# THE CONNARACEAE 

a taxonomic study with special emphasis on Africa.

## C.C.H. JONGKIND

Indumentum, stomata, fruit, seedlings, phylogeny of the genus Rourea, and a revision of the genera Agelaea, Manotes, and Rourea.

## R.H.M.J. LEMMENS

Geography, heterostyly, pollen morphology, phylogeny and a revision of the genera Cnestis, Connarus and Ellipanthus

Proefschrift
ter verkrijging van de graad van doctor in de landbouwwetenschappen, op gezag van de rector magnificus, dr. H.C. van der Plas, in het openbaar te verdedigen op vrijdag 2 juni 1989 des namiddags te 14.45 uur in de aula van de Landbouwuniversiteit te Wageningen

## STELLINGEN

I
De verwantschappen binnen Connaraceae duiden op de kust van Tanzania en Kenya als plaats waar Madagascar zou hebben vastgezeten aan Gondwanaland, zoals verondersteld door Wild.

Wild, H. 1975. Phytogeography and the Gondwanaland position of Madagascar. Boissiera 24: 107-117.

## II

Gezien het feit dat binnen sommige genera de soorten van Afrika en Azië nauwelijks van elkaar verschillen, moet de familie der Connaraceae als een oude groep worden beschouwd, die, althans ten dele, sinds lang weinig is geëvolueerd.

## III

Heterostylie en andere bestuivingssystemen zijn sterk adaptief, hetgeen de grote variatie in vormen bij Connaraceae en sommige andere families verklaart.

Vuilleumier, B.S. 1967. The origin and evolutionary development of heterostyly in the Angiosperms. Evolution 21: 210-226.

## IV

Het genus Jollydora neemt een aparte plaats in binnen de Connaraceae op basis van veel meer kenmerken dan Schellenberg aanvoert.

Schellenberg, G. 1938. Connaraceae. Engler, Das Pflanzenreich 103 $(4,127): 18$.

## V

Het niet onderwerpen van een gerevideerde plantengroep aan fylogenetische beschouwingen moet voor de systematiek als een gemis en voor de botanicus als een gemiste kans worden beschouwd.

## VI

Een scheiding van taxonomie en fylogenie als aparte disciplines moet worden gezien als een kunstmatige classificatie.

VII
De vermelding van geavanceerde apparatuur op een aanvraag voor subsidie van wetenschappelijk onderzoek verhoogt de kans op toewijzing aanzienlijk.

## VIII

Natuurbeschermings-programma's voor ontwikkelingslanden dienen op andere gebieden dan de natuurbescherming grote voordelen te bieden voor de bevolking willen ze enige kans van slagen hebben.

## IX

Kalksteengroeven in Zuid-Limburg kunnen korte tijd na het beeindigen van de exploitatie-activiteiten bijzonder waardevol zijn in natuurwetenschappelijk opzicht. Wanneer hiermee beter rekening zou worden gehouden bij het maken van bestemmings- en inrichtingsplannen voor afgewerkte groeven, zoals op de St. Pietersberg, dan zou kalksteenwinning op het plateau van Margraten onder bepaalde voorwaarden ook door natuurbeschermers in een ander licht kunnen worden gezien.

## X

Voor een verbetering van de samenwerking met andere vakgebieden dan de biologie en voor meer inspraak in multi-disciplinaire projekten is het voor veel biologen van groot belang dat zij eindelijk hun 'geitenwollensokken-image' verliezen.

## XI

Het afschaffen van het gemengd dubbel in de landelijke tenniscompetitie zou een negatieve invloed hebben op het spelpeil van de vrouwelijke spelers.

[^0]Wageningen, 2 juni 1989

## STELLINGEN

I
Het feit dat alleen Connaraceae soorten met een grote ecologische amplitude op verafgelegen vulkanische eilanden groeien maakt het aannemelijk dat niet de afstand maar het milieu op die eilanden de belangrijkste beperkende faktor voor vestiging is.

## II

De verwantschappen binnen de Connaraceae wijzen erop dat het kontakt tussen tropisch Zuid Amerika en Afrika veel eerder verbroken werd dan dat tussen tropisch Azië en Afrika en niet anders om zoals de recente uitwerking van Wegener's theorie door Dietz en Holden doet vermoeden.

R.S. Dietz \& J.C. Holden<br>The breakup of Pangea<br>Scientific American 223, 4: 30-41 (1970)

## III

Dat de Connaraceae, althans ten dele, evolutionair beslist nog in beweging zijn, wordt bewezen door het bestaan van soorten die onderverdeeld zijn in vele blijkbaar genetisch gedeeltelijk geïsoleerde microspecies', zoals Agelaea pentagyna en Cnestis corniculata.

## IV

De onderdrukking van de ontwikkeling tot zaad van het tweede ovulum bij bijna alle Connaraceae soorten, is waarschijnlijk een aanpassing aan de manier van openen van de deelvruchten. Bij de enige soort die regelmatig twee zaden per deelvrucht heeft, Jollydora duparquetiana, blijven de vruchten dan ook gesloten.

## V

Als andere families op het gebied van huidmondjes en andere epidermisstrukturen net zo veel soort- of genusspecifieke kenmerken opleveren als de Connaraceae, dan loont het zeker de moeite deze gegevens in kaart te brengen. Dit zou ondubbelzinnige identificatie van vegetatief materiaal mogelijk maken.

## VI

Tegenover een toenemende belangstelling van het Nederlandse publiek voor het tropisch regenwoud staat een afnemende zorg van de overheid voor het behoud van dit regenwoud, hetgeen tot uiting komt in de afnemende mate waarin het wetenschappelijk onderzoek dat hiervoor nodig is wordt gesteund.

## VII

De schijnbare grotere soortenrijkdom aan paddestoelen in de bossen in onze streken in vergelijking met de bossen aan de evenaar, wordt waarschijnlijk eerder veroorzaakt door de gebrekkige inventarisatie van het tropisch bos dan door een werkelijk verschil in soortenrijkdom.

VIII
Het streven van moderne dierentuinen om de dieren in een benadering van hun natuurlijk milieu aan het publiek te tonen, levert een beter begrip voor de ingewikkeldheid van ekosystemen en daardoor ook meer algemeen begrip voor een verantwoorde natuurbescherming op.

IX
Schone auto valse hoop: alleen drastische beperking van het privé autoverkeer kan ons land leefbaar houden (weer leefbaar maken).

## X

Het veelvuldig gebruik van ingewikkelde ordeningsapparatuur als computers door onderzoekers leidt er veelal toe dat diens inventiviteit zich meer richt op de middelen dan op het doel.

## XI

Het gefaseerd terugdringen van schadelijke drijfgassen voor spuitbussen is te vergelijken met de situatie waarin een gevaarlijk misdadiger, bij arrestatie, nog eerst de resterende patronen in zijn vuurwapen in het wilde weg mag afschieten, alvorens dit in te leveren.

[^1]Abstract<br>C. C. H. Jongkind

In the general part of this work the author of this thesis treats the leaves, flowers and fruits of Connaraceae. Additional chapters reflect upon the phylogeny of the genus Rourea, the phytochemistry of the family, and the relationship of Connaraceae with other families.

In the taxonomic part a description of the family is presented together with keys to the genera. A revision of the genera Agelaea, Manotes, and Rourea is presented with special emphasis on Africa, including descriptions of the genera and differential keys to the species.

In the revision of the genus Agelaea six species are recognized including the Asiatic species.

Manotes is only found in Africa and comprises five species.
The genus Rourea is revised for Africa only, twelve species are recognized for this area. The American and Asiatic species are studied but not revised. New combinations are made for American and Asiatic species that are transferred to this genus. The American species are classified into clusters. In this work Rourea also includes Bernardinia, Byrsocarpus, Jaundea, Roureopsis, Santaloidella, Santaloides, Spiropetalum, and Paxia, formely recognized as separate genera.

The treatment of the African species comprises full synonymy, literature, diagnosis, a distribution map, and ecological notes. In most cases an illustration is presented as well.

The author studied and collected most species of Agelaea, Manotes, and Rourea on location in the rain forest in Gabon.

## Samenvatting

## C. C. H. Jongkind

In het algemene deel van het boek behandelt de auteur van dit proefschrift de bladeren, bloemen en vruchten van de Connaraceae. Tevens beschrijft de auteur wat er bekend is over de fytochemie en de verwantschap van Connaraceae met andere families. Ook wordt de fylogenie van het genus Rourea gerekonstrueerd.

In het taxonomische deel wordt een beschrijving gegeven van de familie, gevolgd door sleutels tot de genera. Tevens worden de genera Agelaea, Manotes en Rourea behandeld als onderdeel van de komplete revisie van de Connaraceae met nadruk op Afrika. Hierbij wordt een beschrijving van de drie genera gegeven samen met sleutels tot de soorten.

Het genus Agelaea wordt voor zijn gehele verspreidingsgebied gerevideerd, dit verspreidingsgebied omvat Afrika en Azië. In dit genus worden zes soorten onderscheiden.

Het genus Manotes is beperkt tot Afrika, telt vijf soorten en wordt hier in zijn geheel gerevideerd.

Het genus Rourea wordt alleen voor Afrika bewerkt en omvat daar twaalf soorten. De niet-Afrikaanse soorten zijn wel bestudeerd. Nieuwe kombinaties worden gemaakt voor Amerikaanse en Aziatische soorten die naar dit genus zijn overgebracht. De Amerikaanse soorten worden in clusters ingedeeld. Het genus Rourea omvat hier ook de veelal als aparte genera erkende Bernardinia, Byrsocarpus, Jaundea, Roureopsis, Santaloidella, Santaloides, Spiropetalum en Paxia. Een nieuwe sectie-indeling is uitgewerkt voor het gehele genus.

De behandeling van alle Afrikaanse soorten omvat de synonymie, literatuur, een diagnose, verspreidingskaart en, voor zover bekend, ekologische gegevens. Van bijna alle soorten is een tekening bijgevoegd.

De auteur heeft gedurende twee maanden veldstudies verricht in Gabon en in die tijd de meeste van de door hem behandelde soorten verzameld.

Abstract<br>R. H. M. J. Lemmens

In the general part of this work the author of this thesis treats the geography, habit, morphology of stems and branches, and inflorescences of Connaraceae. The phenomenon of heterostyly, its expression and evolutionary developments are dealt with in a separate chapter. Additional chapters reflect upon the phylogeny of the genera within the family and on mutual relations of the species in the genus Cnestis. The author has assembled what is known about the pollen morphology, and provides supplementary original information.

In the taxonomic part a revision of the genera Cnestis, Connarus, and Ellipanthus is presented, with special emphasis on Africa, including descriptions of the genera and differential keys to the species. Additional keys are presented for plants that are either exclusively flowering or fruiting.

In the genus Cnestis 13 species are recognized, including the Asiatic C. palala and two new species, C. bomiensis and C. uncata. Compared to Schellenberg's monograph on Connaraceae (1938) the number of species is extensively reduced.

Connarus comprises seven species in Africa, including the new species C.gabonensis, while Ellipanthus has two African species, of which one was collected only once on Madagascar.

The treatment of each species comprises its full synonymy, literature, diagnosis, an illustration, a distribution map, and ecological and botanical notes.

The author studied and collected five species of Cnestis, and two species of Connarus on location in the rain forest in Gabon.

## Samenvatting

R. H. M. J. Lemmens

In het algemene deel van het boek behandelt de auteur van dit proefschrift de geografie en voorts de habitus, de stengels en takken en de bloeiwijzen van Connaraceae. Het verschijnsel heterostylie bij Connaraceae wordt besproken, evenals de ontwikkelingen hierbinnen. In een kort hoofdstuk vat de auteur samen wat bekend is over de pollenmorfologie, aangevuld met eigen waarnemingen. Er wordt een reconstructie gemaakt van de fylogenie van de genera binnen de familie en van de soorten binnen het genus Cnestis.

In het taxonomisch deel worden de genera Cnestis, Connarus en Ellipanthus behandeld als onderdeel van de complete revisie van de Connaraceae met speciale nadruk op Afrika. Bij deze drie geslachten worden een genusbeschrijving en determinatiesleutels tot de soorten gegeven. Bij Cnestis en Connarus zijn drie sleutels opgenomen: respectievelijk voor planten met bloemen én vruchten, voor bloeiende en voor vruchtdragende planten.

In het genus Cnestis worden dertien soorten behandeld, inclusief de Aziatische C. palala (de enige niet-Afrikaanse soort) en twee nieuwe soorten: C. bomiensis en C. uncata. De reductie van het aantal soorten is aanzienlijk in vergelijking met de monografie van Schellenberg (1938).

Connarus omvat in Afrika zeven soorten, inclusief C. gabonensis, een nieuwe soort. Ellipanthus heeft twee Afrikaanse soorten, één in Oost Afrika en éen op Madagascar.

De behandeling van elke soort omvat de synonymie, literatuur, een diagnose, tekening, verspreidingskaart en, voor zover bekend, oecologische en gebruiksgegevens. In de meeste gevallen zijn opmerkingen toegevoegd.

De auteur verrichtte veldstudies en heeft herbariummateriaal verzameld van vijf Cnestis- en twee Connarus-soorten in het tropisch regenwoud van Gabon.

## Curriculum vitae

Carel Christiaan Hugo Jongkind werd op 9 januari 1954 geboren te 's-Gravenhage. Hij behaalde in 1974 zijn Atheneum B diploma aan het Haags Montessori Lyceum. Daarna studeerde hij biologie aan de Landbouwuniversiteit te Wageningen, alwaar hij in 1984 zijn doctoraal examen met goed gevolg aflegde met als hoofdvakken vegetatiekunde en plantentaxonomie. Tijdens zijn studie vervulde hij van september 1975 tot juni 1977 zijn vervangende dienst aan het Rijks Instituut voor Natuurbeheer in Leersum. Van maart 1987 tot maart 1989 was hij in tijdelijke dienst als assistent in opleiding (A.I.O.) bij de vakgroep Plantentaxonomie van de Landbouwuniversiteit.

Roeland Hendrikus Maria Julien Lemmens werd op 14 november 1954 geboren te Maastricht. Na het Gymnasium B diploma aan het Henric van Veldeke College in zijn geboortestad behaald te hebben, studeerde hij biologie aan de Landbouwuniversiteit te Wageningen. In 1984 legde hij het doctoraal examen met goed gevolg af, met als hoofdvakken natuurbeheer en vegetatiekunde en als bijvak plantentaxonomie. Tevens behaalde hij de aantekening onderwijsbevoegdheid in de biologie. In hetzelfde jaar was hij werkzaam bij de Stichting tot Instandhouding van Kleine Landschapselementen te Roermond. Vanaf september 1984 tot maart 1989 werkte hij bij de vakgroep Plantentaxonomie van de Landbouwuniversiteit als wetenschappelijk assistent. Vanaf januari 1988 is hij bovendien werkzaam als taxonoom bij het PROSEA-project, eveneens verbonden aan de Landbouwuniversiteit.

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## Introduction

In 1938 Schellenberg published his monograph of the pantropical family Connaraceae. In his treatment the family comprises 24 genera and 385 species. In Africa it is very well represented by 16 genera and 154 species. Asia and America are not so rich, having respectively 9 genera with 142 species and 5 genera with 89 species. Most African floras are based on Schellenberg's work and, as it seems, without very much alteration of the genus and species concept.

Leenhouts undertook a thorough revision of Schellenberg's work when he prepared the contribution for Flora Malesiana (1958b). His revision led to a considerable reduction of the number of species and also to a substantial reduction of genera: 9 genera and 142 species for Asia and adjacent areas in Schellenberg, 6 genera and 36 species for Malesia in Leenhouts treatment. Although Asia and adjacent areas contain some more species than Malesia alone, the reduction is nevertheless very significant.

A similar result is experienced in the revision of the African species: a reduction from 154 species in 16 genera in Schellenberg to 49 species in 10 genera now. The most significant reduction on the specific level is found in Agelaea (including Castanola): from 58 to 6 species (Africa + Asia). On the generic level the reduction in the number of genera is most apparent when considering Rourea: 9 separate genera in Schellenberg are now referred to synonymy. It is interesting to note that this last reduction does not involve a high number of new combinations in Rourea. Only 9 (4 for Africa, 4 for Asia, 1 for America) were necessary, as most species were originally described in Rourea!

Forero's recent (1983) treatment of the American representatives does not demonstrate the same result as experienced with the Asiatic and African treatments viz. a great reduction in the number of taxa. Where Schellenberg accepted for America 89 species in 5 genera, Forero treats 101 species in the same 5 genera. As a result the American continent now ranks first in species diversity (see table 1). In our opinion this is most likely due to a different species concept and does not necessarily reflect a greater diversity of species.

The present revision, which was initially undertaken to revise the African representatives only, now deals with the family in a much wider context. As in Africa 10 out of the 12 genera occur, a complete revision of the family on the generic level was undertaken, which resulted in a new subdivision of the family in 4 tribes. For genera with their main distribution in Africa the extra African species are revised as well (e.g. Agelaea, Cnestis). The heterostyly phenomenon which is so well represented in this family, is thoroughly investigated and so are the leaf epidermis and the wood anatomy.

The taxonomic part of Eimunjeze's publication on the genus Hemandradenia (1976) is reprinted in this work with some additionalinformation on new collections.

Finally it may be observed that only 3 new species are described, two based on rather recently collected material, the third, also on old material which was overlooked by previous authors. This may prove that Africa, at least as far as Connaraceae are concerned, is rather well explored.

Wageningen, February 1989
F.J. Breteler

## GENERAL PART

# 1. History of the family 

by F.J. Breteler

The genus Connarus was published by Linnaeus in 1753. He classified it in Monadelphia Decandria. Aublet (1775) used the same system to classify his new genus Rourea. When A.L. de Jussieu (1789) described Cnestis, he placed it in his Terebintaceae under 'Genera Terebintaceis affina', together with genera which are now placed in families like Rutaceae and Sapindaceae. The genera Connarus and Rourea were, apparently, considered as true Terebintaceous. Robert Brown (1818) was the first author to separate the three known genera from the Terebintaceae, placing them together in the new family Connaraceae. Omphalobium of Gaertner (1788) is considered by him a synonym of Connarus. Brown's concept of the family is essentially the same as ours.

De Candolle (1825) did follow De Jussieu rather than Brown in placing the genera of Connaraceae, treated as a tribe, in Terebintaceae. The generic concept of Connarus is expanded to accommodate Aublet's Rourea, a genus with 5 instead of 1 carpel per flower. Next to Connarus Gaertner's genus Omphalobium is maintained, accommodating like Connarus, 5-carpellate as well as 1-carpellate species. This confusing situation ended when Planchon in 1850 reinstalled Connaraceae as a distinct family, reducing Omphalobium unambiguously into a synonym of Connarus by making the necessary new combinations. Planchon (l.c.) also added five new genera: Agelaea, Bernardinia (now treated as a synonym of Rourea), Cnestidium, Manotes, and Roureopsis (now also in Rourea). He divided the family in two tribes, the Connareae and the Cnestideae, based on differences in the aestivation of the sepals and the presence of endosperm. J.D. Hooker (1862) followed Planchon in his generic treatment of the family. Four genera were added: Ellipanthus and Taeniochlaena of himself, Tricholobus Blume (1850), and Troostwykia Miquel (1860). Of these only Ellipanthus is maintained here.

When Gilg (1891) made his treatment for 'Die Natürlichen Pflanzenfamilien' he maintained Planchon's tribes. Radlkofer's genus Pseudoconnarus, published in 1886, was added. In his supplements to this work of 1891, 1894, and 1897 the family was enriched with the genera Paxia Gilg (1891), Spiropetalum Gilg (1891), Jaundea Gilg (1894), Dinklagea Gilg (1897), and Jollydora of Pierre (1896). In his third supplement Gilg divided the Connaraceae in two subfamilies, Connaroideae and Jollydoroideae, to underline the separate position of Jollydora, while Planchon's tribes are maintained.

Schellenberg (1910) made a new subdivision of the family. Two subfamilies were distinguished namely Connaroideae (including Jollydora) and Cnestoideae. The Connaroideae are divided in two tribes the Connareae and the Roureeae. The latter tribe is further divided into two subtribes. It is interesting to note that the fundamental difference within Connaraceae of flowers having five or
a single carpel is not used by Schellenberg in this new subdivision as both subfamilies consist of a mixture of 5-carpellate and 1-carpellate genera. In 1938 Schellenberg reverts to Gilg's subdivision into two subfamilies Connaroideae and Jollydoroideae. Again one or five carpels per flower is not considered to be fundamentally important by him (see also paragraph 10.1 and Fig. 54). In this last treatment of Schellenberg the number of genera has reached 24. Subsequently this number was reduced by Leenhouts (1958 b) and even further in the present work, to half this amount (see also the introduction).

# 2. Geographical distribution 

by R.H.M.J. Lemmens

Connaraceae are almost exclusively found in the tropics. They are largely restricted to lowland rain forest. More rarely they are found in mountain or savanna vegetations, where they usually grow in thickets or in remnants of forest. Only a few species surpass the 20th degrees of latitude, e.g. Cnestis polyphylla in southern Africa and some Connarus species on the Asiatic mainland, and some Rourea species in all continents.

Table 1 shows that the largest number of genera, representing all 4 tribes, is found in Africa, followed by Asia and then America, each with 2 tribes. Only a few genera represented in Africa have many species in Asia and/or South America, i.e. Connarus, Rourea (both in Asia and South America), and Ellipanthus (Asia).

In Africa the main centre of distribution is Central Africa, as shown in table 2. In West Africa (Gambia to Nigeria) 29 species in 7 genera are found. East and South Africa (Kenya, Uganda, Tanzania, and further south) have 12 species in 7 genera. In Central Africa (the remaining part of the continent south of the Sahara) 40 species in 7 genera occur, of which 36 are found in Cameroun and Gabon. When the part of Nigeria east of the Niger River is added to Central Africa, the number for West Africa is reduced to 20 species in 6 genera. In Central Africa representatives of all 4 tribes are found.

Table 1. Distribution of Connaraceae

| Genus | Africa | Asia ${ }^{*}$ | America ${ }^{* *}$ |
| :--- | :---: | :---: | :---: |
|  |  |  |  |
| Agelaea | 4 | 2 | 0 |
| Burttia | 1 | 0 | 0 |
| Cnestidium | 0 | 0 | 2 |
| Cnestis | 12 | 1 | 0 |
| Connarus | 7 | ca 19 | 51 |
| Ellipanthus | 2 | 4 | 0 |
| Hemandradenia | 2 | 0 | 0 |
| Jollydora | 3 | 0 | 0 |
| Manotes | 5 | 0 | 0 |
| Pseudoconnarus | 0 | 0 | 5 |
| Rourea | 12 | ca 16 | $43^{* * *}$ |
| Vismianthus | 1 | 1 | 0 |
| Total species | 49 | ca 43 | 101 |
| genera | 10 | 6 | 4 |

[^2]Table 2. Distribution of Connaraceae in Africa

|  | Number of <br> species | Number of <br> genera | Number of <br> tribes |
| :--- | :--- | :--- | :--- |
| Area of FWTA | 29 | 7 | 4 |
| W of Niger River | 20 | 6 | 3 |
| Central Africa (E of Niger River) | 40 | 7 | 4 |
| E and S Africa | 12 | 7 | 2 |
| Madagascar | 5 | 4 | 2 |
| Total for Africa | 49 | 10 | 4 |

In Madagascar 5 species in 4 genera occur, of which only a single species, Ellipanthus madagascariensis, is endemic (see also note under this species). According to Dietz \& Holden (1970) and Wild (1975, on phytogeographical grounds) Madagascar, prior to the fragmentation of Gondwanaland, is supposed to have been joined to the Somalia-Kenya-Tanzania coast. This could explain the pattern of distribution of Cnestis polyphylla linked to its morphological variation, i.e. the intermediate position of the Kenya material between the distinct populations of Madagascar and those of Southeast Africa. At the separation of Madagascar from the African continent possibly a major part of the genepool remained on this island, resulting in the wide variation within this species. It is not likely that the comparatively large seeds of Cnestis polyphylla have come across the Mozambique channel, but it cannot be excluded either, as the species is also found on Reunion and Mauritius, islands of volcanic origin at a distance of more than 700 km from Madagascar. The distance between Madagascar and South Mozambique is ca 900 km , while Madagascar and South Kenya lie almost 1400 km apart. The genus Ellipanthus shows a comparable distribution: E. hemandradenioides along the coast in Kenya and Tanzania and E. madagascariensis in NW Madagascar. Another species with a more or less comparable area of distribution to Cnestis polyphylla is Rourea orientalis.

Some species inhabit a very large area in Africa, e.g. Agelaea pentagyna, A. paradoxa, Manotes expansa, Rourea thomsonii, R. coccinea, Cnestis corniculata, and C. ferruginea. Rourea minor is even found outside Africa in Malaysia and on islands in the Indian Ocean and in the Pacific. In several genera as Agelaea, Connarus, Ellipanthus, Rourea, and Vismianthus very closely related species are found in Africa and Asia.

Apparently evolution in these species has been very slow since the separation of the continents, as their large seeds are not likely to be dispersed over long distances, and they are not likely to have been distributed by man. Possibly this also applies to some species from East Africa and Madagascar, as discussed above.

The relations between the taxa of the African and American tropics are less close. While not a single genus is restricted to Asia, two of the four genera are
endemic to South and Central America, i.e. Pseudoconnarus and Cnestidium. However it must be noted that some American Connarus species show a remarkable resemblance with some African and Asiatic species.

Africa and the Indian plate drifting northward, were possibly connected for a comparatively long time by islands in the Indian Ocean, that allowed some exchange between populations. The rupture of South America and Africa is supposed to have taken place later than the breakup of the eastern part of Gondwana (see Dietz \& Holden, 1970), but it was more abrupt, limiting the possibilities for exchange.

Some species are very restricted in their distribution. In the same area often a closely related species is found, with a much larger area of distribution. This is the situation in Cnestis yangambiensis and C. corniculata, C. uncata and C. urens, C. bomiensis and C. racemosa, Jollydora pierrii and J. duparquetiana respectively.

Disjunct distributions are found in Cnestis macrantha, Manotes macrantha, Hemandradenia mannii, and Connarus congolanus. The last three species occur in Liberia and/or Ivory Coast, as well as in Central Africa, but not in a large area in between: Ghana, Togo, Benin, and often also West Nigeria. Possibly these species once had a large area of distribution. In times with a more dry climate they became confined to refuges from which they migrated again when the climate became moister. This may also have been the case in Rourea solanderi and Agelaea paradoxa. The disjunct distribution is in these species less marked as the gap in their distribution is less wide. However, it cannot be ruled out completely that some species may be present in the distributional gap, but that they simply have not been collected there. This is not likely, as the area from Ghana to Nigeria is comparatively well-collected.

# 3. Systematic position of the family 

by C.C.H. Jongkind

Unambiguous relationships of Connaraceae with other families have not been demonstrated so far. Most often close relationship with Leguminosae and Rosaceae has been postulated, as was advocated by Planchon (1850: 411), Bentham \& Hooker (1862: 430), Gilg (1891: 63), Schellenberg (1938: 16, 17), and Dickinson (1971: 81, 86; 1972: 129, 136; 1973: 137). Affinities with other families, not necessarily in conflict with this rather classic view, were proposed by some of these authors as well. Planchon (1850: 411), Bentham \& Hooker (1862: 430), and Schellenberg (1938: 17) considered Oxalidaceae to be affiliated, while Bentham \& Hooker (1862: 430) also took Anacardiaceae into account. This was by no means a new point of view as de Jussieu in 1789 classified the genera of Connaraceae known by him in the affinity of his Terebinthaceae, a taxon that included among others present-days Anacardiaceae. Hutchinson's opinion (1964: 162), emphasizing a link with Dilleniaceae, should not be disregarded either.

If views of these authors on the affinities of Connaraceae are supported by specific characters at all, they are invariably limited in number. Pinnate leaves and apocarpous, pod-like, fruits support their relationship with Leguminosae while the exstipulate leaves and the presence of a sarcotesta emphasize affinities with Sapindaceae.

In 1976 Corner thoroughly analyzed the carpels and seeds of species of many different families and among them ten species of Connaraceae. The results of his investigations combined with the pinnate, exstipulate character of the Connaraceae leaves led him to consider affinity with Meliaceae.

When Connaraceae are regarded to form a link between Rosales and Sapindales they may be placed in the latter order, as was done by Cronquist (1968: 263-266). In harmony with the view of the first authors mentioned in this paragraph they are often referred to Rosales as did Thorne (1976). Hutchinson, however, eventually preferred to classify them in Dilleniales.

Any preference expressed as to the position of Connaraceae in any of the orders mentioned, leaves them with part of their characters in disagreement with that position. This led Takhtajan (1969:224) to place them into an order of their own, the Connarales.

Recently Dickinson (1978: 36-45) tried to sort out the systematic position by means of all available anatomical and morphological data, but he did not arrive at a simple conclusion. In this work Dickinson mentioned heterostyly as one of the important characters in order to determine possible relationships between families. Therefore it is remarkable that he did not consider Oxalidaceae, as one of the possible related groups. This family is similar to Connaraceae in showing heterostyly and also shares other characters. Oxalidaceae resemble

Connaraceae to such an extent that a American species of Rourea, R. blanchetiana, was first described in Oxalidaceae.

The present revision did not reveal any important new characters for the classification of the family. It is possible that future phytochemical research may produce more information. However, the results of further research on larger and more variable families as Leguminosae, Sapindaceae, and Rosaceae is indispensable in order to elucidate the affinities of Connaraceae.

## 4. Morphology

### 4.1 Habit and growth

by R.H.M.J. Lemmens

Many species of Connaraceae are lianescent, but Ellipanthus, Hemandradenia, Vismianthus, Burttia, Jollydora, some species of Rourea and Connarus, and possibly a single Cnestis species do not show any lianescent tendencies, and are usually shrubs. Some Asiatic Ellipanthus species are recorded by Leenhouts (1958b) as medium-sized trees, up to 30 m high and $50-60 \mathrm{~cm}$ in diameter. Also some Connarus species from Asia can have a tree-like habit, up to 17 m high.


Fig. 1. Cnestis corniculata: liana in forest (van der Maesen 5612; phot. L.J.G. van der Maesen).


Fig. 2. Cnestis corniculata: young shoot (phot. L.J.G. van der Maesen).

Forero (1983) describes the habit of some South American Connarus species as a small tree, sometimes up to 20 m high. In Africa Hemandradenia mannii is occasionally a small tree up to 15 m , and Ellipanthus hemandradenioides up to 10 m . Jollydora shows the habit of a small, usually unbranched treelet, up to 7 m high.

When found in savannas that are regularly burned off, Rourea coccinea and $R$. orientalis develop rhizomatous shrublets with often strongly suberized bark. Moreover, in savannas both species are deciduous, like Rourea fluminensis from South America, while most other species of the family are evergreen.

Burttia prunoides and Vismianthus punctatus are also deciduous shrubs with leaves crowded at the end of the otherwise often aphyllous shoots, resembling certain Prunus species in appearance.

Many species are polymorphic. For instance, Cnestis ferruginea, probably due to environmental conditions, may be either a shrub or small tree, or a large forest liana.

In the undergrowth of rain forest in Gabon small shrubs of several species, particularly of Agelaea, are common. These plants often hardly show any growth for many years (Caballé, 1986). When the canopy of the forest opens they produce long shoots rapidly and become lianas. The same phenomenon is reported for other lianescent species, e.g. Dichapetalum (Breteler, 1973).

The lianas usually employ the winding end of young branches for attachment. In Manotes macrantha however, the reduced leaves, transformed to woody hooks, support the winding stems. According to Caballé (1986) some Rourea species use small, hook-like lateral branches for climbing and Cnestis and Manotes occasionally employ the swelling of the pulvinus at the base of the petiole for this purpose in bringing the leaf rachis in a hook-like position.

### 4.2 Stems and branches

by R.H.M.J. Lemmens

Among the lianescent species the main stem varies in shape in cross section. Usually it is (sub)cylindrical (fig. 3), but in Rourea parviflora and R. minor it


Fig. 3. Manotes griffoniana: cross section of main stem, 3 cm diam. (Breteler 1708; phot. F.J. Breteler).
is often strongly ridged and these ridges show a number of concentric rings (see also Caballé, 1986: fig. 44 and 45). These species have included phloem, as occasionally found in other species, e.g. Agelaea pentagyna.

Sometimes partition-like structures in the main stem are present, as is reported by Caballé for Agelaea paradoxa.

Main stem and shoots are occasionally strongly intertwined.
The bark is usually smooth, more rarely fissured and in some species sometimes strongly suberized (Rourea coccinea, R. orientalis, and the Asiatic Connarus suberosus). Lenticels are usually present on the branchlets. They are conspicuous in many Connarus species and particularly so in Rourea orientalis.

In Connarus wounded phloem produces a sticky, reddish exudate, like some papilionoid lianas. Some other species, e.g. Rourea myriantha and R. solanderi, exude a pale slime. Latex tubes are present in the wood of Connarus (see chapter on wood anatomy).

Wood samples have been scarcely collected and the characters mentioned for them cannot always reliably be extrapolated for the species they represent. A more comprehensive study of the wood anatomy has been made by den Outer \& van Veenendaal (see chapter 8).

### 4.3 Indumentum

by C.C.H. Jongkind

In Connaraceae six different types of hairs can be distinguished, two glandular and four non-glandular. These six types are described below and their presence is indicated.

1. Multi-cellular glandular hair, consisting of a stalk-like part and a usually strikingly coloured head. The stalk is one to many cells long and one cell wide. The head is one to three cells wide and one to four cells long. This hair type is found in the genera Cnestis, Connarus, Jollydora, Manotes, and Rourea. The hairs very variable in shape and size (fig. 4.1-3). In Cnestis mannii the hair is a chain of about twelve cells long of which the upper two cells form the head. In Rourea callophylla it has the shape of a very tiny mushroom with a short stalk of about two cells and a large flat head of about six cells.
2. The second type of glandular hair is uni-cellular and very small with a little globular top. This type is only found in all Manotes species (fig. 4.4).
3. The most common non-glandular hair is an often thick-walled uni-cellular hair with an acute apex. It is found in all genera except in Jollydora. It varies in shape from an erect, straight, one-armed hair to an appressed hair with two unequal or equal opposite arms (fig. 4.5-4.12 \& 5.1-5.2). The one-armed form is most common. The two-armed form can be observed readily in Burttia, Connarus, Hemandradenia and Vismianthus and in some species of Rourea. In Agelaea section Agelaea the one-armed form is often fascicled in four (fig.5.3). The


Fig. 4. Different hairtypes: 1-3. multi-cellular glandular hairs; 4. uni-cellular glandular hair; 5-12. uni-cellular non-glandular hairs; 13,14. multicellular non-glandular hairs.
long stinging hairs on the fruits of Cnestis species and the smaller ones on the fruits of Agelaea borneensis are a modification of this hair type. These stinging hairs differ from the usual hairs by their more rigid cell wall and their decreasing diameter from the middle down to the base.
4. A hair type consisting of a chain of the above mentioned two-armed unicellular hairs is exclusively found in many Connarus species (fig. 4.14). It resembles a miniature spiral staircase. This hairtype has not been observed in African Connarus species.
5. The fifth type is a multicellular hairs of one cell wide that looks like the one-armed form of type 3 (fig. 4.13). The walls between the cells are perforated and are orientated in sharp angles to the direction of the hair. The indumentum of Jollydora consists of this type mixed with type 1.
6. This type consists of more than a hundred cells and it is many cells wide and long. The cells are stretched lengthwise. It is up to a few cm long and is usually flattened. It stands erect on branches, petioles, and rachis, and it is exclusively found in Rourea parviflora (see note 2 under this species).

### 4.4 Leaves

by C.C.H. Jongkind

Connaraceae are evergreen or deciduous. The leaves are always alternate, exstipulate, and exstipellate. Most genera and species have pinnate leaves. In Agelaea, Pseudoconnarus, and in some species of Connarus the leaves are trifoliolate, and unifoliolate leaves are characteristic for Burttia, Ellipanthus, Hemandradenia, and Vismianthus. The petiole is always pulvinate at the base and the petiolules are entirely so. In the unifoliolate species this implies that petioles have a pulvinus at the base and at the apex. The leaflets are always entire, and they may be opposite or not. They are chartaceous to coriaceus. In many species the apex is mucronate, and in Hemandradenia, Vismianthus, and many species of Connarus glands can be found in the surface. The nervation is open except in Manotes where it terminates in a closed pattern of very fine parallel veinlets.

### 4.5 Leaf epidermis and stomatal patterns

by C.C.H. Jongkind

### 4.5.1 Introduction

In Connaraceae the pattern of the stomata in the epidermis is a useful additional taxonomic character. It is often rather easy to recognize and it enables us, in combination with other leaf characters, to identify sterile samples down to species or at least to genus level (see tab. 23). It has been an important tool in the clustering of the South American species of Rourea (presented on pag. 368). It also reflects affinities between the taxa.

Apart from the stomata the leaf epidermis of Connaraceae provides four other characters of taxonomical value that are used in this revision.

First and most frequent is the presence of a papillose lower epidermis in many species of Cnestis, Pseudonnarus and Rourea.

Second are the mucous cells that may be present in the upper epidermis. In living specimens they are often difficult to observe, but in herbarium specimens
they show as small pits in the surface. If the pits are densely distributed they are easy to recognize. They may be readily observed in the species of Agelaea section Troostwykia and in some species of Rourea such as R. erythrocalyx and less often in $R$. solanderi or $R$. thomsonii.

Third is the occurrence of a pattern of more or less parallel lines in the lower epidermis (fig. $5.4 \& 6.1$ ). This pattern is only visible through a microscope.

Fourth is a pattern of numerous small pits in the outer cell walls of the lower epidermis. They may number about a score on a single wall of one epidermis cell.

The lower epidermis of most species in the family has been investigated with the exception of a number of Connarus species and a few rare species of Rourea: R. laurifolia, R. omissa, and R. pseudospadicea. In Connarus 35 species representing all continents have been studied. As these do not show much difference in their epidermis structure, it is felt that in the other species not much differences can be expected either.

The four epidermis characters will be discussed hereafter with exception of the occurrence of mucous cells, this is macroscopical in character and is presented in the description of the species.

### 4.5.2 Methods

Small fragments of the leaflets of herbarium specimens were rehydrated in boiling water. Manually prepared sections were made from the lower surface. These sections were then bleached in diluted household bleach. The resulting preparations were not conserved, but of 90 preparations photographs were taken. Specimens from which such sections were photographed are indicated by !. The photographs remain available in the photograph collection of the Laboratory of Plant Taxonomy (WAG).

### 4.5.3 Results

The stomatal patterns encountered in Connaraceae are of diverse nature. The terminology by Wilkinson (1979) is used to describe the stomata. A paracytic pattern is found in Cnestis and some species of Rourea, anisocytic including helicocytic in Agelaea, Cnestidium, and some species of Rourea, anomo-cyclocytic in Burttia, Connarus, Ellipanthus, Hemandradenia, Manotes, Vismianthus, and again some species of Rourea, and bicyclic in Jollydora (fig. 6-14). Rourea is the only genus with a wide variation in stomatal patterns, therefore the results for Rourea are not given for the genus but in detail for sections or for particular species.

Apart from the stomatal pattern the size of the vestibule as expressed by the size of the outer ledge of the stomata can also be an important character. This ledge is particularly large and very conspicuous in all Connarus species and in Rourea section Roureopsis.

Within the Connaraceae it seems that the sequence from primitive to advanced


Fig. 5. Hairs and leaf epidermis: 1. Connarus griffonianus, unequal two armed hair (arrow pointing at the base), $\times 950 ; 2$. Connarus culionensis, unequal two armed hair (arrow pointing at the base), $\times 270 ; 3$. Agelaea pentagyna, fascicled hairs, $\times 380 ;$ 4. Rourea calophylla, cuticula with more or less parallel lines, $\times 380$. (1.J.J. de Wilde 625; 2. Elmer 12877; 3. Bos 5346; 4. Zenker 1963).


Fig. 6. Hairs, leaf epidermis, and stomata: 1. Manotes macrantha, cuticula with many more or less parallel lines, $\times 380 ; 2$. Manotes expansa, stomata and glandular hair, $\times 380 ; 3$. Vismianthus punctatus, stoma, $\times 950$; 4. Burttia prunoides, stoma, $\times 950$. (1. Reitsma 1728; 2. Breteler \& Lemmens 8377; 3. Semsei 647; 4. Peter 34193A).


Fig. 7. Stomata: 1. Hemandradenia mannii, $\times 950 ;$ 2. Ellipanthus hemandradenoides, $\times 950$; 3. Jollydora duparquetiana, $\times$ 950; 4. Agelaea paradoxa, $\times$ 950. (1.J.J. de Wilde 8321; 2. Faulkner 2109; 3. Bos 6730; 4. Breteler \& Lemmens 8192).


Fig. 8. Stomata: 1. Connarus congolanus, $\times$ 380; 2. Connarus longistipitatus, $\times 540$; 3. Connarus griffonianus, $\times 950$; 4. Connarus incomptus, $\times 950$. (1. Leeuwenberg 5091; 2. van Meer 1822; 3. Tisserant 1586; 4. Maas \& Westra 3654).


Fig.9. Stomata: 1. Rourea obliquifoliolata, $\times 380 ; 2$. Rourea acutipetala, $\times 540 ; 3$. Rourea myriantha, $\times$ 950; 4. Rourea calophylloides, $\times$ 950. (1. Breteler \& Lemmens 8356; 2. Cockburn FRI 8493; 3. De Giorgi 1377; 4. Le Testu 5444).


Fig. 10. Stomata and leaf epidermis: 1. Rourea erythrocalyx, $\times 950 ; 2$. Rourea camptoneura, cuticula with many more or less parallel lines, $\times 380$; 3. Rourea fluminensis, $\times 540 ; 4$. Rourea coccinea subsp. coccinea var. coccinea, $\times$ 950. (1. Reitsma 1488; 2. Ule 5056; 3. Kuhlmann 2350; 4. Jansen 2620).


Fig. 11. Stomata: 1. Rourea orientalis, $\times 1350$; 2. Rourea minor (Philippines), $\times 380$; 3. Rourea minor, (Thailand), $\times 380$; 4. Rourea minor, (Cameroun), $\times 540$. (1. Peter 20165; 2. Ramos 39603; 3. BKF 57548; 4. Bos 4940).


Fig. 12. Stomata: 1. Rourea parviflora, $\times 950$; 2. Cnestis racemosa, $\times 380$; 3. Cnestis polyphylla, $\times$ 950; 4. Cnestis corniculata, $\times$ 950. (1. Breteler \& Lemmens 8141; 2. Baldwin 10779; 3. Rakato 2907; 4. J. Louis 2556).


Fig. 13. Stomata: 1. Cnestidium guianense, $\times 1350$; 2. Rourea adenophora, $\times 540 ; 3$ \& 4: Rourea adenophora, $\times 950$. (1. Borsboom 12265; 2. Dodson et al. 10001; 3. \& 4. Croat 8447).


Fig. 14. Stomatal types: 1. actinocytic; 2. anomocytic; 3. cyclocytic; 4-5. paracytic; 6. bicyclic; 7. anisocytic; 8. helicocytic.

Stomata in transverse section (after Schellenberg 1910): 9. Rourea coccinea (Byrsocarpus coccineus); 10. Cnestis ferruginea; 11. Manotes expansa (M. sanguineo-arillata); 12. Rourea myriantha (Paxia scandens), a. vestibule, b. outer stomatal ledge; 13. Hemandradenia mannii.
stomata types is either from anomo-cyclocytic to bicyclic or from anomo-cyclocytic via paracytic to anisocytic and helicocytic.

The presence of a papillate lower surface is not always of taxonomical significance. This character constitutes a generic difference between Connarus and Pseudoconnarus, but in Cnestis and Rourea some species are quite indifferent regarding this character.

A pattern of more or less parallel lines in the lower epidermis has only been found in two species of Rourea, R. calophylla and R. camptoneura and in Manotes macrantha.

The taxonomical value of the pattern of many microscopical pits in the outer cell walls of the lower epidermis is still obscure. It is only found in the leaves of Rourea prancei, at present exclusively represented by its type specimen.

If only a single stomata type is reported, it means that $95-100 \%$ of the observed stomata of this taxon is of that type.

If appropriate the origin of herbarium specimens and species is indicated with Af. for Africa, Am. for America, and As. for Asia.

Agelaea: Stomata anisocytic, often in majority helicocytic (fig. 7.4 \& 14.7-8). Vestibule small with a narrow outer stomatal ledge.

Burttia: Stomata actino-cyclocytic (fig. 6.4 \& 14.1-2). Vestibule small with a narrow outer stomatal ledge.

Cnestidium: Stomata in majority anisocytic (fig. $13.1 \& 14.7$ ). Vestibule small with a narrow outer stomatal ledge.

Cnestis: Stomata almost pure paracytic (fig. $12.2 \& 14.5$ ). Vestibule small with a narrow outer stomatal ledge (fig. 14.10). Lower epidermis smooth to strongly papillate, apparently without taxonomical significance at species level.

Connarus: Stomata surrounded by 4-7 epidermal cells, which can be larger than, equal to, or smaller than the other epidermal cells (actino-, anomo- or cyclocytic) (fig. $8 \& 14.1-3$ ). It is not clear whether the shape of these cells may have any taxonomical significance for the Asiatic or American species of the genus, for the African it has not. All species studied have a wide outer stomatal ledge enclosing a spacious vestibule.

Ellipanthus: Stomata (anomo-)cyclocytic (fig. 7.2 \& 14.2-3). Outer stomatal ledge medium, in size between those of Connarus and those of most other genera e.g. Cnestis.

Hemandradenia: Stomata cyclocytic with very distinctly submerged subsidiary cells (fig. $7.1 \& 14.3$ ). Outer stomatal ledge large and conspicuous, enclosing a spacious vestibule (fig. 14.13).

Jollydora: The only genus of the Connaraceae with pure bicyclic stomata (fig. 7.3 \& 14.6). Outer stomatal ledge medium, in size between those of Connarus and those of most other genera e.g. Cnestis.

Manotes: Stomata irregularly cyclocytic, cell walls between subsidiary cells thinner than the walls between other epidermal cells (fig. 6.1, 6.2, \& 14.3). Outer stomatal ledge medium in section Manotes (fig. 14.11). Outer stomatal ledge large in section Dinklagea. Epidermal cuticula of M. macrantha with many more or less parallel lines (fig. 6.1).

Pseudoconnarus: Stomata probably paracytic but very hard to discern because the lower epidermis cells are always strongly papillate.

Rourea section Bernardinia (Am.): Stomata in majority paracytic, other part anomo- cyclocytic (fig. $10.4 \& 14.4-5$ ). Vestibule small with a narrow outer stomatal ledge.

Rourea section Byrsocarpus (Af.): Stomata $75-100 \%$ paracytic other part anomocytic (fig. 10.4, $11.1 \& 14.4-5$ ). Vestibule small with a narrow outer stomatal ledge (fig. 14.9).
R. cassioides has a papillate lower leaf epidermis.

Rourea section Rourea (Af., Am., and As.): Stomata anomo-cyclocytic, paracytic, anisocytic, or partly or entirely intermediate between these three patterns (fig. 12.1, 13.2-4, \& 14.2-5). Vestibule small with a narrow outer stomatal ledge. Taxa:

Rourea accrescens: Stomata 50-80\% paracytic, other wise anomo-cyclocytic.
Rourea acropetala: Stomata $50-75 \%$ paracytic, other wise anomo-cyclocytic. Lower epidermis strongly papillate in the collections from Sumatra and not papillate in the collections from the continent.

Rourea blanchetiana: Stomata probably anomocytic with a strong tendency to paracytic. Cellwalls fragile and easily destroyed. Lower epidermis papillate.

Rourea camptoneura cluster: Stomata 30-70\% paracytic, other part anomocyclocytic. Epidermis cuticula often with a pattern of more or less parallel lines (fig. 10.2).

Rourea frutescens cluster: Stomata anisocytic to anomo-cyclocytic with a strong tendency to anisocytic (fig. 13.2-4).

Rourea gardneriana cluster: Stomata 40-95\% paracytic and other part anomocyclocytic with a tendency to paracytic.

Rourea induta cluster: Stomata anomo-cyclocytic mixed with paracytic in varying proportions.

Rourea krukovii: Stomata paracytic. Lower epidermis cells papillate.
Rourea martiana cluster: Stomata in majority paracytic, the other part anomocytic, or anomocytic with 3-6 subsidiary cells with a tendency to paracytic. Lower epidermis often papillate. Walls between epidermis cells always thin.

Rourea parviflora: Stomata paracytic (fig. 12.1).
Rourea pinnata: Stomata paracytic.
Rourea prancei: Stomata ca $80 \%$ paracytic. Epidermis with a pattern of many microscopical pits, ca 20 per epidermis cell.

Rourea pubescens: Stomata paracytic.
Rourea revoluta cluster: Stomata paracytic. Lower epidermis often papillate.
Rourea suerrensis cluster: Stomata anomo-cyclocytic.
Rourea section Roureopsis (Af., As.): Stomata 75-100\% paracytic, other part anomo-cyclocytic in R. acutipetala, R. asplenifolia, R. confundens, R. dictyophylla, R. emarginata, R. stenopetala (fig. 9.2). Stomata cyclocytic with a strong tendency to paracytic in R. calophylla, R. erythrocalyx, R. myriantha, R. obliquifoliolata, R. solanderi (fig. 9.1, 9.4, \& 10.1). Or stomata cyclocytic with a tendency to bycyclic and paracytic in R. calophylloides (fig. 9.4). All species have stomata with a large and conspicuous outer stomatal ledge enclosing a spacious vestibule (fig. 14.12).

Epidermal cuticula of $R$. calophylla with many more or less parallel lines (fig. 5.4).

Rourea section Santaloides (Af., As.): Stomata 90-100\% paracytic (fig. 11.2-4 \& 14.4-5). Vestibule small with a narrow outer stomatal ledge.

Some species with a papillate lower leaf surface like in $R$. balansea, $R$. harmandiana, R. mimosoides, and R. prainiana or without in $R$. minor and R. rugosa. $R$. fulgens and $R$. radlkoferiana papillate or not.

Vismianthus: Stomata anomo-cyclocytic (fig. 6.3). Vestibule small with a narrow outer stomatal ledge.

Connaraceae spec. nov. (Af.): Stomata anomo-cyclocytic.

### 4.5.4. Specimens examined $(!=$ photograph in WAG $)$

Agelaea borneensis (As.): Au \& Chai S. 24131 (L); Axelius 382 (L).
Agelaea macrophylla (As.): Cockburn FRI 7538 !(L); Leeuwenberg 13241 (WAG).
Agelaea paradoxa (Af.): Bokdam 3348 (WAG); Breteler 1889 !(WAG); Breteler \& Lemmens 8192 !(WAG).

Agelaea pentagyna (Af.): Bos 3534 (WAG); 5346 (WAG); Breteler 1738 (WAG); Chase 432 (SRGH); Decary s.n. anno 1926 (L); J.J. de Wilde et al. 247 !(WAG); Dummer 1265 (Z); Goldsmith 64-61 (SRGH); Gossweiler 8098 (COI); Lam \& Meeuse 5308 (L); 5552 (L); 5838 (WAG); Leeuwenberg 11246 (WAG); Stoop v.d. Kasteele 207 (WAG); Welwitsch 4641 (K); Zenker 2271 (WAG).

Agelaea poggeana (Af.): Arends et al. 659 !(WAG); Bos 5514A (WAG); N.Hallé 1190 (P); Raimond et al. 479 (LISC); Young 454 (BM).
Agelaea rubiginosa (Af.): Breteler 1749 (WAG); Letouzey 14061 (WAG); Liben 2285 !(BR); Louis et al. 499 !(WAG); 686 (WAG); Stam 131 (L); Zenker 545 (WAG); 2543 (BR).

Burttia prunoides: Burtt 1978 (EA); Peter 34193 !(B).
Cnestidium guianense: Borsboom 12265 !(WAG); Breteler 3773 !(WAG).
Cnestidium rufescens: Coelingh 880 (U); de Bruijn 1779 (WAG).
Cnestis bomiensis (Af.): Jansen 2288 (WAG).

Cnestis corniculata (Af.): Bos 5183 (WAG); 6896 (WAG); Claessens 473 (BR); Dewevre 715B (BR); W. de Wilde 2822 (WAG); de Wit 7543 (WAG); d’Orey 386 !(COI); Leeuwenberg 4010 (WAG); 8281 (WAG); Liben 2916 (BR); J. Louis 2556 !(BR); 6957 (BR); 10516 (BR); Morton \& Gledhill SL 504 (K); Mildbraed 4208 (HBG); Mullenders 2051 (BR); Pynaert 168 (BR); Sapin s.n. (Gombé) (BR); Stoop v.d.Kasteele 255 (WAG); Vanderyst 22988 (BR); van der Zon 296 (WAG); Wingfield \& Lucas 1949 (K); Zenker 2157 (WAG).

Cnestis ferruginea (Af.): Bos 4252 (WAG); Breteler 1041 !(WAG); W. de Wilde 1622A (WAG); de Wit \& Morton A2856 (WAG); Risopoulos 648 (BR); Thijssen 100 (WAG); van der Zon 300 (WAG); van Meer 1566 (WAG).

Cnestis macrantha (Af.): Binuyo 45402 (P); D. Thomas 3326 (WAG).
Cnestis macrophylla (Af.): Leroy s.n. (P); Zenker 947 (K).
Cnestis mannii (Af.): Binyo \& Daramolo FHI 35455 (P); J.J. de Wilde et al. 253 (WAG); Le Testu 8378 !(BM); Mann 2264 (K); Talbot 1707 (K).

Cnestis mildbraedii (Af.): Dummer 5422 !(K); Eggerling 1553 (BR).
Cnestis palala (As.): Clemens 3805 (L); W. de Wilde 14512 (L); Gaudichaud 93 (L); Geesink
\& Hiepko 7867 (L); Griffith 1255 (L); B.Hussin S18514 (L); Shah \& Samsuri MS 1738 !(L).
Cnestis polyphylla (Af.): Boivin 1888 (P); s.n. (C. boiviniana) (P); s.n. (C. lurida) (P); Faden \& Faden 72/68 (EA); Rakoto 2907 !(K); Rakotozafy \& Nicoll 4004 (WAG); Rudatis 1119 (WAG); van der Schijf 6217 (PRE).

Cnestis racemosa (Af)): Baldwin 10779 !(WAG); Bos 2578 (WAG); Jansen 2475 (WAG).
Cnestis uncata (Af.): Breteler \& Lemmens 8304 (WAG).
Cnestis urens (Af.): Bequaert 2004 !(BR).
Cnestis yangambiensis (Af.): J. Louis 13623 (BR); Mandango 1457 !(BR).
Connarus africanus (Af.): Bos 2574 (WAG); 5347 (WAG); de Koning 5541 !(WAG); Jansen 1525
(WAG); Morton SL 616 !(WAG).
Connarus agamae (As.): Sinanggul 57255 (L).
Connarus brachybotryosus (Am.): Tuerckheim 4027 (U).
Connarus championii (As.): Waas 1919 (L).
Connarus cochinchinensis (As.): Geesink 6349 (L); Teyse 6016 (L).
Connarus conchocarpus (As.): Irvine 846 (L).
Connarus congolanus (Af.): Leeuwenberg 5091 !(WAG); Sapin D24 (BR).
Connarus coriaceus (Am.): Maas et al. 3483 (U); Schultz 7610 (U); N.T. Silva 1879 (U); A.C.
Smith 3572 (U).
Connarus culionensis (As.): Elmer 12877 !(L); Leighton 102 (L).
Connarus detersus (Am.): Harley 15653 (U).
Connarus erianthus (Am.): Croat 20754 (U); Oldenburger et al. 331 (U); Pires et al. 51100 (U);
Vilhena et al. 217 (U).
Connarus euphlebius (As.): James et al. S35074 (L).
Connarus fasciculatus (Am.): Prance et al. 16044 (U).
Connarus ferrugineus (As.): Lewis 128 (L).
Connarus gabonensis (Af.): Breteler \& de Wilde 494 !(WAG).
Connarus grandis (As.): Elmer 14888 (L).
Connarus griffonianus (Af.): J.J. de Wilde 625 !(WAG); Gilbert 14202 (BR); Tisserant 1586
!(WAG); 1668 (WAG).
Connarus incomptus (Am.): Maas \& Westra 3654 !(U).
Connarus lambertii (Am.): Cuatrecuasas 14076 (U); Lundell 19044 (U).
Connarus longistipitatus (Af.): A. Léonard 2816 (BR); van Meer 1822 !(WAG).
Connarus marlenei (Am.): Prance et al. 11242 (U).
Connarus monocarpus (As.): Kostermans 24846 (L); 28060B (L); Robyns 6974 (L).
Connarus odoratus (As.): Chai S19704 (L); Elmer 21058 (L).
Connarus ovatifolius (Am.): Harley 17399 (U).
Connarus paniculatus (As.): Geesink et al. 6787 (L).
Connarus perrotteti (Am.): Prance et al. 25769 (U); A.C. Smith 2817 (U).
Connarus punctatus (Am.): N.T. Silva 2411 (U).
Connarus regnellii (Am.): Mendes Magalhaes 19264 (U).

Connarus reticulatus (Am.): Howard 5848 (U).
Connarus rigidus (Am.): Steyermark \& Bunting 102467 (U).
Connarus ruber (Am.): Croat 20017 (U).
Connarus salomoniensis (As.): Kajewski 2017 (L); Whitemores collectors BSIP 2881 (L).
Connarus semidecandrus (As.): Elsener H90 (L); Langlasse 248 (L); Maxwell 75-509 (L); Sörzing
5272 !(L).
Connarus staudtii(Af.): Klaine 1961 !(P); Lecuwenberg 5622 (WAG).
Connarus suberosus (Am.): Fosberg 43291 (U); Hunt 6119 (U).
Connarus thonningii (Af.): Warnecke 446 !(K).
Connarus winkleri (As.): Elmer 13411 !(L); Leopold \& Kodoh SAN 81387 (L).
Connarus spec. Nw Guinea: Pullen 8266 (L).
Ellipanthus beccarii (As.): J. Singh SAN 22777 (L).
Ellipanthus hemandradenoides (Af.): Faden 74/292 (WAG); Faulkner 2109 !(BR).
Ellipanthus tomentosus (As.): Koorders 24160B (L).
Hemandradenia chevalieri: de Wit 9020 (WAG).
Hemandradenia mannii: J.J. de Wilde 8321 !(WAG); Koufani 153 (WAG); Léonard 583 (WAG);
Raynal 10751 (YA); Wagemans 1543 (BR).
Jollydora duparquetiana: Bos 6730 !(WAG); J.J. de Wilde 309 (WAG); Zenker 3438 (E).
Jollydora glandulosa: Letouzey 13416 (P).
Jollydora pierrei: Klaine 2884 (P).
Manotes expansa: Allard 212 (BR); Breteler \& Lemmens 8377 !(WAG).
Manotes griffoniana: Louis et al. 1088 (WAG).
Manotes lomamiensis: Delvaux 341 (BR); Gillardin 213 (BR).
Manotes macrantha: Breteler et al. 8715 (WAG); Breteler 9012 (WAG); de Wilde \& Jongkind 9330 (WAG); Jansen 2400 !(WAG); Reitsma 1728 !(WAG).

Pseudoconnarus macrophyllus: Wessels Boer 2336 (U).
Pseudoconnarus rhynchosioides: Krukoff 8304 (NY).
Rourea accrescens (Am.): Krukoff 6795 (U); Mori et al. 9091 (K); Prance et al. 2853 (NY).
Rourea acropetala (As.): Bartlett 8161 (L); Chevalier 37426 (P); Clemens 3365 (P); Rahmat si Toroes 2342 (L); 4912 (L); Harmand in Herb. Pierre 3292 (L).

Rourea acutipetala (As.): Cockburn FRI 8493 !(L); P. Sangkhachand 1221 (L).
Rourea adenophora (Am.): Allen 887 (K); Croat 8447 !(MO); Dodson et al. 10001 !(MO).
Rourea amazonica (Am.): Prance et al. 59302 (U); Ule 5054 (L).
Rourea antioquensis (Am.): Metcalf \& Cuatrecasas 30045 (MO).
Rourea araguaensis (Am.): Agostini \& Farinas 29 (U).
Rourea asplenifolia (As.): Korthals in Herb. Bogor 1920 (L); H.Wiriadinata 707 (L).
Rourea bahiensis (Am.): Pinheiro 1656 (NY).
Rourea balansea (As.): McKee 4443 (L).
Rourea blanchetiana (Am.): Salzmann s.n. (P).
Rourea calophylla (Af.): Breteler et al. 8634 (WAG); Klaine 3319 (P); Le Testu 6415 (WAG); Zenker 1963 !(WAG).

Rourea calophylloides (Af.): Le Testu 5444 !(BM).
Rourea camptoneura (Am.): Boom 4034 (U); Krukoff 1660 (U); 4899 (U); 4906 (U); 6289 (U); 7004 (U); Prance et al. 12933 (U); 13360 (U); 13704 (U); Rushby 1360 (K); 1370 !(K); Spruce 2168 (K); Ule 5056 !(K).

Rourea cassioides (Af.): Compere 1160 (BR); W. de Wilde 2637 (WAG); Jongkind 707 (WAG); Le Testu 4645 (WAG); Lisowski 40462 !(BR).

Rourea chrysomalla (Am.): Irwin \& Soderstrom 6001 (K); Mori et al. 10532 (K).
Rourea cnestidifolia (Am.): Warming 1849 (K).
Rourea coccinea ssp. coccinea var. coccinea (Af.): de Koning 6974 (WAG); Jansen 2620 !(WAG); Morton SL 1329 (WAG).

- ssp. coccinea var. viridis (Af.): Leeuwenberg 11426 !(WAG); Lisowski 17404 !(BR); A.Louis et al. 1325 (WAG).
- ssp. boiviniana (Af.): Gomes \& Sousa 4638 (WAG); 4680 !(WAG); Kuchar 13484 (EA); Musyoki \& Hansen 1022 (EA).

Rourea confundens (As.): Larsen et al. 32221 (L).
Rourea cuspidata (Am.): Bamps 5388 (BR); Krukoff 8375 (U); Prance et al. 2508 (U); 15034 (U); Spruce 1901 (K); 1924 (K); 2036 (K); 2376 (K); 3273 (K).

Rourea dictyophylla (As.): King 5425 (L).
Rourea discolor (Am.): Duarte 6118 (NY); Riedel s.n. anno 1821 (NY).
Rourea doniana (Am.): Don 41 (BR); Moore 291 (BM).
Rourea duckei (Am.): Pires et al. 50895 (K).
Rourea emarginata (As.): Bakhuizen v.d. Brink 7697 !(L); Boerlage s.n. (L); Rahmat si Toroes 3369 (L).

Rourea erythrocalyx (Af.): Breteler et al. 7696(WAG); Le Testu 6081 (BM); 7651 (WAG); Reitsma 1488 !(WAG); Toussaint 242 (BR).

Rourea fluminensis (Am.): J.G. Kuhlmann 2350 !(NY); Pires \& Black 3242 (U); Ule 2405 !(U).
Rourea frutescens (Am.): Broadway 5791 (K); De La Cruz 2719 (K); Maguire \& Fanshawe 22910
(U); Melinon anno 1842 (U); Prance et al. 1688 (U); Steyermark 87419 (U).

Rourea fulgens (As.): Falconer 560 (L); Y.C. Chan FRI 18183 (L).
Rourea gardneriana (Am.): Gardner 962 (K); Ratter et al. 4496 (K).
Rourea glabra (excl.S Brasil) (Am.): Aristeguieta 7051 (U); de Bruijn 1399 (WAG); Ekman 10428
(K); $17387(\mathrm{~K})$; Gentle $636(\mathrm{~K})$; $7615(\mathrm{BM})$; Harris $11981(\mathrm{~K})$; Holm \& Iltis $266(\mathrm{~K})$; Howard 5625
!(U); Jellez 1926 (BM); I. Johnston 485 (U); Mc Fadyem s.n. (K); Mexia 9248 (U); Novelo et al.
211 (U); Proctor et al. 24862 (U); 27238 (U); 36267 (U); Steyermark \& Allen 17175 (U).
Rourea glabra (S Brasil only): Luschnath s.n. (H.Fl.Br. 1267) !(BR).
Rourea glazioui (Am.): Simard in Herbarium Glaziou 3625 (P).
Rourea gracilis (Am.): Hatschbach 20829 (WAG); 26944 (K).
Rourea grosourdyana (Am.): Eiten \& Eiten 8496 (K); Prance et al. 9152 (U); 9563 (K); A. Smith 3149 (U); Ule 7898 (K).

Rourea harmandiana (As.): Harmand in herb. Pierre 6371 (L).
Rourea induta (Am.): Argent R. 6781 (U); Argent et al. 6518 (U); Burchell 8394 (K); Goldsmith
125 (K); Irwin et al. 10542 (U); 16637 !(K); Prance et al. 18852 (U).
Rourea kappleri (Am.): Oldenburger et al. 1264 (U).
Rourea krukovii (Am.): Maguire et al. 56706 (U); Prance et al. 10658 (K).
Rourea latifoliolata (Am.): Allen \& Allen 5242 (MO); Kennedy 2006 (MO).
Rourea ligulata (Am.): Archer 7920 (K); Burchell 9449 (K); 9981 (K); Rosa et al 4103 (U); Tutin 357 (K).

Rourea martiana (Am.): Rose \& Russell 19932 (NY).
Rourea mimosoides (As.): Beumée 6728 (L); Hansen \& Smitinand 12489 (L); Maxwell 82/203 (L).

Rourea minor (Af.): Bos 4940 !(WAG); De Graer 157 (BR); Espirito Santo 2674 (WAG); Lisowski 51507 (BR); Pierlot 840 (BR); Quarre 5820 (BR). (As.): BKF 57548 !(L); Kostermans 28060A (L); Ramos 39603 !(L); Vidal 720 (P).

Rourea myriantha (Af.): De Giorgi 1377 !(BR); de Wilde et al. 8071 (WAG); Donis 2140 (BR); Germain 4743 (BR); J. Louis 12097 (BR); Zenker 3720 (P).

Rourea neglecta (Am.): Spruce 2952 (BR).
Rourea obliquifoliolata (Af.): Badre 147 (WAG); Breteler \& Lemmens 8356 !(WAG); J.J. de Wilde 8438A (WAG); Louis et al. 515 (WAG); 938 (WAG).

Rourea orientalis (Af.): Malaisse 11181 (BR); Pawek 5057 !(SRGH); Peter 20165 !(B).
Rourea paraensis (Am.): Campbell et al. P22419 (U); Prance et al. 1835 (U); 22903 (U).
Rourea parviflora (Af.): Breteler \& Lemmens 8141 (WAG); A. Léonard 2879 (WAG); Louis et al. 1497 (WAG); J. Louis 2722 (BR); Mann 1795 (P); Tisserant 1555 (BM); Zenker 540 (WAG).

Rourea pinnata (As.): Ramos 1485 (L).
Rourea pittieri(Am.): Alonzo et al. 5105 !(MO); Duke 15710 !(MO); Sullivan 670 !(MO).
Rourea prainiana (As.): Sinclair 3869 (L); Whitemore FRI 12903 (L).
Rourea prancei (Am.): Prance \& Silva 58625 (NY).
Rourea psammopphila (Am.): Burchell 7880 (K).
Rourea puberula (Am.): Croat 19242 (WAG); Krukoff 1655 (K); Maguire 56884 (K); Steinbach 6735 !(U); 7608 (U).

Rourea pubescens (Am.): Sagot s.n. (K); Talbot s.n. (K).
Rourea radlkoferiana (As.): Hollrung 766 (L).
Rourea revoluta (Am.): V. Graham 458 (K); Schomburgk 125 (K).
Rourea rugosa (As.): Everett FRI 14229 (L).
Rourea schippii (Am.): Peck 889 (K); Schipp 1168 (K).
Rourea solanderi (Af.): Baldwin 11310 (WAG); Bos 5238 (WAG; 5274 !(WAG); 6156 (WAG); de Koning 3457 (WAG); Jansen 776 (WAG); Stoop v.d. Kasteele 219 (WAG); Zenker 2540 (WAG).

Rourea sprucei (excl.var. rondonensis) (Am.): Krukoff 8719 (U); Prance et al. 3256 (K); 10072 (K); Spruce 2760 !(BR).

Rourea sprucei var. rondonensis (Am.): Prance et al. 8458 (K); 8951 (K).
Rourea stenopetala (As.): Beusekom 2930 (L); Geesink et al. 5337 (L); 6783 (L).
Rourea suerrensis (Am.): Pittier 16103 (BM); Smith 6466 (K).
Rourea surinamensis (Am.): Breteler 4963 (WAG); Broadway 1891 (K); de Bruijn 1650 (WAG); Eggers 1246 (K); Ekman 11109 (K); Florschutz \& Maas 2757 (U); Howard \& Nevling 15486 (U); Lindeman et al. 730 (U); Maas et al. 5553 !(U); Sandwith 183 (U); Sintenis 5728 (WAG); Steyermark 88447 (U).

Rourea tenuis (Am.): Pohl s.n. (BR).
Rourea thomsonii (Af.): Bos 4579 (WAG); de Koning 2857 !(WAG); J. de Wilde 405 !(WAG); Schlieben 2794 (B).

Vismianthus punctatus: Schlieben 5757 (B); Semsei 647 !(K).
Vismianthus sterculiaefolius: Prain s.n. anno 21 Nov. 1889 (BM).
Connaraceae spec. nov. (Af.): Hallé 1727 !(P) see imperfectly known species (pag. 375)

### 4.6 Inflorescences

by R.H.M.J. Lemmens

The inflorescences of Connaraceae are basically axillary panicles. They are often located in the axils of rudimentary or very young leaves situated towards the apex of young branches. This often gives the impression of a compound terminal inflorescence, particularly in Manotes (fig. 15), Agelaea, Pseudoconnarus, Connarus, and some Cnestis and Rourea species (Fig. 16 A).

In many Connarus species the upper leaves of the main and lateral branches are reduced, forming a very large, strongly compound pseudoterminal inflorescence. The actual inflorescences are small and few-flowered. The leaves situated at the base rarely develop more or less normally, showing the true nature of this inflorescence, as in a specimen of Connarus africanus, Roberty 10749 (Fig. 16 B ).

Terminal inflorescences, as described by Schellenberg (1938) for many species in the larger part of the genera, and by Leenhouts (1958b) for Connarus and Agelaea, are not found in Connaraceae. Branches resembling a terminal inflorescence are always ending in a vegetative bud, that sometimes continues the branch after flowering, but it usually shrivels. Schellenberg (1938) considered the position of the inflorescence, either axillary or terminal, as very important in order to distinguish genera and even tribes in Connaraceae. The absence of true terminal inflorescences in the family seriously undermines Schellenberg's classification in tribes (see also paragraph 10.1 on phylogeny of the family).


Fig. 15. Manotes griffoniana: branch with axillary panicles (J. de Wilde \& Jongkind 9589; phot. C.C.H. Jongkind).

In Ellipanthus, Hemandradenia, Burttia and Vismianthus the inflorescences are always located in the axils of normal developed leaves, in the last two genera more particularly at the apex of the branchlets (Fig. 16 C).

The panicles are often reduced to pseudoracemes, e.g. in some Cnestis species. In Cnestis urens and C. uncata this reduction even results in single-flowered inflorescences. Occasionally the peduncle and axis of the panicle are so strongly reduced in length that the flowers form glomerules, as in Hemandradenia mannii and Rourea obliquifoliolata. In the latter species the glomerules are located particularly on the very long whip-like extremities of branches without well-developed leaves (Fig. 16 D).

In many species apparently more than one inflorescence is located in a single leaf axil. In some species this may be interpreted as a single panicle with a


Fig. 16. Different types of inflorescences in Connaraceae. For explanation see text.
strongly reduced peduncle and axis, while the developed branches look like separate inflorescences, e.g. Rourea minor and Ellipanthus hemandradenioides. In other species this may be the result of the reduction of an entire lateral branch maintaining its inflorescences in the axils of reduced leaves, e.g. Cnestis and Rourea species (Fig. 16E).

In cauliflorous species such completely reduced lateral branches produce the inflorescences. This is also known in other cauliflorous species such as Cercis (Leguminosae) and is found in Jollydora, Cnestis urens, C. uncata, C. corniculata, Rourea calophylloides, and Manotes macrantha. As flowering in these species occurs each year again on the same spot, large nodose proliferations are formed, that bear the flowers (Fig. 16 F).

In Cnestis large pseudoterminal panicles are considered as primitive, while cauliflory is advanced (see also paragraph 10.2 on phylogeny of Cnestis).

### 4.7 Flowers

by C.C.H. Jongkind

Connaraceae have flowers with five sepals, five petals, ten stamens in two whorls and either one or five carpels. All species are probably sweet scented and pollinated by insects (H.G. Baker, 1962: 208; Schellenberg, 1938: 11). Most species have a jointed pedicel.

The sepals are glabrous or hairy on one or both sides. They are valvate in Manotes and more or less in species of Cnestis, Connarus, Ellipanthus and Hemandradenia. They are imbricate in all other species. In Rourea solanderi they are almost entirely united, in all other species of the family the sepals are free or nearly free. They are quite often persistent and in Rourea and Manotes they are accrescent in fruit.

The petals are glabrous or hairy on the outside or on both faces. They may have glandular hairs and in Connarus, Manotes and Vismianthus they can have sessile glands on the surface. They are usually imbricate, they can be lorate and inrolled as well in Cnestis and Rourea. In Agelaea, Connarus, Hemandradenia, and Rourea they are often (strongly) connivent near base or middle.

A distinct androgynophore is found only in species of Manotes.
The inner, epipetalous whorl of stamens is shorter or subequal to the outer episepalous whorl. It is staminodial in Ellipanthus, Hemandradenia, and in some species of Connarus (see chapter about heterostyly).

The filaments have some kind of indumentum in Connarus, Ellipanthus, Hemandradenia, and Manotes but they are glabrous in all other genera.

The carpels are partly to entirely hairy in most species of the family, sometimes also with glandular hairs as in Manotes griffoniana. In some species like $R$. minor and R. emarginata they are almost glabrous.

As a rule there are two ovules per carpel.
The ovules are usually hemitropous but in Burttia prunoides they are anatropous.

### 4.8 Fruits and seeds

## by C.C.H. Jongkind

When there are five carpels present in flowers of Connaraceae, they usually do not develop collectively into five follicles. Usually some remain small while in many Rourea species only a single follicle is produced.

Connaraceae have two ovules in each carpel and in most species only one of them develops into seed. In Jollydora duparquetiana usually both ovules mature, while exceptionally there may be two seeds per carpel in Agelaea paradoxa, Ellipanthus hemandradenoides, and Rourea solanderi.


Fig. 17. Fruits of Hemandradenia chevalieri (phot. H.C.D. de Wit).


Fig. 18. Fruit of Jollydora duparquetiana (de Wilde \& Jongkind 9462, phot. C.C.H. Jongkind).
The fruits are usually dehiscent and orange to red, advertising the often twocoloured seeds to birds who are responsible for their dispersion. At the moment of dehiscing the funiculus is severed from the seed. The fruits of Jollydora and Hemandradenia are indehiscent. This is linked with an other rare feature in Connaraceae as they are both not lianas or savanna shrubs but understory treelets in the rain forest. Their seed coat is almost entirely fleshy and lacks contrasting colours while it remains hidden in the indehiscent follicle that are produced in often cauliflorous situations. Birds will readily detect the often abundant colourfull fruits on savanna shrubs or lianas of the canopy, but those of the understory treelets may escape their attention and these are more likely to be detected and harvested by small mammals, assuming the responsability for their dispersal instead.


Fig. 19. Fruits of Rourea obliquifoliolata (Breteler \& Lemmens 8111, phot. R.H.M.J. Lemmens).

The fruits of Cnestis and those of many Connarus species are hairy on the inside, but they are glabrous inside in all other genera. In Connarus these hairs may be partly glandular, or even exclusively so.

A striking character all Connarus species share is the stage in fruit development where the follicle is already fully expanded including a developing seed that is still not much bigger than a pin's head.

One of the characters all Connaraceae have in common is the at least partially fleshy character of their seed coat. The fleshy part is usually situated at the chalaza, positioned at the lower end of the seed as observed in the follicle. The colour of the sarcotesta is often strongly contrasting with the thin part of the testa as well as with the exocarp of the fruit. In Agelaea, Burttia, Cnestis, and


Fig. 20. Fruits of Agelaea pentagyna (Breteler \& Lemmens 8359, phot. R.H.M.J. Lemmens).
many species of Rourea ca $3 / 4$ of the seed is squeezed out of the follicle that retains a firm grip on the part that remains inside. In Manotes and Vismianthus the seed is almost completely released from the follicle, dangling near the base of it. It remains attached to the endocarp by means of a threadlike appendix of the sarcotesta. The apex of this apendage remains wedged in the narrowly funnel shaped bottom part of the follicle. These two genera are also the only ones in which endocarp and exocarp separate from each other at maturity.

In 1976 Corner published an excellent description of the fruits and seeds of ten Connaraceae species. In the present revision no distinction is made between the term sarcotesta for the fleshy part entirely fused with the seed and the term aril for the free part of the arilloid as Corner did. For both the term sarcotesta


Fig. 21. Fruits of Cnestis corniculata (Breteler, Lemmens, \& Nzabi 8154, phot. R.H.M.J. Lemmens).
is preferred here because the arilloid is clearly continuous, exclusively produced by the testa and, except in a few cases (see below) well separated from the hilum.

As Corner did not deal with fruits of all genera, his family diagnosis based on only ten species needs some modifications. Evidently he was not familiar with the seeds of Rourea orientalis or Rourea cassioides where the testa is fleshy except for a very small area around the hilum and the micropyle, and Manotes macrantha with an entirely fleshy testa. These three species also lack a thin testa along the preraphal side as is the case in species with a comparable large sarcotesta like Rourea thomsonii or Jollydora duparquetiana.

Many African Connaraceae have large seeds compared to those of other continents. The largest seeds ever found are from Rourea thomsonii measuring up to $4 \times 3 \mathrm{~cm}$. Other examples of African Connaraceae with big seeds are Agelaca paradoxa with seeds up to $3 \times 1.5 \mathrm{~cm}$, Connarus congolanus measuring $3.4 \times$ 2.5 cm, C. staudtii up to $3.5 \times 2 \mathrm{~cm}$, and Rourea solanderi reaching dimensions of $3 \times 2 \mathrm{~cm}$. Only a few Asiatic Connarus species have comparable large seeds like C. agamae and C. grandis with seeds that may measure up to $3.5 \times 2 \mathrm{~cm}$. All American Connaraceae have distinctly smaller seeds. Connarus congolanus, C. staudtii, and Rourea solanderi seems to have invariable big seeds, but in Agelaea paradoxa and Rourea thomsonii the largest seeds are found in Cameroun and Gabon while in other parts of Africa they produce seeds of strikingly smaller dimensions. The reason why in these species such big fruits are restricted to Cameroun and Gabon is still unknown as well as the general situation of large seeds being produced particularly in Africa.

The structure of the seeds concerning endosperm and cotyledons is very variable. It varies from seeds with small, thin, and flat cotyledons embedded in abundant endosperm in Manotes and some species of Cnestis to planoconvex cotyledons without endosperm in the seeds of Agelaea, Connarus, Jollydora, and Rourea. Intermediary combinations are represented by Burttia, Pseudoconnarus, and some species of Cnestis with flat but slightly fleshy cotyledons, embedded in abundant endosperm and planoconvex cotyledons with scarce endosperm in Cnestidium, Ellipanthus, Hemandradenia, and Vismianthus.

A character which is not mentioned by Corner is the position of the radicle. It seems to be generally assumed that the radicle is located near the micropyle, but in Connaraceae this is not always so. In part of the species of Rourea and Connarus the radicle is more or less ventrally or dorsally situated while the micropyle is found apically like it is in all other Connaraceae. In Connarus staudtii and C. congolanus the situation is otherwise, there the radicle is found in the centre of the seed and quite hidden between the peltate cotyledons, the radicle pointing more or less dorsally. These characters enable the segregation of groups of African species from their nearest relatives in Africa or Asia. Such groups are represented by Rourea erythrocalyx \& R. obliquifoliolata, $R$. coccinea \& $R$. thomsonii, and R. solanderi, R. myriantha, R. calophylla, \& R. calophylliodes. Each of these three groups is characterized by a ventral position of the radicle in the seed, away from the apical micropyle. A fourth group of African species comprising Connarus africanus, C. congolanus, and C. staudtii, respectively, is characterized by a gradual transition of the position of the radicle, from dorsal in the first to central in the last two species. Moreover C. africanus has a close relative in Asia, C. monocarpus. There the position of the radicle is intermediate between the dorsal position in C. africanus and the apical position of the radicle found in all other Connarus species (see also pag. on C. africanus). In Asiatic Connarus species with oblique fruits and almost round seeds it is sometimes difficult to establish the apical position. Fortunately the micropyle and the radicle are still located at the same spot in these species. These abberrant positions of the radicle in the seeds of Connaraceae are phenomena that are almost exclusively restricted to Africa. In not-African species only Connarus monocarpus and Rourea minor have their radicles in not exactly apical position. There seems to be no obvious explanation for these abberant positions, but they might be linked with the behaviour of some seed eating animals.

### 4.9 Seedlings

by C.C.H. Jongkind
Classification of the seedlings of Connaraceae has been rather neglected so far, probably due to lack of suitable conserved material. At present seedling material is available for most genera and an attempt is made to classify it according to de Vogel (1980: 56).


Fig. 22. Seedlings of Hemandradenia chevalieri (Eimunjeze s.n., phot. H.C.D. de Wit).

In genera where seedling collections of more than one species are available, differences between them proved to be very limited. Therefore a general seedling description is given for each genus, often based on only part of its constituent species. It is felt there will be a fair chance that seedlings of species that have not yet been investigated will prove to match these descriptions eventually. With each of the genera treated hereafter, all species to which the investigated seedlings were referred are listed. The pertinent conserved seedling material is cited with the taxonomic treatment of the relevant species.

De Vogel's key appeared to over emphasize the importance of the persistance of the testa when applied to Connaraceae. For instance in Rourea the single difference between the seedlings of various closely related species is persistance or deciduousness of the testa on the cotyledons. In de Vogel's classification these seedlings represent widely diverging types.

## Agelaea

Primary root well developed. Hypocotyl only slightly elongated. Cotyledons sessile, at most slightly spreading, without testa, fleshy, glabrous. First leaves scalelike.

Sloanea type, Palaquium subtype.
Species: A. paradoxa (fig. 25.1), A. pentagyna.


Fig. 23. Seedling of Cnestis ferruginea (seed from Bos 2952, phot. H.C.D. de Wit).

## Cnestidium

Primary root well developed. Hypocotyl only slightly elongated. Cotyledons with a short petiole, remaining hidden in testa and endosperm. First leaves scalelike.

Horsfieldia type, Horsfieldia subtype.
Species: C.rufescens (fig. 26.1).

## Cnestis

Primary root well developed. Hypocotyl strongly elongated, velutinous. Coty-


Fig. 24. Seedlings of Cnestis ferruginea (seeds from Louis et al. 186, phot. H.C.D. de Wit).
ledons sessile, flat, coriaceus, horizontal spreading, nervation clearly visible, hairy above. First leaves opposite or in a whorl of three, pinnate.

Sloanea type, Sloanea subtype.
Species: C. corniculata, C. ferruginea (fig. 23, 24, \& 26.5).

## Connarus

Primary root well developed. First internode sometimes with accessory roots. Hypocotyl usually only slightly but sometimes clearly elongated. Cotyledons sessile, at most slightly spreading, fleshy, glabrous, the testa persistent entirely or in parts. First leaves opposite and unifoliolate or scalelike.

Sloanea type, Sloanea or Palaquium subtype or Endertia type, Endertia subtype.

Species: C. africanus (fig. 26.6), C. grandis (de Vogel, 1980: 217-219), C. griffonianus, C. odoratus (de Vogel, 1980: 219-221), C. panamensis (Duke, 1969: 148).

Note: In my opinion de Vogel's seedling type for C. odoratus is artificial, as in this case the entire fruit was collected from the plant. Without interference by man only individual seeds are dispersed (see chapter on fruit).

## Hemandradenia

Primary root well developed. Hypocotyl strongly elongated, velutinous. Coty-


## Wーホ

Fig. 25. Seedlings, $2 / 3 \times$ : 1. Agelaea paradoxa; 2. Rourea coccinea subsp. coccinea var. coccinea; 3. Rourea surinamensis. (1. de Koning 5752 (WAG); 2. de Koning 5953 (WAG); 3. N.M. Heyde 703 (U)).



Fig. 27. Seedlings, $2 / 3$ x: 1. Hemandradenia chevalieri; 2. Hemandradenia mannii. (1, Eimunjeze s.n (WAG); 2, de Bruijn 2038 (WAG)).
ledons sessile, fleshy, glabrous or hairy at base, horizontally spreading. First leaves opposite, unifoliolate (like all leaves of Hemandradenia).

Sloanea type, Sloanea subtype.
Species: H. chevalieri (fig. 22, 26.3, \& 27.1), H. mannii (fig. 27.2) (the only two species of the genus).

## Manotes

Primary root hardly developed, many accessory roots developing instead. Hypocotyl strongly elongated and somewhat thickened at base, velutinous. Cotyledons with a short petiole, remaining within the testa with the endosperm, soon caducous. First leaves opposite, uni- or trifoliolate.

Horsfieldia type, Pseuduvaria subtype.
Species: M. expansa, M. griffoniana (fig. 26.4).

## Rourea

Primary root well developed. Hypocotyl only slightly elongated. Cotyledons sessile, at most slightly spreading, fleshy, glabrous, testa sometimes persistent. First leaves opposite, sometimes unifoliolate but usually scalelike.

Sloanea type, Palaquium subtype or Horsfieldia type and subtype.
Species: R. coccinea (fig. 25.2), R. minor (de Vogel, 1980: 221-223), R. obliquifoliolata, R. solanderi, R. surinamensis (Duke, 1965:332) (fig. 25.3), R. thomsonii.

An exceptional case is $R$. parviflora (fig. 26.2), with aberrant seedlings that look more like those of Cnestis or Manotes: No primary root, only accessory roots growing from the base of the hypocotyl. Hypocotyl strongly elongated. Cotyledons sessile, horizontally spreading, succulent, no nervation visible, glabrous. First leaves in a whorl, pinnate.

## 5. Heterostyly

by R.H.M.J. Lemmens

### 5.1 Introduction

In Connaraceae, heterostyly was first reported by Burck (1887) in some of the Asiatic species of Connarus. However, heterostyly was already noticed by Thonning who annotated specimens he collected in Ghana to that effect. When Schumacher dealt with these specimens he concluded that they represented two distinct species: Byrsocarpus coccineus with short styles and $B$. puniceus with long styles. They represent in fact the two types of styles of a single species: Rourea coccinea. It is peculiar that Schellenberg (1938) hardly pays attention to heterostyly in his monograph on Connaraceae. He pointed out that as a rule trimorphic flowers are found. Hemsley (1956) reports a well-marked dimorphy in the East African species. Leenhouts (1958b) only mentioned the fact that in the entire family the flowers are distinctly heterostylous. Finally, Baker (1962) discussed heterostyly in Connaraceae, with special reference to Byrsocarpus coccineus. He questions the existence of heterotristyly in the family.

Some species are reported to be dioecious or to 'represent a stage in a trend towards dioecism' (Hemsley). This is done by Hemsley (1956) for the East African species, and by Schellenberg (1938) and Leenhouts (1958b) for Ellipanthus (including Pseudellipanthus).

Leenhouts (1958b) and Baker (1962) stated that in order to solve the questions concerning heterostyly and dioecism, observations of living material within the tropics should provide the most reliable data. This may be true, but I think that detailed investigation of a sufficient amount of herbarium specimens may give a great deal of information about these breeding systems as well.

### 5.2 Types of heterostyly in Connaraceae

The length of pistils and stamens was accurately measured in almost all of the African species. In addition some Asiatic and South American species were selected in order to either represent the non-African genera, or types of heterostyly absent in Africa, and these were measured also. The result is reproduced in fig. 28, each diagram representing a species. The number of specimens investigated varies from 33 in much collected species as Cnestis corniculata, to 2 in rare species as Vismianthus punctatus. In each diagram, the specimens are arranged according to increasing pistil length. All flowers of a single specimen invariably are of the same type.

- (apparently) fertile pistil(s)

O rudimentary pistil(s)

+ (apparently) fertile stamens
$\Delta$ rudimentary stamens


Fig. 28. Diagrams of 21 species of Connaraceae, showing the pistil and stamen lengths of the specimens investigated. In each diagram the specimens are arranged according to increasing pistil length. For explanation see text.



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Heterostyly in Connaraceae can be classified in 8 different types, as shown in fig. 29 and 30.

1. Heterotristyly

Species in several genera are heterotristylous. This is the case in most Agelaea species (fig. 31), excepting some from Asia, in all Manotes species except $M$. macrantha, in Jollydora duparquetiana and probably also in the other Jollydora species. Thus, true heterotristyly is found in two 5-carpellate genera and in one 1 -carpellate genus.

In all heterotristylous species, the number of individuals of each type ( $a, b$ and c) is roughly equal, except in Jollydora duparquetiana, where the number of short-styled specimens is larger than the numbers of medium- and long-styled ones. However, statistically this difference is not significant, as the distribution of the numbers does not differ significantly from an equal distribution of the three types. The larger number of short-styled specimens may be due to chance. However, as is demonstrated by Breteler \& van Ziel in their treatise on Jollydora, short-styled plants only rarely produce fruits. Additionally, functionally male plants do flower more frequently, which could explain the larger number of short-styled plants collected.
2. Heterostyly, transitional between heterotristyly and heterodistyly

Several species of 4 different genera show a type of heterostyly, that can be considered neither as true heterodistyly, nor as true heterotristyly. It is found in Cnestis polyphylla, C. racemosa, Cnestidium rufescens, Pseudoconnarus macrophyllus, and Agelaea macrophylla.

In these species flowers occur that have pistils about as long as the stamens of one whorl (d and e), called semi-homostyly by Ganders (1979), pistils that are longer or shorter than the stamens ( $a$ and $c$ ), or sometimes pistils of intermediate length (in between the lengths of the stamens from the two whorls; b). This type is only found in 5-carpellate species.
3. Heterodistyly with 10 fertile stamens and short or long styles

This is the most common type of heterostyly in Connaraceae. It is found both in 1-carpellate species (Burttia prunoides, Vismianthus punctatus), and in 5-carpellate species (Rourea, most Cnestis species, Manotes macrantha, Agelaea borneensis).

It is characterized by pistils and stamens clearly differing in length while the two whorls of stamens are subequal. It is possibly derived from heterotristyly by loss of the medium-styled form.
4. Heterodistyly with rare extreme forms

In this type of heterodistyly stamens and pistils are frequently almost equal in length ( h and i ) while in more rare cases they do differ distinctly ( $f$ and g ). It is found in the Asiatic Cnestis palala.


Fig. 29. The hypothetical evolution of heterostyly in 5-carpellate Connaraceae. For explanation see text. The numbers and letters correspond to the types of heterostyly discussed in the text.



Fig. 31. Agelaea pentagyna: medium-styled flower (phot. H.C.D. de Wit).

## 5. Homostyly

Cnestis ferruginea always has flowers that have both whorls of stamens and the pistils approximately equal in length (fig. 32). The stamens may be slightly longer as well as slightly shorter than the pistils ( j and k ).

When the pistils are longer than the stamens, the styles are curved towards the anthers. Compared to other Cnestis species the flowers are small.

## 6. Heterodistyly with 10 fertile stamens, and a medium or long style

In some African and Asiatic species of Connarus a type of heterodistyly is found with 10 apparently fertile stamens. The pistil is either intermediate between the lengths of the stamens of both whorls (b), or it is longer than the stamens (c). This type is thought to be derived from heterotristyly by loss of the short-styled form. It is limited to the 1 -carpellate representatives Connarus africanus, C. congolanus, C. longistipitatus and many Asiatic Connarus species.

It should be noted that in American Connarus species the short-styled form is still present.
7. Heterodistyly with 5 fertile stamens

In 1-carpellate species such as Connarus staudtii, C. griffonianus, C. thonningii, some Asiatic Connarus species, Hemandradenia mannii, H. chevalieri, Ellipanthus hemandradenioides, E. madagascariensis, and E. tomentosus, heterodistyly with 5 fertile and 5 rudimentary stamens is found.

This may have evolved from the type discussed under 6. Sometimes it is almost impossible to establish whether the short stamens are fertile or not. Burck (1887) pointed out already that in Asiatic Connarus the short stamens are apparently fertile but they do not open.

## 8. Dioecism

Ellipanthus beccarii, an Asiatic species, is dioecious. Male plants have 5 fertile stamens, 5 rudimentary ones and at most a rudimentary pistil. Female plants have 5 sterile stamens (lacking pollen), 5 rudimentary stamens and a fertile pistil. This situation is probably derived from heterodistyly with 5 fertile stamens and a fertile pistil, as found in other Ellipanthus species.

In American Connarus species there also seems to occur a tendency towards dioecism.

### 5.3 The hypothetical evolution of heterostyly in Connaraceae

Heterotristyly is found in Jollydora, Manotes and Agelaea. These genera are considered as comparatively primitive while they are not closely related to each other. For this reason heterotristyly may be considered a plesiomorphic charac-ter-state in Connaraceae while all other types of heterostyly may be derived from it.

Heterostyly in general in Connaraceae seems to have evolved in two directions:


Fig. 32. Cnestis ferruginea: flower showing small stamens and curved styles (phot. H.C.D. de Wit).
one towards dioecism in 1-carpellate Connaraceae, and the other towards homostyly in 5-carpellate Connaraceae. Thus, in 1-carpellate and in 5-carpellate Connaraceae the evolution seems to have followed, at least partly, a different course. See fig. 30 and 29. In both pathways heterodistyly, either with 10 or 5 fertile stamens, is an intermediate stage.

The two most advanced types of heterostyly are discussed below.
a. Dioecism

In Connaraceae dioecism is rare. Only the Asiatic Ellipanthus beccarii is unquestionably dioecious. However, in this species seemingly bisexual flowers may occur as well, while in other Asiatic, usually bisexual Ellipanthus species, unisexual flowers may be present (e.g. the closely related E. tomentosus). In several South American Connarus species unisexual flowers are found as well, but this was not sufficiently investigated as there was not much material available. Functionally female flowers often seem to possess normally developed long stamens, but the anthers are empty or they contain poorly developed pollen only. Functionally male flowers may have a carpel that is either distinctly rudimentary or only somewhat reduced in size, i.e. with a somewhat smaller ovary and a poorly developed stigma. Leenhouts (1958b) remarked that 'in the protandrous $E$. tomentosus var. gibbosus it is sometimes difficult to establish whether the
stamens have been or the pistil will be fertile'. It is sometimes difficult to establish whether flowers are uni- or bisexual.
b. Homostyly

A situation close to homostyly is found in one species only: Cnestis ferruginea. It resembles the situation called quasi-homostyly by Ganders (1979). Possibly Cnestis ferruginea is self-compatible. Wyatt (1983, as modified from Ornduff, 1969) published a list of characteristics that often differ between outcrossing species and their selfing derivates. Table 3 shows the character-states, found in C.ferruginea that may indicate autogamy, and outcrossing respectively, compared to the list of Wyatt. This species shows rather many characteristics, that are usually found in autogamous plants and that consequently indicate possible self-compatibility.

As a rule, plants with homostyly, as derived from heterostyly, are self-compatible and self-pollinating (Ganders, 1979).

It is curious, however, that a plant grown in the greenhouse in Wageningen flowers regularly, but it never sets fruit. Possibly some activity by insects is necessary in order to accomplish pollination, as is known in some other autogamous plants.

### 5.4 Comparison of heterostyly and dioecism in Connaraceae with other families

Heterostyly is known in plants of many different families, that are not necessarily related (table 4). Consequently, heterostyly must have evolved independently on several occasions. According to Vuilleumier (1967), breeding systems are adaptive or flexible under different environmental conditions. This could explain the convergent evolution of heterostylous breeding systems, and the many different types of heterostyly, found in some families, like Connaraceae. For a survey see Ganders (1979).

Considering heterostyly as a polyphyletic breeding system, it is rather surprising that heterostylous species in different families show many similar structures,

Table 3. Character-states of Cnestis ferruginea indicating possible outcrossing and autogamy respectively, as compared to the list of Wyatt (1983)

## outcrossing

Flowers many

## autogamy

Petals small
Anthers adjacent to stigma
Pistils short
Stamens equal in length to pistil
Many follicles maturing per flower
Wide distribution

Table 4. Families with heterostylous species
Heterodistylous species Heterotristylous species
Boraginaceae
Clusiaceae
Connaraceae Connaraceae
Erythroxylaceae
Gentianaceae
Iridaceae
Leguminosae
Linaceae
Linaceae
Loganiaceae
Lythraceae
Lythraceae
Menyanthaceae
Olacaceae
Oleaceae
Oxalidaceae
Oxalidaceae
Plumbaginaceae
Polygonaceae
Primulaceae
Rubiaceae
Santalaceae
Saxifragaceae
Sterculiaceae
Turneraceae
tendencies, and developments. In many aspects Connaraceae agree with other heterostylous families, as illustrated below.

1. Like in all other heterostylous species with two whorls of stamens, the inner (epipetalous) stamens of Connaraceae are shorter than the outer (episepalous) stamens.
2. The morphological differences in pistils and stamens shown by heterostylous flowers are usually related to a physiological self-incompatibility system. In Connaraceae, information about this system is scarce. According to Baker (1962) Rourea coccinea is largely, but not completely, self-incompatible. Seed setting usually followed 'legitimate' cross-pollination (long $\times$ short and vice versa).
3. Heterotristyly is rare and found only in a few species in Pontederiaceae, Lythraceae, Oxalidaceae, Linaceae, and Connaraceae. In all these families, closely related di- or monomorphic species, are found. The trimorphic species are usually regarded as primitive. Lewis (1975) found a situation comparable with Connaraceae in Pemphis (Lythraceae), as did Ornduff (1964), while Weller \& Denton (1976) did so in Oxalis.
4. Just as the transition of tristyly towards distyly is commonplace, according to Vuilleumier (1967) a development towards dioecy and homostyly occurs just as frequently.

Darwin (1877) was the first to suggest that a dioecious species (Rhamnus catharticus) had a heterostyled ancestor. Later, more examples of evolution of dioecy from heterostyly (usually distyly) have been reported. See Bawa (1980) for a survey.

In all dioecious taxa that have evolved from distylous ancestors, male flowers apparently are derived from short-styled and female from long-styled flowers. Bawa also states that unisexuality is often found in taxa with large, few-seeded, animal-dispersed fruits. These phenomena occur in Connaraceae.
5. Compared to their heterostylous relatives, the homostyles often inhabit a larger area of distribution (Weller \& Denton, 1976; Ganders, 1979) and they often have a more 'weedy' character (Ornduff, 1964; Vuilleumier, 1967). Cnestis ferruginea, the only Connaraceae that is approximately homostylous, is widespread, and is one of the most common species of Connaraceae in many countries, often found on formerly cultivated places and in secondary regrowths.
6. Ganders (1979) reconstructed pathways by which on the one hand distyly and on the other tristyly may have evolved into other breeding systems. According to Ganders the evolutionary breakdown of heterodistyly leads to homostyly, monomorphy, and dioecy, and that of heterotristyly results in quasi-homostyly, semi-homostyly, monomorphy, and distyly. It is surprising how well the schematic representation of the hypothetical evolution of heterostyly in Connaraceae fits in Gander's diagrams. In fact, it combines both diagrams, illustrating the enormous diversity of heterostyly in this family.

Connaraceae differ in some other aspects from most other heterostylous families.

1. The stigmas of the floral morphs may differ in shape, size or, more commonly, in the size of the stigmatic papillae. In many species of Connaraceae such differences in the stigmas are found, but they are not or hardly related to the length of the style, except in species with functionally unisexual flowers. Andreas \& Prop (1954) observed differences in the stigmas of Cnestis palala, but these also were not distinctly related to the style length.
2. Heterostylous species usually show differences in pollen size and number of pollen grains produced by each anther and each flower. Less frequently differences in pollen shape, colour or exine sculpturing are observed. Normally, pollen of long stamens is larger. However, in Connaraceae differences in pollen size and shape are not found. In 6 specimens of different species pollen grains from different whorls of stamens were measured (see table 5 and 6). Baker (1962)

Table 5. Mean diameter in $\mu \mathrm{m}$ of pollen grains in some heterotristylous species of Connaraceae

|  | short stamens | medium stamens | long stamens |
| :--- | :--- | :--- | :--- |
| Agelaea paradoxa |  | $28.3 \times 26.2$ | $27.0 \times 24.1$ |
| Agelaea rubiginosa | $24.4 \times 23.3$ |  | $25.8 \times 22.8$ |
| Manotes expansa | $20.2 \times 16.4$ | $21.3 \times 18.3$ |  |
| Manotes griffoniana | $22.3 \times 18.9$ | $23.8 \times 20.3$ |  |

Table 6. Mean diameter in $\mu \mathrm{m}$ of pollen grains in some heterodistylous species of Connaraceae

|  | short stamens | long stamens |
| :--- | :--- | :--- |
| Connarus africanus <br> (long-styled) | $30.0 \times 22.7$ | $31.0 \times 22.2$ |
| Rourea thomsonii <br> (short-styled) | $21.0 \times 21.7$ | $21.6 \times 20.4$ |

found no differences in pollen size in Rourea coccinea. Burck (1887) did find differences in pollen size in long and short stamens of medium-styled specimens of Connarus falcatus ( = probably C. monocarpus ssp. malayensis). But he also observed that the anthers of the short stamens never open: evidently pollen of the short stamens is not fertile.

There is no family in which such a diversity in forms of heterostyly is known. This would be a stimulus for experimental research, but the habit of the plants (large forest lianas, shrubs or small trees) does not permit simple cultivation in a greenhouse. However difficult, further investigations are most desirable, particularly in genetics, compatibility, pollination, and fertility of pollen.

## 6. Pollen morphology

by R.H.M.J. Lemmens

Pollen of some species of Connaraceae has already been described by Erdtman (1952). Forero (1976) studied pollen of a number of South American species, while Eimunjeze (1976) compared pollen of Hemandradenia and Ellipanthus species. In 1979 Dickison made a survey of the pollen morphology of Connaraceae. Mondal \& Mitra (1982) recorded biaperturate pollen to occur along with the normal triaperturate ones in some specimens of Rourea minor (as R. santaloides).

Pollen grains of some, mainly African, representatives of most genera were studied by the present author (see table 7).

Table 7. Selected pollenmorphological features of Connaraceae

|  | 1 | 2 | 3 | 4 | 5 | 6 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Agelaea paradoxa | $28 \times 25$ | 1.12 | PS | $3-\mathrm{c}$. | fr | 2.0 |
| A. rubiginosa | $25 \times 23$ | 1.09 | PS | 3-c. | fr | 2.1 |
| Cnestis corniculata | $22 \times 20$ | 1.10 | PS | $3-\mathrm{c}$. | fr | $1.3^{*}$ |
| C. polyphylla | $25 \times 21$ | 1.19 | SP | $3-\mathrm{c}$. | r | 1.4 |
| C. racemosa | $22 \times 20$ | 1.10 | PS | 3-c. | fr | 1.6 |
| Connarus africanus | $31 \times 23$ | 1.35 | P | 3-c. | r | 1.8 |
| C.griffonianus | $30 \times 23$ | 1.30 | SP | 3-c. | r | 2.6 |
| C. monocarpus ssp. malayensis | $30 \times 25$ | 1.20 | SP | 3-c. | r | 2.4 |
| C. monocarpus ssp. monocarpus | $39 \times 31$ | 1.26 | SP | 3-c. | r | 2.4 |
| C. semidecandrus | $32 \times 28$ | 1.14 | SP | 3-c. | r | 2.5 |
| C. staudtii | $31 \times 28$ | 1.11 | PS | 3-c. | r | 3.0 |
| C. thonningii | $34 \times 28$ | 1.21 | SP | 3-c. | r | 2.3 |
| Ellipanthus hemandradenioides | $33 \times 35$ | 0.94 | OS | 3-c. | r | 2.6 |
| E. tomentosus | $30 \times 30$ | 1.00 | S | 3-c. | r | 2.7 |
| Jollydora duparquetiana | $38 \times 53$ | 0.72 | O | 4-c. | cr | 2.9 |
| J. pierrei | $41 \times 62$ | 0.66 | O | 4-c. | cr | 3.0 |
| Manotes expansa | $21 \times 17$ | 1.24 | SP | 3-c. | fr | 1.5 |
| M. griffoniana | $23 \times 20$ | 1.15 | SP | 3-c. | fr | 1.8 |
| Roureamyriantha | $22 \times 24$ | 0.92 | OS | 3-c. | fr | 1.9 |
| R. solanderi | $21 \times 22$ | 0.95 | OS | 3-c. | fr | 1.5 |
| R. thomsonii | $21 \times 21$ | 1.00 | S | 3-c. | fr | 1.6 |

1. Average pollen grain size in equatorial view ( $\mu \mathrm{m}$ ) $P \times E$
2. Ratio of polar to equatorial axes $P / E$
3. Shape classification: $\mathrm{O}=$ oblate; $\mathrm{OS}=$ oblate spheroidal; $\mathrm{S}=$ spheroidal; $\mathrm{PS}=$ prolate spheroidal; $\mathbf{S P}=$ subprolate $; \mathbf{P}=$ prolate
4. Aperture type: 3-c. $=3$-colporate; 4-c. $=4$-colpate
5. Sculpturing type: $\mathrm{fr}=$ finely reticulate; $\mathrm{r}=$ reticulate; $\mathrm{cr}=$ coarsely reticulate
6. Average wall thickness

* In the specimen J. de Wilde 8058 aberrant pollen with large bulges is found, comparable with pollen from a specimen of Penianthus zenkeri (Engl.) Diels (Menispermaceae) as found by Dekker (1983).


Fig. 33. Scanning electron micrograph of tricolporate pollen of Hemandradenia mannii ( $\times 1500$; phot. V.E. Eimunjeze).

Preparations were made according to Erdtman's acetolysis method (1952) with minor modifications as described by Arends (1989, in press), and subsequently mounted in glycerine jelly. They were studied by means of a light microscope.

Dickison (1979) studied pollen of all genera, except Hemandradenia, of which pollen was investigated by Eimunjeze (1976). Dickison found that pollen of Connaraceae is rather uniform, with the exception of that of Jollydora. He also described some characters that show some evolutionary advancement. Of these characters, grain size and shape can be studied already by means of a light microscope.

According to Dickison evolutionary advancement is demonstrated by increase in grain size. This trend has been described in a number of unrelated families by various authors. Pollen is comparatively small in the 5 -carpellate genera Manotes, Rourea, Cnestis, and Agelaea, and according to Dickison also in Cnestidium and Pseudoconnarus. But he described very large pollen in Rourea martiana from South America. In the 1-carpellate genera pollen grains are usually distinctly larger, but according to Dickison some Connarus species from South America have small pollen, just as Schellenbergia sterculiifolia (now a synonym of Vismianthus sterculiifolius) from Asia. In the preliminary stages of our Connaraceae programme van den Berg made an investigation of pollen of Vismianthus sterculiifolius. He found no differences with the rather large pollen of Vismianthus punctatus and that of Burttia prunoides. Pollen is largest in Jollydora.

Dickison considered sphaerical and subsphaeroidal to be primitive, and oblate or prolate as advanced. Both last states are rare, oblate is only found


Fig. 34. Scanning electron micrograph of tetracolpate pollen of Jollydora duparquetiana ( $\times 1500$, phot. R.G. van den Berg).
in Jollydora, while prolate occurs only in some Connarus species and, according to Dickison and Forero (1976), in some Rourea species from South America as well.

Generally it can be stated that pollen in the tribes Cnestideae and Manoteae is sphaerical or subsphaeroidal and small, with a thin wall and a finely reticulate ornamentation. In Connareae it is suboblate to subprolate and larger, with a thicker wall, and more coarsely reticulate (fig. 33). Jollydora (Jollydoreae) shows a completely different pollen type compared to the other genera of the family. Its pollen is large, oblate and tetracolpate, with a thick wall and a coarse reticulum (fig. 34). This most unusual type is not found in any other genus of Dicotyledons with the single exception of Impatiens (Erdtman, 1952; Dickison, 1979). Combined with other characters unique in Connaraceae, such as habit and number of seeds per carpel (see paragraph 10.1 on phylogeny of the family), this justifies the separate position of Jollydora in the family.

Pollen of Manoteae and Cnestideae is probably primitive. In Connareae and particularly in Jollydora, it is considered to be advanced. Within the tribes and genera evolutionary advancement, as described by Dickison, is sometimes found as well.

With the exception of Jollydora, the study of pollen grains does not provide a useful delimitation of the genera but it does support the assumed relationships of the genera in the family as well as the proposed classification in tribes.

## 7. Chromosome numbers

by J.C. Arends

The 2 n chromosome numbers as found in the various species are presented in Table 8. At present, there is karyological information on African taxa only. The information pertains to 10 out of 50 species and 6 out of 10 genera recognized in this study.

The numbers indicate that there are two groups, one group comprises taxa with $2 \mathrm{n}=32$ and the other $2 \mathrm{n}=28$ or, in a single case $2 \mathrm{n}=26$.

In 1976 I presented evidence that Hemandradenia chevalieri has $2 \mathrm{n}=32$ (see Eimunjeze, 1976). At that time it was suggested that there might be infraspecific

Table 8. Chromosome numbers in species of Connaraceae



Fig. 35. Hemandradenia chevalieri: Metaphase plate in root tip cell, $2 \mathrm{n}=32$.
chromosomal variation in that species, as Mangenot \& Mangenot $(1959,1962)$ reported $2 \mathrm{n}=28$. H. chevalieri belongs to the tribe Connareae, of which Connarus griffonianus has $2 \mathrm{n}=32$ as well. It is possible that the count of $2 \mathrm{n}=28$ by Mangenot $\&$ Mangenot (op. cit.) is either a misinterpretation of the cells analyzed, or has been found in a seedling of another species. This cannot be verified as these authors did not refer to any collection. In the two root tips of a single young seedling of Connarus griffonianus $2 \mathrm{n}=31$ and $2 \mathrm{n}=34$ has been counted as well. The preparation was rather difficult of analysis, and further material is needed before it can be ascertained that its chromosome number is $2 \mathrm{n}=32$ indeed.

The remainder of the species listed in the Table belong to either the tribe Manoteae or Cnestideae. These sections are characterized by $2 \mathrm{n}=28$.

The somatic chromosomes of the Connareae have a length ranging from $\mathbf{c}$. 0.5 to $1 \mu \mathrm{~m}$ (see Fig. 35), reproduced from Eimunjeze, 1976), whereas those seen in the present study in the Manoteae and Cnestideae range from c. 1 to $2 \mu \mathrm{~m}$. Thus it appears that the karyotype in the Connareae differs from that in the other tribes in both number and length of the chromosomes.

Although the present evidence is far from conclusive, it could be postulated that $2 \mathrm{n}=32$ represents a derived chromosomal condition, as it is found in the tribe that is characterized by quite a few other advanced character states (see paragraph 10.1). Further investigation is needed to support this hypothesis.

# 8. Wood anatomy 

by R.W. den Outer and W.L.H. van Veenendaal

### 8.1 Summary

The secondary xylem of 54 species belonging formerly to 19 genera of Connaraceae was studied, in order to contribute to a natural classification and generic delimitation in the family.

A general wood anatomical description is given of the family, based on our investigations and measurements made by Veenendaal (1964). Separate generic descriptions are also presented. Dickison's (1972) wood anatomical data on this family have been incorporated in the descriptions and discussion. Wood anatomically four groups of genera are recognized, mainly based on the composition of the ground tissue. Two of these groups are divided into smaller subgroups. These groups of genera are:
A. Manotes;
B. 1. Rourea with Byrsocarpus, Jaundea and Paxia; 2. Santaloidella, Santaloides, Spiropetalum and Pseudoconnarus; 3. Cnestidium, Cnestis and Bernardinia. The first two genera of subgroup 3 cover a wide range of wood anatomical characters;
C. Agelaea with Castanola;
D. 1. Connarus with Ellipanthus and Hemandradenia; 2. Jollydora and Burttia.

In the series mentioned above Manotes has the most primitive wood structure, Connarus with Burttia as an extreme has the most advanced wood anatomy. Within each group the genera resemble each other in many aspects. The reduction however of all group genera to the representing group genus (Manotes, Rourea, Agelaea and Connarus, respectively), based on wood anatomical characters only, is not justified. On the other hand support can be found in wood characters to place some genera in synonymy under the representative one, e.g. the reduction of Byrsocarpus to Rourea and Castanola to Agelaea. Also the genera Santaloidella, Santaloides and Spiropetalum can be reduced to a single genus, and Hemandradenia placed in Ellipanthus.

### 8.2 Introduction

All members of the homogenous, natural, pantropical family Connaraceae are woody. There are 16 (Heywood, 1979) to 24 (Record, 1947; Stoffers, 1982) genera of usually small trees, erect or scandent shrubs, climbers and lianas. Several plant taxonomists feel that the large number of genera has to be reduced. Wood anatomical evidence is often useful in matters of generic delimitation.

Metcalfe and Chalk (1950) have summarized the earler wood anatomical literature on the family. Dickison's study of 1972 is the most comprehensive account of wood anatomical diversity to date. Since he mainly discussed the taxonomic relationships of the family Connaraceae as a whole and not or only to a minor extent generic delimitation, the present investigation was undertaken. The samples used by Dickison and by us are almost entirely different. We mainly studied African samples, whereas Dickison (1972) has used material from South America and Asia. Data from both studies may give a more representative wood anatomical description of the family and provide more reliable differences between the genera.

### 8.3 Materials and methods

This investigation is mainly based on material from tropical Africa but also some material from tropical South America was used. The species studied are listed below, arranged alphabetically, viz. 99 samples belonging to 54 species and 19 genera. The Uw (v) material was investigated by Veenendaal (1964; 34 samples belonging to 20 species and 9 genera); the results of his measurements were used in this study. The results of the measurements by Dickison (1972; table II of his publication) were added to our general wood anatomical descriptions. Dickison (1972) investigated 81 samples, belonging to 45 species and 13 genera (Manotes excluded). Only 8 samples of these are the same as those used by us.

Anatomical features were studied in transverse, radial and tangential sections and macerations. All sections were embedded in Kaiser's gelatin-glycerin. Means and ranges of the different characters are based on at least twenty-five individual measurements. Tangential vessel diameters are given and vesselmember length was measured including the tails. In the wood description quantitative data are given as mean values between extremes, usually followed by the range of means. We have used the definition of libriform fibres and fibre-tracheids given by Reinders (1935) and Janssonius (1940), viz.:

Fibre-tracheid. Moderately elongated; commonly with thick and apparently somewhat swollen walls, rarely with mucilaginous layers; hardly ever septate; never containing starch; rather often annularly or spirally thickened; having rather large bordered pits with lenticular to slit-like apertures. The pits are comparatively numerous in the tangential walls, in many instances outnumbering those in the radial. When such fibres constitute the ground tissue, the pits towards the vessels ordinarily have borders of much the same size as those of pits in the walls of contact of two vessels.

Libriform wood fibre. Much elongated; mostly with relatively thick walls, without swollen appearance and rather often with mucilaginous layers; hardly ever annularly or spirally thickened; sometimes septate by very thin, commonly unpitted partition walls formed after secondary thickening of the fibre walls, the septate and non-septate types often occurring together; often containing
starch (in sapwood) or crystals; having simple pits or pits with narrow borders and slit-like apertures (or rarely both kinds). In the tangential walls, pits are commonly much less numerous than in the radial and may be entirely lacking; in the parts of the wall adjacent to vessels they are absent or few. The bordered pits leading to parenchyma cells are often more numerous and their borders somewhat larger than those to fibres of the same kind.

## List of studied material

Each name is followed by an abbreviation of the location of wood sample and herbarium voucher, collector and number, geographical origin, and habit. Lw = state herbarium University of Leiden; Uw = systematic botany, University of Utrecht; Uw(v) = systematic botany, University of Utrecht (slides and measurements made by Veenendaal were used); WLw $=$ department of Plant Cytology and Morphology, Agricultural University, Wageningen; WTw = Plant Taxonomy, Agricultural University, Wageningen; $-=$ name adopted in this revision (arguments are only partly based on wood anatomical characters, except in three cases indicated by *, which are entirely based on Forero's (1983) Flora treatment).

Agelaea pentagyna (Lam.) Baill.: Uw(v), Breteler 1777, Cameroun, liana, syn. A. dewevrei De Wild. et Dur.; WTw and Uw(v), Breteler 1351 and 1738, Cameroun, liana, syn A. floccosa Schellenb.; WLw, Versteegh and Jansen 767, Liberia, liana, syn. A. nitida Sol. ex Planch.; WLw, Versteegh and Den Outer 140, Ivory Coast, shrub, syn. A. obliqua (P. Beauv.) Baill.; Uw(v), Breteler 1280, 2330 and 2949, Cameroun, liana, syn. A. obliqua (P. Beauv.) Baill.

Agelaea rubiginosa Gilg: WTw and Uw(v), Breteler 1749, Cameroun, liana.
Agelaea poggeana Gilg: WTw, Bos 5514A, Cameroun, liana.
Bernardinia fluminensis (Gardn.) Planchon var. fluminensis: WTw, De SaintHilaire Cat. C2, no27, Brazil, - Rourea fluminensis (Gardn.) Jongkind.

Burttia prunoides Bak. f. et Exell: WTw, Burtt 3035, Tanzania, shrub.
Byrsocarpus coccineus Thonn. ex Schum.: WLw, Versteegh and Den Outer 238, Ivory Coast, liana, - Rourea coccinea (Thonn. ex Schum.) Benth. ssp. coccinea var. coccinea.

Byrsocarpus maximus Baker: Uw, Schlieben 5454, Tanzania, small tree, Rourea coccinea (Thonn. ex Schum.) Benth. ssp. boiviniana (Baill.) Jongkind.

Byrsocarpus orientalis (Baill.) Baker: Uw, Schlieben 5444, Tanzania, small tree, - Rourea orientalis Baill.

Byrsocarpus viridis (Gilg) Schellenb.: WTw and Uw(v), Breteler 2831, Cameroun, liana, - Rourea coccinea (Thonn. ex Schum.) Benth. ssp. coccinea var. viridis (Gilg) Jongkind; Uw(v), Breteler 2961, Cameroun, liana, - Rourea coccinea (Thonn. ex Schum.) Benth. ssp. coccinea var. viridis (Gilg) Jongkind.

Castanola paradoxa (Gilg) Schellenb. ex Hutch. et Dalz.: WLw, Versteegh and Den Outer 651, Ivory Coast, liana, - Agelaea paradoxa Gilg; WTw and Uw(v), Breteler 1889, Cameroun, liana, - Agelaea paradoxa Gilg.

Cnestidium guianense (Schellenb.) Schellenb.: Uw, Stahel and Gonggrijp 269, Suriname, liana; Uw, Van Donselaar 3077, Suriname, liana; WTw, Breteler 3773, Venezuela, liana.

Cnestis corniculata Lam.: WTw, Breteler 8154, Gabon, liana; WTw, Breteler 8286, Gabon, lianescent treelet.

Cnestis ferruginea Vahl ex DC.: Uw(v) and WTw, Breteler 868, Cameroun, liana; WLw, Versteegh and Jansen 806, Liberia, shrub.

Cnestis cf. longiflora Schellenb.: WLw, Versteegh and Den Outer 124, Ivory Coast, shrub, - C. corniculata Lam.

Cnestis polyphylla Lam.: WLw, Van Veenendaal and Den Outer 1182, Madagascar, shrub.

Cnestis uncata Lemmens: WTw, Breteler 8304, Gabon, lianescent shrub.
Connarus africanus Lam.: WTw, Leeuwenberg 5091, Cameroun, liana, - C. congolanus Schellenb.

Connarus coriaceus Schellenb.: Uw and Uw(v), Lanjouw and Lindeman 1870, Suriname, liana.

Connarus erianthus Benth. ex Baker var. stiptatus Forero: Uw and Uw(v), Krukoff 6042, Brazil, small tree.

Connarus fasciculatus (DC.) Planchon spp. fasciculatus: WTw, Wessels Boer 1569, Suriname, small tree.

Connarus fasciculatus (DC.) Planchon spp. pachyneurus (Radlk.) Forero: Uw, Krukoff 6240, Brazil, syn. C. klugii Standley.

Connarus griffonianus Baill.: Uw(v), Breteler 846, Cameroun, liana; Uw(v) and WTw, Breteler 1850, Cameroun, liana.

Connarus klugii Standley: Uw(v), Krukoff 6240 and 6977, Brazil, small tree, - *C. fasciculatus (DC.) Planchon ssp. pachyneurus (Radlk.) Forero.

Connarus lambertii (DC.) Sagot: Uw, exchange Florence (Italy), South America, liana.

Connarus marlenei Forero: Uw, Prance and Maas 11242, Brazil, shrub.
Connarus nervatus Cuatr.: Uw, Cuatrecasas 17349, Colombia, liana, syn. C. spucei Baker.

Connarus patrisii (DC.) Planchon: Uw, Lindeman and Heyde 90, Suriname, liana.

Connarus perrottetii(DC.) Planchon var. perrottetii: Uw, Maguire et al. 51504, Brazil, liana.

Connarus perrottetii (DC.) Planchon: WTw, Breteler 3873, Venezuela, liana, - *C. perrottetii (DC.) Planchon var. angustifolius Radlk.; Uw(v), Maguire and Stahel 24897, Suriname, liana, - *C. perrottetii (DC.) Planchon var. perrottetii; Uw(v), Lanjouw and Lindeman 2043, Suriname, shrub- liana.

Connarus punctatus Planchon: Uw and Uw(v), Lanjouw and Lindeman 1409, Suriname, liana-shrub.

Connarus rostratus (Vell.) L.B. Smith: Uw and Uw(v), Reitz 14896, Brazil, liana-shrub.

Connarus spec.: Uw(v), Lindeman 5116, Suriname, liana,-*C. punctatus Planchon.

Ellipanthus tomentosus Kurz var. luzoniensis Vidal: Lw, Van Balgooy 3950, Celebes (Sulawesi, Indonesia), tree.

Hemandradenia mannii Stapf.: WTw, De Wilde 8321, Cameroun, tree.
Jaundea pubescens (Baker) Schellenb.: WTw, Bos 5421, Cameroun, lianasmall tree, - Rourea thomsonii (Baker) Jongkind.

Jollydora duparquetiana (Baill.) Pierre: WTw, Leeuwenberg 5039, Cameroun, tree; WTw, Louis et al. 1256, Gabon, treelet; WTw, Louis et al. 1332, Gabon, treelet.

Manotes expansa Sol. ex Planch.: WLw, Versteegh and Den Outer 549, Ivory Coast, shrub, syn. M. longiflora Baker; WTw, Breteler 8078, Gabon, lianescent shrub.

Manotes griffoniana Baill.: WTw and Uw(v), Breteler 1677, Cameroun, liana, syn. M. zenkeri Gilg ex Schellenb.; Uw(v), Breteler 1276, 1302 and 1708, Cameroun, liana, syn. M. zenkeri Gilg ex Schellenb.

Paxia myriantha (Baill.) Pierre: WTw, De Wilde et al. 511, Gabon, liana, Rourea myriantha Baill.

Pseudoconnarus agelaefolius Cuatr.: Uw, Cuatrecasas 17334, Colombia, liana. Pseudoconnarus rhynchosioides (Standley) Prance: Uw, Krukoff 8304, Brazil, liana.

Pseudoconnarus subtriplinervis (Radlk.) Schellenb.: Uw, Van Donselaar 2363, Suriname, liana.

Rourea accrescens Forero: Uw and Uw(v), Krukoff 6795, Brazil, liana, syn. R. rectinervia A.C. Smith.

Rourea calophylloides (Schellenb.) Jongkind:WTw, Breteler 8007, Gabon, liana.
Rourea cf. cuspidata Benth. ex Baker: Uw(v), Lindeman 6891, Suriname.
Rourea frutescens Aubl.: Uw, Irwin et al. 47891, Brazil, liana- shrub.
Rourea krukovii Steyerm.: Uw, Maguire et al. 56706, Brazil, liana.
Rourea paraensis Forero: Uw, Van Donselaar 3502, Suriname, liana.
Rourea puberula Baker: Uw, Maguire et al. 56884, Brazil, liana.
Rourea pubescens (DC.) Radlk. var. spadicea (Radlk.) Forero: Uw, Van Donselaar 3502, Suriname, liana; Uw(v), Lindeman 4807, Suriname, liana.

Rourea surinamensis Miq.: Uw(v), Lindeman 6857, Suriname, liana; Uw, Van Donselaar 3794, Suriname, liana.

Rourea thomsonii (Baker) Jongkind: WTw, Breteler 8096, Gabon, liana.
Santaloidella gilletii Schellenb.: WTw and Uw(v), Breteler 1649, Cameroun, liana, - Rourea parviflora Gilg; Uw(v), Breteler 1304, Cameroun, liana, - Rourea parviflora Gilg.

Santaloides afzelii (R. Br. ex Planch.) Schellenb.: WLw, Versteegh and Den Outer 468, Ivory Coast, small tree-liana, - Rourea minor (Gaertn.) Alston.

Santaloides spec.: Lw, Jacobs 9634, West New-Guinea, liana, - Rourea minor (Gaertn.) Alston.

Spiropetalum heterophyllum (Baker) Gilg: WTw and Uw(v), Breteler 1217, Cameroun, liana, - Rourea solanderi Baker.

Spiropetalum reynoldsii (Stapf) Schellenb.: WLw, Versteegh and Den Outer 79, Ivory Coast, liana, - Rourea solanderi Baker.

### 8.4 Results

A general description of the secondary xylem of the Connaraceae is given below. The wood appears to be comparatively uniform. Yet in our opinion four groups of genera can be distinguished, viz. a Manotes (A)-, Rourea (B)-, Agelaea (C)- and Connarus (D)-group. A short description of these four genera, mainly based on differences from the general description, and the genera belonging to these groups are also given. A summary of characters of the investigated genera is represented in table 9 ; furthermore an identification key is given for the genera or groups of genera in table 10. See also figs.36-51.

## General family description

Growth rings are generally present (absent in Manotes and Hemandradenia) but not always distinct, often marked by smaller radial diameters of the late wood fibres and/or crystals in the late wood fibres; wood diffuse-porous.

Vessels exclusively solitary or solitary, in short radial multiples and in clusters, very rarely in chains (some Agelaea and Cnestis species); variable in size (medi-um-sized vessels next to small ones), number and arrangement even in the same specimen (in lianous members two distinct patterns of xylem development may be present, see Dickison, 1972); round to oval in cross section; average number per square mm 26 (range of means $3-410$ per square mm ); tangential diameter (15-) $125(-420) \mu \mathrm{m}$ (range of means $25-215 \mu \mathrm{~m}$ ); thin-walled ( $2-3 \mu \mathrm{~m}$ ). Vesselmember length (140-) $535(-1250) \mu \mathrm{m}$ (range of means $220-910 \mu \mathrm{~m}$ ); perforations exclusively simple, slightly oblique to transverse; spiral thickenings occasionally present in vessel ligules (Hemandradenia, Spiropetalum heterophyllum); intervessel (tracheal) pits bordered (vestured in Santaloides afzelii), not crowded, usually alternate, main horizontal diameter $7 \mu \mathrm{~m}$ (range of means $4-11 \mu \mathrm{~m}$ ). Besides with rays, vessels usually in contact with tracheids, often also with libriform fibres, sometimes with axial parenchyma. Vessel-ray pitting very distinctive, simple, sometimes half bordered, horizontal diameter $10 \mu \mathrm{~m}$ (range of means $6-20 \mu \mathrm{~m}$ ); vessel-axial parenchyma pits are also conspicuous and mostly simple. Tyloses rather common (in $35 \%$ of the samples), but very changeable. Gum-like substances present in vessels of Spiropetalum.

Ground tissue usually libriform fibres together with fibre-tracheids (in the surroundings of vessels) and/or vasicentric tracheids, sometimes only fibre-tracheids (Manotes), or only libriform fibres (Connarus, Jollydora, Hemandradenia, Burttia and Ellipanthus).

Libriform fibres usually moderately thin-walled, mean wall-thickness $4 \mu \mathrm{~m}$ (range of means $3-4 \mu \mathrm{~m}$ ), septate (in Connarus marlenei partly septate and in Cnestidium guianense non-septate); with simple, sometimes minutely bordered pits with slit-like inner apertures, equally infrequent on both radial and tangential walls; length (220-) $760(-1280) \mu \mathrm{m}$ (range of means $340-1085 \mu \mathrm{~m}$ ); often chambered and crystalliferous; very rarely with spiral thickenings (Hemandradenia, Spiropetalum heterophyllum, Connarus griffonianus, Agelaea). Regularly
two types of libriform fibres present, viz. one type with thick walls, outline in cross section more or less rectangular, without intercellular spaces or with narrow spaces, without starch; the other type with thinner walls, outline in cross section circular, with large intercellualr spaces between them and/or differing in contents (often starch). In transverse sections these thin-walled fibres resemble bands or patches of axial parenchyma.

Fibre-tracheids with large bordered pits on both radial and tangential walls, somewhat shorter than libriform fibres; occasionally with spiral thickenings; no contents.

Parenchyma (axial) absent or very scanty diffuse, diffuse in aggregates and paratracheal (Agelaea, Castanola); only in Manotes rather abundant, often banded. Sometimes in long crystalliferous strands among the fibres, for instance in Ellipanthus (cf. Janssonius, 1918).

Rays exclusively uniseriate or with a few biseriates, in Agelaea, Castanola and Burttia (1-)2(-3)-seriate, in Connarus lambertii (1-)2(-4)-seriate, in Connarus klugii (1-)3(-5)-seriate; heterocellular (only in $9 \%$ of the samples homocellular), but rather often composed of predominantly square or upright cells ( $52 \%$ of the samples; only in $5 \%$ of the samples composed of predominantly procumbent cells); height (1-)11(-80) cells (range of means $4-22$ cells) or $275(-2450) \mu \mathrm{m}$ (range of means $125-650 \mu \mathrm{~m}$; (2-)15(-25) per tangential mm (range of means $4-20$ per tangential mm ); often filled with brown, gummy substances, sometimes with silica globules (Connarus, Agelaea, Santaloidella, Rourea) or crystals; sheath cells only found in Connarus klugii; pits to vessels large (see under vessels).

Crystals often present (in $68 \%$ of the samples), usually in crystalliferous fibres, less frequently in axial parenchyma, seldom in ray parenchyma cells; rare or absent in Rourea, Byrsocarpus, Spiropetalum and Pseudoconnarus; exclusively solitary, prismatic or pyramidal in shape.

Silica grains occur in the parenchymetous tissues of neotropical genera Pseudoconnarus and Rourea, none were observed in Cnestidium and Connarus; the African species Connarus griffonianus, unlike the neotropical species of this genus, contains silica in the ray cells (Ter Welle, 1976). According to Mennega and Veenendaal (unpublished results; Ter Welle, 1976) all samples of Agelaea from Cameroun show the same silica distribution pattern as Pseudoconnarus, Byrsocarpus, Jaundea and Rourea.

Latex tubes (or mucilage canals) longitudinal and/or radial, observed in Connarus.

Pith flecks regularly present (in 19\% of the samples), rather often in Agelaea, Byrsocarpus, Jaundea and Rourea.

Intercellular canals of the vertical type often present in libriform tissue of the second type with thin-walled fibres.

Included phloem of the concentric type often present in Agelaea, Santaloidella and Santaloides.

## A. Manotes

Growth rings indistinct.
Vessels exclusively solitary; average number per square mm 11 (range of means 7-31 per square mm ); tangential diameter (15-)190(-415) $\mu \mathrm{m}$ (range of means $70-215 \mu \mathrm{~m}$ ). Vessel-member length (255-) $730(-960) \mu \mathrm{m}$ (range of means $385-865 \mu \mathrm{~m}$ ); inter-vessel pits $7 \mu \mathrm{~m}$ (range of means $6-8 \mu \mathrm{~m}$ ). Besides with ray parenchyma, vessels in contact with fibre-tracheids and axial parenchyma. Main horizontal diameter vessel-ray pits $11 \mu \mathrm{~m}$ (range of means $10-13 \mu \mathrm{~m}$ ). Tyloses absent.

Ground tissue, composed of fibre-tracheids; length (560-)895(-1280) $\mu \mathrm{m}$ (range of means $745-945 \mu \mathrm{~m}$ ); mean wall thickness $5 \mu \mathrm{~m}$ (range of means 4-6 $\mu \mathrm{m}$ ).

Parenchyma in long tangential bands, 4-8 cells wide, (1-) often 3 per radial mm ; also aliform; chambered crystalliferous cells often present.

Rays 1(-2)-seriate, heterocellular with predominantly square and upright cells; height (1-) $15(-52$ ) cells (range of means $12-18$ cells) or $340(-1295) \mu \mathrm{m}$ (range of means $320-355 \mu \mathrm{~m}$ ); (11-)18(-20) per tangential mm (range of means 13-19 per tangential mm).

Crystals always present.

## B. Rourea

Growth rings fairly distinct.
Vessels solitary but sometimes also in radial multiples and clusters; average number per square mm 10 (range of means 6-14 per square mm); tangential diameter (25-)165(-400) $\mu \mathrm{m}$ (range of means $110-210 \mu \mathrm{~m}$ ), Dickison's measurements (26-)124(-323) $\mu \mathrm{m}$ (range of means $53-199 \mu \mathrm{~m}$ ). Vessel-member length (200-) $600(-1040) \mu \mathrm{m}$ (range of means $400-825 \mu \mathrm{~m}$ ), Dickison's measurements (145-)609(-1024) $\mu \mathrm{m}$ (range of means 474-673 $\mu \mathrm{m}$ ); diameter inter-vessel pits $7 \mu \mathrm{~m}$ (range of means $6-8 \mu \mathrm{~m}$ ). Besides with ray parenchyma, vessels usually in contact with fibre-tracheids. Vessel-ray pits simple, mean horizontal diameter $11 \mu \mathrm{~m}$ (range of means $8-20 \mu \mathrm{~m}$ ).

Ground tissue libriform fibres and up to $40 \%$ fibre-tracheids (and/or vasicentric fibre-tracheids). Mean wall thickness of libriform fibres $4 \mu \mathrm{~m}$ (range of means $3-6 \mu \mathrm{~m}$ ); length ( $320-$ ) $850(-1120) \mu \mathrm{m}$ (range of means $705-1010 \mu \mathrm{~m}$ ), Dickison's measurements (242-)739(-1131) $\mu \mathrm{m}$ (range of means 603-857 $\mu \mathrm{m}$ ); libriform often in two types: one with large intercellular spaces in earlywood and/or lumina of fibres of $16-20 \mu \mathrm{~m}$, and the other with small intercellular spaces in latewood and/or fibre lumina of $8-12 \mu \mathrm{~m}$.

Parenchyma absent or rare.
Rays 1(-2)-seriate, often exclusively uniseriate; heterocellular without domination of a certain cell type; height (1-)11(-50) cells (range of means 7-17 cells) or $300(-1120) \mu \mathrm{m}$ (range of means $200-445 \mu \mathrm{~m}$ ), Dickison's measurements
(1-)9(-32) cells (range of means $8-11$ cells); (9-)15(-20) per tangential mm (range of means 14-17 per tangential mm ); ray cells regularly with silica bodies.

Crystals usually rare; when present in chambered crystalliferous cells with up to 25 compartments.

Pithflecks sometimes present.
In Byrsocarpus the arrangement of the vessels is more in radial multiples; tangential vessel diameters are smaller ( 80 against $165 \mu \mathrm{~m}$ ), but the number per square mm is larger ( 49 against 10 per square mm ); vessel-member length and libriform fibre length are shorter ( 420 against $600 \mu \mathrm{~m}$ and 550 against $850 \mu \mathrm{~m}$ respectively); crystals are absent. The same trends are found in Paxia, Jaundea, Cnestis, Cnestidium and Bernardinia with the exception that in Cnestis and Cnestidium the arrangement of the vessels is the same as in Rourea, and crystals are more abundant in the last three mentioned genera. Also in Spiropetalum the tangential vessel diameters are slightly smaller ( 135 against $165 \mu \mathrm{~m}$ ), the number per square mm larger ( 21 against 10 per square mm ), and the vessel-member length and libriform fibre length shorter ( 485 against $600 \mu \mathrm{~m}$ and 695 against $850 \mu \mathrm{~m}$ ); in Spiropetalum heterophyllum (Bret. 1217) moreover, spiral thickenings, vertical latex ducts and patches included phloem are present. The genera Santaloidella and Santaloides too resemble Rourea in many aspects; only in Santaloidella included phloem is always present and crystals are more common, whereas in Santaloides included phloem is usually present and crystals absent.

In Pseudoconnarus the vessel-member length is shorter ( $450 \mu \mathrm{~m}$ against 600 $\mu \mathrm{m}$ ); ground tissue libriform fibres are slightly shorter ( 805 against $850 \mu \mathrm{~m}$ ) but fibre-tracheids comprise $50 \%$ of the axial system; crystals are absent.

## C. Agelaea

Growth rings fairly distinct, boundaries often marked by smaller radial lumina of the fibres (regularly fibre-tracheids) and more chambered crystalliferous cells.

Vessels usually exclusively solitary, sometimes some radial multiples present; average number per square mm 13 (range of means $10-16$ per square mm ); tangential diameter ( $20-$ ) $150(-340) \mu \mathrm{m}$ (range of means $80-210 \mu \mathrm{~m}$ ), Dickison's measurements (32-)146(-323) $\mu \mathrm{m}$ (range of means $86-204 \mu \mathrm{~m}$ ). Vessel-member length (195-) $550(-1250) \mu \mathrm{m}$ (range of means $410-910 \mu \mathrm{~m}$ ), Dickison's measurements (204-) $577(-945) \mu \mathrm{m}$ (range of means $495-658 \mu \mathrm{~m}$ ); inter-vessel pits bordered, alternate, mean horizontal diameter $5 \mu \mathrm{~m}$ (range of means $4-7 \mu \mathrm{~m}$ ). Besides with ray parenchyma, vessels in contact with fibre-tracheids and very seldom with axial parenchyma. Vessel-ray pitting simple, mean horizontal diameter $10 \mu \mathrm{~m}$ (range of means 6-12 $\mu \mathrm{m}$ ).

Ground tissue libriform fibres and up to 20-30\% fibre-tracheids (and/or vasicentric fibre-tracheids). Libriform fibres thin-walled, mean wall thickness $4 \mu \mathrm{~m}$; length (395-)710 (-1120) $\mu \mathrm{m}$ (range of means 520-960 $\mu \mathrm{m}$ ), Dickison's measurements (296-)804 (-1644) $\mu \mathrm{m}$ (range of means 722-965 $\mu \mathrm{m}$ ); sometimes with spiral thickenings, contents often starch, intercellular canals present.

Parenchyma rare or absent.
Rays (1-)2(-4)-seriate, heterocellular, often composed of more than three storeyes; height (1-)12(-65) cells (range of means 7-22 cells) or $220(-1110) \mu \mathrm{m}$ (range of means 145-360 $\mu \mathrm{m}$ ), Dickison's measurements (1-)17(-56) cells (range of means $8-50$ cells); (8-)15(-20) per tangential mm (range of means $12-18$ per tangential mm ); regularly filled with globular silica grains, gum and/or brown deposits.

Crystals always present, usually in crystalliferous fibres.
Pith flecks sometimes present.
Included phloem of concentric type, often present.
Latex ducts only present in one sample of A. pentagyna (Bret. 1280).
In Castanola the tangential vessel diameter is slightly smaller ( 125 against $150 \mu \mathrm{~m}$ ), but the number of vessels per square mm is larger ( 31 against 13 per square mm ); also the diameter of the inter-vessel pits is somewhat larger ( 7 against $5 \mu \mathrm{~m}$ ). The libriform fibre walls are slightly thicker ( 6 against $4 \mu \mathrm{~m}$ ). The main difference between Castanola and Agelaea is the absence of included phloem in Castanola; also spiral thickenings are absent from the fibre walls.

## D. Connarus

Growth rings fairly distinct, boundaries often marked by chambered crystalliferous cells.

Vessels in radial multiples of often more than 4 vessels and in clusters; average number per square mm 22 (range of means $3-50$ per square mm ); tangential diameter (15-) $105(-330) \mu \mathrm{m}$ (range of means $35-180 \mu \mathrm{~m}$ ), Dickison's measurements (15-)94(-307) $\mu \mathrm{m}$ (range of means $39-156 \mu \mathrm{~m}$ ). Vessel-member length (200-) $530(-1040) \mu \mathrm{m}$ (range of means $360-720 \mu \mathrm{~m}$ ), Dickison's measurements (210-) $575(-997) \mu \mathrm{m}$ (range of means $398-711 \mu \mathrm{~m}$ ); mean horizontal diameter of inter-vessel pits $9 \mu \mathrm{~m}$ (range of means $5-11 \mu \mathrm{~m}$ ). Besides with ray parenchyma, vessels usually in contact with libriform fibres and for a smaller part with fibretracheids. Vessel-ray pitting simple, horizontal diameter $11 \mu \mathrm{~m}$ (range of means 6-17 $\mu \mathrm{m}$ ). Tyloses sometimes present.

Ground tissue usually exclusively libriform fibres; fibre-tracheids absent or rare and vasicentric. Wall thickness of libriform fibres $4 \mu \mathrm{~m}$ (range of means 3-6 $\mu \mathrm{m}$ ); libriform fibres partly septated in C. marlenei (Prance et Maas 11242); length (380-) $755(-1180) \mu \mathrm{m}$ (range of means $560-1040 \mu \mathrm{~m}$ ), Dickison's measurements (237-)743(-1293) $\mu \mathrm{m}$ (range of means 517-980 $\mu \mathrm{m}$ ). Libriform fibres usually in two (sometimes three) types, viz. alternating bands of earlywood fibres with large intercellular spaces, large fibre lumina, starch or brown deposits, associated with latex tubes, and bands of latewood fibres with small intercellular spaces, smaller fibre lumina, without starch, brown substances or latex tubes. Spiral thickenings sometimes present, e.g. in C. griffonianus (Bret. 1850).

Parenchyma rare or absent, in C. lambertii (exchange Florence) more abundant, vasicentric and even confluent.

Rays exclusively uniseriate, only in C. lambertii (exchange Florence) (1-)2(-6)-seriate; cells predominantly square or upright, regularly homocellular (no procumbent cells at all); height (1-) $10(-44$ ) cells (range of means 4-19 cells) or $285(-1040) \mu \mathrm{m}$ (range of means $140-495 \mu \mathrm{~m}$ ), Dickison's measurements (1-)7(-28) cells (range of means $5-10$ cells); (3-)15(-20) per tangential mm (range of means 4-20 per tangential mm).

Crystals always present, often abundant.
Latex tubes always present, vertical and/or horizontal ones (in rays), sometimes only in rays.

In Jollydora, Hemandradenia, Ellipanthus and Burttia the tangential vessel diameters are smaller (35, 50, 50 and $25 \mu \mathrm{~m}$ respectively against $105 \mu \mathrm{~m}$ ) than in Connarus, but the number of vessels per square mm is larger ( $47,45,34$ and 410 respectively against 22 per square mm ). The vessel-member length in Ellipanthus is also shorter ( 390 against $530 \mu \mathrm{~m}$ ), in Burttia ( $220 \mu \mathrm{~m}$ ) much shorter. Libriform fibre length is longer in Jollydora ( 960 against $755 \mu \mathrm{~m}$ ) and much shorter in Burttia ( 340 against $755 \mu \mathrm{~m}$ ). Both in Jollydora and Burttia the libriform fibres are not arranged in alternating tangential bands and are partly nonseptate. In Burttia the rays are (1-)2(-3)-seriate. The main difference however between Connarus and the other mentioned genera is the presence of latex tubes in Connarus, and the absence in the other genera.

### 8.5 Discussion

The secondary xylem of the Connaraceae is anatomically rather uniform and moderately highly specialized according to standards given by Tippo (1938, 1946), Koek-Noorman and Hogeweg (1974), Carlquist (1975) and others (see also Dickison, 1972). This rather high level of evolutionary advancement is partly caused by the fact that many species of the family are climbers or lianas. Lianous species in general show trends of specialization or phylogenetic advancement, like wider and shorter vessel elements, which are not present in species of the same family with the habit of a shrub, treelet or tree.

In spite of the homogeneity of the family, it is possible to arrange the taxa into four groups. These groups mainly differ in the composition of the ground tissue; however, also characters mentioned in Table 11 and the habit of the genera, are involved in our considerations about the group composition and arrangements. Ground tissue composition as main characteristic for the arrangement of the taxa, is also based on phylogenic views about parallel development or reversion within the family in relation to habit (liana or non-liana) transformation given by Dickison (1972). The ground tissue may consist only or nearly only of fibre-tracheids (Manotes group), of fibre-tracheids and libriform fibres in which case libriform fibres usually dominate (Rourea and Agelaea group) and can be composed only or nearly only of libriform fibres (Connarus group). In this last mentioned group a differentiation has taken place in the
libriform tissue, viz. libriform fibres with thin walls, circular outline, large intercellular spaces and/or with distinct contents (starch) and libriform fibres with thick walls, rectangular outline, and without intercellular spaces or starch. These four groups can be placed in the above mentioned sequence in three successive organization levels of the hydro-system proposed by Braun (1970), namely the Manotes group in Braun's organization level II (Fibre-tracheid-Vessel level), the Rourea and Agelaea group in III (limited Fibre-tracheid-Vessel level) and the Connarus group in Braun's organization level IV (Vessel-Libriform fibre level). The average ray width in all groups is 1 -seriate, only in the Agelaca group 2-seriate and in the genus Burttia as a member of the Connarus group. Burttia occupies an extreme position in comparison with the other genera, not only concerning wood anatomical characters. The parenchymatous primary cortex contains sclereids in varying number in all genera investigated by Dickison (1973b), except in Burttia (and Vismianthus). In addition most parenchyma cells contain dark-staining deposits in all genera except Burttia (Dickison, 1973b).

A comparison of the measurements performed by Dickison (1972; calculated from his table II) and those obtained by us, reveals that Dickison's vesselmember lengths and fibre lengths are somewhat longer, the tangential vessel diameters about equal or somewhat smaller (except Jaundea which is much larger) than ours (table 9). From table 9 and 11 it is clear that several wood anatomical characters gradually change if one considers the series Manotes, Rourea, Agelaea, Connarus and Burttia. For instance the vessel-member length and fibre length decrease, as do the percentage fibre-tracheids of the ground tissue, ray height (also the number of cells per ray) and average number of rays per tangential mm. Also the tangential vessel diameter decreases within the series mentioned above, but the number of vessels per square mm increases. This means that the vulnerability index (diameter of vessels divided by the number of vessels per square mm; Carlquist, 1977) decreases. According to criteria summarized among others by Koek-Noorman et al. (1974) and Carlquist (1975 and 1977) all characters mentioned in table 11, with the exception of tangential vessel diameter and amount of axial parenchyma, indicate that within the series Manotes and Connarus (Burttia) constitute the extremes, Manotes having the most primitive wood structure and Connarus (Burttia) the most advanced wood. The number of carpels per flower (five in the groups A, B and C and one in group D ) are not opposed to the above mentioned statement. Also on bases of leaf anatomy (Dickison, 1973a) Connarus (and Jollydora but also Bernardinia) is considered to be more derived with multilacunar nodes. In all other more primitive genera the fundamental nodal pattern in both compound and simpleleaved genera, is trilacunar, three-traced.

On the basis of all wood anatomical characters investigated, the remaining genera of the family can be arranged, with the above mentioned group representatives, into groups of genera viz. A, B, C and D in a sequence with in each case a higher degree of evolutionary development. Group B is subdivided into three, group D into two separate smaller subgroups (see results). These genera groups are:
A. Manotes;
B. 1. Rourea with Byrsocarpus, Jaundea and Paxia; 2. Santaloidella, Santaloides, Spiropetalum and Pseudoconnarus; 3. Cnestidium, Cnestis and Bernardinia. The first two genera of subgroup 3 possess wood anatomical characters with a large variation and might be placed elsewhere;
C. Agelaea with Castanola;
D. 1. Connarus with Ellipanthus and Hemandradenia; 2. Jollydora and Burttia. This despite the fact that only Connarus possesses latex tubes.

Though all genera of a group present many similarities, the successive groups being more specialized, this does not mean that within a group the genera can be placed in all cases in synonymy under the group representative. Especially Cnestis and Cnestidium within the Rourea group take a somewhat exceptional position, like Burttia in the Connarus group.

For several authors there are no objections against some reductions of the number of genera. For instance Dickison (1972) does not find wood characters which are in contradistinction to the reduction of Santaloides and Jaundea to Rourea; for Byrsocarpus this is less certain. Veenendaal (1964) had the same opinion about Byrsocarpus, and even suggest to arrange the genus under Agelaea. Leenhouts (1958b) on the other hand placed Byrsocarpus in Rourea. We too find many similarities between these latter two genera, but also between Rourea and Jaundea together with Paxia. In our opinion also Spiropetalum, Santaloidella and Santaloides can be reduced to a single genus.

Veenendaal (1964) and Dickison (1972) find support in wood characters for the reduction of Castanola to Agelaea. Also from our findings it is clear that both genera resemble each other in great extent, despite the fact that included phloem is often present in Agelaea and absent in Castanola. Dickison (1973b) and Leenhouts (1958b) support the opinion that the genus Hemandradenia should be placed in Ellipanthus. Also in our point of view the last two mentioned genera could be combined, but not placed in synonymy under Connarus since latex tubes are absent.

Legends to figures 36-51.
Transverse sections of the secondary xylem of Connaraceae; 10 mm on the photographs represents $150 \mu \mathrm{~m}$.
Position cambium near the top side of the photographs.
$\overrightarrow{\mathrm{L}}=$ growth-ring boundary; $\mathrm{L}=$ libriform fibres; $\mathrm{Lg}=$ libriform fibres with gelatinous layers;
$\mathrm{L} 1=$ libriform fibres with large lumina and intercellular canals; $\mathrm{Lt}=$ latex tubes; $\mathrm{P}=$ metatracheal
parenchyma; $\mathrm{T}=$ fibre-tracheids; $\mathrm{V}=$ vessels,$-=$ name adopted in this revision.
Fig. 36. Manotes griffoniana Baill. (Breteler 1677). Growth-ring boundaries indistinct to absent. Vessels exclusively solitary. Ground tissue fibre-tracheids; metatracheal parenchyma bands only present in this genus.

Fig. 37. Pseudoconnarus subtriplinervis (Radlk.) Schellenb. (Van Donselaar 2363). Growth-ring boundaries fairly distinct. Vessels exclusively solitary. Ground tissue libriform fibres and a large number of vasicentric fibre-tracheids. Ray-parenchyma cells with brown deposits. Notice tyloses formation.

Fig. 38. Rourea frutescens Aubl. (Irwin et al. 47891). Growth-ring boundaries fairly distinct; three present on the photograph. Ground tissue like in Pseudoconnarus but much less fibre-tracheids.

Fig. 39. Byrsocarpus maximus Baker (Schlieben 5454) - Rourea coccinea (Thonn. ex Schum.) Benth. ssp. boiviniana (Baill.) Jongkind. Growth-ring boundaries fairly distinct. Vessels solitary but also in radial multiples and clusters. Ground tissue libriform fibres; some vasicentric fibre-tracheids.

Fig. 40. Jaundea pubescens (Bak.) Schellenb. (Bos 5421) - Rourea thomsonii (Bak.) Jongkind. Ground tissue libriform fibres with large lumina and intercellular canals; fibre-tracheids scarcely present, vasicentric but above all terminal.

Fig. 41. Paxia myriantha (Baill.) Pierre (De Wilde et al. 511) - Rourea myriantha Baill. Vessels exclusively solitary only in the first growth-ring. Ground tissue libriform fibres.

Fig. 42. Cnestidium guianense (Schellenb.) Schellenb. (Van Donselaar 3077). Growth-ring boundaries indistinct. Ground tissue (non-septate) libriform fibres, partly with gelatinous layers.

Fig. 43. Cnestis polyphylla Lam. (Van Veenendaal and Den Outer 1182). Growth-ring boundaries fairly distinct. Vessels usually solitary, sometimes in chains. Ground tissue libriform fibres.

Fig. 44. Bernardinia fluminensis (Gardn.) Planchon var. fluminensis (De Saint-Hilaire Cat. C2, no 27) - Rourea fluminensis (Gardn.) Jongkind. Vessels arranged in radial multiples but also in radial or oblique chains. Ground tissue libriform fibres; some vasicentric fibre-tracheids.

Fig. 45. Agelaea pentagyna (Lam.) Baill. (Breteler 1351). Growth-ring boundaries fairly distinct; four present on the photograph. Vessels exclusively solitary. Ground tissue libriform fibres; vasicentric fibre-tracheids present.

Fig. 46. Castanola paradoxa (Gilg) Schellenb. ex Hutch. et Dalz. (Breteler 1889) - Agelaea paradoxa Gilg. Growth-ring boundaries fairly distinct. Vessels exclusively solitary. Ground tissue libriform fibres; some vasicentric fibre-tracheids.

Fig. 47. Connarus perrottetii (DC.) Planchon var. angustifolius Radlk. (Breteler 3873). Growth-ring boundaries distinct; five present on the photograph. Ground tissue libriform fibres; fibre-tracheids absent. Notice latex tubes and tyloses formation.

Fig. 48. Hemandradenia mannii Stapf. (De Wilde 8321). Growth-ring boundaries absent. Ground tissue libriform fibres, arranged in more or less alternating tangential bands with large intercellular canals, large fibre lumina, and bands without or small intercellular canals and small fibre lumina; vasicentric fibre-tracheids absent.

Fig. 49. Ellipanthus tomentosus Kurz var. Iuzoniensis Vidal (Van Balgooy 3950). Growth-ring boundaries indistinct. Ground tissue arranged like in Hemandradenia.

Fig. 50. Jollydora duparquetiana (Baill.) Pierre (Leeuwenberg 5039). Growth-ring boundaries distinct; four present on the photograph. Ground tissue libriform fibres; fibre-tracheids absent.

Fig. 51. Burttia prunoides Baker f. et Exell (Burtt 3035). Growth-ring boundaries fairly distinct. Many, very small vessels in radial multiples and solitary. Ground tissue libriform fibres, partly non-septate; vasicentric fibre-tracheids almost absent. Rays often 2-seriate.





Table 9. Secondary xylem characters of the investigated genera

| genera studied | growth rings | vessels |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | arrangements | tg diam. in $\mu \mathrm{m}$ |  | number per sq mm | diam. <br> interv. <br> pits in <br> $\mu \mathrm{m}$ | $\begin{aligned} & \text { tylo- } \\ & \text { ses } \end{aligned}$ | member length in $\mu \mathrm{m}$ |  |
| Manotes | - | exs |  | 190 | 11 | 7 | - |  | 730 |
| Rourea | $\pm$ | exs or rdm | 165 | 145 | 10 | 7 | $\pm$ | 600 | 605 |
|  |  |  | 124 |  |  |  |  | 609 |  |
| Byrsocarpus | $\pm$ | rdm | 80 | 70 | 49 | 7 | - | 420 | 454 |
|  |  |  | 42 |  |  |  |  | 555 |  |
| Jaundea | $+$ | rdm | 45 | 120 | 32 | 7 | - | 490 | 595 |
|  |  |  | 159 |  |  |  |  | 649 |  |
| Paxia | $+$ | rdm or exs |  | 50 | 70 | 7 | - |  | 425 |
| Santaloidella | $\pm$ | rdm or exs |  | 185 | 15 | 7 | - |  | 590 |
| Santaloides | $\pm$ | exs | 130 | 140 | 12 | 6 | - | 525 | 550 |
|  |  |  | 156 |  |  |  |  | 603 |  |
| Spiropetalum | $\pm$ | exs |  | 135 | 21 | 8 | $\pm$ |  | 485 |
| Pseudoconnarus | $\pm$ | exs | 175 | 175 | 11 | 7 | $\pm$ | 480 | 490 |
|  |  |  | 177 |  |  |  |  | 517 |  |
| Cnestidium | $\pm$ | exs or rdm | 100 | 130 | 19 | 6 | - | 505 | 525 |
|  |  |  | 161 |  |  |  |  | 544 |  |
| Cnestis | $\pm$ | exs, ch | 85 | 90 | 36 | 7 | - | 410 | 440 |
|  |  |  | 99 |  |  |  |  | 603 |  |
| Bernardinia | + | rdm |  | 45 | 55 | 7 | - |  | 410 |
| Agelaea | $\pm$ | exs | 150 | 150 | 13 | 5 | $\pm$ | 550 | 550 |
|  |  |  | 146 |  |  |  |  | 577 |  |
| Castanola | $\pm$ | exs | 125 | 120 | 31 | 7 | $\pm$ | 595 | 565 |
|  |  |  | 116 |  |  |  |  | 512 |  |
| Connarus | $\pm$ | rdm, cl | 105 | 100 | 22 | 9 | - | 530 | 550 |
|  |  |  | 94 |  |  |  |  | 575 |  |
| Ellipanthus | $\pm$ | $\mathrm{cl}, \mathrm{rdm}$ | 70 | 50 | 45 | 9 | - | 390 | 565 |
|  |  |  | 54 |  |  |  |  | 606 |  |
| Hemandradenia Jollydora | - | rdm |  | 50 | 34 | 8 | - |  | 490 |
|  | + | rdm | 35 | 35 | 47 | 7 | - | 580 | 660 |
|  |  |  | 33 |  |  |  |  | 743 |  |
| Burttia | + | rdm | 25 |  | 410 | 8 | - | 220 |  |

## Symbols and abbreviations in table 9:

$+=$ present; - = absent; $+=$ scarcely present; aggr. = aggregates; $\mathrm{av} .=$ average; ch = chain; $\mathrm{cl}=$ cluster; comp. = composed; diam. = diameter; diff. = diffuse; exs = exclusively solitary; gel. = gelatinous layer; incl. = included; int. = intercellular canals; interv. = intervessel: $1=$ non-septate libriform fibres; $\mathrm{ls}=$ septate libriform fibres; $\mathrm{ls}(2)=$ septate libriform fibres in two types, viz. with and without intercellular canals and/or brown substances, usually arranged in alternating tangential bands; muc. $=$ mucilage; mult. $=$ multiseriate; pred. $=$ predominant; rdm $=$ radial multiples; $s=$ simple crystals, generally in chambered crystalliferous cells, except in Spiropetalum and only partly in Rourea. In these genera crystals are usually rare; $\mathrm{sq}=\mathrm{square} ; \operatorname{tg}=$ tangential; th. = thickness; $\operatorname{tr}=$ fibre-tracheids; vas. = vascular.
(Table 9 continued)

| fibres |  |  |  |  | rays |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| ground tissue | length in $\mu \mathrm{m}$ |  | wall <br> th. <br> in $\mu \mathrm{m}$ | also <br> pre- <br> sent | av. height in cells |  | av. <br> height <br> in $\mu \mathrm{m}$ | seriate | comp: <br> of $>3$ <br> storeyes |
| tr |  | 895 | 5 | - |  | 15 | 340 | 1(-2) | - |
| 1s(2) | 850 | 790 | 4 | tr | 11 | 10 | 300 | 1(-2) | - |
|  | 739 |  |  |  | 9 |  |  |  |  |
| Is | 550 | 575 | 3 | tr | 11 | 12 | 260 | 1(-2) | - |
|  | 610 |  |  |  | 13 |  |  |  |  |
| 1 s | 730 | 735 | 4 | tr | 16 | 12 | 360 | 1(-2) | - |
|  | 738 |  |  |  | 11 |  |  |  |  |
| 1 s |  | 730 | 3 | tr |  | 12 | 350 | 1 | - |
| 1 s |  | 910 | 4 | tr |  | 7 | 175 | 1(-2) | - |
| 1 s | 910 | 855 | 4 | tr | 8 | 8 | 195 | 1(-2) | - |
|  | 954 |  |  |  | 8 |  |  |  |  |
| 1 s |  | 695 | 3 | tr |  | 13 | 295 | 1(-2) | - |
| 1 s | 805 | 785 | 3 | tr |  | 11 | 230 | 1 | - |
|  | 735 |  |  |  |  |  |  |  |  |
| $1(1 \mathrm{~s})$ | 690 | 705 | 4 | $\pm$ tr | 12 | 10 | 450 | 1(-2) | - |
|  | 717 |  |  |  | 9 |  |  |  |  |
| 1 s | 645 | 660 | 4 | tr | 15 | 13 | 275 | 1(-2) | $\pm$ |
|  | 727 |  |  |  | 9 |  |  |  |  |
| 1 s |  | 580 | 3 | tr |  | 17 | 400 | 1 | - |
| 1s | 710 | 735 | 4 | tr | 12 | 15 | 220 | (1-)2(-3) | + |
|  | 804 |  |  |  | 17 |  |  |  |  |
| 1 s | 765 | 770 | 6 | tr | 13 | 12 | 270 | (1-)2(-3) | $+$ |
|  | 776 |  |  |  | 12 |  |  |  |  |
| $\mathrm{ls}(2)$ | 755 | 750 | 4 | - (tr) | 10 | 8 | 285 | 1 | - |
|  | 743 |  |  |  | 7 |  |  |  |  |
| 1s(2) | 670 | 750 | 3 | - | 4 | 5 | 125 | 1 | - |
|  | 769 |  |  |  | 5 |  |  |  |  |
| 1 s (2) |  | 685 | 6 | - |  | 8 | 225 | 1 | - |
| $1 \mathrm{~s} / 1$ | 960 | 920 | 5 | - | 7 | 9 | 220 | 1(-2) | - |
|  | 883 |  |  |  | 10 |  |  |  |  |
| 1s/1 |  | 340 | 3 | - |  | 14 | 280 | (1-)2(-3) | - |

Wood-ray type: $\mathrm{I}=$ uniseriate rays and multiseriate rays with long uniseriate tails; $\mathrm{II}=$ uniseriate rays and multiseriate rays with short uniseriate tails; III = only uniseriate rays present; $\mathrm{He}=$ heterogeneous, procumbent and upright and/or square cells are present; $\mathrm{Ho}=$ homogeneous, only procumbent or only upright and/or square cells are present.
$165 \quad 145=$ the first column gives the average $t g$ vessel diameter obtained by our measurements (165), followed by the one calculated from Dickison's (1972) table II (124); the second column represents the average tg diameter of all measurements, or only ours if those of Dickison were not available (145).
(Table 9 continued)

| genera studied | rays |  |  |  | axial parenchyma |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | pred. <br> cell <br> type | type | number <br> per <br> $\operatorname{tg~mm}$ | diam. <br> pits to <br> vessels <br> in $\mu \mathrm{m}$ | rare or absent | diff. <br> or diff. <br> in aggr. | mult. tg bands |
| Manotes | sq, up | He I (III) | 18 | 11 | - | - | + |
| Rourea | - | He III | 15 | 11 | $+$ | - | - |
| Byrsocarpus | - | He III | 14 | 11 | + | - | - |
| Jaundea | - | He III | 16 | 8 | + | - | - |
| Paxia | sq, up | He III | 15 | 9 | $+$ | - | - |
| Santaloidella | - | He III | 12 | 11 | $+$ | - | - |
| Santaloides | - | He I/III | 16 | 10 | $+$ | - | - |
| Spiropetalum | - | He III | 14 | 12 | $+$ | - | - |
| Pseudoconnarus | sq, up | He III | 15 | 11 | $+$ | - | - |
| Cnestidium | sq, up | Ho III | 14 | 9 | + | - | - |
| Cnestis | - | He I/III | 15 | 10 | + | - | - |
| Bernardinia | sq, up | He III | 16 | 7 | + | - | - |
| Agelaea | - | He I/II | 15 | 10 | + | - | - |
| Castanola | - | He I/II | 17 | 7 | + | + | - |
| Connarus | sq, up | $\mathrm{He}(\mathrm{Ho}) \mathrm{I}$ | II 15 | 11 | + | - | - |
| Ellipanthus | sq, up | He III | 12 | 9 | + | - | - |
| Hemandradenia | sq, up | He III | 14 | 11 | + | + | - |
| Jollydora | sq, up | He III | 9 | 14 | $+$ | + | - |
| Burttia | - | He I | 14 | 5 | + | - | - |

(Table 9 continued)

| crystals | miscellaneous |  |  | further information |
| :---: | :---: | :---: | :---: | :---: |
| type | pith <br> flecks | latex, oil, muc. canals | incl. <br> phloem |  |
| s | - | - | - | tg. par. bands 4-8 cells wide, (1) often $3 / \mathrm{rd} \mathrm{mm}$, also aliform |
| s | $\pm$ | - | - | tr. vas.; crystals abundant in Lind. 4807 |
| - | $\pm$ | - | - | tr vas.; int. between ls |
| - | + | - | - | tr vas. and terminal; int. mainly in early wood ls ; crystals in pith |
| - | - | - | - | tr vas.; int. between ls; secretory cells in pith |
| $s$ | - | - | $+$ | tr vas. $40 \%$; ray cells with silica grains |
| - | - | - | $+$ | tr vas. (very few); vestured vessel pits in V. and 0.468 |
| s | - | - | - | tr vas. $30 \%$; int. between ls; Bret. 1217 aberrant (vertical latex ducts, spiral thickenings and incl. phloem present) |
| - | - | - | - | $\operatorname{tr} 50 \%$, mainly in late wood; large int. between early wood ls |
| S | - | - | - | 1 with gel. layer; vestured vessel pits in Van Dons. 3077 |
| $s$ | - | - | - | tr vas.; int. between ls; somewhat ring-porous in V . and 0.1182 |
| s | - | - | - | tr vas. and terminal; very small int. between ls |
| s | $\pm$ | - | $+$ | tr vas.; int. between ls; ray cells with gum and silica grains |
| s | - | - | - | tr vas.; int. between Is; vert. gum canals in Bret. 1889 |
| s | - | + | - |  |
| s | - | - | - | vessel pits with coalescent apertures |
| s | - | - | - | spiral thickenings in vessel tails and ls ends |
| s | - | - | - | int. between Is (not always septate) |
| s | - | - | - | tr absent or rare; $30 \% \mathrm{l}$; small int. in I |


|  |  | sensu Schellenberg (1938) | sensu Breteler (1989) |
| :---: | :---: | :---: | :---: |
| 1a | Ground tissue fibre-tracheids, libriform fibres absent or very sparce; axial parenchyma rather abundant, often banded | Manotes | Manotes |
| b | Ground tissue libriform fibres or libriform fibres with fibre-tracheids; axial parenchyma absent or scanty diffuse, diffuse in aggregates and/or paratracheal | 2 |  |
| 2a | Ground tissue libriform fibres; fibre-tracheids more or less abundant | 3 |  |
| b | Ground tissue libriform fibres; fibre-tracheids absent or almost absent | 10 |  |
| 3a | Ground tissue libriform fibres, but fibre-tracheids comprise about $50 \%$ of the axial system | Pseudoconnarus | Pseudoconnarus |
| b | Ground tissue libriform fibres; fibre-tracheids less frequent (maximal $40 \%$ ), usually only vasicentric | 4 |  |
| 4a | Latex-tubes present | Connarus | Connarus |
| b | Latex-tubes absent | 5 |  |
| 5 a | Wood rays $1(-2)$-seriate | 6 |  |
| b | Wood rays (1-)2(-3)-seriate | 9 |  |
| 6a | Included phloem present | Santaloidella | Rourea |
|  |  | Santaloides |  |
|  |  | Spiropetalum heterophyllum |  |
| b | Included phloem absent | 7 |  |
| 7 a | Crystals, usually in chambered crystalliferous cells, abundant | Cnestis | Cnestis |
|  |  | Cnestidium | Cnestidium |
|  |  | Bernardinia | Rourea |
| b | Crystals, usually in chambered crystalliferous cells, absent to rare | 8 |  |
| 8 a | Average tangential vessel diameter smaller than $100 \mu \mathrm{~m}$; number of vessels per square mm more than 30 |  |  |
|  |  | Byrsocarpus <br> Paxia | Rourea |
|  |  | Jaundea |  |
| b | Average tangential vessel diameter larger than $100 \mu \mathrm{~m}$; number of vessels per square mm less than 30 | Rourea Spiropetalum | Rourea |
| 9a | Vessels on average less than 20 per square mm; axial parenchyma rare or absent; included phloem often present | Agelaea | Agelaeasection Agelaea |
| b | Vessels on average more than 20 per square mm ; axial parenchyma diffuse or diffuse in aggregates; included phloem absent | Castanola | Agelaeasection Troostwykia |

(Table 10 continued)

| 10a Latex-tubes present | Connarus | Connarus |
| :---: | :---: | :---: |
| b Latex-tubes absent | 11 |  |
| 11a Tangential bands libriform fibres without intercellular spaces, alternate with tangential bands with intercellular spaces | 12 |  |
| b Not so | 13 |  |
| 12a Average wall thickness libriform fibres $6 \mu \mathrm{~m}$; average wood ray heigth 8 cells | Hemandradenia | Hemandradenia |
| b Average wall thickness libriform fibres $3 \mu \mathrm{~m}$; average wood ray heigth 4 cells | Ellipanthus | Ellipanthus |
| 13a Average number of vessels per square mm about 50 | Jollydora | Jollydora |
| b Average number of vessels per square mm about 400 | Burttia | Burttia |

Table 11. Some secondary xylem characters of the group representatives and Burttia. ( $\mathrm{M}=$ Manotes, $\mathrm{R}=$ Rourea, $\mathrm{A}=$ Agelaea, $\mathrm{C}=$ Connarus and $\mathrm{B}=$ Burttia $)$.

| Characters | Decreasing <br> in the sequence | Increasing <br> in the sequence |
| :--- | :--- | :--- |
|  | MRACB |  |
| vessel-member length <br> fibre length | MRCAB |  |
| ratio fibre-tracheids $/$ libriform fibres | MRACB |  |
| average ray height (in $\mu \mathrm{m}$ ) | MRCBA |  |
| average number of rays per tangential mm <br> vulnerability index (vessel diameter/number of <br> vessels per square mm) | MRACB |  |
| vessel area percentage of cross surface <br> tangential vessel diameter <br> amount of axial parenchyma | MRACB |  |
| number of vessels per square mm | MABCR | MARCB |

# 9. Phytochemistry 

by C.C.H. Jongkind

Hegnauer (1964) reported that the phytochemistry of Connaraceae has been rather neglected, probably in want of species that have the interest of the pharmaceutical industry. Although this revision does by no means compensate for this lack of knowledge, there are indications that many species of the family contain phytochemically interesting substances. The seeds of many species from different parts of the tropics are reported to be very poisonous. Most of these are used as dog-poison and they seem to be poisonous for other animals like sheep, goats, and rats as well (Burkill, 1985: 523). Species that have been cited for such qualities are Burttia prunoides (see pag. ), Cnestis palala (Vidal, 1962: 14), Cnestis polyphylla (Schellenberg, 1938: 17), Connarus ferruginea (Leenhouts, 1958: 531), Rourea fluminensis (Schellenberg, 1938: 17, as Bernardinia), Rourea glabra (Forero, 1976: 28), Rourea minor (Vidal, 1962: 37), Rourea orientalis (Schellenberg, 1938: 17, as Byrsocarpus), and Rourea thomsonii (Troupin, 1952: 86, as Jaundea pubescens). The seeds of Connarus africanus are reported to be an anthelmintic drug (Burkill, 1985: 522).

The roots of many species are reported to be poisonous as well, although less vehemently than the seeds. Some are also used as dog-poison. Diluted in small doses, many are used as medicine against stomach-ache and dysentery. Such species are Agelaea macrophylla (Leenhouts, 1958: 504, as A. trinervis), Cnestis ferruginea (Burkill, 1985: 520), Rourea coccinea (Burkill, 1985: 518, as Byrsocarpus), Rourea glabra (Hegnauer, 1964: 546), Rourea fulgens (Leenhouts, 1958: 519), Rourea minor (Leenhouts, 1958: 516), and Rourea rugosa (Leenhouts, 1958: 514).

Miscellaneous literature and herbarium labels give indications of medical applications of leaves, bark, and sometimes even flowers of a number of species, but the substances responsible for their curative effects remain unknown.

# 10. Phylogeny 

### 10.1 Phylogeny of the family

by R.H.M.J. Lemmens

### 10.1.1 Introduction

According to Stuessy (1987) there are three principal approaches to biological classification: cladistics, phenetics, and evolutionary classification. 'Cladistics is the determination of branching patterns of evolution, phenetics is classification by overall similarity, without regard for evolutionary considerations. Evolutionary classification attemps to consider all meaningfull aspects of phylogeny and to use these as a basis for making a classification. This latter approach has always been done intuitively, i.e. without explicit methods'.

One of the fundamental and laudable aims of botanists practising numerical taxonomy (phenetics) as well as cladists is to decrease the amount of subjectivity and intuition. In that sense, an attempt is made here to reconstruct the phylogeny of Connaraceae, and to designate the similarities and relations between the genera, using more or less generally customary methods. A taxonomic division of the family above the genus level is based on the result.

Two different ways of classification are practised here, one based on overall similarity (phenetics), the other on phylogeny. These are discussed and compared.

All characters useful for the phenetic classification are discussed below. Often, but not always, these characters could also be used for the phylogenetic classification. In such cases, the determination of polarity is discussed.

### 10.1.2 The characters

1. Habit. The family comprises shrubs or treelets as well as lianas. Many genera have always a shrub- or tree-like habit, others are (nearly) always lianescent. Some genera are polymorphic in habit, like Rourea and Connarus. The habit is not phylogenetically useful, because of its variability in some genera and since the direction of its evolution is questionable, although many authors consider lianas as derived.
2. Leaves. Pinnate leaves occur as well as trifoliolate and unifoliolate ones. Only in Connarus and, more rarely, in Rourea both pinnate and trifoliolate leaves may be present. It is highly probable that the direction of the evolution is from pinnate towards tri- and unifoliolate.
3. Veinlets. In all genera the fine veinlets of the leaflets are reticulate, but
in Manotes they are distinctly parallel. Because the latter character-state is probably a specialization and as it is found only in Manotes, it is considered here as derived.
4. Inflorescences. In some genera the flowers are arranged in large, often pseudoterminal panicles, in others they occur in small panicles, racemes or fascicles, often cauliflorous. Variation in inflorescence type within several genera occurs to such an extent that this character is not useful for the phylogeny (see also paragraph 4.6 on inflorescences).
5. Heterostyly. This is discussed in chapter 5. Although many types are distinguished, only two character-states are used here: heterotristyly versus all other types. Heterotristyly is considered as primitive.
6. Androgynophore. An androgynophore is only found in Manotes and it is here considered as a similar evolutionary development as the parallel venation in this genus.
7. Sepals. Imbricate sepals are common, valvate ones occur in Manotes and sometimes in Cnestis, Cnestidium, Connarus and Ellipanthus. Because of the often intermediate or variable state of this character in the latter four genera it is not considered phylogenetically useful.
8. Petals. Free petals are most common, coherent ones are found in several species in some genera. Because of this the character has not been used in phylogeny.
9. Hairs and glands on petals and/or filaments. Pilose or glandular filaments and/or petals are found in 4 genera. In the other genera they are (almost) glabrous. Pilose and glandular is considered as a primitive condition, glabrous as derived. The evolutionary line is supposed to be directed towards loss of hairs.
10. Number of fertile stamens. Usually 10 fertile stamens are present, but in some genera there are only 5. In Connarus both character-states occur, but most often 10 (apparently) fertile stamens are found. Reduction of the 5 epipetalous stamens clearly indicates the direction of evolution, as discussed in chapter 5 on heterostyly.
11. Number of carpels. Six genera have 5 carpels to a flower, the other six have only a single carpel. Here a reduction in number indicates the evolutionary line.
12. Shape of follicle. In many genera the follicle has the recognizable shape of a leaf-like carpel, i.e. distinctly narrowed at the base and at the apex. In other genera the follicle is different in shape, often rounded at the base and often at the apex as well. The latter condition is considered as derived.
13. Dehiscence of follicle. Mostly the follicle is dehiscent, but in Jollydora and Hemandradenia it is indehiscent. Indehiscence is probably derived, in accordance with the views of various authors on this situation in other families.
14. Indumentum of follicle. The follicle is often pilose outside, but in several genera it is glabrous. In some genera both states occur, as in Connarus, where the follicles are often initially pilose, but they become glabrous later. Because of the intermediate or variable state of this character in some genera, it is not used in phylogenetical considerations here.
15. Indumentum of endocarp. Usually the endocarp is glabrous, but in Cnestis it is always densely pilose, while in Connarus it is often either pilose or glandular. Glabrous is considered here as derived, in accordance with the loss of hairs in other parts of the plants, like petals, filaments and the surface of follicles. However, this remains debatable. It cannot be ruled out that a pilose endocarp is in fact derived, i.e. a specialized condition, especially in Cnestis, where the endocarp is provided with many, long, often caducous and more or less stinging hairs.
16. Separating endocarp. In Manotes and Vismianthus the endocarp separates from the pericarp. It is striking that this is combined with the presence of a long appendix to the sarcotesta. This condition is considered as specialized and consequently derived.
17. Number of seeds. Usually Jollydora has two seeds in each carpel, all other genera have one seed, only very rarely two. The reduction in number indicates the direction of evolution.
18. Place of attachment of seed. The seed is attached either to the ventral side of the follicle, or (almost) to the base. The latter condition is considered as derived (see also paragraph 4.8 on fruits and seeds). In Burttia seeds are attached near the top of the follicle. This is considered as equivalent to a ventral attachment, as the place of attachment is merely shifted somewhat towards the apex.
19. Endosperm. In several genera endosperm is abundant, in others it is absent. In some genera, particularly in Cnestidium and Ellipanthus, endosperm is often present, but only in a thin layer, while the cotyledons are thick. It is generally accepted that the presence of abundant endosperm is primitive, while absence of endosperm and thick cotyledons are considered as derived conditions. A thin layer of endosperm is also considered as derived.

Two characters that can only be studied using a microscope are added to the morphological characters:
20. Epidermis cells adjacent to stomata. These cells may be different from the other epidermis cells in shape and position. Uniformity is considered as primitive, while all other deviating conditions are derived. See also paragraph 4.5.
21. Pollen. Jollydora has pollen that is completely different from the pollen of all other genera. This is considered by various authors as derived (see also chapter 6). In other genera apart from Jollydora the pollen is variable, but this variation more or less represents a continuum in which different character-states cannot be distinguished.

Characters of wood anatomy are not used. These are discussed in chapter 8 , as well as their phylogenetical significance.

### 10.1.3 Classification by overall similarity (see table 12 and 13)

For the construction of a phenogram the 21 characters discussed above are used, each with two character-states, A and B. Only in the character 'number of leaflets' three character-states, A, B, and C, are distinguished. An intermediate

Table 12. Characters and character-states of the genera of Connaraceae used for the construction of phenograms

|  | A | B | C |
| :---: | :---: | :---: | :---: |
| 1. Habit | Shrubs or treelets | Lianas |  |
| 2. Leaves | Pinnate | 3-foliolate | 1-foliolate |
| 3. Fine venation | Reticulate | Parallel |  |
| 4. Flowers | In large panicles | In small panicles, racemes or fascicles |  |
| 5. Heterostyly | Trimorphic | Dimorphic or different |  |
| 6. Androgynophore | Absent | Present |  |
| 7. Sepals | Imbricate | Valvate |  |
| 8. Petals | Free | Coherent |  |
| 9. Petals and/or filaments | Pilose | Glabrous |  |
| 10. Number of fertile stamens | 10 | 5 |  |
| 11. Number of carpels | 5 | 1 |  |
| 12. Follicle | Carpel-shaped | Different |  |
| 13. Follicle | Dehiscent | Indehiscent |  |
| 14. Follicle | Pilose outside | Glabrous outside |  |
| 15. Endocarp | Pilose | Glabrous |  |
| 16. Endocarp | Not separating | Separating |  |
| 17. Seeds per carpel | Often 2 | Usually 1 |  |
| 18. Attachment of seed | Ventral | Basal |  |
| 19. Endosperm | Present | Absent |  |
| 20. Epidermis cells adjacent to stomata | Different in shape | Not different in shape |  |
| 21. Pollen | Small, 3-colporate | Large, 4-colpate |  |

state is noted as AB. Basically all characters useful for the determination of the genera, were to be used, but an exception was made for those characters that did not allow to distinguish only two or three character-states. For this reason characters of the sarcotesta and the position of the radicle within the seed were not considered. These characters are extremely variable, showing a very large number of conditions.

In table 14 the overall similarity is calculated by comparing each genus with all other ones. The numbers of shared character-states are filled in. In this calculation, 0.5 is scored when in one of two genera compared an intermediate charac-ter-state (AB) is present.

High figures indicate that the compared genera share many character-states. The highest scoring genera are the first to be entered in the phenogram (fig. 52 A and B). These are Cnestis and Cnestidium scoring 18.5. Next the level of

Table 13. Matrix of character-states in the genera of Connaraceae. The numbers correspond to the characters discussed in the text and table 12.

|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Ag | B | B | A | A | A | A | A | AB | B | A | A | A | A | A | B | A | B | B | B | B | A |
| Bu | A | C | A | B | B | A | A | A | B | A | B | B | A | A | B | A | B | A | A | A | A |
| Cm | B | A | A | A | B | A | AB | A | B | A | A | B | A | A | B | A | B | B | AB | B | A |
| Cn | B | A | A | AB | $\mathrm{B}^{*}$ | A | AB | A | $\mathrm{B}^{*}$ | A | A | AB | A | A | A | A | B | B | A | B | A |
| Co | AB | AB | A | A | AB | A | A | AB | A | AB | B | A | A | AB | AB | A | B | A | B | A | A |
| El | A | C | A | B | AB | A | AB | A | A | B | B | A | A | A | B | A | B | A | AB | A | A |
| He | A | C | A | B | B | A | A | AB | A | B | B | B | B | A | B | A | B | A | A | A | A |
| Jo | A | A | A | B | $\mathrm{A}^{*}$ | A | A | B | B | A | B | A | B | B | B | A | A | A | B | B | B |
| Ma | B | A | B | A | A | B | B | A | A | A | A | A | A | A | B | B | B | A | A | AB | A |
| Ps | B | B | A | A | B | A | A | A | B | A | A | A | A | B | B | A | B | B | A | B | A |
| Ro | AB | A | A | AB | B | A | A | AB | B | A | A | B | A | AB | B | A | B | B | B | B | A |
| Vi | A | C | A | B | B | A | A | A | B | A | B | A | A | B | B | B | B | A | B | A | A |

$\mathrm{AB}=$ intermediate character-state or both character-states present

* = alternative or intermediate character-state rarely present
$\mathrm{Ag}=$ Agelaea $; \mathrm{Bu}=$ Burttia $; \mathrm{Cm}=$ Cnestidium $; \mathrm{Cn}=$ Cnestis; $\mathrm{Co}=$ Connarus; $\mathrm{El}=$ Ellipanthus;
$\mathrm{He}=$ Hemandradenia; $\mathrm{Jo}=$ Jollydora; $\mathrm{Ma}=$ Manotes; $\mathrm{Ps}=$ Pseudoconnarus; Ro $=$ Rourea; $\mathrm{Vi}=$ Vismianthus
connection in the phenogram is calculated as a quotient, i.e. the number of shared character-states divided by the total number of characters considered: $18.5 / 21=0.88$. In this way the genera are grouped in the phenogram and their level of connection is indicated. Where a group of genera is to be compared either with another group or with a single genus two different methods have been followed. When the average of the shared characters in the group is used this leads to group-average clustering as is shown in fig. 52 A . But when the highest number of shared character-states within the group is considered this leads to single-linkage clustering as was done in fig. 52 B.

Table 14. Summation of character-states shared between the genera of Connaraceae

|  | Ag | Bu | Cm | Cn | Co | El | He | Jo | Ma | Ps | Ro | Vi |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Ag |  | 11.5 | 16.5 | 15 | 14 | 11 | 9 | 11.5 | 12 | 17.5 | 16.5 | 11.5 |
| Bu |  |  | 14 | 14 | 13 | 16.5 | 17.5 | 11 | 9.5 | 13 | 14 | 17 |
| Cm |  |  |  | 18.5 | 11.5 | 11.5 | 10.5 | 9 | 12.5 | 17 | 18 | 11 |
| Cn |  |  |  |  | 11 | 11 | 10 | 8.5 | 12 | 16.5 | 16.5 | 10.5 |
| Co |  |  |  |  |  | 15.5 | 13.5 | 11.5 | 11 | 12.5 | 13.5 | 14 |
| El |  |  |  |  |  |  | 17 | 10.5 | 11 | 10.5 | 10.5 | 15.5 |
| He |  |  |  |  |  |  |  | 10.5 | 8 | 9.5 | 11.5 | 13.5 |
| Jo |  |  |  |  |  |  |  |  | 6.5 | 10 | 12 | 13 |
| Ma |  |  |  |  |  |  |  |  |  | 11.5 | 9.5 | 9.5 |
| Ps |  |  |  |  |  |  |  |  |  |  | 16 | 13 |
| Ro |  |  |  |  |  |  |  |  |  |  |  | 13 |
| Vi |  |  |  |  |  |  |  |  |  |  |  |  |



Fig. 52. Phenograms for the genera of Connaraceae, using group average clustering (A) and single-
linkage clustering (B). For explanation see text.

## Discussion

The phenograms fig. 52 A and fig. 52 B resulting from group-average and single-linkage clustering respectively, are slightly but not fundamentally different. Four groups can be distinguished. Manotes is the single representative of a group, as is Jollydora. The other two groups consist of the remaining 5-carpellate and of the remaining 1-carpellate genera, respectively.

It should be noted that some genera, particularly Connarus, show many intermediate character-states. Several characters that hardly vary in other genera, are strongly variable in Connarus.

### 10.1.4 Phylogenetic classification

For the construction of a cladogram, 16 characters, each with two characterstates, have been considered. For each character the polarity was determined, as discussed before (table 15). An apomorphic character-state is noted in the matrix (table 16) as 1 . The characters are the same as used for the classification by overall similarity, but 5 of them had to be omitted, either because no decision about the polarity could be made, or because one or more genera show an intermediate character-state. This is also discussed under the characters.

The Wagner Groundplan-Divergence Method was used for the construction of the cladograms. The procedure followed was taken from Cronquist, 1987, p.47:
' 1 . Delimited and characterize the species by normal taxonomic methods.
2. Remove species of hybrid origin from the set. These may be reinserted later, after the basic cladogram has been produced.
3. Determine polarity of characters, from whatever evidence is available, including but not limited to outgroup-comparison.

Table 15. Polarity of characters of the genera of Connaraceae useful for phylogenetic classification and selected from table 12

|  |  | Plesiomorphic | Apomorphic |
| :--- | :--- | :--- | :--- |
| a | Leaves | pinnate | tri- or unifoliolate |
| b | Parallel venation in leaflets | absent | present |
| c | Heterostyly | trimorphic | dimorphic or different |
| d | Androgynophore | absent | present |
| e | Petals and/or filaments | pilose | glabrous |
| f | Number of fertile stamens | 10 | 5 |
| g | Number of carpels | 5 | carpel-shaped |
| h | Follicle | dehiscent | different |
| i | Follicle | pilose | indehiscent |
| j | Endocarp | not splitting apart | glabrous |
| k | Endocarp | 2 | splitting apart |
| l | Seeds per carpel (usually) | ventral | basal |
| m | Place of attachment of seed | present | absent |
| n | Endosperm | not different | different |
| o | Epidermis-cells adjacent to stomata | small, tricolporate | large, tetracolpate |
| p | Pollen |  |  |

Table 16. Apomorphic character-states in the genera of Connaraceae. The letters correspond to the characters cited in table 15. An apomorphic character-state is noted in the matrix as 1 .

|  | a | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Ag | 1 |  |  |  | 1 |  |  |  |  | 1 |  | 1 | 1 | 1 | 1 |  |  |
| Bu | 1 |  | 1 |  | 1 |  | 1 | 1 |  | 1 |  | 1 |  |  |  |  |  |
| Cm |  |  | 1 |  | 1 |  |  | 1 |  | 1 |  | 1 | 1 |  | $*$ | 1 |  |
| Cn |  |  | 1 |  | 1 |  |  | $*$ |  |  |  | 1 | 1 |  | 1 |  |  |
| Co | $1^{*}$ |  | $1^{*}$ |  |  | $*$ | 1 |  |  | $*$ |  | 1 |  | 1 |  |  |  |
| El | 1 |  | $1^{*}$ |  |  | 1 | 1 |  |  | 1 |  | 1 |  |  | $*$ |  |  |
| He | 1 |  | 1 |  |  | 1 | 1 | 1 | 1 | 1 |  | 1 |  |  |  |  |  |
| Jo |  |  |  |  | 1 |  | 1 |  | 1 | 1 |  |  |  | 1 | 1 | 1 |  |
| Ma |  | 1 |  | 1 |  |  |  |  |  | 1 | 1 | 1 |  | 1 | $1^{*}$ |  |  |
| Ps | 1 |  | 1 |  | 1 |  |  |  |  | 1 |  | 1 | 1 |  | 1 |  |  |
| Ro |  |  | 1 |  | 1 |  |  | 1 |  | 1 |  | 1 | 1 | 1 | 1 |  |  |
| Vi | 1 |  | 1 |  | 1 |  | 1 |  |  | 1 | 1 | 1 |  | 1 |  |  |  |

* = alternative or intermediate character-state rarely present

4. Hypothesize a common ancestor primitive (plesiomorphic) in all characters considered. This putative ancestor represents the groundplan.
5. Set up a chart (familiarly called Wagner's bull's-eye) with concentric semicircles about a common base-point that represents the groundplan. Occasionally there may be an actual existing species at this base-point. The first semicircle (nearest the base-point) represents divergence from the groundplan in one character; the second represents divergence in two characters, etc.
6. Following a relatively simple set of logical rules explained by Wagner, and starting with the species that diverge the least from the groundplan, manually construct the most parsimonious cladogram. Branch-points on the cladogram may be represented by existing species or extinct hypothetical species. Species that have diverged in the fewest characters from the groundplan appear on the semicircle(s) nearest the base-point. Species that have diverged in more characters appear on progressively remote semicircles. All species are eventually connected by lines to the base-point (representing the groundplan) on an assumption of maximum parsimony in the evolution of individual apomorphics. Thus both the cladistic relationships and the degree of evolutionary advancement are shown on the chart, which limits the number of acceptable taxonomic arrangements but does not proscribe the acceptance of paraphyletic groups.

All this can be done manually if relatively few species are to be considered, and if parallelisms and reversals are not numerous...'

## Discussion

The important subjective component in the construction of a cladogram consists chiefly of two separate choices. The first of these is which character is used and which is ignored. The second one is the determination of polarity. The methods used by cladists to determine polarity are the following:

1. Outgroup-comparison. The outgroup should preferably be the sister group of the group under study, i.e. the most closely related natural taxon. If only one of a pair of character-states under consideration is found in the outgroup, that state is considered to be plesiomorphic in the ingroup.
2. Correlation of transformation series. Wiley (1981) cites Hennig's criterion of the correlation of several series of transformation: 'if two characters each with three or more progressive states in allied taxa are always correlated (a with $b$, $a^{\prime}$ with $b^{\prime}, a$ " with $b$ '), and if polarity can be established for one of the series, it will be the same for the correlated series'.
3. Fossil record. When fossils are known in the group under study and when the characters under consideration can be studied in them, it may be possible to determine polarity from those fossils.
4. Geography. Occasionally the geographical distribution can be useful to determinate polarity.
5. Adaptation. Specialization and adaptation in characters is often recognizable and is of course considered as derived.

According to Cronquist (1987) we should use whatever evidence we may find in order to establish polarity, and such evidence is not necessarily restricted to the methods enumerated above.

In Connaraceae, the determination of polarity was often problematic. Out-group-comparison was not possible, because the position of the family is uncertain as a closely related family is not available, nor are fossils. In some characters a reduction of organs is thought to indicate the polarity, e.g. number of leaflets, fertile stamens, carpels, and number of seeds per carpel. In other characters a trend, generally observed in Angiosperms, is assumed, e.g. dehiscence of the follicle, presence or absence of endosperm, shape and position of epidermis-cells adjacent to stomata and characters of the pollen. In the remaining characters an even more subjective choice for the establishment of polarity is made. For instance the polarity of the indumentum of the inside of the follicle is uncertain, as discussed before (under this character). In general, pilose is considered as plesiomorphic, glabrous as apomorphic. Finally, the presence of apparently specialized structures, only found in a single genus or sometimes in two genera, is considered as an apomorphic condition, e.g. presence of a parallel venation in the leaflets and of an androgynophore in the flowers of Manotes, and the separating endocarp in Manotes and Vismianthus.

Hutchinson $(1964,1969)$ considered pinnate leaves, 5 carpels, imbricate sepals, and a dehiscent follicle as primitive, and tri- and unifoliolate leaves, 1 carpel, valvate sepals, an indehiscent follicle, cauliflory, and unisexual flowers as advanced. My views agree with these assumptions, and also with the major evolutionary trends as supposed by Dickison (1981).

The two cladograms presented (fig. 53 A and 53 B ) show only dichotomous branching, and they are the most parsimonious ones that could be constructed. Two more equally parsimonious cladograms can be constructed, when the position of the branch(es) comprising Cnestis, Cnestidium, and Rourea is inter-


Fig. 53. Two of the most parsimonious cladograms for the genera of Connaraceae. The letters indi-
cate apomorphic character-states and corrent cate apomorphic character-states and correspond to the characters cited in table 15. For explanation
see text.
changed between the two cladograms. The cladograms show an equal number of parallelisms and this number is high, 19 in 10 characters. Cronquist (1987) states: 'There is so much evolutionary parallelism among the Angiosperms that we should not balk at accepting something more than the absolute minimum number of steps if the additional parallelism (or avoided reversals) make sense in other respects...'. However, when accepting also cladograms with a slightly larger number of parallelisms, the number of cladograms strongly increases. For that reason only two of the most parsimonious cladograms are taken into consideration here. Cronquist also states that when two or more equally parsimonious cladograms are available, the cladist must choose the one he intuitively prefers, or he must accept only those features that are common to the other or most of the others of these parsimonious cladograms, leaving the remaining decisions unresolved.

According to Cronquist it must be taken into account that 'cladograms of higher-level taxa are almost always oversimplifications of evolutionary history'. Still, 'such an extrapolation of the method is not fatal nor even inherently improper'. In fact, Wagner himself has used his method for genera. In practice, the utility at the higher levels is progressively limited.

The cladograms show that all genera have many apomorphic character-states and that no genus can be considered as very primitive and close to the common ancestor.

Ellipanthus is ancestral to Hemandradenia and Cnestidium is it to Rourea, while Cnestis can be considered ancestral to Cnestidium and Rourea. Cronquist (1987) states that in most current cladistic theories, no existing species can be ancestral to any other existing species. In the process of producing two descendant species, the ancestral species must cease to exist. He considers this as palpably untrue. It is generally accepted that many new species arise as geographically peripheral isolates of other species. The acceptance of an existing species to be ancestral to another must be considered as an advantage. Wagner accepts existing species as ancestral to other and according to Cronquist, Wagner avoids the most important errors in cladistic theory and practice by casting a wider net for data bearing on polarity of characters, and most importantly in his acceptance of paraphyletic taxa.

Cronquist's assertion that in most current cladistic theories an extant species cannot be ancestral to another calls for comment. In fact, the cladograms resulting from the Wagner Groundplan Divergence Method and those resulting from most other cladistic methods, do not differ as much as Cronquist suggests. The ancestral taxon is situated in a different position in both types of cladograms. In Wagner's 'bull's-eye' it is situated on the main axis, in other cladograms it terminates a distinct branch. This difference in the position of ancestral taxa does not imply that only Wagner's method accepts the existence of an ancestral taxon. Whether this ancestral taxon is situated on the main axis or its situation is represented in a terminal position on its own branch is not relevant. The main issue is the presence of apomorphic character-states on the branch of the cladogram between the positions of the ancestral and the descendant taxon.

### 10.1.5 Comparison of phenetics and cladistics

The resulting cladograms and phenograms are to a certain extent in agreement with each other. In both, Jollydora and Manotes are clearly separated from the other genera. The remaining 5 -carpellate as well as the remaining 1-carpellate genera are clustered together. Yet, the two methods are directed toward different ends. The phenogram is intended to show similarities, without regard to phylogeny, whereas the cladogram is intended to show phylogeny, with only secondary attention to phenetic features. Of course, it must be kept in mind that usually similarities are largely the result of relations.

### 10.1.6 Arrangement in tribes

In his monograph Schellenberg (1938) made a phylogenetic classification of Connaraceae, which is reproduced in fig. 54. Apparently he did this after he had established the infrafamiliar taxa above the genus level. So Schellenberg first delimited his subfamilies and tribes and placed these in the phylogenetic tree afterwards. He considered certain characters of primary importance. For instance, the fact that Jollydora often has two seeds per carpel was important enough to him to distinguish Jollydora from all other Connaraceae and to place it in a separate subfamily Jollydoroideae. Schellenberg placed Cnestis in the tribe Cnestideae as a primitive group at the base of the phylogenetic tree of Connaroideae. For the construction of the tree he considered the type of inflorescence as very important, terminal or axillary. Proceeding from the point of furcation near Cnestis, the tree shows four main branches, each considered as a tribe by Schellenberg. They are Agelaeeae with the genera Agelaea, Manotes and Hemandradenia; Connareae with Cnestidium, Rourea and Connarus; Byrsocarpeae with Pseudoconnarus, Vismianthus, Burttia and 8 other genera, now placed in Rourea, and finally Castanoleae with Ellipanthus, Schellenbergia (now placed in Vismianthus), Castanola (now in Agelaea) and Taeniochlaena (now in Rourea). It should be noted that Schellenberg in three separate instances referred parts of what is in our view a single genus, to different tribes! This concerns the genera Agelaea, Rourea, and Vismianthus.

It is remarkable that Schellenberg did not assess characters such as the number of carpels and the number of leaflets.
The classification by overall similarity and the phylogenetic classification, as presented here, are based on the genera and their differentiating characters. The following division of the family in tribes is based on these classifications. The main characters are summarized, and the constituent genera are listed.

1. Connareae, first used by Planchon, 1850: 411; Gilg, 1897: 64; Schellenberg, 1938: 191.

Lianas, shrubs or small trees with unifoliolate leaves (except Connarus with trifoliolate or pinnate leaves), a single carpel, a dehiscent follicle with 1 seed,

## Stammbaum der Connaraceen.



Fig. 54. Schellenberg's phylogenetic tree. Copied from Schellenberg (1938) p. 19.
ventrally attached, tricolporate pollen. Type: Connarus. Burttia, Connarus, Ellipanthus, Hemandradenia, and Vismianthus.
2. Jollydoreae (Gilg) Lemmens, comb. \& stat. nov. Jollydoroideae Gilg, 1897: 189; Schellenberg, 1938: 24.
Usually unbranched treelets with large, pinnate leaves, a single carpel, an indehiscent follicle with often 2 seeds, ventrally attached, tetracolpate pollen. Type: Jollydora, the only genus.
3. Manoteae Lemmens, trib. nov.

Liana. Folia imparipinnata, foliola striata. Flos androgynophoro. Carpella 5. Folliculi dehiscentes. Semen in carpidio solitarium, hilo ventrali.

Lianas with pinnate leaves and striately nerved leaflets, an androgynophore, 5 carpels, dehiscent follicles with 1 seed, ventrally attached, tricolporate pollen. Type: Manotes, the only genus.
4. Cnestideae Planchon, 1850: 438; Gilg, 1897: 67; Schellenberg, 1938: 28.

Lianas or shrubs with pinnate or trifoliolate leaves, 5 carpels, dehiscent follicles with 1 seed, basally attached, tricolporate pollen. Type: Cnestis. Agelaea, Cnestidium, Cnestis, Pseudoconnarus, and Rourea.

This subdivision of the family differs widely from the one given by Schellenberg. Only the distinct position of Jollydora in the family is maintained, although at a lower level.

### 10.2 Phylogeny of the genus Cnestis

by R.H.M.J. Lemmens

### 10.2.1 Introduction

In analogy to the pertinent chapter concerning the phylogeny of the family, the different approaches discussed there to arrive at a classification have been applied on the genus Cnestis. All characters useful for the phenetic classification are discussed below. Often, but not always, these characters could also be used for the phylogenetic classification. In such cases, the determination of polarity is discussed.

The methods used in order to designate similarities and phylogenetics of the species of the genus, are the same as discussed in paragraph 10.1 on phylogeny of the family. The determination of polarity in some characters is also discussed in this paragraph.

### 10.2.2 The characters

Characters that are considered useful for phylogeny, are compared with those of Manotes, which is chosen as the outgroup (see 10.2.4).

1. Habit. Only C. mildbraedii is probably always a shrub or small tree. All other species show lianescent tendencies, dependent on environmental condi-
tions. Usually a shrubby or tree-like habit is considered as primitive, a lianescent habit as derived.
2. Number and size of leaflets. Leaflets are few and large or numerous and small. However, the number and shape of the leaflets varies strongly within several species. For that reason this character is phylogenetically not useful.
3. Apex of leaflets. The leaflets are often acuminate, sometimes rounded at the apex. Again some species are variable and therefore this character cannot be used in phylogenetical considerations.
4. Petiolules. C. macrophylla has very long petiolules. It could be supposed that long petiolules are derived, as they are not found in the outgroup and only in a single Cnestis species. In other characters of the leaves C. macrophylla seems to be primitive. The direction of evolution of petiolule-length is uncertain, and as such this character seems not to be useful phylogenetically.
5. Inflorescences. Three types of inflorescences can be distinguished: often pseudoterminal large panicles, rather small (pseudo)racemes, and glomerules of flowers on old branches and stems. Large pseudoterminal inflorescences are considered as primitive, small ramiflorous ones as derived. A reduction of the inflorescence from paniculate to racemose and to glomerulate flowers is also assumed, the last two conditions thus being derived. The outgroup, Manotes, has large, pseudoterminal panicles, except for M. macrantha.
6. Flowers. These can be comparatively large or small. But there is so much variation within several species, that this character is not useful phylogenetically.
7. Heterostyly. In Cnestis many types of heterostyly are found, as discussed

Table 17. Characters and character-states of the species of Cnestis used for the construction of phenograms

|  |  | A | B | C |
| :---: | :---: | :---: | :---: | :---: |
| 1. | Habit | Shrubs | Lianas |  |
| 2. | Leaflets | Large, few | Small, numerous |  |
| 3. | Leaflets | Acuminate at apex | Rounded at apex |  |
| 4. | Petiolules | Short ( $<6 \mathrm{~mm}$ ) | Long ( $>6 \mathrm{~mm}$ ) |  |
| 5. | Flowers | In large panicles | In small racemes | In fascicles |
| 6. | Flowers | Large | Small |  |
| 7. | Heterostyly | Dimorphic | Obscurely heterostylous | Almost homostylous |
| 8. | Sepals | Not reflexed | Reflexed |  |
| 9. | Sepals | Pilose inside | Glabrous inside |  |
| 10. | Petals | Shorter than sepals | About as long as sepals | Longer than sepals |
| 11. | Glandular hairs | Present | Absent |  |
| 12. | Follicle | Small | Large |  |
| 13. | Follicle | Distinctly stiped at base | Not distinctly stiped at base |  |
| 14. | Follicle | Short-rostrate <br> (-obtuse) | Long-rostrate |  |
| 15. | Follicle | With soft, short hairs outside | With hispid, long hairs outside |  |

Table 18. Matrix of character-states in the species of Cnestis. The numbers correspond to the characters discussed in the text and table 17.

|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| bo | B | B | B* | A | B | B | A | B | B | C | B* | B | AB | AB | A |
| co | B | AB | A | A | B | AB | AB | B* | B | BC | B* | AB | A | B | B |
| fe | AB | AB | A | A | A | B | C | A | A | A | A | AB | B | B | A |
| mc | $B^{*}$ | B | B | A | A | A | A | A | A | A | A | B | B | B | A |
| mp | B | A | A | B | B | A | AB | A | B | B | B | AB | A | B | A |
| mn | B | A | A | A | A | A | A | A | A | A | B* | B | A | B | A |
| mi | A | AB | A | A | B | A | B | A | B* | B | B | AB | A | B | A |
| pa | AB | B | AB | A | B | AB | BC | A | A | AB | A | AB | A | AB | A |
| po | AB | AB | AB | A | B | AB | B | B | AB | B | B | A | B | A | A |
| ra | AB | A | A | A | B | B | B | B | B | B | B | A | A | A | A |
|  | $\mathrm{B}^{*}$ | AB | A | A | C | A | A | B | B | C | B | ${ }^{\text {A }}$ | A | A | A |
|  | B | B | B | A | C | A | A | B | B | C | B* | AB | A | B | B |
|  | B | B | A | A | B | B | AB | B | B | C | B B | AB | A | B | B |

in chapter 5. Three types are distinguished here for the classification by overall similarity: heterodistyly, a type possibly intermediate between heterodistyly and -tristyly, and an almost homostylous type, only found in C.ferruginea. For phylogenetical considerations only the last type is assumed to be derived.
8. Sepals. These are either reflexed or not. Outgroup-comparison leads to the assumption that non-reflexed, i.e. slightly spreading, is a primitive condition, and thus reflexed sepals are derived.
9. Inner side of sepals. The sepals can be pilose or glabrous inside. In accordance with several characters regarding the indumentum, the evolutionary line is supposed to be directed towards loss of hairs.
10. Length of petals. Petals can be distinctly shorter than the sepals, about as long, or distinctly longer. It proved that the second condition was correlated with primitive character-states of other characters, especially of flowers and inflorescences. For that reason petals as long as sepals is considered as the most primitive condition, both other situations derived.
11. Glandular hairs. Glandular hairs are usually present in three species, particularly on inflorescences, pedicels and sepals. They are less common in some other species. In Manotes glandular hairs are always present and consequently this condition is considered as primitive.
12. Size of follicle. The follicle may be large or small, but an intermediate state occurs in many species. As such this character is not useful for phylogenetical considerations.
13. Base of follicle. A distinct stipe is often present, but several species have a follicle rounded at the base. It is assumed that the latter condition is derived,
as discussed in the paragraph 10.1, where the 'carpel-shaped' follicle is considered as primitive.
14. Apex of follicle. A distinct beak is present in most species. A short beak is found in some species, sometimes only a short mucro is present, resembling the follicles of Manotes, rarely the follicle is obtuse or rounded, as sometimes found in C. polyphylla. Shortly beaked, mucronate and obtuse or rounded follicles are considered as primitive, because they resemble the follicles of Manotes.
15. Indumentum of follicle. On the outside the follicle is provided with either soft and rather short hairs, or with hispid and long hairs. The latter characterstate is specialized and not found in the outgroup, and is consequently considered as derived.

### 10.2.3 Classification by overall similarity (see table 17 and 18)

For the construction of phenograms, 12 characters with two character-states (A and B), and 3 with three character-states (A, B, and C) are used. In the matrix (table 18) an intermediate state is noted as $\mathrm{AB}, \mathrm{BC}$, or AC .

In table 19 the highest scoring species are C. urens and C. uncata with 13.5. These species are connected in the phenogram at the level $13.5 / 15=0.90$, i.e. the quotient of number of shared character-states and the number of characters taken into consideration.

The resulting phenograms are figured in fig. 55 A and 55 B , using groupaverage and single-linkage clustering respectively, as discussed in the paragraph on phylogeny of the family.

## Discussion

The phenograms resulting from group-average and single-linkage clustering, fig. 55 A and fig. 55 B respectively, are somewhat different, especially as regards the position of C. mildbraedii, C. macrophylla and C. bomiensis. In both pheno-

Table 19. Summation of character-states shared between the species of Cnestis

| bo | co | fe | mc | mp | mn | mi | pa | po | ra | un | ur | ya |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| bo | 9.5 | 5.5 | 8 | 6 | 7 | 7 | 7.5 | 8.5 | 8.5 | 9 | 10 | 10 |
| co |  | 6 | 5 | 11.5 | 8 | 10.5 | 8 | 9 | 10 | 12.5 | 11 | 11 |
| fe |  |  | 10.5 | 5 | 9.5 | 7.5 | 10 | 7 | 6 | 5.5 | 4 | 5.5 |
| mc |  |  |  | 5 | 11 | 6 | 9 | 5.5 | 2.5 | 6 | 7.5 | 4.5 |
| mp |  |  |  |  | 9 | 11 | 7 | 6.5 | 8.5 | 10 | 8.5 | 7.5 |
| mn |  |  |  |  |  | 9 | 8 | 5.5 | 6.5 | 9 | 7.5 | 4.5 |
| mi |  |  |  |  |  |  | 9.5 | 9.5 | 10.5 | 9 | 7.5 | 6.5 |
| pa |  |  |  |  |  |  |  | 9 | 8 | 5.5 | 6 | 6 |
| po |  |  |  |  |  |  |  |  | 12 | 6.5 | 6 | 10 |
| ra |  |  |  |  |  |  |  |  |  | 7.5 | 6 | 10 |
| un |  |  |  |  |  |  |  |  |  |  | 13.5 | 9.5 |
| ur |  |  |  |  |  |  |  |  |  |  |  | 9 |
| ya |  |  |  |  |  |  |  |  |  |  |  |  |



Fig. 55. Phenograms for the species in Cnestis, using group average clustering (A) and single-linkage clustering (B). For explanation see text.
grams three groups of species can be distinguished, the first of which comprises C. palala, C. ferruginea, C. mannii and C. macrantha, the second C. polyphylla and C. racemosa, and the third C. corniculata, C. urens and C. uncata.

It should be noted that three species, i.e. C. polyphylla, C. palala, and C. corniculata, show many intermediate character-states. They are strongly variable, as is discussed in the taxonomic treatment of these species.

### 10.2.4 Phylogenetic classification

For the construction of cladograms, 11 characters, each with two characterstates, have been considered. After determination of the polarity (table 20), as discussed under 'the characters' and by using Manotes as an outgroup, an apomorphic character-state is noted in table 21 as 1 . The characters are the same as those used for the classification by overall similarity, but 4 of them are omitted, either because no decision about the polarity could be made, or because one or more species show an intermediate character-state. This is also discussed under 'the characters'.

For the construction of the cladograms the Wagner Groundplan-Divergence Method is used once again.

Two of the most parsimonious cladograms (fig. 56 A and fig. 56 B ) are presented here. They differ in the position of the group of C. macrantha, C.ferruginea and C. mannii, that of C. mildbraedii, while the positions of C. corniculata and C. uncata have been switched. Two more equally parsimonious cladograms can be constructed, when the positions of the four species within the group of C. corniculata are interchanged between the two cladograms. In this group exclusively dichotomous branching was not possible.

## Discussion

As discussed in paragraph 10.1 on the phylogeny of the family, determination of polarity is often problematic. For the genus Cnestis outgroup-comparison

Table 20. Polarity of characters of the species of Cnestis useful for phylogenetic classification and selected from table 17

|  |  | Plesiomorphic | Apomorphic |
| :--- | :--- | :--- | :--- |
| a | Habit | shrub | liana |
| b | Inflorescences | large, pseudoterminal | small, ramiflorous |
| c | Flowers | in panicles or racemes | in fascicles |
| d | Flowers | heterostylous | almost homostylous |
| e | Sepals | not reflexed | reflexed |
| f | Sepals | pilose inside | glabrous inside |
| g | Petals | as long as sepals | shorter or longer than sepals |
| h | Glandular hairs | present | absent |
| i | Base follicle | distinctly stiped | not distinctly stiped |
| j | Apex follicle | indistinctly or short-rostrate | long-rostrate |
| k | Follicle | with short, soft hairs | with long, hispid hairs |

Table 21. Apomorphic character-states in the species of Cnestis. The letters correspond to the characters cited in table 20. An apomorphic character-state is noted in the matrix as 1.

|  | a | b | c | d | e | f | g | h | i | j | k |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| bo | 1 | 1 |  |  | 1 | 1 | 1 | 1 | 1* |  |  |
| co | 1 | 1 |  |  | 1 | 1 | $1^{*}$ | 1 |  | 1 | 1 |
| fe | $1^{*}$ |  |  | 1 |  |  | 1 |  | 1 |  |  |
| mc | 1 |  |  |  |  |  | 1 |  | 1 |  |  |
| mp | 1 | 1 |  |  |  | 1 |  | 1 |  | 1 | 1 |
| mn | 1 |  |  |  |  |  | 1 | 1 |  | * |  |
| mi |  | 1 |  |  |  | 1 |  | 1 |  | * |  |
| pa | 1* | 1 |  | * |  |  | * |  |  |  |  |
| po | 1* | 1 |  |  | 1 | * |  | 1 | 1 |  |  |
| ra | ${ }^{*}$ | 1 |  |  | 1 | 1 |  | 1 |  |  |  |
| un |  | 1 | 1 |  | 1 | 1 | 1 | 1 |  |  | 1 |
| ur | 1 | 1 | 1 |  | 1 | 1 | 1 | 1 |  | 1 | 1 |
| ya | 1 | 1 |  |  | 1 | 1 | 1 | 1 | 1 |  | 1 |

* = alternative or intermediate character-state rarely present
became possible when the phylogeny of the family was reconstructed and the relations of the genera were designated. Three different choices for the outgroup were considered: Manotes, Jollydora, and a genus from the group of 5-carpellate genera. As a result Manotes is considered as the sistergroup of Cnestis, and consequently it is used as the outgroup. Manotes is primitive in many characters and probably more closely related to Cnestis than Jollydora, although it should be noted that this is debatable, as is demonstrated by one of the cladograms dealing with the genera of the family. The other 5 -carpellate genera are considered to be distinctly more derived than Cnestis. Because of that they were not chosen as the outgroup, although these genera are probably more closely related to Cnestis than Manotes is. For most of the characters, polarity is determined by comparison with Manotes. The character-states found in the sister group are considered to be plesiomorphic. For two characters (habit and length of petals) it proved that a character-state, not found in Manotes, is always correlated with plesiomorphic character-states of other characters. In these cases the character-state concerned is also considered to be plesiomorphic. By using an outgroup, the determination of polarity within Cnestis possibly has been more objective than it was when treating the genera of the family. On the other hand, for the reconstruction of the phylogeny of the family a larger number of characters could be used.

The number of characters used to construct the cladograms of Cnestis was 11. It should be kept in mind that errors made, for instance in the determination of the polarity, can have great consequences for the position of species in the cladograms, particularly when a limited number of characters is used.

In the most parsimonious cladograms the number of parallelisms is not as high as was found for the genera: 13 parallelisms in 7 characters.
The cladograms show that C. palala and C. mildbraedii, and the group consist-


Fig. 56. Two of the most parsimonious cladograms for the species in Cnestis. The letters indicate apomorphic character-states and correspond to the characters cited in table 20. For explanation see text.
ing of C.ferruginea, C. macrantha and C. mannii can be considered as comparatively primitive and close to the common ancestor. The group comprising C. yangambiensis, C. corniculata, C. uncata, and C. urens is apparently derived. C. palala is in both cases ancestral to 8 other species, while either $C$. uncata or C. corniculata is the ancestor of $C$. urens.

A remark should be made about the position of C. macrophylla. As discussed in the taxonomic treatment, C. macrophylla only differs in the long petiolules from a form of C. corniculata. This character, however, is not used in the phylogeny. C. macrophylla has spreading sepals and petals as long as the sepals, conditions considered as primitive. C. corniculata only rarely shows these characterstates and is considered as derived in regard to the sepals and petals.

### 10.2.5 Comparison of phenetics and cladistics

The resulting cladograms and phenograms are in agreement with each other to a certain extent. In both, C. ferruginea, C. mannii and C. macrantha are situated closer to each other than to the other species. C. palala is clearly separated from the other species, while C. polyphylla and C. racemosa are clustered together.

However, the cladograms and phenograms distinctly differ in the position of some other species. C. mildbraediii is distinctly separated from the other species in the cladograms, but not in the phenograms. The separate position of this species in the cladograms is particularly due to its habit. C. mildbraedii is either a shrub or a small tree, while all other species are basically lianas. It should be noted however, that material of $C$. mildbraedii is scarce and that notes on the habit of the plants collected are not always available.

The species having follicles with stinging hairs, i.e. C. macrophylla, C. corniculata, C. yangambiensis, C. urens, and C. uncata, are situated together in the cladograms. In the phenograms some other species, particularly C. mildbraedii and C. bomiensis, are clustered together with 'the stinging species'.

The phenograms show two distinct groups, the first of which comprises $C$. palala, C. ferruginea, C. mannii, and C. macrantha, the second consists of the remaining species. These groups are not found in the cladograms, although the four species of the first group are situated close to each other at the base of the tree.

However, as was discussed in the paragraph on phylogeny of the family, cladograms and phenograms are hardly comparable. The cladograms are based on the relations of the species, the phenograms only partly so. Overall similarity can also be the result of adaptation and specialization, independently originated in several species and due to environmental conditions.

No subdivision of the genus based on the classification in the phenograms and cladograms is proposed above the species level. One could consider to distinguish two separate groups, the first comprising C. ferruginea, C. mannii, C. macrantha, and C. palala, the second consisting of the remaining species. But
then the position of C. mildbraedii remains dubious. Besides this, the first group of species would be paraphyletic, because the descendants of C. palala are excluded from the group. Finally, the groups are not as distinctly separated as are the groups of genera in the family, that are accepted as tribes.

### 10.3 Phylogeny of the genus Rourea

## by C.C.H. Jongkind

After dealing for over four years with the African species of Rourea it is felt that the evolutionary relationship between these species is better reflected upon without employing special cladistic methods. Such methods require the expression of character states in a contrasting numerical manner that does not sufficiently allow for subtle distinctions in value. This does not imply that I do not see possibilities for a fruitful application of cladistics in order to reveal the phylogeny of other taxa. My approach towards the phylogeny on Rourea has resulted in a diagram (fig. 57) reflecting the possible course of evolution in this genus.


Fig. 57. Phylogeny of the genus Rourea


Table 22. Comparison of the sections of Rourea with the 'ancestral species'. + : This character is in all species the same as in the ancestral species; $\pm$ : in some species the same as in the ancestral species; - : in all species different from the ancestral species; -* : in all species different from the ancestral species but not equal to that in other aberrant section.

The length of the branches in this diagram are without value, only the bifurcations are important.

The ancestral species, X in this diagram, was probably a liana with anomocytic stomata in its leaves, and flowers with inrolled petals. The calyx was not clasping the fruit. More than one follicle developed per flower, and the fruit was velutinous. The testa was fleshy for ca $1 / 4$ and the seed had an apical radicle.

The characters for the ancestral species have been selected after comparison of Rourea with the other genera of Connaraceae and establishment of the pattern of distribution of the character states among the species of the genus.

1. All species of Rourea are lianas or scandent shrubs so it is plausible that the ancestral species was a liana.
2. The only stomata pattern that is found in both five-carpellate and onecarpellate Connaraceae is the cyclocytic pattern. This pattern is also found in some species of Rourea, so this seems to be the primitive pattern in this genus.
3. Flowers with inrolled petals are found in the sections Roureopsis and Byrsocarpus in Rourea and also in some species of Cnestis. I suppose this character state to have been developed only once in a common ancestor of Cnestis and Rourea and therefore to have been present in the ancestral species of Rourea.
4. The only genus beside Rourea with five-carpellate flowers and an accrescent calyx is Manotes, and there this calyx is not at all clasping the fruit (see fig. 147.7), so this seems to be the primitive state.
5. In some species of Rourea and in all other genera with five carpellate flowers more than one follicle usually developes into fruit, one developed follicle per flower clearly is a derived character state.
6. Velutinous indumentum is the most common indumentum on the fruits of this family. It is found in most genera in the five-carpellate group and it is common in the genera in the one-carpellate group as well. Therefore it is considered to be primitive. Other kinds of indumentum such as an indumentum of glandular hairs or long sometimes stinging hairs mixed with short velutinous hairs are considered to be derived just as the glabrous fruits.
7. A testa that is fleshy for ca $1 / 4$ is found in most species of Rourea and in all other genera with five-carpellate flowers with the exception of Manotes. Because Rourea is clearly more related to five-carpellate genera like Cnestis or Agelaea than to Manotes, the character state as found in the first two is considered to be primitive for Rourea.
8. The radicle is apical in seed in almost all Connaraceae (see chapter 4.8) so a ventral or dorsal radicle is considered to be a derived character state.

Other characters of Rourea are either not variable or hard to segregate in a primitive and a derived state.

The different sections are classified according to the amount of differences with this ancestral species and the amount of similarities with each other. In tab. 22 the sections are compared with the ancestral species. The characters to distinguish the sections are given on pag. 313. Key characters for the first bifurcations within the sections are the place of the radicle in the seed: ventral (1A) or apical (1B), and the indumentum of the fruit: velutinous ( 2 A ) or glabrous (2B).

The only African species in section Rourea is R. parviflora. Except for dimensions there is no character in flower or fruit that separates this species from all other species in this section. This maybe the only species in this section with deeply furrowed branches, but this could not yet be verified in some of the other species.

In section Santaloides the Afro-Asiatic species $R$. minor can be separated from the others on leaf characters only. However, in several divisions of its area of distribution these may be reinforced by some fruit characters as well.
R. orientalis and $R$. cassioides of section Byrsocarpus are very similar, the only important difference between these species is the location of the inflorescence. The other two species in this section, R. thomsonii and R. coccinea, are not hard to separate. $R$. thomsonii is distinct from $R$. coccinea in the shape of the petals and in the shape of the sarcotesta.

The Asiatic species of section Roureopsis are situated on two different branches, one for the species with velutinous fruits (1) and one for the species with glabrous fruits (2).

The group of four species marked with an asterisk need some special explanation. They are located at the end of a branch that started with the character of velutinous fruits (2A), but the fruits of R. myriantha are glabrous and those of $R$. calophylla have only glandular hairs. However, because of the similarity in the shape of the follicles and of the calyx in fruit, it is felt that these two species are close relatives of $R$. solanderi, a species with velutinous fruits. Their position in the diagram implying repeated instances of a relapse towards loss of indumentum is preferred over an alliance with species with glabrous fruits and subsequent acquisition of indumentum. Within this group of four species R. calophylloides is branched off first because the follicle and calyx in fruit are more like those of the Asiatic species with velutinous fruits rather than those of the remaining three species. Flower or fruit characters do not provide terms for a further phylogenetical classification of these three species. R. calophylla
is branched off first by means of distinct vegetative characters. The remaining two species are almost impossible to separate when sterile.
R. erythrocalyx and R. obliquifoliolata differ mainly in the shape of the inflorescence, the dimensions of the calyx in fruit, and the shape of the leaves.

## TAXONOMIC PART

# Description of the family and keys to the genera 

by C. C. H. Jongkind

## Description of the family

Lianas climbing by means of the winding ends of young branches, sometimes additionally provided with reduced leaves transformed into woody hooks, less often shrubs or small trees. Stems may be deeply furrowed to fluted, lenticellate or not. Wood sometimes with interxylary phloem. Leaves alternate, imparipinnate, trifoliolate or unifoliolate, exstipulate, exstipellate; petiole pulvinate at base; petiolules entirely so; leaflets entire, opposite or not. Flowers in axillary panicles, racemes or rarely in fascicles; often numerous inflorescences grouped together towards the end of a branch accompanied by strongly reduced leaves suggesting a single large terminal inflorescence, sometimes partly cauliflorous or uniformly so. Pedicel usually jointed. Flowers bisexual or rarely unisexual, pentamerous or rarely tetramerous, actinomorphic. Sepals imbricate or valvate, free or united at base, or almost entirely fused in bud (Rourea solanderi), caducous to persistent and sometimes somewhat accrescent in fruit to strongly so. Petals imbricate, free to connivent near the base. Androgynoecium usually heterodistylous or heterotristylous; Stamens in two whorls, free or united at base, the outer episepalous, longer than the inner epipetalous ones, the latter staminodial in a limited number of species; anthers dorsifixed, dehiscing lengthwise, introrse. Carpels superior, free, either one or five present, of the five carpels often only a reduced number develops into ripe follicles, in many species even only a single one; ovules two, collateral, nearly basal to nearly apical, anatropous to hemitropous; micropyle always directed upwards. Fruits dry or more-or-less fleshy, usually dehiscing by a ventral suture, sometimes along the dorsal side as well, rarely circumscissile at the base, or indehiscent, Two or more follicles of a single flower sometimes connate at base. Seed one or two per follicle, with or without endosperm; hilum lateral to basal; testa partly to entirely fleshy, sarcotesta sometimes partly free; cotyledons thin and flat to planoconvex; radicle central covered by the cotyledons or situated at their margin, apical, ventral, or dorsal. Seedlings hypogeal or epigeal.

A circumtropical family with twelve genera and 110-200 species depending on the species concept used (see Introduction).

Three keys to the genera are presented. For the first one, the general key, flowers and fruits are needed for identification. In this key all 12 genera are covered. The second and the third key are for identification of flowering and fruiting material respectively. These two keys are made for the African genera only. Identification with these keys, i.e. of material with either flowers or fruits,


Table 23. Vegetative characters of the genera of Connaraceae. + : character present in one or more
species of the genus. species of the genus.
is more difficult than of complete material, especially so when only flowers arepresent.For sterile material table 23 may be a useful help to determine the genus.In this table vegetative characters of all 12 genera are presented.
General key to the genera
1a Flowers with five carpels. ..... -2
b Flowers with one carpel only. ..... -8
2a Follicles (nearly) glabrous. ..... $-3$
b Follicles covered with a continuous indumentum of (sometimes glandular) hairs. ..... -4
3a Seed with abundant endosperm. Leaves always trifoliolate. (America)
Pseudoconnarus
b Seed (almost) without endosperm. Leaves pinnate (branches with unifolio- late or trifoliolate leaves may occur). (circumtropical) Rourea
4a Flowers with a distinct androgynophore. (Africa) ..... Manotes
b Flowers without a distinct androgynophore ..... -5
5a Follicles hairy inside. (Africa, Asia) Cnestis
b Follicles glabrous inside. ..... $-6$
6a Sepals in fruit strikingly accrescent. (circumtropical) ..... Rourea
b Sepals in fruit inconspicuous or caducous. ..... $-7$
7a Leaves trifoliolate. (Africa, Asia) ..... Agelaea
b Leaves with more leaflets. (America) Cnestidium
8a Leaves unifoliolate. ..... $-9$
b Leaves with more than one leaflet. ..... $-12$
9a Follicles glabrous. (Africa, Asia) ..... Vismianthus
b Folicles velutinous. ..... $-10$
10a Petals glabrous. Fruits dehiscent. Seeds with abundant endosperm; cotyle- dons thin and flat. (Africa) ..... Burttia
b Petals hairy. Fruits dehiscent or not. Seeds with or without endosperm; cotyledons flat to planoconvex. ..... $-11$
11a Follicles dehiscent. Testa for about $1 / 4$ fleshy. (Africa, Asia) . Ellipanthus
b Follicles indehiscent. Testa almost entirely fleshy. (Africa)
Hemandradenia
12a Understory treelet. Petals and filaments glabrous. Follicles indehiscent. 1-2-seeded. (Africa) Jollydora
b Treelet, shrub or liana. Petals and/or filaments with many (sometimes glan- dular) hairs. Follicles dehiscent, 1 -seeded. (circumtropical) . . . Connarus
Key to the African genera based on flowering material
1a Flowers with five carpels. ..... -2
b Flowers with one carpel only. ..... -8
2a Flowers with a distinct androgynophore. ..... Manotes
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b Flowers without a distinct androgynophore. ..... -3
3a Leaves trifoliolate. Most hairs fascicled and sepals fringed with multicellu-lar hairs, or leaflets at the uppersurface with many mucous cells (look likesmall pits in herbarium specimens).Agelaea
b Plants otherwise or mature leaves not available. ..... $-4$
4a Sepals longer than petals and/or reflexed when flowering. ..... Cnestis
b Sepals shorter than petals and not reflexed when flowering. ..... -5
5a Petals connivent and/or twice or more times as long as sepals. ..... -6
b Petals not connivent and shorter than twice the sepals. ..... $-7$
6a Sepals ca three times as long as wide, never entirely covered with glandularhairs outside; petals twice as long as sepals or longer, never connate. Petiolemore than 1 cm long.Cnestis corniculata
b Plants otherwise. Rourea
7a Inflorescences on older, full-grown branches, sometimes together with young shoots. Cnestis
b Inflorescences on young shoots in the axil of immature or reduced leaves.Rourea cassioides
8a Leaves unifoliolate. ..... -10
b Leaves with more than one leaflet ..... -9
9a Understory treelet. Petals and filaments glabrous. ..... Jollydora
b Small tree, shrub or liana. Petals and/or filaments with many (sometimes glandular) hairs. ..... Connarus
10a Petals glabrous. Petiole about half the length of leaf-lamina or longer ..... $-11$
b Petals hairy. Petiole considerably shorter. ..... $-12$
11a Lower surface of leaflet with many small glandular dots. Vismianthusb Lower surface of leaflet without glandular dots
Burttia
12a Petals with many hairs inside. East Africa \& Madagascar. Ellipanthus
b Petals (almost) glabrous inside. West \& Central Africa Hemandradenia
Key to the African genera based on fruiting material.
la Follicles (nearly) glabrous outside. ..... $-2$
b Follic ..... 5
2a Understory treelet. Follicles indehiscent, never more than one per flower, often with two seeds. Central Africa. Jollydora
b Lianas or shrubs. Follicles dehiscent, one to five per flower, rarely withmore than one seed$-3$
3a Shrub. Leaves unifoliolate, crowded at the top of the shoot. East Africa.
b Lianas or shrubs. Leaves pinnate (branches with unifoliolate leaves mayoccasionally occur), leaves more or less evenly distributed, not confined
to the apex of shoots. Whole tropical Africa. . . . . . . . . . . . . . . -4
4a Seed attached basally in the follicle.
b Seed attached ventrally in the follicle.
5a Seed (almost) without endosperm; cotyledons planoconvex. ..... -6
b Seed with abundant endosperm; cotyledons flat. ..... -10
6a Seed attached basally in the follicle. ..... $-7$
b Seed attached ventrally in the follicle. ..... -8
7a Calyx in fruit inconspicuous or caducous. Leaves always trifoliolate. Folli- cles always velutinous. ..... Agelaea
b Calyx in fruit accrescent and reddish, never inconspicuous. Leaves rarely trifoliolate. Follicles velutinous or not.8a Leaves unifoliolate.-9
b Leaves with more leaflets. ..... Connarus
9a Follicles dehiscent. East Africa \& Madagascar. ..... Ellipanthus
b Follicles indehiscent. West \& Central Africa. ..... Hemandradenia
10a Follicles hairy inside. ..... Cnestis
b Follicles glabrous inside. ..... -11
11a Leaves unifoliolate. Shrub or treelet. ..... $-12$
11b Leaves with more leaflets. Shrub or liana. ..... Manotes
12a Follicles indehiscent. West \& Central Africa. ..... Hemandradenia
12b Follicles dehiscent. East Africa. ..... Burttia

# Revision of the genera in alphabetical order 

Agelaea Sol. ex Planchon

by C. C. H. Jongkind

History of the genus
Agelaea was first published by Planchon in 1850 and based on three species, two in Africa and one in Madagascar. In the present work they are considered to be conspecific and they are placed in Agelaea pentagyna (Lam.) Baill.

The genus Castanola was published by Llanos in 1859 based on C. trinervis from the Philippines. When Llanos described Castanola trinervis he noticed its similarity with Connarus pentagynus Lam. (= Agelaea pentagyna (Lam.) Baill.) from Madagascar. He clearly was ignorant of Agelaea published nine years earlier by Planchon. In the next year two almost identical new genera Hemiandrina Hooker fil. and Troostwykia Miquel were described. These only differ from Castanola in the number of sepals and/or ovaries, and are obviously based on collections with deformed flowers. Castanola, Hemiandrina, and Troostwykia have been separated from or included in Agelaea at various occasions. When the name Agelaea was generaly accepted, many species from the 'Castanola' group were described in the genus Agelaea (see Leenhouts 1958). In 1908 and 1918 Merrill transferred the Castanola/Hemiandrina species names known to him to Agelaea and in 1910 Schellenberg proposed Agelaea subgenus Troostwykia for this group of species.
In his monograph of the Connaraceae (1938) Schellenberg changed his mind and he removed the genus Castanola with twelve species from Agelaea. He even referred Castanola to another tribe, based on the axillary inflorescences of Castanola species. The axillary inflorescences of Agelaea were interpreted by him as terminal ones. Leenhouts (1958) rejected this separation and he moved a strongly reduced 'Castanola' group back into Agelaea again.

The number of published species in Agelaea was growing rapidly when De Wildeman (1900-1911) and later Schellenberg (1923) described many new species, most of them on vegetative characters only. In the present work all those names are reduced into synonyms. In Schellenberg's monograph of the family (1938) Agelaea comprises forty-six African species apart from Castanola with another twelve species for Africa and Asia. From 1938 till now another six Agelaea species have been described.

The present work recognizes a species described by Gilg in 1895, A. poggeana, as the most recent new discovered species.

Delimitation of the genus
Among Connaraceae with five carpellate flowers Agelaea is sharply delimitated by a combination of the following characters: trifoliolate leaves, no androgynophore, follicles glabrous inside and velutinous outside, sepals inconspicuous or caducous in fruit, and seeds without endosperm.

Description of the genus
Agelaea Solander ex Planchon, 1850: 437; Bentham \& Hooker, 1862: 432; Baker, 1868: 453; Baillon, 1870: 18; Gilg, 1890: 65; Schellenberg, 1910: 60,132; 1923: 200; 1938: 65; Troupin, 1952: 97; Hemsley, 1956: 9; Keraudren, 1958: 9; Leenhouts, 1958: 500; Hutchinson, 1964: 167; Mendes, 1966: 616; Mendes, 1969: 3; Liberato, 1980a: 8; 1980b: 9.

Type species: A. villosa Solander ex Planchon (illegitimate name for Cnestis trifolia Lamarck $=$ A. trifolia $($ Lam. $)$ Baill. $=$ A. pentagyna $($ Lam. $)$ Baill. $)$.

Omphalobium section 2 De Candolle, 1825: 86.
Castanola Llanos, 1859: 505; Schellenberg, 1938: 169; Troupin, 1952: 113; Hutchinson, 1964: 167. Type species: C. trinervis Llanos (=Agelaea macrophylla (Zoll.) Leenh.).

Hemiandrina Hooker f., June 1860: 171,tab.28. Type species: H. borneensis Hooker f. ( = Agelaea borneensis (Hook.f.) Merr.).

Troostwykia Miquel, November 1860: 531; Bentham \& Hooker, 1862: 434; Gilg, 1890: 69. Type species: T. singularis Miquel ( $=$ Agelaea borneensis (Hook.f.) Merr.).

Large lianas. Branches cylindric to deeply furrowed, often ending in a tendrilloid tip. Some species frequently with interxylary phloem. Leaves 3 -foliolate; leaflets entire, symmetric or asymmetric; tertiary venation more or less clearly showing a pattern of very small squares and crosses (fig. 58). Inflorescence axillary, paniculate, usually many flowered, frequently several inflorescences grouped in the same axil and often one or more together at the end of a leafy branch, thus resembling a terminal inflorescence, the supporting leaves rudimentary. Flowers pentamerous, heterotristylous or heterodistylous, sweet scented; pedicel always with a distinct joint. Sepals nearly free, imbricate in bud, never accrescent in fruit. Petals as long as or longer than the sepals, free or connivent near the base, white, often with a trace of yellow or red, glabrous. Stamens in two whorls, shortly united at base, filaments glabrous, the five stamens opposite the sepals longer than the five opposite the petals. Carpels five, free. Fruit a follicle, one to five per flower, pyriform or ellipsoid with a constricted base, beaked or not, with many coarse protuberances or not, orange to red, velutinous, dehiscing by a ventral suture. Seed solitary subovoid or ellipsoid; testa partly fleshy and yellow to red (sarcotesta), other part of the testa thin, black and shiny; hilum basal; endosperm absent; cotyledons planoconvex, glabrous; radicle apical.

A genus of six species, four in tropical Africa and two in Asia. In Africa ranging from Guinea Bissau to $S$ Sudan and southwards to Mozambique, Angola and Madagascar.

Note 1: Leenhouts who found no evidence to maintain Castanola as a separate genus is followed.

Note 2: The protuberances on the follicles of some species have nothing to do with fungi as Schellenberg (1923: 205) stated. The presence or absence of this character is clearly genetically determined.

Sectional arrangement
Schellenberg (1910: 67) divided Agelaea in two subgenera. The subgenus Troostwykia has mucous cells in the upper surface of the leaflets and the subgenus Agelaea has fascicled hairs. These subgenera are identical to the sections Troostwykia (Miq.) Jongkind and Agelaea in the present work. The section Troostwykia is also identical to Castanola. A character Schellenberg ignored but that proved to be valuable is the fringed edge of the sepals in species of the section Agelaea. The section Agelaea is represented in the present work by the African species A. pentagyna, A. poggeana, and A. rubiginosa while the section Troostwykia comprises the Asiatic A. borneensis and A. macrophylla, and A. paradoxa from Africa (see also paragraph on the Asiatic species of this genus).

Section Troostwykia (Miq.) Jongkind comb. \& stat. nov.
Basionym: Troostwykia Miq. as a genus.
Type species: T. singularis Miq. ( = Agelaea borneensis (Hook.f.) Merr.). Synonym: Castanola Llanos, Hemiandrina Hook.f.

Key to the sections and the African species
1a Sepals $1.5-2 \mathrm{~mm}$ long, not fringed with multicellular hairs. Leaflets with many mucous cells in the upper surface. Those mucous cells look like small pits in dried material. Hairs not fascicled. Section
b Sepals (2.5-)3-4(-5) mm, fringed with multicell Troostwykia: A. paradoxa leaflets absent. Most hairs fascicled, 3 or 4 together hairs. Mucous cells on
2a Follicles with many coarse protuberances. Hairs. Section Agelaea . . -2 . Hairs on branchlets at most 0.5 on the midrib (caflets glabrous or with some remnants of indumentum on the midrib (on Principe the lower surface with small hairs). The basal pair of main lateral nerves of the terminal leaflet always longer than the others. Central and Eastern W Africa. . . . . . . . . . . . . A. rubiginosa
b Follicles without coarse protuberances but sometimes wrinkled when dry. Branchlets sometimes also with hairs much longer than 0.5 mm . Adult leaflets glabrous to hairy. The basal pair of main lateral nerves of the terminal leaflet either shorter or longer than the others. Africa and Madagascar. . -3


Fig. 58. Agelaea paradoxa var. paradoxa: 1. flowering branchlet, $2 / 3 \times$; 6 . open follicle, $2 / 3 \times$; 7. seed, ventral side, showing the hilum and small part of the sarcotesta, $2 / 3 \times$.

Agelaea paradoxa var. microcarpa: 2-3. flower, $8 \times ; 4$. stamens and pistils of a short-styled flower, $8 \times$; 5 . pistils, $14 \times ; 8$. open follicles, $2 / 3 \times$; 9 . seed, dorsal side, showing sarcotesta, $2 / 3 \times$. (1. A.Louis 514; 2-5. de Koning 2072; 6-7. A.Louis 556; 8-9. Bamps 2146).

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3a Terminal leaflet always with a pinnate venation; the basic pair of main lateral nerves always distinctly smaller than the next. Young leaflets entirely covered by a white and slightly shining arachnoid indumentum; older leaflets glabrous on both sides or with some remnants of arachnoid indumentum on the midrib. Rachis $0.1-1 \mathrm{~cm}$.
A. poggeana
b Terminal leaflet usually with a palmate but sometimes with a pinnate venation; the basal pair of main lateral nerves never distinctly smaller than the others. Young leaflets rarely with an arachnoid indumentum, old leaflets glabrous to hairy. Rachis up to 4 cm .
A. pentagyna

## Agelaea paradoxa Gilg

Fig. 58-60
For literature, synonyms and typification see under the varieties.
Large liana up to 40 m long. Branchlets puberulous to nearly glabrous. Wood usually without interxylary phloem, xylem furrowed. Petiole 4-19 cm long; rachis $0.5-5 \mathrm{~cm}$ long; petiolules $2-7 \mathrm{~mm}$ long; leaflets elliptic to ovate, puberulous to glabrous, on the upper surface with many mucous cells, looking like small pits in dried material, 3-5 pairs of main lateral nerves; apex acuminate; terminal leaflet 4-26 $\times 2-13 \mathrm{~cm}$; lateral leaflets asymmetric, $2.5-24.5 \times 1-11 \mathrm{~cm}$. Inflorescence up to $6(-15) \mathrm{cm}$ long, often more than one in the axil of a sometimes rudimentary leaf, puberulous to glabrous. Flowers heterotristylous. Pedicel above the joint ca 1 mm long. Sepals $1.5-2 \times 0.7-1 \mathrm{~mm}$, velutinous outside. Petals $4-5 \times 1.5 \mathrm{~mm}$, concave, glabrous. Long stamens $1.5-4.5 \mathrm{~mm}$ long, short stamens $0.5-3 \mathrm{~mm}$ long. Pistil $0.5-3.5 \mathrm{~mm}$ long, unequal to the stamens; style sparsely hairy; ovary pubescent. Developed follicles one to five per flower, $20-45 \times 10-28$


Fig. 59. Distribution of Agelaea paradoxa.


Fig. 60. Distribution of Agelaea paradoxa var. paradoxa in combination with distribution of $A$. paradoxa var. microcarpa in the same area. Dots: var. paradoxa. Asterisks: var. microcarpa.
mm , sometimes with many coarse protuberances, velutinous, beaked. Seed 15-30 $\times 7-14 \mathrm{~mm}$; testa for ca $1 / 4$ fleshy and yellow to red. Seedling hypogeal; first pair of leaves opposite and usually scalelike or abortive; first fully developed leaves unifoliolate.

Distribution: From Senegal to E Zaire.
Key to the varieties
1a Follicles smooth or rugulose, ca $20 \times 10 \mathrm{~mm}$. A. paradoxa var. microcarpa lb Follicles with many coarse protuberances, ca $35 \times 20 \mathrm{~mm}$.
A. paradoxa var. paradoxa

## Agelaea paradoxa Gilg var. paradoxa

A. paradoxa Gilg, 1891b: 318; Schellenberg, 1910: 67; 1923: 205 p.p. Type: Cameroun, sin. loc., J.Braun 52 (holo: B $\dagger$; lecto: M; iso: B). Castanola paradoxa (Gilg) Schellenberg ex Hutchinson \& Dalziel, 1928: 516 ı.p.; Schellenberg, 1929: 550 p.p.; 1938: 174 p.p.; Troupin, 1952: 113 p.p.; Heper, 1958: 746 p.p.; Irvine, 1961: 570 p.p.; Mangenot, 1965 p.p.; Adam, 1971: :67 p.p.; Burkill, 1985: 519 p.p; Caballé, 1986: 216,228. Basionym: A. paradoxa Jilg (see above).

Follicles up to $45 \times 28 \mathrm{~mm}$ but usually ca $35 \times 20 \mathrm{~mm}$, with many coarse rotuberances. Seed up to $30 \times 14 \mathrm{~mm}$.

Distribution: E Nigeria, Cameroun, Gabon, SW Congo and SW Zaire.
Ecology: Rain forest and gallery forest, from sealevel up to 760 m alt.
Selection of 42 examined specimens:

Nigeria: Oban (fl.) Talbot 1300 (K, Z).
Cameroun: Lake Tissongo, 16 km ESE Mouanko (fr. Sept.) Asonganyi 700 (P, YA); 11 km from Źribi (fl. Oct.) Bos 5538 (K, P, WAG); 45 km S of Kribi (y.fr. Dec.) Letouzey 15329 (P); Bipindi y.fr.) Zenker 1601 (B, G, GOET, K, L, M, P, WAG, Z).

Gabon: region de l'estuaire (fr. Sept.) Floret et al. 1479 (P); La Nke (fr. Oct.) Floret et al. 1769 P); Belinga (fr. Nov.) N.Hallé 3711 (P); between Mouila and Saint Martin (fr. Sept.) Le Testu 021 (BM, BR, P, WAG); Guidouma (fl. Nov.) Le Testu 5069 (BM, BR, P); Liyanga (fl., fr. Nov.) e Testu 7692 (BR, P); Lastoursville (fl., fr. Nov.) Le Testu 8502 (BR, K, P, WAG); 35 km SW Vdende (fr. Dec.) Louis et al. 1148 (LBV, WAG); Oveng (fr. May) Reitsma 906 (WAG).
Congo: Moussoumou (fr. Aug.) Farron 4477 (P).
Zaire: Gimbi, Fuka valley (fr. Dec.) Toussaint 713 (BR).
tgelaea paradoxa Gilg var. microcarpa Jongkind var.nov.
Type: Ivory Coast, Morokro, 12 km N of N'Douci, Oldeman 985 (holo: WAG; so: B, BR, K, MO, P).
A. fragrans Gilg, 1896: 209. Type: Cameroun, Lolodorf, Staudt 378 (holo: B ; lecto: K; iso: E, G, Z).
A. brevipaniculata Cummins, 1898: 73. Type: Ghana, Kumasi, Cummins 30a holo: K).
Castanola paradoxa (Gilg) Schellenberg ex Hutchinson \& Dalziel, 1928: 516 ग.p.; Schellenberg, 1929: 550 p.p.; 1938: 174 p.p.; Troupin, 1952: 113 p.p.; Hepeer, 1958: 746 p.p.; Irvine, 1961: 570 p.p.; Mangenot, 1965 p.p.; Adam, 1971: 367 p.p.; de Koning, 1983: 281; Burkill, 1985: 519 p.p.

Differt at A. paradoxa var. paradoxa folliculus circ. $20 \times 10 \mathrm{~mm}$, interdum rugulosus (non circ. $45 \times 28 \mathrm{~mm}$, nec plurituberculatus) et semen maximus $14 \times 7 \mathrm{~mm}$ (non maximus $30 \times 14 \mathrm{~mm}$ ).

Follicles ca $20 \times 10 \mathrm{~mm}$, smooth or rugulose, beaked. Seed up to $14 \times 7$ mm .

Distribution: From Senegal to Gabon and E Zaire.
Ecology: Rain forest, gallery forest and semideciduous forest, from sea level up to 800 m alt.

Selection of the more than 200 examined specimens
Guinea: Macenta (fl. May) Jacques-Félix 921 (P).
Sierra Leone: Pujehun (fr. Feb.) N.W.Thomas 8182 (K).
Liberia: Tappita (fl. Aug.) Baldwin 9115 (K); Vahun (y.fr. Nov.) Baldwin 10244 (K); Nimba Mts (fl. July) Leeuwenberg \& Voorhoeve 4635 (B, P, WAG).
Ivory Coast: Tienkula (fr. March) Bernardi 8393 (G, K, M, WAG); Banco F.R. (fr. Dec.) de Koning 5061 (WAG); W of Soubré (fl.b. June) W.de Wilde 294 (P, WAG, Z); Mbaso (fl. July) Oldeman 224 (B, P, WAG); Morokro (fr. Feb.) Oldeman 985 (B, BR, K, MO, P, WAG, type).

Ghana: Bobisi F.R. (fl. June) Andoh 5574 (B, BR, K); Asukese F.R. (fr. March) Enti FE 1288 (BR, K); Asamankese (fl. Aug.) Howes 936 (K); Begoro fall (fr. Jan.) Morton A2676 (K).

Nigeria: Okomu F.R. (fr. Feb.) Brenan 9093 (BR, P); Omo F.R. (fl. Aug.) Okeke \& Binuyo FHI 36900 (K, WAG); 8 mls NE of Ute Enugu (fl.b. Aug.) Onochie FHI 33427 (K).
Cameroun: Banga F.R. (fr. March) Binuyo \& Daramola FHI 35622 (P); logging road AsiaBedoumo (fr. April) Letouzey 3910 (P, WAG); near Nteigne (fr. Jan.) Letouzey 11870 (BR, K, P, WAG).
Central African Republic: 35 km NE of Bayanga, Caroll 113 (WAG); Boukoko (fr. Jan.) Equipe Tisserant 621 (BR, P, WAG); Haut Sangha (fl. Sept.) Tisserant s.n. (P, WAG); Mbomou R. (fl. Sept.) Tisserant 3668 (BM, BR).

Gabon: 23 km Moanda-Franceville (fl., fr. Oct.) Breteler 6769 (WAG); M’Passa (fr. June) Hladik 2346 (P); Mont de Casque, ca 20 km NW of Booue (fl., y.fr. May) Reitsma et al. 3393 (WAG).

Congo: Gamboma (fl. June) Descoings 6933 (P); near Owando (Fort Rousset) (fl.b. July) Descoings 8670 (P); Louhoulou Forest along the road M'Poka-Meya (fr. July) Sita 2927 (P).
Zaire: Penghe (fr. Feb.) Bequaert 2237 (BR); Lubutu-Kirundu (fl. Feb.) Bequaert 6880 (BR); Bambesa (fl. Oct.) Gerard 5058 (BR, WAG); Bombo R. (fr. Dec.) Breyne 3160 (BR); Maduda (fr. Nov.) Breyne 4517 (BR); Kakuluba (fr. Sept.) Callens 4278 (BR); Eala (fl. Feb.) Corbisier 1294 (B, BR); Dundusana (fl. June) De Giorgi 1041 (BR); INEAC Boketa (fr. Feb.) Evrard 196 (BR, M); Bulumbu (y.fr. April) A.Léonard 3756 (BR); between Lubire and Bena-Makinia (fl. May) 1910 Sapin s.n. (BR).

Cult.: Seedlings, de Koning 5743, 5752, and 5977 (WAG).
Note 1: Of the two related species $A$. paradoxa and $A$. borneensis with comparable variable fruit shape only $A$. paradoxa has been divided in two varieties. The differences in fruitshape in the African A. paradoxa are greater than in the Asiatic $A$. borneensis and there are almost no intermediates. In $A$. borneensis intermediates are as common as the extremes.
Note 2: There are some small differences in the texture of the leaflets of the two subspecies. It seems not practicable to describe these differences, but they make it possible to refer part of the flowering collections to the varieties by comparing them with already named fruiting collections.


Fig. 61. Agelaea pentagyna: flowering branchlet (phot. H.C.D. de Wit).

Agelaea pentagyna (Lam.) Baill.
Fig. 20, 61-65
A. pentagyna (Lam.) Baillon, 1882: 345; Drake de Castillo, 1902: 31; Schellenberg, 1910: 63; 1923: 220; 1938: 89; Keraudren, 1958: 13, fig. 3.
Basionym: Connarus pentagynus Lamarck, 1786: 95.
Type: Madagascar, sin. loc., Commerson s.n. (holo: P).
A. trifolia (Lam.) Baillon, 1867: 237; Schellenberg, 1938: 83; Hepper, 1958:

745; Irvine, 1961: 568; Adam, 1971: 865; Berhaut, 1975: 15; Liberato, 1980a:


Fig. 62. Agelaea pentagyna: detail from fig. 61, showing fringed sepals (phot. H.C.D. de Wit).

8; Hall \& Swaine, 1981: 117; de Koning, 1983: 278; Burkill, 1985: 517. Basionym: Cnestis trifolia Lamarck, 1789: 24. Type: Sierra Leone, sin. loc., Smeathmann s.n. (holo: BM).
A. villosa (DC.) Solander ex Planchon, 1850: 438 (nom. ill. superfl.); Baker, 1868: 454; Schellenberg, 1910: 65. Basionym: Omphalobium villosum De Candolle, 1825: 86; G.Don, 1832: 91. Type: the same as for A. trifolia (Lam.) Baill. above.
A. obliqua (P.Beauv.) Baillon, 1867: 238; Baker, 1868: 454; Schellenberg, 1910:

62; 1923: 217; 1938: 90; Hepper, 1958: 745; Aubréville, 1959: 13; Irvine, 1961: 567; Adam, 1971: 863; Berhaut, 1975: 14; Hall \& Swaine, 1981: 115; Ern, 1984: 164; Burkill, 1985: 516. Basionym: Cnestis obliqua Palisot de Beauvois 1804: 97; G.Don, 1832: 91. Type: Nigeria, Oware, Palisot de Beauvois s.n. (holo: G).
A. obliqua (P.Beauv.) Baill. var. usambarensis Gilg, 1895a: 192. Type: Tanzania, Usambara, Nderema, Holst 2234 (holo: B $\dagger$; lecto: K).
A. obliqua (P.Beauv.) Baill. var. cordata (Schellenb.) Exell, 1944: 148; Hepper, 1958: 745; Liberato, 1980b: 8. Basionym: A. cordata Schellenb. (see below).
A. lamarckii Planchon, 1850: 438; Baker, 1868: 453; 1877: 64. Type: the same as for $A$. obliqua (see above).
A. nitida Solander ex Planchon, 1850: 437; Hiern, 1896: 188; Schellenberg, 1923: 217; 1938: 88; Hepper, 1958: 745; Adam, 1971: 863; Hall \& Swaine, 1981: 115; Burkill, 1985: 516. Type: Sierra Leone, sin. loc., Afzelius s.n. (holo: BM).
A.emetica Baillon, 1887: tab.15; 1867: 239; Schellenberg, 1910: 62. Lectotype: Baillon, 1887: tab. 15.
A. thouarsiana Baillon, 1867: 240; Schellenberg, 1938: 70; Keraudren, 1958: 10, fig. 2. Type: Madagascar, sin. loc., Du Petit-Thouars s.n. (holo: P).
A. koneri O. Hoffmann \& Hildebrandt ex O. Hoffmann, 1881: 321. Type: Madagascar, Lokobé, Hildebrandt 2943 (syn: B $\dagger$; lecto: P).
A. heterophylla Gilg, 1895b: 66; Schellenberg, 1910: 62; 1938:75; Hemsley, 1956: 11, fig. 4; Mendes, 1966: 618, 619; Mendes, 1969: 4; Troupin, 1978: 361; Troupin, 1982: 223. Type: Tanzania, Morogoro, Uluguru Mts, Stuhlmann s.n. anno 1894 (holo: $\mathrm{B} \dagger$ ). Neotype: Tanzania, Lushoto, Proctor 3387 (holo: BR; iso: EA).
A. preussii Gilg, 1896: 210; Schellenberg, 1910: 64; 1923: 217; 1938: 86. Type: Cameroun, Victoria-Bimbia, Preuss 1277 (holo: B $\dagger$ ). Neotype: Cameroun, 6 km SW of Masok, Leeuwenberg 5370 (holo: WAG; iso: B, C, LISC, MO, P).
A. punctulata (Hiern) Schellenberg, 1938: 88; Troupin, 1952: 103. Basionym: Connarus (?) punctulatus Hiern, 1896: 189. Type: Angola, Quetta, Welwitsch 6685 (holo: BM). Flowers from Agelaea pentagyna (Lam.) Baill. (Welwitsch 6685a), leaves from a non Connaraceae species (Welwitsch 6685b).
A. dewevrei De Wildeman \& Durand, 1899b: 190; Schellenberg, 1938: 73; Troupin, 1952: 104, fig. 8; Hepper, 1958: 745; Burkill, 1985: 516. Type: Zaire, Lufu R., Dewèvre 435 (holo: BR).
A. demeusei De Wildeman \& Durand, 1900c: 61. Type: Zaire, Bangala, Demeuse 213 (holo: BR).
A. duchnesnei De Wildeman \& Durand, 1900c: 59; Schellenberg, 1910: 61; 1923: 210; 1938: 78; Troupin, 1952: 107. Type: Zaire, Umangi, Duchnesne 26 (holo: BR).
A. hirsuta De Wildeman, 1909: 100, tab. 25; Schellenberg, 1923: 205; 1938: 67; Troupin, 1952: 100; Hepper, 1958: 745; Adam, 1971: 863; Burkill, 1985: 516. Type: Zaire, Lukolela, Pynaert 185 (holo: BR).
A. hirsuta De Wildem. var. likimensis De Wildeman, 1911: 257. Type: Zaire, Likimi, Malchair s.n. anno 1910 (holo: BR).
A. hirsuta De Wildem. var. malchairi De Wildeman, 1911: 257. Type: Zaire, Likimi, Malchair 173 (holo: BR).
A. leopoldvilleana De Wildeman, 1909: 102, tab.12; Schellenberg, 1938: 82; Troupin, 1952: 109.Type: Zaire, Kinshasa (= Leopoldville), M.Laurent 466 (lecto: BR), 460 (para: BR).
A. lescrauwaetii De Wildeman, 1909: 103, tab.12; Schellenberg, 1938: 81; Troupin, 1952: 109; Exell \& Mendonça, 1954: 144. Type: Zaire, Lubi, Lescrauwaet 201 (holo: BR).
A. pynaertii De Wildeman, 1909: 104, fig.12. Type: Zaire, Lukolela, Pynaert 175 (holo: BR).
A. sublanata De Wildeman, 1909: 105. Type: Zaire, Lukolela, Pynaert 175b (holo: BR).
A. tricuspidata Gilg ex Schellenberg, 1910: 64; 1923: 206; 1938: 68. Type: Cameroun, Bipindi, Zenker 3447 (holo: B $\dagger$; lecto: MO; iso: BM, BR, E, G, GOET, M, Z).
A. claessensii De Wildeman, 1911a: 256; Schellenberg, 1938: 70; Troupin, 1952: 102.Type: Zaire, Katako-Kombe, Claessens 408 (holo: BR).
A. glandulosissima Gilg, 1911: 231; Troupin, 1952: 102; Exell \& Mendonça, 1954: 144.Type: Zaire, Beni-Irumu, Mildbraed 2848 (holo: B $\dagger$ ). Neotype: Zaire, sin. loc., van der Gucht s.n. anno 1912 (holo: BR).
A. mildbraedii Gilg, 1911: 230; Schellenberg, 1938: 70; Troupin, 1952: 101; Burkill, 1985: 516. Type: Zaire, Bomili-Panga, Mildbraed 3264 (holo: B $\dagger$ ). Neotype: Zaire, Kinshasa (Leopoldstad), Achten $207 b$ (holo: BR).
A. annobonensis Schellenberg, 1923: 207; 1938: 72. Type: Annobon, Quiveo, Mildbraed 6680 (holo: $\mathbf{B} \dagger$ ). Neotype: Annobon, Ambo, Wrigley \& Melville 232 (holo: K; iso: BM).
A. australis Schellenberg, 1923: 218; Exell \& Mendonça, 1954: 143; Liberato: 1980b: 10. Type: Angola, Golungo Alto, Queta, Welwitsch 4641 (syn: $\mathrm{B} \dagger$; lecto: COI; iso: BM, C, G, K).
A. conraui Schellenberg, 1923: 207; 1938: 73. Type: Cameroun, Bangwe, Conrau 268 (holo: $\mathrm{B} \dagger$ ). Neotype: Gabon, 30 km SE of Doussala, Reitsma 1677 (holo: WAG).
A. cordata Schellenberg, 1923: 222; 1938: 92. Type: Sao Tomé, on the beach, Quintas 76. (syn: B†; lecto: K).
A. elegans Schellenberg, 1923: 213; 1938: 84. Type: Cameroun, Bodje on Mt Cameroun, Lederman 307 (holo: $\mathrm{B}_{\dagger}$ ). Neotype: Cameroun, 6 km S of Kribi, Bos 5240 (holo: WAG; iso: K, P).
A. floccosa Schellenberg, 1923: 210; 1938: 79; Hepper, 1958: 745. Type: Cameroun, Abonando, Rudatis 64 (holo: $\mathrm{B} \dagger$; lecto: Z ; iso: G).
A. grisea Schellenberg, 1923: 208; 1938: 73; Hepper, 1958: 745. Type: Cameroun, Bipindi, Zenker 3022 (holo: B; iso: G, GOET, M, MO, WAG, Z).
A. longecalyculata Schellenberg, 1923: 208; 1938: 77. Type: Cameroun, Songolong near Ribau, Ledermann 2109, on Lake Tibati, Ledermann 2421 (syn: B $\dagger$ ). Neotype: Cameroun, Station de Cacaoyer de N'Koemvone, J.J.de Wilde 8112 (holo: WAG).
A. longifoliolata Schellenberg, 1923: 212. Type: Zaire, Kwa Muera near Fort Beni, Mildbraed 2282, near Irumu in the direction of Ngombe-Nyama, Mild-
braed 2871 (syn: B $\dagger$ ). Neotype: Zaire, Haut Uele, Ikela, Jespersen 6 (holo: BR). A. lucida Schellenberg, 1923: 217; 1938: 87. Type: Gabon, Sibange Farm, near Libreville, Soyaux 27 (holo: B $\dagger$; lecto: Z ; iso: GOET, P).
A. macrocarpa Schellenberg, 1923: 214; 1938: 85. Type: Liberia, Fishtown, Dinklage 1866 (holo: B; iso: WAG).
A. marginata Schellenberg, 1923: 221; 1938: 92; Troupin, 1952: 110. Type: Zaire, Kimuenza, Mildbraed 3551 (syn: B $\dagger$; lecto: BR); Zaire, sin. loc., Gillet s.n. anno 1901 (syn: B $\dagger$; iso: BR).
A. neglecta Schellenberg, 1923: 211; 1938: 81. Type: Cameroun, Mbo's-Sardi, Mildbraed 8544 (holo: $\mathrm{B} \dagger$ ). Neotype: Gabon, sin. loc., Klaine 1934 (holo: B; iso: P ).
A. obovata Schellenberg, 1923: 215; 1938: 86. Type: Cameroun, Mimfia near Bipindi, Zenker 4664 (syn: $\mathrm{B} \dagger$; lecto: MO; iso: BR, G, GOET, L, Z).
A. oligantha Gilg ex Schellenberg, 1923:214; 1910: 63; 1938: 85; Hepper, 1958: 745. Type: Liberia, Gran Bassa, Fishtown, Dinklage 1711 (holo: B).
A. ovalis Schellenberg, 1923: 218; 1938: 87. Type: Annobon, ascending at the Quioveo, Mildbraed 6679, on the upper rim of the Northern Crater, Mildbraed 6606 (syn: $\mathrm{B}_{\dagger}$ ). Neotype: Gabon, Oveng, Louis et al. 416 (holo: WAG; iso: LBV).
A. phaseolifolia Gilg ex Schellenberg, 1923: 220; 1938: 90. Type: Cameroun, Bipindi, Zenker 4202 (lecto: B; iso: BM, E, G, GOET, K, L,M, MO, Z).
A.pseudobliqua Schellenberg, 1923: 216; 1938: 86; Troupin, 1952: 108; Adam, 1971: 865. Type: Cameroun, Kribi, Winkler 790 (syn: B $\dagger$; lecto: Z).
A. setulosa Schellenberg, 1923: 211; 1938: 81; Hemsley, 1956: 12, fig.4. Type: Tanzania, Useguha, Makinjubi am Pangani, Scheffler 247 (holo: B $\dagger$; lecto: K; iso: $\mathrm{BR}, \mathrm{Z}$ ).
A. ugandensis Schellenberg, 1923:219; 1938: 81; Andrews, 1952: 353; Hemsley, 1956: 12, fig.4; Mendes, 1966: 618. Type: Uganda, sin. loc., Scott Eliot 7397 (lecto: K); Uganda, Entebbe, Dawe 271 (para: K).
A. ustulata Schellenberg, 1923: 212; 1938: 82; Adam, 1971: 865. Type: Cameroun, on Njui R. near Jukaduma, Mildbraed 4647 (holo: B $\dagger$ ). Neotype: Congo, Oubangui, Thollon s.n. anno 1889 (holo: P; iso: B, K).
A. zenkeri Schellenberg, 1923: 215; 1938: 86. Type: Cameroun, Bipindi, Zenker 2271 (holo: B; iso: BM, G, GOET, M, MO, WAG, Z).
A. baronii Schellenberg, 1938: 79; Keraudren, 1958: 12, fig.2. Type: Madagascar, sin. loc., Baron 5591 (holo: K).
A. mayottensis Schellenberg, 1938: 74; Keraudren, 1958: 16,fig.3. Type: Mayotte, Boivin s.n. (holo: P).
A. pilosa Schellenberg, 1938: 83; Hepper, 1958: 745; Burkill, 1985: 517. Type: Nigeria, Degema, Talbot 3670 (holo: K; iso: BM).
A. coccinea Exell, 1944: 147; Liberato, 1980b: 10. Type: Principe, SW of Esperanca, Exell 669 (holo: BM).
A. phaeocarpa Exell, 1944:148; Liberato, 1980b:9. Type: Principe, Oquê Pipi, Exell 489 (holo: BM).
A. reticulata Exell, 1944: 150; Liberato, 1980b: 12. Type: Principe, Oquê Pipi, Exell 488 (holo: BM).
A. katangensis Troupin, 1951: 366; 1952: 106. Type: Zaire, Katanga, Karavia, Quarré 3679 (holo: BR).

Omphalobium pentagynum (Lam.) De Candolle, 1825: 86; G.Don, 1832: 91. Type the same as for A. pentagyna (Lam.) Baillon.

Omphalobium nervosum G.Don, 1832: 90. Type: Sierra Leone, sin. loc., Afzelius s.n. (holo: BM).

Connarus pinnatus auct. non Lamarck, De Candolle, 1825: 86 syn. Omphalobium pentagynum, sphalm.

Cnestis obliqua Bojer, 1837: 84 (Ill. name) non P.Beauv. Type: Mauritius, Grand Port, Bojer s.n. herb. Hooker (holo: K).

Large liana up to 25 m . Wood frequently with interxylary phloem. Branches sometimes deeply furrowed; branchlets glabrous to tomentose. Petiole $1-26 \mathrm{~cm}$; rachis $0.1-9 \mathrm{~cm}$; petiolules $1-9 \mathrm{~mm}$; leaflets elliptic to ovate or cordate, glabrous to tomentose, 3-8 pairs of main lateral nerves, the basal ones are as long as or longer than the next ones, they usually originate at the very base of the leaflet, tertiary nerves sometimes in a distinct parallel pattern; apex acuminate; terminal leaflet 2.2-30 $\times 1.5-17 \mathrm{~cm}$; lateral ones $1.8-24 \times 1.4-12,5 \mathrm{~cm}$ usually asymmetric. Inflorescence up to 35 cm , glabrous to tomentose. Flowers heterotristylous. Pedicel ca 1 mm long. Sepals 2.5-5 $\times 1 \mathrm{~mm}$, fringed with multicellular hairs, velutinous outside; petals $3-5.5 \times 1 \mathrm{~mm}$, often connivent near the base, glabrous. Long stamens $2.5-6 \mathrm{~mm}$ long, short stamens $1-4.5 \mathrm{~mm}$ long. Pistil $2-5.5 \mathrm{~mm}$ long, unequal to the stamens; style hairy; ovary velutinous. Developed follicles one to five per flower, $15-25 \times 8-16 \mathrm{~mm}$, pyriform and usually not beaked, never with coarse protuberances. Seed 10-15 $\times 5-10 \mathrm{~mm}$; testa for ca one fourth fleshy and yellow to red.

Distribution: West, Central and East Africa, Fernando Poo, Principe, Sao Tomé, Annobon, Archipel Des Comores, Madagascar and Mauritius.

Ecology: In all kinds of forests, from the seashore to montane forest and from primary rain forest to forest patches in the savanna, from sea level up to 2100 m alt.

Selection of the more than 1000 examined specimens:
Senegal: Oussouye, Adam 18235 (K); Kaeme, Berhaut 6947 (BR); Kaheme (fl. March) Berhaut 7261 (BR).

Guinea Bissau: Cacine (fl., fr. Aug.) Espirito Santo 610 (COI, LISJC); Fulacunda (fl., fr. May) Espirito Santo 2038 (COI, K, LISC); Pobreza (fl., fr. June) Espirito Santo 3211 (COI, LISC, LISJC); Cadabe (fr. Jan.) Raimundo \& Guerra 819 (LISC).

Guinea: Macenta, Adam 4169 (K); Between La Santa and Limbo (fl. March) Chevalier 12585 (P); Kindia (fl.b. March) Chevalier 13110 (P); Friguiagbe-Telinkowie (y.fr. May) Chillon 1964 (P); Nunez R. (fr.) Heudelot 730 (G, K, P); Pongo (fl., fr.) Heudelot 894 (G); M’Zerekore (fl. Sept.) Jacques-Félix 1131 (P); Kakoulima (fr. April) Roberty 17664 (G).

Sierra Leone: Makeni (fl. Dec.) Morton SL281 (WAG); Lungi (fl. April) Morton SL1233 (WAG);
Freetown (fr. July) Morton SL1374 (WAG); Ronietta (fl.b. Nov.) N.W.Thomas 5374 (K, Z); sin. loc. (fr.) N.W.Thomas 6239 (K, Z); Magbile (fl.) N.W.Thomas 6308 (K, Z).


Fig. 63. Agelaea pentagyna: 1. flowering branchlet, $2 / 3 \times ; 2-3$. leaves, $2 / 3 \times ; 4$. sepal, $8 \times ; 5$. fruit, $2 \times$; 6. length section follicle, showing a cotyledon and the apical radicle, $2 \times ; 7$. sepal, $8 \times ; 5$. sarcotesta and hilum, $2 \times$. (1. Hart 448; 2. de Kruif 127; 3. da Silva 2266; 4. van Veldhuizen 762 ;
$5-7$. Bos 3534 ).

Liberia: Ganta (fl., y.fr. Sept.) Baldwin 9213 (K, WAG); Chien (fl., fr. Jan.) Bos 2829 (WAG); Fishtown (fl. Aug.) Dinklage 1711 (B, type A. oligantha); (fr. Oct.) Dinklage 1866 (B, WAG, type A. macrocarpa); N of Bomi Hills (fr. Nov.) Jansen 2287 (WAG); Gola N.F.R. (fl. Aug.) Stoop v.d. Kasteele 207 (WAG); Grand Bassam (seedlings) Toilliez 314 (BR, P); NE of Suacoco Gbarnge (fl. Sept.) Traub 286 (BR, G); Gola N.F.R. (fl. Aug.) Voorhoeve 57 (WAG, Z); Zorzor area (fl., fr. March) Woelfel 32 (WAG).

Ivory Coast: Mt Tonkoui (fl. March) Aké Assi 9934 (BR); between Tate and Tabou (fr. Aug.) Chevalier 19823 (P); Iringou R. (fl. Feb.) Geerling \& Bokdam 2033 (K, MO, WAG); between Port Bouet and Grand Bassam (fl., fr. May) de Koning 615 (WAG); Banco F.R. (fl. March) de Koning 3412 (WAG); (fr. Jan.) de Koning 5112 (WAG); 7 km W Abidjan (fl. Oct.) J.J.de Wilde 3131 (K, WAG); Grand Bassam (fl., fr. Feb.) Leeuwenberg 2664 (K, WAG, Z); 25 km SW Gueyo (fr. March) Leeuwenberg 3761 (B, WAG); Kokodi (fr. Oct.) Roberty 12381 (G, Z).

Ghana: Axim (fl. Nov.) Hall 1803 (K); U.S.T. Kumasi (fl. Nov.) Obeng-Darko 5669 (BR, WAG); Cape Coast Castle (fl. Oct.) Roberty 12827 (G, Z); Abesi (fl. Jan.) de Wit \& Morton 2843 (WAG).

Togo: Apeyeme (fl.b. Dec.) Ern 2718 (B, K); Avetonou (fl. Dec.) Ern 2740 (B, K); Tomegbe near Badou (fr. Dec.) Ern 2816 (B); N of Kpalime (fr. May) Hakki et al. 801 (B); near Lome (fl. Aug.) Mahoux s.n. (L).

Benin: Abomey (fl. Feb.) Chevalier $23139 b$ (BR, K); Banigbe (fr. March) Froment 1171 (BR); Adjohon (fl., fr. Dec.) v.d. Zon 299 (WAG).

Nigeria: Akwaijantar Forest (fl. Feb.) Chapman 5274 (K); Abinsi (fl., fr. April) Dalziel 780 (Z); a few km from dispensary Iba (fr. June) Daramola \& Osanyiniusi FHI 90124 (WAG); near Dogo Kusmi (fr. May) Lawton 1844 (K); Ilashe (fl. April) Leeuwenberg 11344 (WAG); 20 km S of Obubra (fr. April) Pilz 2029 (B, WAG);

Cameroun: Kribi (fr. Dec.) Bos 3534 (K, P, WAG); (fr. April) Bos 4253 (P, WAG); (fl. May) Bos 4478 (K, P, WAG); (fl. Aug.) Bos 5240 (K, P, WAG, type A. elegans); Bertoua (fl., fr. April) Breteler 1280 (K, LISC, WAG); (fr. April) Breteler 2769 (B, K, M, WAG); Masok (fl. April) Leeuwenberg 5370 (B, C, LISC, MO, P, WAG, type A. preussii); 20 km W Yokadouma (fl. July) Leeuwenberg 6180 (K, LISC, WAG); Abonando (fl.) Rudatis 64 (G, K, Z, type A. floccosa); Deng Deng Forest (fr. June) Satabié 763 (P, YA); Bipindi (fl. Feb.) Zenker 237 (B, C, G, WAG); (fl. April) Zenker 544 (BR, C, G, MO, WAG); (fr. May) Zenker 578 (B, C, G, MO, WAG).

Central African Republic: Mpoko R. (fr. Sept.) Breyne 1529 (BR); Camp Koumbala (fl. March) Fay 4347 b (K); Yalinga (fl. Jan.) Le Testu 4490 (BM, BR, P, WAG); (fl.) Le Testu 4508 (BM, BR, P, WAG); Boukoko (fl. Jan.) Equipe Tisserant 1346 (BM, BR); (fr. July) Equipe Tisserant 1519 (BR, P, WAG); (fl.b. April) Equipe Tisserant 2092 (BR, P, WAG); (fr. March) Equipe Tisserant 2401 (BR, WAG); (fr. June) Equipe Tisserant 2540 (BR, P, WAG).

Sudan: Valley of Yei R. near source (fl. Feb.) Dandy 515 (BM); Imatong Mts (fl. Nov.) Friis \& Vollesen 362 (C, K); Gilo (fl. Feb.) Friis \& Vollesen 927 (C, K); Talanga, Friis \& Vollesen 1056 (C, K); Iwatoka (fr. March) Hoyle 811 (BM); Yei R. (fr. Oct.) Sillitoe 376 (K).

Equatorial Guinea: Rongui R. (fl. Sept.) Mann 1820 (K); Annobon (fl., fr. Aug.) Wrigley \& Melville 232 (BM, K, type A. annobonensis); Fernando Po, Moka (fr. Sept.) Wrigley 638 (K).

Sao Tomé \& Principe: Sao Tomé, Monte Mario-Porto Alegre (fl. Jan.) J.J.de Wilde 247 (WAG); Sao Tomé, Mt Cafe (y.fr. Jan.) Espirito Santo 184 (LISJC); Sao Tomé, Pinheira (fr. April) Espirito Santo 4385 (LISJC); Principe, Oque Pipi (fr.) Exell 488 (BM, type A. reticulata); Principe, SW Esperanca (fr.) Exell 669 (BM, type A. coccinea); (fr. Dec.) Exell 672 (BM); Principe, sin. loc. (fl.) Mann s.n. anno 1861 (K); Sao Tomé, Prainha (fl., fr. ) Quintas 1418 (BM, COI, K, LISJC, LISU, Z).

Gabon: W of Belinga (y.fr. July) Bos \& v.d. Laan 10710 (LBV, WAG); between Mouila and Yeno (fl. Sept.) Breteler \& Lemmens 8022 (LBV, WAG); road Libreville-Kango (fr. Oct.) Breteler \& Lemmens 8359 (LBV, WAG); Fernan-Vaz Lake (fl. Sept.) Fleury 26494 in herb. Chevalier (P, WAG); Mts de Cristal, 40 km E SEF (fl. Sept.) Leeuwenberg \& Persoon 13586 (LBV, WAG); Lastoursville (fl. Nov.) Le Testu 7598 (BM, BR, WAG); Bitam (fl. April) Le Testu 9561 (BR, P, WAG); 45 km S of Doussala (fl. Oct.) Reitsma 1742 (WAG).

Congo: Isle facing Pikounda (fr. Aug.) Bouquet 1697 (P); Zemio Rd (fl.b. Dec.) Descoings 12247 (P); Bonga on the Sanga R. (fl. July) Schlechter 12653 (Z); Chaillu (fl. Oct.) Sita 3977 (P).

Zaire: Damaga (fr. July) Bamps 259 (BR, K); Penghe (fl. Jan.) Bequaert 2204 (BR); Bambesa (fr. June) du Bois 308 (BR); ETSAV Reserve (fr. Dec.) Bokdam 4405 (WAG); Basoko (fl. July)


Fig. 64. Distribution of Agelaea pentagyna

Claessens 676 (BR); Bangala (fl. Feb.) De Giorgi 273 (BR); Boende (fr. Aug.) Dubois 902 (BR); Bombura (fr. May) Evrard 873 (BR); Ngondo on the Ngiri R. (fl. March) Evrard 5876 (BR, K); Ikela (fl. June) Germain 7343 (BR); Likimi (fl. March) Goossens 4162 (BR); Nyabibwe (fl. Sept.) Gutzwiller 3272 (BR, WAG); Mumvu Gallery (fl. June) Herman 2164 (BR); Ibali (fl. Nov.) E.\& M.Laurent s.n. (BR); Mwenga, A.Léonard 4959 (BR); Wamaza (fl. Aug.) A.Léonard 5731 (BR); Lubi ( fr. Sept.) Lescrauwaet 201 (BR, type A. lescrauwaetii); Kamukugwi ( fl.b. July) Liben 3337 (BR, WAG); Yangambi (fr. July) Louis 5604 (B, BR); (fl. Sept.) Louis 11103 (B, BR); Kimuenza (fl. Oct.) Mildbraed 3710 (HBG); Lutendele (fr. March) Pauwels 4924 (BR, WAG); Makengo (fl. Feb.) Pogge 728 (K); Lukolela (fl. July) Pynaert 175 (BR, type A. pynaertii); Karavia (fl. Dec.) Quarré 3679 (BR, type A. katangensis); Gimbi (fl. Sept.) Toussaint 490 (BR); Lazaret S.Jules (fl. Sept.) Vanderyst 2207 (BR).

Angola: Melange (fr. Sept.) da Silva 225 (LISC, WAG); Pungo Andongo (fr. Aug.) da Silva 2133 (COI, LISC); Zavula Zalazar (fr. Jan.) da Silva 2266 (LISC); Mt Belo (y.fr.) Gossweiler 5424 (BM, COI, LISJC, LISU); Quetta (fr.) Gossweiler 5571 (BM, COI, LISJC, LISU); N' Dalatando, Gossweiler 5951 (BM, COI, K, LISJC, LISU); Cabinda, Buca Zau (fl.) Gossweiler 6706 (BM, COI, LISJC, LISU); Cabinda, Seva (fl.) Gossweiler 8098 (BM, COI, LISJC, LISU); Ponta de Quiombe (fl. April) Gossweiler 8665 (BM, K); Quela (fl.) I.Nolde 312 (BM); Ikoka (fl. Aug.) Raimundo et al. 843 (LISC, WAG); between Buenga Sul and Buenga Norte (fl. Sept.) Raimundo et al. 914 (LISC); Queta (fl.) Welwitch 4641 (BM, C, COI, G, K, type A.australis).

Rwanda: Nyongwe (fl. Oct.) Troupin 11215 (BR); Uwinka (fl. July) Troupin 12417 (BR).
Burundi: Makamba, Lewalle 1318 (BR); Bubanza (fr.) Lewalle 6507 (BR, WAG); Bubanza (fr. Jan.) Reekmans 1480 (BR); Munini-Kumuyange (fl. Sept.) Reekmans 3621 (BR).

Uganda: Mukono Hill (fl. Nov.) Dummer 1265 (Z); Namauve Forest (fr. April) Eggeling 585 (EA); Lolui I. (fl. May) Jackson u36 (K); Entebbe (fl. March) Liebenberg 748 (K); Bugoma Forest (fl. Feb.) Purseglove 1247 (EA, K); Ishasha Gorge (fl. May) Purseglove 3410 (BR, EA, K); Buambara (fl. Nov.) Purseglove 3523 (EA); Kalinzu (fr. Nov.) Synnott 427 (EA); Kimaka Hill (fl. Aug.) Wood 324 (EA, K).

Kenya: Tana R. N.F.R. (fr. Oct.) Adamson 164 (EA, G); Mt Kenya (fl., fr.) Battiscombe 691 (EA, K); Kuja R. (fl. April) Glasgow 46/33 (EA); Mbololo Hill (fl. Oct.) Joana 9079 (EA); Kitondu Hill (fr. March) Mhauton 1797 (EA).

Tanzania: Amani (fr. March) Braun 693 (EA); (fl., fr. Oct.) Braun 1405 (B, EA); Ukerewe I. (fr.) Conrads 6033 (EA, K); Mlinga Peak (fl.b. March) Drummond \& Hemsley 1436 (B, BR, K); Bukoba (fl. July) Eggeling 6240 (EA, K); Kibsha (fl. July) Harris et al. 5819 (EA); Njala-Usangi (fl. Feb.) Peter 14240 (B); Kiwanda (fr. Feb.) Peter 19344 (B); Lushoto (fl. Dec.) Proctor 3387 (BR, EA, type A. heterophylla); Derema (fl.) Scheffler 144 (BR, EA, K, P, Z); Iringi (fl. Oct.) Schlieben 1347 (B, BM, BR, G, HBG, Z); Kyimbila (fr.) Stolz 1796 (K, Z); Zanzibar (fl. Oct.) Vaughan 1626 (EA, K); (fr.) Vaughan 1994 (EA).

Zambia: near Kawambwa (fr. Oct.) Angus 689 (BR, K); Makutus (fl. Oct.) Fanshawe 11544 (K, SRGH); Samfya (fr. Nov.) Mutimushi 1166 (BR); Kambole escarpment (fl. Sept.) Richards 13226 (SRGH).

Zimbabwe: Chirinda Forest (fr. Jan.) Chase 432 (SRGH); Ngosima Reserve (fr. Jan.) Chase 8229 (BR, SRGH); Vumba Mts., Drummond 5079 (BR, PRE); Gungunyanga F.R. (fl. Aug.) Goldsmith 64/61 (K, M, SRGH); (fl. Nov.) Goldsmith 121/67 (BR, M, SRGH); Kasipiti (fl. Sept.) Loveridge 1160 (B, BR, K); Mt Maruma (fl. Oct.) Swynnerton 640 (K, SRGH, Z).
Malawi: Misuku Forests (fl.b. Sept.) Chapman 251 (BR, K); Misuku Hills (fr. Dec.) Pawek 3232 (K); Mughesse (fr. Jan.) Pawek 7767 (P, SRGH, WAG); (fr. Jan.) Pawek 13505 (BR, K, SRGH, WAG).

Mozambique: Milange, serra do Chierone (fr. April) Correia \& Marques 2443 (WAG); Morrumbala (fr. 30 Dec. 1858) Kirk s.n. (K); Manica e Sofala, base of Mt Tchianganhi (fr. Nov.) Pereira \& Marques 795 (SRGH); Manica e Sofala, Mossurize (fr. Oct.) Torre 6158 (COI, K, LISC, PRE, SRGH); Mozambique, Ribáuè (fr. Jan.) Torre \& Paiva 10219 (COI, K, LISC, SRGH); Manica e Sofala, Bàruè, (fr. Dec.) Torre \& Correia 13603 (COI, LISC, SRGH, WAG); Mozambique, serra Mepálué (fr. Dec.) Torre \& Correia 16368 (LISC).

Comores: Mayotte (fr.) Boivin s.n. (P, type A. mayottensis).
Madagascar: Nossi-Bé (fr. Dec.) Bernardi 11819 (G, P); Moramanga (fr.) Decary 15318 (B, P); Foulpointe (fr.) Decary 17000 (K, P); N of Mananjary (fr. March) Dorr et al. 3900 (MO, WAG); Nossi-Bé (fr. Sept.) Hildebrandt 3194 (BM, G, K, P); (fl. Sept.) Hildebrandt 3198 (G, GOET, K, M, P); Roussettes at Ankazobe, Homolle 158 (P), 183 (P); between Sakamalaza and Anonokambo (fr. Jan.) Homolle \& Cours 2648 (BR); Ivohimbe (fl. Nov.) Humbert 3379 (B); pass at Fitana, Humbert 6034 (P); Antongondriha, Humbert 23961 (P); Sambava (fr. Nov.) Humbert 24441 (G, P); Andlazazaolea(?) Forest (fr. March) Keraudren 1763 (G, P); Soanierana-Antasibé (fl. Dec.) Lam \& Meeuse 5838 (BR, K, L, WAG); beach 26.2 km N of Tampolo (fr. Nov.) Leeuwenberg \& Ralimanana 4406 (MO, WAG); Maroa (fl.b.) Mocquerys 42 (G); (fl.) Mocquerys 76 (G); Matinanana, Perrier 6257 (P), 6318 (P); Fort Dauphin (fl. Oct.) Reserve Nat. 3426 (BR, P); Ambodiriana (fl.) Reserve Nat. 4526 (K, P); Tamatave (fl. Nov.) Schlieben 8011 (B, BR, G, M).
Mauritius: sin. loc. (y.fr.) Bouton s.n. before 1864 (K); sin. loc. (fl., fr.) Carmichael s.n. anno 1813 (K); Bassin Blanc, Lorence \& Edgerly 2701 (K, MO); sin. loc. (fl.) Neraud s.n. (G); sin. loc. (fl.) du Petit-Thouars s.n. (K).

Culta: Wageningen in greenhouse (fl.) van Veldhuizen 762 (WAG, alc.), seeds from de Koning 615 (Ivory Coast).

Note 1: In my view A. pentagyna is a complex of many micro species or forms which seem to be partly genetically isolated. In the field one can find two or


Fig. 65. Agelaea pentagyna. A: area of distribution. The numerals indicate prevalent occurence of corresponding shapes of the top leaflet (fig. 65B). In the shaded area no such prevalence was detected.
B: Shape of the top leaflet
B: Shape of the top leaflet, 1-9 each represent one or more of the former Agelaea species: 1. A. trifolia; 2. A. obliqua \& A. grisea; 3. A. duchnesei; 4. A. hirsuta \& A. dewevrei; 5. A. heterophylla; 6. A. australis; 7. A. ugandensis; 8. A. pentagyna s.s.; 9. A. zenkeri.
more forms together while most of their offspring (often very abundant on the forest floor) looks very similar to the parent. As heterostylous species usually have a strong barrier against self-fertilization, this could lead to the conclusion that consequently this would result in the description of such species based on differences in leaf shape and/or indumentum as Schellenberg did (1923: 200; 1938: 65), flowers and fruits are all similar. The resulting list of species will prove to be nearly endless because each new accession, especially those from Gabon and Cameroun, will represent 'new species' with new combinations of characters often virtually bridging the gap between already described taxa. Therefore, although there are many partly isolated forms, they constitute in my opinion only a single variable species: A. pentagyna. In this way, out of more than forty species recognized by Schellenberg in his revision of 1938, only two more species are retained here: A. rubiginosa and A.poggeana (see notes under these species).
Note 2: See fig. 65 for an impression of the variability of the leaflet shape of this species.

Note 3: The neotypes for $A$. glandulosissima, A. mildbraedii, and A. longifoliolata were designated by Troupin in 1951 in the herbarium of Brussel. They are published here for the first time.


Fig. 65b.

Note 4: In the region of Sierra Leone and Guinea the leaflets of this species have sometimes prominent galls caused by a Cecidomyiidae species. They are ca 1 cm in diameter and have a velutinous indumentum. They are well developed on Adam 27501 (BR), Schnell 7548 (P), and N.W.Thomas 4531 (K).
A. poggeana Gilg, 1895b: 65; Schellenberg, 1923: 209; 1938: 78; Troupin, 1952: 110.

Type: Zaire, Mukenge, Pogge 726 \& 734 (syn: B $\dagger$ ).
Neotype: Zaire, Mbau, Vanderyst 16371 (holo: BR).
A. ferruginosa De Wildeman, 1909: 99. Type: Zaire, Lac Foa, Lescrauwaet 218 (holo: BR).
A. tenuinervis Schellenberg, 1923: 209; 1938: 78. Type: Equatorial Guinea, Makonanam near Nkolentangan, Tessmann 425 (holo: B $\dagger$ ). Neotype: Gabon, W flank of Mt Doudou, Arends et al. 659 (holo: WAG; iso: LBV).
A. villosiflora Schellenberg, 1923: 206; 1938: 68; Troupin, 1952: 100. Type: Zaire, Kimuenza, Mildbraed 3542 (syn: $\boldsymbol{B} \dagger$; lecto: BR).

Large liana up to 20 m . Wood often with interxylary phloem. Branches glabrous, often clearly furrowed; branchlets with a white arachnoid indumentum sometimes mixed with long simple hairs. Petiole $1-20 \mathrm{~cm}$; rachis $0.1-1 \mathrm{~cm}$; petiole and rachis with the same indumentum as the young branches but more persistent; petiolules $1-4 \mathrm{~mm}$; leaflets ovate or oblong-ovate to elliptic with a pinnate nervation; 5-8 pairs of main lateral nerves, the basal pair never the largest; young leaflets with arachnoid indumentum (sometimes mixed with long simple hairs?);


Fig. 66. Agelaea poggeana: young branchlet showing white arachnoid indumentum (Breteler et al. 8780; phot. C.C.H. Jongkind).


Fig. 67. Agelaea poggeana: 1. branchlet with flowers and fruits, $2 / 3 \times$; 2 . flower, $8 \times$; 3. follicles, one showing seed, $2 / 3 \times$; 4. follicle seen from above, showing seed, $2 \times ; 5$. seed, showing sarcotesta (darker part) and hilum surrounded by sarcotesta, $2 \times$. (1. Gilbert 14515; 2. Tisserant 569; 3-5. Arends et al. 659).


Fig. 68. Variation in terminal leaflet in Agelaea: 1,2. Agelaea poggeana; 3-5. Agelaea rubiginosa.
old leaflets glabrous or with some remnants of indumentum on the midrib; apex rounded to acuminate; terminal leaflet $1.8-25 \times 1.2-8.5 \mathrm{~cm}$; lateral leaflets $1.6-17.5 \times 1-7.5 \mathrm{~cm}$, asymmetric. Inflorescence up to 20 cm , often one or more together at the end of a leafy branch and resembling a terminal inflorescence, puberulous to tomentose. Flowers heterotristylous. Sepals ca $4 \times 1 \mathrm{~mm}$, fringed with multicellulair hairs. Petals ca $4.5 \times 1 \mathrm{~mm}$, glabrous. Long stamens 2.5-5.5 mm long, short stamens $1-4 \mathrm{~mm}$ long. Pistil $2-5.5 \mathrm{~mm}$ long, unequal to the stamens; style hairy; ovary velutinous. Developed follicles one to five per flower, $12-18 \times 6-8 \mathrm{~mm}$, pyriform without coarse protuberances. Seed ca $10 \times 5 \mathrm{~mm}$; testa for ca $1 / 4$ fleshy and yellow to red, the thin part black and shiny.

Distribution: Central Africa.
Ecology: Rain forest and gallery forest from sea level up to 850 m alt.
Specimens examined:
Nigeria: Uri? (fl.) 1909 Kitson 109 (BM).
Cameroun: 15 km from Kribi, Bos $5514 b$ (WAG).
Central African Republic: Boukoko (fl. Dec.) Equipe Tisserant 569 (BM, P, WAG); (fl. Dec.) Equipe Tisserant 1962 (BM, P, WAG).

Gabon: W flanc Mt Doudou (fr. Dec.) Arends et al. 659 (LBV, WAG, type A. tenuinervis); ca 24 km N of Koumameyong, Breteler et al. 8565 (LBV, WAG); 35 km NE of St Germain, Breteler et al. 8780 (WAG); 15 km N of Doussala, de Wilde \& Jongkind 9472 (LBV, WAG); 10 km S of Makokou, Florence 1397 (P); Florence 1975 (P); Makokou, Hallé 1190 (P); 40 km SW of Doussala (y.fr. Aug.) Reitsma 1363 (WAG); Lopé Reserve (fr. Nov.) Reitsma 2626(WAG).

Congo: Djoumouna Forest (fl., y.fr. Sept.) Bitsindou 411 (P, WAG); 25 km W Sibiti, Farron 4490 (P); Plateaux Batékés, Farron 5127 (P).

Zaire: Kimbuba (fr. Feb.) Callens 4774 (BR); Bomandja (fl. Feb.) Evrard 3494 (BR, K); Bokone/s/ Tshuapa (fl. Jan.) Evrard 5622 (BR); Ndjili-Brasserie (fl. Aug.) Evrard 6374 (BR); Panza (fl., fr. July) Gilbert 14515 (BR); Kimuenza, Gillet s.n. (BR); Lutendele (fr. Oct.) Jans 94 (BR); Lac Foa (fr. Sept.) Lescrauwaet 218 (BR, type A. ferruginosa); Musoko (fl., y.fr. Aug.) Liben 3517 (BR); Kimuenza (fl. Sept.) Mildbraed 3542 (BR, type of A. villosiflora); Kimbuba (fr. Sept.) Pauwels 403


Fig. 69. Distribution of Agelaea poggeana
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Sapin s.n.(BR); Mbau(fl.) Vanderyst 16371 (BR, type); (fl.) Vanderyst 16386 (BR); Sanga, Vanderyst 25396 (BR).

Angola: Rio Zadi-Beu (fr. Oct.) Raimondo et al. 479 (LISC); Dundo (fl. Aug.) Young 454 (BM, COI).

Note: A. poggeana is the only species kept separate from A. pentagyna on the basis of vegetative characters only, because this is the only one with a combination of leaf and indumentum characters that have no clear intermediates to one or more forms of $A$. pentagyna. Characters such as the shiny arachnoid indumentum and the small first main lateral nerves have not been observed in A. pentagyna.

## Agelaea rubiginosa Gilg

Fig. 68, 70-72
A. rubiginosa Gilg, 1891b: 319; Schellenberg, 1910: 64; 1923: 210; 1938: 79; Troupin, 1952: 111.

Type: Zaire, Monbuttu-land, Kibali, Schweinfurth 3537 (holo: B $\dagger$ ). Neotype: Zaire, Doruma, De Graer 587 (holo: BR).
A. schweinfurthii Gilg, 1891b: 319. Type: Zaire, Niamniam-land, Dingbe, Schweinfurth 3099 (syn: B $\dagger$; lecto: K).
A. laurentii De Wildeman, 1909: 101,tab.12. Type: Zaire, Eala, Pynaert 463 (lecto: BR); M.Laurent 897 (para: BR).
A. macrophysa Gilg ex De Wildeman, 1909: 102; Schellenberg, 1910: 62. Type: Cameroun, Bipindi, Zenker 2543 (holo: BR; iso: B, E, G, GOET, K, L, M, MO, Z).
A. gracilis Schellenberg, 1923:213; 1938: 84. Type: Equatorial Guinea, Bebai, Tessmann 580 (holo: $\mathrm{B} \dagger$; lecto: HBG; iso: K).
A. vanderystii Schellenberg, 1938: 73; Troupin, 1952: 107. Type: Zaire, Kikwit, Vanderyst 10047 (holo: BR).
A. principensis Exell, 1944: 148, fig.7c; Liberato, 1980b: 11. Type: Principe, Oquê Pipi, Exell 491 (holo: BM; iso: BR, COI).
A. kivuensis Troupin, 1951: 367; 1952: 110. Type: Zaire, Walikale-Kalehe, Lebrun 5251 (holo: BR; iso: K).

Large liana up to 20 m long and in diameter up to 9 cm . Wood often with interxylary phloem. Branches glabrous, often clearly furrowed; branchlets puberulous. Petiole $2-15 \mathrm{~cm}$; rachis $0.5-5 \mathrm{~cm}$; petiolules $2-8 \mathrm{~mm}$; leaflets ovate to elliptic with a more or less palmate venation, full-grown leaflets glabrous or nearly so; 3-5 pairs of main lateral nerves, basal pair longer than the others but not always originating at the very base of the leaflet; apex (slightly) acuminate; terminal leaflet $5-23 \times 2.5-11 \mathrm{~cm}$; lateral leaflets $3.5-23 \times 2-11 \mathrm{~cm}$, more or less asymmetric. Inflorescence up to $15(-35) \mathrm{cm}$, often one or more together at the end of a leafy branch and resembling a terminal inflorescence, puberulous. Flowers heterotristylous. Sepals 3-4.5 $\times 1 \mathrm{~mm}$, fringed with multicellular hairs, puberulous outside. Petals 3.5-5 $\times 1 \mathrm{~mm}$, often connivent near base. Long sta-


Fig. 70. Agelaea rubiginosa: branchlet showing leaf from beneath (Breteler et al. 8774, phot. C.C.H. Jongkind).
mens $3-5 \mathrm{~mm}$ long, short stamens 1-2.5 mm long. Pistil $1-4.5 \mathrm{~mm}$ long, unequal to the stamens; style hairy; ovary velutinous. Follicles one to five per flower, $15-20 \times 8-10 \mathrm{~mm}$, with many coarse protuberances, red velutinous. Seed 10-15 $\times 7 \mathrm{~mm}$; testa for ca $1 / 4$ fleshy and yellow to red, the thin part black and shiny.

Distribution: Central Africa and Principe.
Ecology: Rain forest and gallery forest from sea level up to 1000 m alt.


Fig. 71. Agelaea rubiginosa: 1. flowering branchlet, $2 / 3 \times$; 2. flower, $6 \times$; 3. flower partly, showing connivent petals, $6 \times$; 4. stamens and pistils, $6 \times$; 5 . pistils, $8 \times ; 6$. follicles, one showing seed, $2 / 3 \times ; 7$. seed, showing sarcotesta (dark part) and hilum surrounded by the sarcotesta, $2 \times$. (1-5.
A.Louis et al. $499 ; 6-7$. A.Louis et al. 1211 ).

## Specimens examined:

Nigeria: Oban, P.A.Talbot s.n. anno 1911 (BM).
Cameroun: Bitye (fl.b.) Bates 1331 (BM); 8 km SW Bertoua (fr. Aug.) Breteler 1749 (WAG); 12 km NE Akwaya (fr. July) Letouzey 14061 (BR, P, WAG); 250 km NE Yaounde (fl. March) Mildbraed 8785 (K); Bipindi (fl.) Zenker 1779a (G); (fr.) Zenker 2543 (B, BR, E, G, GOET, K, L, M, MO, Z, type A. macrophysa); (fl. May) Zenker 545 (B, BR, C, G, MO, WAG).
Central African Republic: reg. Bambari (fl. April) Tisserant 498 (P); Boukoko (fl. Feb.) Equipe Tisserant 2390 (BR).
Equatorial Guinea: sin.loc. (fl.) Tessmann 580 (HBG, K, type A. gracilis).
Sao Tome \& Principe: Principe, Oquê Pipi (fr. Dec.) Exell 491 (BM, BR, COI, type A.principensis); Principe, SW Esperanca (fr. Dec.) Exell 670 (BM); sin.loc. (fl.) 1861 Mann s.n. (P).
Gabon: Mouila-Yeno (fl. Sept.) Breteler \& Lemmens 8046 (LBV, WAG); ca 24 km N of Koumameyong, Breteler et al. 8571 (WAG); ca 10 km SE of Mitzic, Breteler et al. 8774 (WAG); near Cape Esterias, 20 km NNW of Libreville, de Wilde \& Jongkind 9651 (WAG); sin.loc. (fl.) Duparquet 52 (P); 10 km S of Makokou, Florence $781 b$ (P); Lastoursville (f1.) Le Testu 7549 (BR, P); Oveng (fl. Nov.) Louis et al. 499 (LBV, WAG); reg. Abeilles (fl. Nov.) Louis et al. 686 (LBV, WAG); 23 km SE of Sindara (fr. Dec.) Louis et al. 1211 (LBV, WAG); 30 km SW of Lastoursville (fr. Nov) van der Maesen \& de Bruijn 5813 (WAG).
Zaire: Yangambi (fr. Aug.) Bamps 661 (BR); Yanange (fl. July) Bolangi Bo Yanguma 30 (BR); Yangambi (fl. March) Bolema 478 (BR); Amboko (fl. April) Claessens 442 (BR); Makanza (Nouvelle Anvers) (fl.) De Giorgi 572 (BR); Doruma (fr. June) De Graer 587 (BR, type); Kelembe R. (fr. May) De Graer 869 (BR); Bangala (fl.) Demeuse 419 (BR); Kiyaka-Kwango (fl. July) Devred 2194 (BR); N.P. Albert (fr. July) J.de Wilde 558 (BR); Bas-Uele (fl. April) Dewulf 789 (BR); Lake Kwada (fl. April) Evrard 721 (BR); Popolo (fr. Aug.) Evrard 1602 (BR); Boende (fl. April) Evrard 4020 (BR); Makayoba R. (fr. June) Fredericq 9525 (BR); Tukpwo (fr. Sept.) Gerard 4063 (BR); Bambesa (fl. April) Gerard 4883 (BR, WAG); Kimuenza (fr.) Gillet 1936 (BR); Bomaneh (fl.) Goossens 1665 (BR); Eala (fl. May) M.Laurent 897 (BR); Bantoï/Ruki (fr. June) Lebrun 526 (BR); Bokuma (fl.) Lebrun 1291 (BR); Walikale-Kalehe (fl. April) Lebrun 5251 (BR, K, type A. kivuensis); Yangambi (fr. July) A.Léonard 942 (BR); Nsadi-Kalende (fr. Jan.) Liben 2285 (BR, WAG); Yangambi (fr.) Louis 2720 (BR), (fr.) Louis 4145 (B, BR, K); (fr.) Louis 4357 (BR, K); (fl.) Louis 8796 (BR, K); (fr.) Louis 10551 (BR, K); (fr.) Louis 11292 (BR, K); (fl., fr.) Louis 13168 (BR, K); (fl.) Louis 14380 (BR, K); (fl.) Louis 14616 (BR); (fr.) Louis 15842 (BR, C, K); (fr.) Louis 16953 (BR); Banga-N Shabunda (fl. Sept.) Paquay 18 (BR); Eala (fl. Sept.) Pynaert 463 (BR, type A. laurentii); (fl. Sept.) Pynaert 1679 (BR); Dingbe (fl. Dec.) Schweinfurth 3099 (K, type A. schweinfurthii); Gangala (fr. July) Stam 131 (L); N.P. la Garamba, Troupin 2160 (BR); Kikwit (fl.) Vanderyst 10047 (BR, type A. vanderystii); sin.loc. (fr.) de Witte 9525 (BR).

Angola: Lunda (fr. Dec.) Cavaco 1326 (P, WAG); Maiombe, Bélize (fr.) Gossweiler 7621 (COI, K, LISU).

Note: Differs from A. pentagyna not only in the shape of the follicles (protuberances) but also in the shape and texture of the leaflets. Because these leaf characters are very hard to describe one can hardly identify flowering or sterile material of this species without comparing it with previously identified specimens.

## Agelaea in Asia

As the only African species of the former genus Castanola, A. paradoxa is rather similar to the 4 Asiatic relatives accepted by Leenhouts, it was necessary to make a careful comparison with these species. When studying the material of $A$. paradoxa, the limited number of collections with intermediary fruit characters contributed to the decision to recognize two varieties within this species.


Fig. 72. Distribution of Agelaea rubiginosa

The Asiatic material of the related species shows a similar cline on fruit characters, but here both extremes are recognized as separate species. Recent collections in the herbaria of Kew, Leiden and Paris contain many specimens that cannot be identified by means of the key in Flora Malesiana (Leenhouts, 1958: $500)$ as their fruit characters are too variable to match properly. In my opinion the distinguishing characters have to be sought in the flowers rather than in the fruits. There is a clear difference in the length of style and stamens of $A$. macrophylla and $A$. trinervis at one hand and $A$. borneensis and $A$. insignis at the other. Further distinction between the two species of each pair according to the characters given in Leenhouts key proves impossible. These characters concern the shape of the leaflets and they are not tenable on many recent collections that demonstrate the variability of them. This leads to the conclusion that there are only two different species of Agelaea in Asia.

Some examples of intermediates between formerly recognized Asiatic species are shown in fig. 73.

In Africa the plants with the different fruit shapes have an almost complementary distribution, but in Asia they have a more diffuse geography. On Sumatra, the Malay Peninsula and on Borneo one can find all different fruit shapes together. In other parts of the area one can only find plants with either smooth or rugulose fruits.

Key to the Asian species
1a Twigs, petioles and leaves at least in the young parts densely pubescent. Pistils 2-3.5 mm in pistil-dominant flowers. Long stamens $2-4 \mathrm{~mm}$ in sta-men-dominant flowers. Follicles smooth to tuberculate, protuberances sometimes almost doubling the diameter of the follicle. . . . A. borneensis


Fig. 73. Variation in terminal leaflet in Agelaea: 1-4. Agelaea borneensis, showing intermediates between the former $A$. borneensis s.s. (1) and A. insignis (4); 5-8. Agelaea macrophylla, showing intermediates between the former A. trinervis (5) and A. macrophylla s.s. (8). (1. Loh FRI 13432; 2. Bumée 6756; 3. Diepenhorst s.n. Sumatra; 4. Ploem s.n. Java; 5. Kostermans 5333; 6. Meijer SAN 28867; 7. Fedilis \& Sumbing SAN 88426; 8. Chai S.34668)

Agric. Univ. Wageningen Papers 89-6 (1989)
b Twigs, petioles and leaves puberulous to glabrous. Pistils $1.3-1.7 \mathrm{~mm}$ in pistil-dominant flowers. Long stamens $1-1.5 \mathrm{~mm}$ in stamen-dominant flowers. Follicles smooth to rugulose, sometimes also with some small warts.
A. macrophylla

Agelaea borneensis (Hook. f.) Merr.
Fig. 73
A. borneensis (Hook. f.) Merrill, 1909: 127; Schellenberg, 1910: 65; Leenhouts, 1958: 503.
Basionym: Hemiandrina borneensis Hooker f., 1860: 171.
Type: N Borneo, Labuan I., Lobb s.n. (holo: K).
A. insignis (Schellenb.) Leenhouts, 1958: 504. Basionym: Hemiandrina insignis Schellenberg, 1924: 26. Type: Sarawak, Kuching, Haviland 867 (holo: K).

Castanola insignis (Schellenb.) Schellenberg, 1938: 176. Basionym: Hemiandrina insignis Schellenb. (see above).

For more literature and synonyms see Leenhouts 1958: 503,504.
Large lianas. Petiole up to 11 cm long; rachis up to 3 cm long; leaflets oblongelliptic to ovate, at least the younger ones tomentose, upper surface with many mucous cells looking like small pits in dried material, 4-11 pairs of main lateral nerves; apex acuminate; terminal leaflet 6-33 $\times 3.5-14 \mathrm{~cm}$; lateral leaflet asymmetric to nearly symmetric, $3-32 \times 1.5-13 \mathrm{~cm}$. Inflorescence up to 5 cm long, often more than one in the axil of a sometimes rudimentary leaf, tomentose. Flowers heterodistylous. Sepals 1.3-3 $\times 0.5-1 \mathrm{~mm}, 2.5-4$ times as long as wide, puberulous outside and inside; petals 2.8-6 $\times 0.4-1.2 \mathrm{~mm}$ glabrous. Long stamens $0.7-1.5 \mathrm{~mm}$ or 2-3.5 mm long; short stamens $0.6-1 \mathrm{~mm}$ or $1.5-2.5 \mathrm{~mm}$ long. Long pistils $2-3.5 \mathrm{~mm}$ long; short pistils $0.7-1.7 \mathrm{~mm}$ long; ovary pubescent. Developed follicles one to five per flower, beaked, smooth to tuberculate, protuberances sometimes almost doubling the diameter of the follicle, velutinous indumentum usually mixed with many larger somewhat stinging hairs.

Distribution: (Burma see note,) Thailand (Peninsula), Malaysia (Peninsula, Sarawak, Sabah), Indonesia (Sumatra, Java, Kalimantan), Philippines.

Ecology: In all kinds of forests, from sea level up to $700 \mathrm{~m}(1300 \mathrm{~m}$ ?) alt.
Selection of examined specimens:
Thailand: Sungei Kolok, Nikom Waeng (fr.) Larsen \& Larsen 32925 (AAU, L); Narathiwat, Waeng (fl. Nov.) Sankhachand BKF 47646 (BKF, L).
Malaysia: Peninsula: Johore, Kuala Sedili new road (fr. June) Kadim \& Noor 168 (A, K, L, LAE, SING); 6 mls S of Kg. Aur Pahang (fr. Feb.) T.Suppiah FRI 14772 (L).
Malaysia: Sarawak:Semengoh F.R. Arboretum (fr. Oct.) Banyeng ak Nudong Benang ak Bubong S. 26296 (L, SAR); Sg. Chipidi (fr. Aug.) P.Chai S. 34668 (L, K, KEP, MO, SAN). Malaysia: Sabah: Benawod logging area (fr. July) Fedelis \& Sumbing SAN 88427 (K, L, SAR); logging area mile 26 Luasong (fl. Feb.) Fedelis \& Sumbing SAN 89721 (L, SAN); Sg. Kinabatangan (fl. Sept.) L.Madani San 78702 (AA, K, L, SAR, SING); Ulu Sg. Kebulu (fl. March) Sundaling SAN 93146 (K, KEP, L, SAN, SAR, SING).

Singapore: Nee Soon swampy forest (fl. Feb.) Axelius 382 (L, WAG).
Indonesia: Sumatra: Palembang (fl., fr. May) Dumas 1572 (BO, L); Upper Riauw, Tenajan R. (fl. Aug.) Soepadmo 248 (BO, L).
Indonesia: Java: Banjar (fr. Dec.) Backer s.n. (BO, L); Nusa Kambangan I. (fr.) Valenton 90 (BO, L).
Indonesia: Kalimantan: G. Tepian Lobang (fl. June) Kostermans 5333 (BO, L).
Philippines: Sibuyan I., Mt. Giting-Giting (fr. May) Elmer 12479 (L); Luzon I., Irosin (fl. Aug.) Elmer 16822 (U); Polillo I., Karlagan (fr. March) Fox PNH 9230 (L, PNH); Samar I., Mt Mahagna (fl., fr. May) Sulit PNH 14578 (L, PNH).

Note: Probably also in Burma (Leenhouts, 1958: 505; Schellenberg, 1938: 174), but the involved herbarium collections have not been examined for the present revision.

Agelaea macrophylla (Zoll.) Leenhouts
Fig. 73
A. macrophylla (Zoll.) Leenhouts, 1958: 502.

Basionym: Erythrostigma macrophylla Zollinger, 1857: 174.
Type: Java, Bogor (Buitenzorg) Zollinger 3277 (holo: L).
A. trinervis (Llanos) Merrill, 1918: 164; Leenhouts, 1958: 502. Basionym: Castanola trinervis Llanos, 1859: 503. Type: Philippines, Luzon, Mt. Maquiling, Merrill: Species Blancoanae No. 1059 (lecto: L).

Castanola macrophylla (Zoll.) Schellenberg, 1938: 171. Basionym: Erythrostigma macrophylla Zoll. (see above).
For more literature and synonyms see Leenhouts 1958: 502.
Large lianas. Petiole up to 15 cm long; rachis up to 4.5 cm long; leaflets ovate to elliptic-oblong, puberulous to glabrous, upper surface with many mucous cells looking like small pits in dried material, 4-11 pairs of main lateral nerves; apex acuminate; terminal leaflet 7-34 $\times 2.5-14 \mathrm{~cm}$; lateral leaflets asymmetric to nearly symmetric, $4-30 \times 2-14 \mathrm{~cm}$. Inflorescence up to 5 cm long, often more than one in the axil of a sometimes rudimentary leaf, puberulous. Flowers more or less heterodistylous. Sepals 1.5-2.2 $\times 0.7-1.3 \mathrm{~mm}, 1.5-2$ times as long as wide, puberulous inside and outside; petals $4-6 \times 0.9-1.5 \mathrm{~mm}$, glabrous. Long stamens $1-1.4 \mathrm{~mm}$ long; short stamens $0.8-1.2 \mathrm{~mm}$ long. Long pistils $1.3-1.7 \mathrm{~mm}$ long, short pistils $0.7-1 \mathrm{~mm}$ long; ovary pubescent. Developed follicles one to five per flower, smooth or rugulose sometimes with small warts, beaked or not, velutinous indumentum never mixed with longer hairs.

Distribution: Thailand, S Laos, Cambodia, S Vietnam, Malaysia (Peninsula, Sarawak, Sabah), Indonesia (Sumatra, Java, Bali, Moluccas, Kalimantan), Philippines.

Ecology: In all kinds of forests, from sea level up to 700 m alt.
Selection of examined specimens:
Thailand: Newng Chik, Krabi (fl. March) A.F.G.Kerr 18618 (K, L).

Laos: Bords du Mekong, fl. Harmand 9 (P).
Cambodia: Siêm Réap, Harmand 5 in Herbarium Pierre 6543 (P).
Vietnam: ca 100 km S of Hue, Clemens 4338 (U).
Malaysia: Malay Peninsula: Tg. Penawar (fr. Feb.) P.F.Cockburn FRI 7583 (L); Ulu Telemong F.R. (fr. Sept.) H.S.Loh FRI 13432 (L); Tg. Penawar (fr. Feb.) P.F.Cockburn FRI 7583 (L); Ulu Telemong F.R. (fr. Sept.) H.S.Loh FRI 13432 (L).

Malaysia: Sarawak: Semengoh Arboretum (y.fr. Oct.) Paie S. 37717 (K, L, SAN, SAR, UA).
Malaysia: Sabah: Merutai Besar (fr. July) Gibet 37139 (K, L); Lahad Datu (fr. July) Talip SAN 70952 (K, L).
Singapore: near Bukit Kallang Reservoir (fl. Aug.) Maxwell 81-203 (L, SING).
Indonesia: Sumatra: Gunung Leuser N.R. (fr. July) de Wilde et al. 18690 (L); Lampung (fr. Feb.) Mochtar $84 a(G, L)$.
Indonesia: Java: Musa Barung I. (fr. May) Jacobs 4783 (A, BO, K, L, LAE, PNH, SING); 19 km E of Pameungpeuk (fl. April) Leeuwenberg 13241 (WAG); Dungus Irvul Nat. Reserve (fl. Sept.) van Steenis 11528 (BO, L).

Indonesia: Bali: G. Kelatakan (fr. Aug.) Sarip 155 (BO, L).
Indonesia: Moluccas: Sula Ils, Sula Sanana (fl. July) Bloembergen 4316 (BO, L); Seram, Wai Minawat (fr. Feb.) Kornassi 1035 (BO, L); W Seram, Kairatu, Gemba (fr. June) Kuswata \& Soepatmo (BO, K, L).
Indonesia: Kalimantan: E Kutai (fl. Aug.) Leighton 1089 (BO, DAV, L).
Philippines: Mindanao I., Mt Urdaneta (fr. July) Elmer 13404 (L); Luzon I., Mt Maquiling (fr. June-July) Elmer 17870 (L); Samar I., sin. loc. (fl. April) Ramos 1659 (L); Biliran I., Mt Suiro (fl. April-May) Sulit PNH 21659 (L, PNH); Leyte I., Wenzal 422 (L, MO).

# Burttia Bak. f. \& Exell 

by F.J. Breteler \& J. Brouwer

History of the genus
Burttia with its only species B. prunoides was first described by Baker and Exell (1931) and named in honour of its collector, Mr. B.D. Burtt. The authors discussed the systematic position of the genus within the Connaraceae but were undecided. They looked to place it near Ellipanthus. This genus and also Hemandradenia both share with Burttia the unifoliolate leaves and the unicarpellate flowers, but unlike it have only 5 fertile stamens. In this respect the later described unifoliolate and unicarpellate Vismianthus seems more closely related as its species have ten fertile stamens like Burttia. However, the differences in fruit and seed characters between Burttia and Vismianthus are considerable. Therefore Burttia's taxonomic position remains rather isolated.

Schellenberg (1938: 98) kept Burttia and Vismianthus separate because of the presence of bifurcate hairs and of dark resinous glands in the flowers and leaves of Vismianthus, whose fruit and seed were unknown to Schellenberg. Burttia, however, also has bifurcate hairs, which is demonstrated by Fig. 14 no. 8 in Schellenberg's revision!

Description of the genus
Burttia Baker and Exell, 1931: 249; Schellenberg, 1938: 96; Brenan and Greenway, 1949: 167; Hemsley, 1956: 5; Mendes, 1966: 620.

Type species: B. prunoides Bak.f. \& Exell.
Shrub or small tree. Leaves unifoliolate, long-petioled. Hairs two-armed. Inflorescence racemose. Flowers heterodistylous. Sepals 5, imbricate in bud, persisting in fruit. Petals 5 , free. Stamens 10 , shortly connate at base. Carpel solitary; ovary hairy, ovules anatropous; stigma (sub)capitate, papillose. Fruit a pubescent, 1 -seeded follicle, dehiscent by ventral suture. Sarcotesta raphal, all along one side of seed, partly free, spreading laterally, slightly lobate. Cotyledons long and narrow, embedded in copious endosperm.

Distribution: Tanzania, Zambia, Mozambique.

## Burttia prunoides Bak.f. \& Exell

Fig. 74, 75
B. prunoides Baker and Exell, 1931: 249; Schellenberg, 1938: 97; Brenan and Greenway, 1949: 167; Hemsley, 1956: 5; Mendes, 1966: 620.


Fig. 74. Burttia prunoides: 1. flowering branchlet, $2 / 3 \times ; 2$. fruiting branchlet, $2 / 3 \times$; 3. flower, sepals and petals partly removed, $3 \times$; 4. dehiscing fruit with seed, $2 \times ; 5$. seed with sarcotesta, $2 \times ; 6$. transverse section of seed, $2 \times ; 7$. section of seed lengthwise, sarcotesta removed, $2 \times$. (1. Bullock 1340; 2. Burtt 5148; 3. Newman 59; 4-7. Greenway \& Pohlhill 11440).

Type: Tanzania, Singida District, Itigi-Saranda-Kasikasi area, Burtt 532 (holo: BM; iso: EA).

Shrub or small tree, up to $4(8) \mathrm{m}$, branching subradially. Branches pale grey, smooth to fibrous, with many lenticels; slash very dull orange yellow. Branchlets greyish brown, pubescent when young, hairs ferruginous with unequal arms, becoming glabrous. Leaves crowded at end of shoots, sometimes also spread out along shoots. Petiole $1.5-4.5 \mathrm{~cm}$ long, very slender, channeled, densely ferruginously pubescent when young with unequally two-armed hairs especially at base of leaflet, glabrescent with age, articulate apically; blade herbaceous to thinly coriaceous, ovate-subcircular to elliptic-obovate, sometimes transversely elliptic, from $2.5 \times 2.5 \mathrm{~cm}$ to $10.5 \times 9 \mathrm{~cm}$, apex acuminate to broadly acute, acumen to 0.3 cm , base rounded to retuse; densely ferruginously pubescent-pilose when young, especially beneath, becoming glabrous with age, longer persistent along main and secondary nerves beneath; secondary nerves 6-8 pairs, generally quite prominent both sides. Inflorescence simple, 1-3 flowered raceme; bracts elliptic-oblong to lanceolate, rounded-apiculate, keeled, up to $5 \times 1-2.5 \mathrm{~mm}$, densely pubescent, (partly) caducous; peduncle $1.5-5 \mathrm{~cm}$ long, densely tomentose to pilose, glabrescent; bracteoles filiform, 2-3.5 $\times$ $0.2-0.3 \mathrm{~mm}$, caducous. Flowers (4)5-merous, $9-18 \mathrm{~mm}$ long; pedicel $0.5-2 \mathrm{~mm}$ long, articulate, ferruginously villose-sericeous. Sepals (sub)equal, ellipticoblong to lanceolate, $3.5-7 \times 1.5-3 \mathrm{~mm}$, very shortly connate, apex obtuse to truncate, ferruginously villose-sericeous, especially at the apex and along centre, imbricate. Petals white, sometimes pink (Richards 2259), (sub)equal, spatulate, $6.5-17 \times 3-8 \mathrm{~mm}$, free, apex obtuse, base narrowly cuneate, glabrous. Stamens 10 , the five episepalous ones $4-6 \mathrm{~mm}$ long in long-styled flowers and $6.5-9 \mathrm{~mm}$ long in short-styled ones, the five epipetalous stamens $2.5-5 \mathrm{~mm}$ and $6.5-7.5 \mathrm{~mm}$ long respectively; filaments filiform, somewhat flattened, glabrous (rarely sparsely sericeous), shortly ( $0.3-1 \mathrm{~mm}$ ) connate at base, sometimes so in pairs to 3.5 mm from base; anthers ovoid, $0.5-1 \mathrm{~mm}$ long, dorsiversatile. Pistil 6-8 mm in long-styled flowers, $3-4.5 \mathrm{~mm}$ in short-styled flowers; style filiform, glabrous; stigma (sub)capitate, more or less bilobed, $0.4-0.7 \mathrm{~mm}$ diameter, papillose; ovary sessile $1-2 \mathrm{~mm}$ long, obliquely ovoid-lenticular, densely sericeous, hairs with two unequal arms; ovules 2 , only 1 developing, attached above middle of ventral suture, anatropous. Fruit a flattened follicle with persistent calyx (and stamens), $14 \times 6-18 \times 8 \mathrm{~mm}$, hardly stalked with up to 3 mm long rostrum, densely brown-pilose-pubescent when young, becoming greyer with age, dehiscing along ventral suture. Seed solitary, attached near top of ventral suture, narrowly ovoid, $11 \times 3-18 \times 8 \mathrm{~mm}$, black and shining with large fleshy, verrucose, slightly lobate crimson raphal sarcotesta, covering whole length of seed on one side.

Distribution: Central and western Tanzania, northern Zambia, Mozambique. Ecology: Thickets and woodlands on sandier soils, often among rocks, at altitudes of 800 to 1500 m . Found in association with Cassipourea, Grewia holstii,


Fig. 75. Distribution of Burttia prunoides

Acacia, Baphia, Landolphia, Combretum, Brachystegia, Isoberlinia, Commiphora and Euphorbia.

## Specimens examined:

Tanzania: Mayoni District, Itigi-Saranda-Kasikasi (fl. Dec.) Burtt 532 (BM, type); Kondoa District, Thlawa (fl. Feb.) Burtt 846 (K); Dodoma District, Kondoa Rd (fr. March) Burtt 1800 (BM, BR, EA, G, K); Kondoa District, Sambala (fr. March) Burtt 1978 (BM, EA, K); Shinyanga District, Tinde Hills, Burtt 2383 (BM, EA, K); Dodoma District (fr. March) Burtt 3035 (EA); Manyoni District, between Mkwese \& Kunguya (fl. Dec.) Burtt 3521 (BM, EA, K); Manyoni District, Hika (fl. Dec.) Burtt 3522 (BM, K); sin.loc., Burtt 3818 (K); Manyoni District, Kazikazi, Burtt 4439 (BM); 4440 (BM); (fl. Dec.) Burtt 4939 (BM, BR); (fl. Dec.) Burtt 4961 (BM, BR); Shinyanga (fr. Feb.) Burtt 5148 (BM, BR, EA, K); 5149 (BM, BR, EA, K); Manyoni (fl. Dec.) Burtt 5402 (BM, BR, K); Shinyanga District, Tinde Hills, Burtt 6409 (BM, BR, K, P); Nindo F.R. (fl. Oct.) Carmichael 845 (EA, K); Mayoni District, E. of Itigi Station (fr. April) Greenway \& Polhill 11446 (K); Singida District, Jiwa s.n. (EA); Tabora Region, Lawton 2142 (K); (fr. Nov.) Lawton 2153 (K); Shinyanga, Lindeman 539 (BM, EA, K); Singida (fl. Dec.) Michelmore 832 (EA, K); Gonga, Newman 18 (EA); Tumbakose (fl. Dec.) Newman 59 (BR, EA); Dodoma Mt. (fr. Dec.) Peter 33087 (B);

Uyansi (fr. Jan.) Peter 34193 (B); W of Dodoma, Peter 45686 (B); (fr. Dec.) Peter 45719 (B, K); Sandawe (fr. Feb.) Phillips in Burtt 1480 (BM); Mangoloma (fr. Feb.) Phillips in Burtt 1801 (EA, K); Chenene (fr. Jan.) Polhill \& Paulo 1249 (B, BR, K, P); Kongwa, Regional Plant Pathologist s.n. (EA); Sumbawanga (fr. Dec.) Richards 7398 (K); Kasanga, Richards 10151 (K); Chenene, Ruffo 1152 (K); Chaya (fl. Nov.) Semsei 3435 (K); Singida District (fr. Dec.) Shabani 1213 (K); Kikuye near Dodoma (fr. Jan.) Wigg 200 (EA).
Zambia: Kasanga (fr. Dec.) Bredo 6407 (BR); Bulaya-Mwewe District (fl. Oct.) Bullock 1340 (BR, K, SRGH); Abercorn, Burtt 5996 (BM, BR, K, P); Lake Tanganyika between Kalambo R. and Mpulungu, Burtt 5997 (BM, BR, EA, K); Great Kalambo, Burtt 5998 (BM, BR, K); Museshia, Fanshawe 4870 (K, WAG); (fl. Oct.) Fanshawe 4880 (K); near Mpulungu (fl.) Richards 2259 (BR, K, SRGH); Mwenda, Richards 9585 (K); Abercorn District (fl. Nov.) White 3693 (BM, BR, K).
Mozambique: Nampula, Monapo (fr. Feb.) de Koning c.s 9603 (WAG); Nampula, Mossuril (fr. Feb.) de Koning c.s. 9746 (WAG).

Notes: The young leaves are salmon pink to crimson and copper beach or silvery and brown veined or pale green and covered with soft, short white hairs, the mature leaves are dark green above, paler below, brilliant in autumn. Flowers and leaves appear with the first rains (Oct-Dec.), the fruits are mature about March.

The 'aril' is sweet and edible, the seeds are used for poisoning animals (Burtt 1978). The wood is reported to be of little value (Brenan \& Greenway, 1949: 167; Burtt 4439).

For observations on the pollen grains see under Vismianthus.
In literature (e.g. Hemsley, 1956: 5) heterostyly is mentioned for B. prunoides. The herbarium material examined showed all to be heterodistylous, having longas well as short-styled flowers. A statement by Mendes (1966: 620) to the effect that the six known gatherings of flowers of B. prunoides in the area of the Flora Zambesiaca concerned either 'short-staminate' flowers or flowers with an 'intermediate stamen-style relationship', is to be doubted. Examination of the three gatherings mentioned explicitly by Mendes showed one to be long-styled and one to be short-styled, while Bullock $1340(\mathrm{BR})$ is long-styled and Bullock 1340 $(\mathrm{K})$ is short-styled. The measurements reported by Mendes (1966) himself (longstaminate i.e. short-styled: stamens up to 10 and 7 mm , pistil up to 5 mm ; shortstaminate i.e. long-styled: stamens up to 7 and 5 mm , pistil up to 9 mm ) also lead to the conclusion that only short- and long-styled specimens are in play. The absolute length of the pistils of short-styled flowers as reported by Mendes, 5 mm , is however intermediate between the absolute lengths of the styles of the long- and short-stamened (short- and long-styled) flowers mentioned by Hemsley (1956) (up to 3 and up to 6 mm respectively; ovary up to 2 mm long); this may explain the confusion.

According to Baker and Exell (1931: 249), followed by Schellenberg (1938: 96), Hemsley (1956:7) and Mendes (1966: 620), there are in B. prunoides sometimes either one or three ovules. This could not be confirmed after the examination of all the herbarium material available for this study.
The ovules in B. prunoides are not erect, as mentioned by Schellenberg (1938: 96) nor are they hemitropous, as might be deduced from the illustrations in Hemsley (1956: 6; also in Mendes 1966: 621).

# Cnestis Juss. 

by R.H.M.J. Lemmens

History and subdivision of the genus
De Jussieu published Cnestis in 1789, based on Commerson-collections from Madagascar, without citing any species. A few months later Lamarck described 4 species, 2 from Madagascar, and 2 from W Africa, one of which belongs to Agelaea. De Candolle (1825) proposed another 7 species, four in Cnestis, two now placed in Rourea, and one in Agelaea. By the end of the 19th century the number of African species had strongly increased particulary due to new species proposed by Gilg. Some 20 years later this was repeated by Schellenberg. In 1938 Schellenberg cites 37 species in his monograph, including 2 Asiatic ones. In 1951 Troupin published another 5 species from Zaire.
Schellenberg (1910) divided the genus Cnestis initially into two subgenera: Eucnestis (= subgenus Cnestis) and Ceratocnestis, based on differences in shape and indumentum of the follicle and in petal length. In Eucnestis the follicle is obtuse at the apex and provided with short hairs, in Ceratocnestis it is beaked and provided with short and long, rigid hairs. The petals in Eucnestis are at most as long as the sepals, in Ceratocnestis they are generally longer, and if they are equal, the sepals are petaloid.
In 1938 Schellenberg reduced his subgenera to sections and divided each section into two subsections: Eucnestis in Brevipetalae and Aequipetalae, and Ceratocnestis in Longipetalae and Macrosepalae. His illegitimate lectotype species C. corniculata Lam. was placed in Ceratocnestis and this is not correct as the type-section of a genus, i.e. Eucnestis ( $=$ section Cnestis), should at least contain the type-species. As Schellenberg did not typify his infrageneric taxa, a formal lectotypification is presented here
C. urens Gilg lectotypifies subgenus and section Ceratocnestis as well as subsection Longipetalae, that should consequently be named subsection Ceratocnestis. C. congolana De Wild. is the lectotype of the other subsection Macrosepalae. Subgenus and section Eucnestis as well as the subsection Aequipetalae are typified by the legitimate lectotype species C.polyphylla Lam., while all these infrageneric taxa should be called Cnestis. The last subsection Brevipetalae has C.ferruginea as lectotype.
In my opinion this subdivision cannot be supported as more varied combinations of the characters occur than Schellenberg allows in his sections. Some species have follicles with short indumentum combined with a distinct beak ( $C$. mildbraedii, $C$. mannii), while $C$. bomiensis has follicles with short indumentum and flowers with petals longer than the sepals. Finally C. yangambiensis produces a follicle with a rigid indumentum but lacking a rostrum.
As it does not seem possible to distinguish well delimitated natural groups
of species within Cnestis, I refrain from proposing any infrageneric classification above the species level (see also paragraph 10.2 on phylogeny of the genus Cnestis).

Description of the genus
Cnestis A.L. de Jussieu, Aug. 1789: 374; Lamarck, Oct. 1789: 23; Gmelin, 1791: 729; De Candolle, 1825: 86; Don, 1832: 91; Blanco, 1837: 385; Planchon, 1850: 440; Sonder, 1860: 527; Hooker f., 1862: 433; Baker, 1868: 460; Hooker f., 1876: 54; Baker, 1877: 64; Gilg, 1891a: 67; Lecomte, 1908: 43; Schellenberg, 1910: 10, 92; 1915: 318; 1938: 28; Troupin, 1952: 114; Hemsley, 1956: 2; Hepper, 1958: 742; Leenhouts, 1958b: 497; Keraudren, 1958: 16; Vidal, 1962: 12; Mendes, 1966: 615; 1969: 2; Liberato, 1980a: 6; 1980b: 6.

Type species: C. polyphylla Lam. See note.
Spondioides Smeathman, nomen in sched.; Lamarck, 1789: 23 (in syn.).
Thysanus de Loureiro, 1790: 284; De Candolle, 1825: 91. Type species: T. palala Lour. ( = Cnestis palala (Lour.) Merr.).

Lianas, shrubs (usually climbing) or rarely small trees. Branches cylindric, sometimes ending in a tendrilloid tip. Leaves imparipinnate; leaflets opposite or not, entire, often asymmetric and often also acuminate. Inflorescences axillary, usually more than one together in the axil of a single leaf, sometimes pseudoterminal (then in axils of rudimentary leaves). Flowers in panicles, racemes or fascicles on the main stem, pentamerous, heterostylous, often heterodistylous, rarely more or less homostylous (C. ferruginea). Pedicels with a distinct joint, but not so in species with flowers in fascicles. Sepals more or less free, imbricate (mostly narrowly) or valvate in bud. Petals shorter, as long as or longer than sepals, free, white, yellowish or red tinged, imbricate in bud, glabrous or with some hairs outside near the base. Stamens 10 (two times 5), epipetalous ones mostly shorter than episepalous ones; filaments shortly united at base or free, glabrous. Carpels 5, free; styles often pilose at base. Follicles 1-5 in fruit, reddish, opening lengthwise along the ventral suture, densely tomentose, sometimes also with long rigid hairs outside, velutinous, sometimes with rigid hairs inside, beaked or not. Seeds solitary, attached to the base of the follicle, ovoid, with a yellow to red sarcotesta at base, surrounding the hilum; testa usually black and shiny; endosperm present, abundant; radicle apical; cotyledons thin, nervate.

A genus of 13 species restricted to tropical Africa, but one species in tropical Asia, usually found in rain forest, sometimes in savanna.

Note: Schellenberg (1938) has chosen C. corniculata Lam. as the type species of the genus. This choice is not legitimate. In the protologue of the genus de Jussieu cited exclusively material from Madagascar and Reunion (Commerson), that belongs in $C$. polyphylla Lam. Consequently the type species of the genus is C. polyphylla Lam.

Three keys are presented here. Specimens are best identified when complete material, i.e. with flowers and fruits, is available. Material with either flowers or fruits is sometimes difficult to identify.

## A. Key to specimens with flowers and fruits

1a Follicle outside with very short, spinelike hairs and long, easily caducous,
stinging hairs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
b Follicle outside with rather short, not stinging hairs . . . . . . . . . . 6
2a Flowers clustered in fascicles on nodose thickenings on the branches . 3
b Flowers in panicles or racemes on the stems and branches . . . . . . . 4
3a Leaves 6-10-jugate; terminal leaflet 4.5-7.5 $\times 2-3.5 \mathrm{~cm}$; leaflets glabrous above, except the midrib; follicle hook-shaped, with broad beak C. uncata
b Leaves 12-21-jugate; terminal leaflet 2-3 $\times 0.5-1 \mathrm{~cm}$; leaflets scattered pilose above; follicle not hook-shaped, with slender beak . . . . C. urens
4a Petiolules 8-11 mm long, blackish . . . . . . . . . . . . . C. macrophylla
b Petiolules up to 5 mm long, usually not blackish
5a Follicle with distinct $5-30 \mathrm{~mm}$ long beak . . . . . . . . . . C. corniculata
b Follicle without a beak, apex obtuse or somewhat acute C. yangambiensis
6a Inflorescences all or at least partly on older branches (ramiflorous), a few to many in the same axil of (fallen) leaves; petals (ob)ovate or elliptic to narrowly oblong, (much) shorter to somewhat longer than sepals; anthers without an appendix. Species from Asia . . . . . . . . . . . . . C. palala
b Above characters not associated. Species from Africa . . . . . . . . . 7
7a Petals circular, elliptic or (ob)ovate, at most half as long as the sepals . 8
b Petals (ob)ovate to narrowly oblong, (much) more than half as long as the sepals
8a Petals circular to very broadly obovate; anthers with an appendix at base; follicle rounded or truncate at base
C. ferruginea
b Petals obovate or elliptic; anthers without an appendix at base; follicle cuneate or rounded at base
9a Leaves 2-5-jugate
C. mannii
b Leaves 10-17-jugate
C. macrantha
b Follicle $3-6.5 \mathrm{~cm}$ long, beak longer than 4 mm (very rarely shorter), slender and distinct or broad and less sharply distinct
11a Leaves 1-2-, rarely 3-jugate; lateral leaflets circular to ovate, with 2-5 nerves
b Leaves 4-14-jugate; lateral leaflets (narrowly) ovate, elliptic or oblong, with 6-12 nerves on each side of the midrib. E African species . . C. polyphylla 12a Sepals reflexed; petals distinctly longer than sepals; follicle with an indistinct, broad beak. Species of Liberia
C. bomiensis

> b Sepals not reflexed; petals about as long as sepals. Follicle with a distinct, slender beak. Species from the eastern part of central Africa $\quad$ C. mildbraedii
B. Key to flowering specimens

1a Flowers clustered in fascicles on nodose thickenings on the branches . 2
b Flowers in panicles or racemes on the stems, branches or pseudoterminal 3

2a Leaves 6-10-jugate; terminal leaflet 4.5-7.5 $\times 2-3.5 \mathrm{~cm}$; leaflets densely pilose with curled hairs beneath, glabrous above except for the midrib
C. uncata
b Leaves 12-21-jugate; terminal leaflet 2-3 $\times 0.5-1 \mathrm{~cm}$; leaflets densely pilose with erect hairs beneath, scattered pilose above . . . . . . . . . C. urens
3a Petiolules 8-11 mm long, blackish
C. macrophylla
b Petiolules up to 5(-6) mm long, usually not blackish . . . . . . . . . . 4
4a Petals circular, elliptic or (ob)ovate, at most half as long as the sepals . 5
b Petals (ob)ovate to narrowly oblong, (much) more than half as long as the sepals8

5a Petals circular to very broadly obovate, anthers with an appendix at the base
C. ferruginea
b Petals obovate or elliptic, anthers without an appendix 6

6a Inflorescences all or at least partly on older branches (ramiflorous), a few to many in the same axil of (fallen) leaves; species from Asia . . C. palala
b Inflorescences only on the apical part of young branches, single in the axils of young or reduced leaves; species from central Africa

7
7a Leaves 2-5-jugate; inflorescence a large panicle, up to 40 cm long
b Leaves 10-17-jugate; inflorescence a raceme or panicle, up to 25 cm long
C. macrantha

8a Sepals not reflexed . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
b Sepals reflexed
11
9a Sepals pubescent inside, pilose outside, usually with many glandular hairs; species from Asia
C. palala
b Sepals glabrous inside, rarely minutely pubescent, but then outside lacking glandular hairs; species from Africa
10a Liana or lianescent shrub; bracts 1-2 mm long; pedicel short, articulation $0-2 \mathrm{~mm}$ below the calyx; petals obtuse or indistinctly retuse at top C. corniculata
b Shrub; bracts $2.5-3 \mathrm{~mm}$ long; pedicel longer, articulation $2-3 \mathrm{~mm}$ below the calyx; petals distinctly retuse at top; species from the eastern part of central Africa
C. mildbraedii

11a Leaves 1-2-, rarely 3-jugate; lateral leaflets circular to ovate, with $2-5$ nerves on each side of the midrib
C. racemosa
b Leaves 3-20, rarely 2-jugate; lateral leaflets ovate to narrowly oblong, with 5-15 nerves on each side of the midrib12
12a Petals obovate, somewhat shorter than sepals, often with some hairs out- side at base; species of Madagascar, SE Africa and S Kenya C. polyphylla
b Petals narrowly obovate to narrowly oblong, at least as long as, but mostlylonger than sepals; petals glabrous13
13a Leaflets (thinly) coriaceous, tertiary nerves prominent above; Liberian spe- cies C. bomiensis
b Leaflets papery, tertiary nerves usually not prominent above ..... 14
14a Leaves (2-)3-13-, rarely more jugate C. corniculata* b Leaves 13-20-jugate; species only collected near Yangambi (Zaire)C. yangambiensis*
*Flowering specimens of C. corniculata and C. yangambiensis collected near Yangambi cannot be separated with complete certainty.
C. Key to fruiting specimens
1a Follicle outside with very short, spinelike hairs and long, easily caducous, stinging hairs ..... 2
b Follicle outside with rather short, not stinging hairs ..... 6
2a Follicles in fascicles; fruit-stalk attached to nodose thickenings on the branches ..... 3
b Follicles in racemes, rarely in panicles ..... 4
3a Follicle hook-shaped, beak broad, $10-13 \mathrm{~mm}$ long, strongly curved towards the ventral side of the follicle; leaves 6-10- jugate, terminal leaflet 4.5-7.5$\times 2-3.5 \mathrm{~cm}$, leaflets densely pilose beneath with curled hairs, glabrousabove, except the midrib
C. uncata b Follicle not hook-shaped, beak slender, (8-) $12-30 \mathrm{~mm}$ long, curved or invo-lute at apex only; leaves 12-21-jugate, terminal leaflet $2-3 \times 0.5-1 \mathrm{~cm}$, leaf-lets densely pilose with erect hairs beneath, scattered pilose above C. urens
4a Petiolules $8-11 \mathrm{~mm}$ long, blackish ..... C. macrophylla
b Petiolules up to 5 mm long, usually not blackish ..... 5
5a Follicl jugate
b Follicle without a beak, apex obtuse or somewhat acute; leaves 13-20-jugate
6a Specimens from SE Asia C. yangambiensis ..... C. palalab Specimens from Africa
7a Follic ..... 7
8
8
b Follicle (2-)3-6.5 cm long, beak longer than 4 mm (very rarely shorter, butdistinct
8a Leaves 2-3-jugate, lateral
on each side of the midrib ..... 9
C. racemosa
b Leaves 4-21-jugate, latera with (5-)6-15
lateral nerves on each side of the midrib C. polyphylla
9a Leaves 6-10-jugate, leaflets coriaceous, 2-8 $\times 1-2.5 \mathrm{~cm}$, with distinct terti- ary nerves above; follicle $3-3.5 \times 1.5 \mathrm{~cm}$, cuneate to somewhat rounded at base, with an indistinct beak; species of Liberia C. bomiensis
b Above characters not associated ..... 10
10a Follicle truncate or rounded at base, with a broad, blunt, indistinct beak11
b Follicle cuneate at base, usually with a rather slender, distinct beak ..... 12
11a Leaflets pilose above with scattered, whitish hairs; sepals $5-6.5 \mathrm{~mm}$ long; bracts 3-5 mm long C. macrantha
b Leaflets usually glabrous above, except midrib, rarely all over pilose; sepals $2-4 \mathrm{~mm}$ long; bracts $1-2 \mathrm{~mm}$ long C. ferruginea
12a Leaves 2-5-jugate, lateral leaflets ovate to elliptic, glabrous above, but mid-rib often piloseC. mannii
b Leaves 6-21-jugate, lateral leaflets ovate to narrowly oblong, often pilose
C. mildbraediiabove (especially when young)

## Cnestis bomiensis Lemmens sp. nov.

Fig. 76, 77
Frutex scandens vel liana ramulis juventute pubescentibus demum glabrescentibus. Folia imparipinnata, 6-10-juga. Foliola coriacea, lateralia inferiora elliptica, superiora anguste oblonga, $2-8 \times 1-2.5 \mathrm{~cm}$, basis rotundata vel subcordata; foliolum terminale obovatum vel ellipticum, $3-8 \times 1.5-3 \mathrm{~cm}$, basi cuneatum vel rotundatum; foliola supra nitida, glabra (sed costa pilosa), subtus dense pilosa. Inflorescentia racemosa, $1.5-2.5 \mathrm{~cm}$ longa. Pedicelli articulati. Sepala reflexa, triangulata vel oblonga, 2-2.5 $\times 0.8-1 \mathrm{~mm}$, extra pilosa, intra glabra. Petala anguste obovata, $3.5-4.5 \times 0.6-0.8 \mathrm{~mm}$, glabra. Stamina subaequalia. Folliculus $3-3.5 \times 1.5 \mathrm{~cm}$, rostro lato indistincto, extus pubescens, intus hispidus.
Type: Liberia, 9 km E of Yoma, 20 km NE of Bomi Hills, Leeuwenberg 4885 (holo: WAG).

Liana. Branches cylindric, branchlets densely brown-pilose, later glabrescent. Leaves 6-10-jugate; petiole $2.5-5.5 \mathrm{~cm}$, rachis $4-19 \mathrm{~cm}$ long, brown-pilose. Leaflets leathery, lateral ones opposite or nearly so, elliptic to narrowly oblong, 2-8 $\times 1-2.5 \mathrm{~cm}$, rounded to subcordate and not or hardly unequal at base, terminal one obovate or elliptic, $3-8 \times 1.5-3 \mathrm{~cm}$, rounded or cuneate at base; all leaflets acute, obtuse or retuse, glabrous (except the midrib) above, densely brownpilose beneath, midrib impressed above, prominent beneath, with $8-15$ lateral nerves on each side, tertiary nerves reticulate, distinct on both sides; petiolules very short, up to 1 mm long, densely pilose. Racemes $1-3$ per leaf-axil on young branches, $1.5-2.5 \mathrm{~cm}$ long, sometimes the supporting leaves reduced resulting in a compound pseudoterminal inflorescence, 5-10-flowered, densely brownpilose. Bracts ovate to (narrowly) triangular, 1-2 mm long. Pedicels indistinctly articulated $0-1 \mathrm{~mm}$ below the calyx, brown-pilose. Sepals reflexed, valvate to


Fig. 76. Cnestis bomiensis: 1. flowering branch, $2 / 3 \times$; 2. leaflet beneath, $2 / 3 \times$; 3. flower, $6 \times$; 4. petal, $10 \times$; 5. sepal, $10 \times$; 6. follicle, $1 \times(1,3-5$. Leeuwenberg 4885; 2,6. Jansen 2288).
narrowly imbricate in bud, triangular to oblong, $2.0-2.5 \times 0.8-1.0 \mathrm{~mm}$, acute at top, densely brown-pilose also with glandular hairs outside, glabrous inside. Petals valvate or narrowly imbricate in bud, narrowly obovate, 3.5-4.5 $\times 0.6-0.8$ mm , cuneate at base, obtuse to retuse at top, glabrous. Stamens free, subequal, $3-4 \mathrm{~mm}$ long, anthers $0.3 \times 0.2 \mathrm{~mm}$. Pistils $1.1-1.4 \mathrm{~mm}$ long; ovaries ca 0.5 mm long, brown-pilose; styles straight, pilose at base; stigmata oblique, indistinctly 2-lobed. Follicles oblique-ellipsoid, $3-3.5 \times 1.5 \mathrm{~cm}$, cuneate at base; beak broad and indistinct, $2-5 \mathrm{~mm}$ long; pericarp velvety outside, with long, stiff, deciduous, yellowish brown hairs inside. Seeds (ob)ovoid, 15-20 $\times 7-11 \mathrm{~mm}$, sarcotesta 6 mm long.

Distribution: Liberia.
Ecology: Secondary rain forest. Flowering around August, fruiting a few
onths later.


Fig. 77. Distribution of Cnestis bomiensis

Specimens examined:
Liberia: Ganta (fr. Nov.) Adam 30209 (K); 5 miles N of Bomi Hills (fr. Nov.) Jansen 2288 (WAG); 9 km E of Yoma, 20 km NE of Bomi Hills (fl. Aug.) Leeuwenberg 4885 (WAG, type).

Notes: 1 . This species is very well characterized by the combination of relatively long petals and follicles lacking stinging hairs. Three other species are found in Liberia: C. racemosa, C. corniculata, and C. ferruginea. From C. racemosa it can be easily distinguished by its more numerous, narrower leaflets, from both the other species by its leaves being of a more leathery nature and showing distinct tertiary nerves. It differs from C. ferruginea by the distinctly longer petals and follicles with an obvious cuneate base, and from C. corniculata by the absence of stinging hairs.
2. It is not known whether heterostylous flowers occur in this species, as in the specimens examined only a single type of flowers is found.

## Cnestis corniculata Lam.

Fig. 78-82
C. corniculata Lamarck, 1789: 23; De Candolle, 1825: 87; G. Don, 1832: 91; Hooker, 1849: 290; Planchon, 1850: 440; Walpers, 1852: 306; Baillon, 1867: 241; Baker, 1868: 461; De Lanessan, 1886: 794; Hiern, 1896: 190; Schellenberg, 1910: 15; 1915: 320; Chevalier, 1920: 166; Schellenberg, 1938: 48; Hepper, 1958: 743; Adam, 1971: 868, pl.404; Berhaut, 1975: 25; Liberato, 1980a: 7.

Type: Sierra Leone, Smeathman s.n. (lecto herb. de Jussieu: P; iso: BM). See note 2.
C. grisea Baker, 1868: 461; Gilg, 1891a: 67, fig. 37f; Schellenberg, 1910: 17;

1915: 320; Chevalier, 1920: 167; Schellenberg, 1938: 48; Hepper, 1958: 743; Irvine, 1961: 572. Type: Nigeria, Old Calabar, Thomson 90 (holo: K; iso: E).
C. ferruginea DC. var. pilosa Dewèvre, 1894: 98 (nomen).
C. calocarpa Gilg, 1895b: 192; Schellenberg, 1910: 17; 1915: 320; 1938: 46; Brenan, 1949: 168; Hemsley, 1956: 5. Type: Tanzania, Uzaramo Distr., Mgambo, Stuhlmann 6388 (holo: $\mathrm{B} \dagger$ ), neo: Ulanga Distr., Funga, Ifakara, Haerdi 514/0 (BR, G, K, WAG).
C. confertiflora Gilg, 1895b: 193; Schellenberg, 1910: 17; 1915: 320; 1938: 45; Brenan, 1949: 168; Hemsley, 1956: 4, fig.1. Type: Tanzania, Uzaramo Distr., Kisserawe, Stuhlmann 6262 (holo: B $\dagger$ ), neo: Dar es Salaam, Peter 44838 (B).
C. confertiflora Gilg f. macrophylla Schellenberg, 1938: 45. Type: Tanzania, Pugu Hills, Holtz 2059 (holo: B $\dagger$ ), neo: Pugu Hills F.R., Wingfield \& Lucas 1949 (WAG).
C. grandiflora Gilg, 1895a: 70; Durand \& Durand, 1909: 121; De Wildeman, 1912: 407; 1929: 539; Schellenberg, 1938: 50; Troupin, 1952: 125; Exell \& Mendonça, 1954: 139. Type: Angola, Lunda, between Chicapa and Luachimo rivers, Marques 266 (holo: $\mathrm{B} \dagger$; lecto: LISU; iso: BM, COI). See note 3.
C. iomalla Gilg, 1895a: 69; De Wildeman, 1905: 91; 1906: 247; 1909: 96; Durand \& Durand, 1909: 121; De Wildeman, 1910b: 188; 1912: 407; Schellenberg, 1915: 320; De Wildeman, 1916: 244; Exell, 1928: 94; De Wildeman, 1929: 539; 1931: 236; Schellenberg, 1938: 50; Gossweiler \& Mendonça, 1954: 140. Type: Zaire, Baschilange, Mukenge, Pogge 930 (holo: $\mathrm{B}_{\dagger}$ ), neo: Stanley Pool, Demeuse 227 (BR).
C. iomalla Gilg var. grandifoliolata De Wildeman, 1906: 247; Durand \& Durand, 1909: 121; De Wildeman, 1910a: 294. Type: Zaire, Madibi, Lescrauwaet 115 (holo: BR).
C. setosa Gilg, 1895a: 70; Durand \& Schinz, 1896: 102; Durand \& De Wildeman, 1898: 113; De Wildeman \& Durand, 1899b: 18; De Wildeman \& Durand, 1901b: 10; De Wildeman \& Durand, 1901a: 56; Durand \& Durand, 1909: 121; De Wildeman, 1912: 407; 1920: 142, 244. Type: Zaire, Luculla ( = Lukula), Laurent s.n. (holo: BR).
C. aurantiaca Gilg, 1896: 216; Schellenberg, 1915: 320; 1938: 50; Hepper, 1958: 743. Type: Cameroun, Yaoundé, Zenker \& Staudt 652 (holo: B $\dagger$; lecto: BM; iso: K ).
C. polyantha Gilg, 1896: 215; Durand \& Durand, 1909: 121. Type: Zaire, Baschilange, Musumba, Pogge 147 (holo: B $\dagger$ ), neo: Kikwit, Vanderyst 2892 (BR).
C. riparia Gilg, 1896: 217; Schellenberg, 1910: 17; 1915: 320; 1938: 45; Brenan, 1949: 168. Type: Tanzania, Uluguru Foothills, Luhangulo, Stuhlmann 8942 (holo: $\mathrm{B} \dagger$ ), neo: Msalwa Estate, Carmichael 126 (K; iso: EA). See note 4.
C. emarginata De Wildeman \& Durand, 1899d: 81; 1900b: 129, pl.65; 1901: 56. Type: Zaire, near Stanley Pool, Dewèvre $715 b$ (holo: BR).
C. lescrauwaetii De Wildeman, 1906: 247; Durand \& Durand, 1909: 121; De Wildeman, 1910a: 294; Exell, 1928: 95; De Wildeman, 1929: 540; Schellenberg, 1938: 44; Gossweiler \& Mendonça, 1939: 90; Troupin, 1952: 118; Exell \& Mendonça, 1954: 139. Type: Zaire, Madibi, Lescrauwaet 88 (holo: BR).
C. congolana De Wildeman, 1909: 96; Schellenberg, 1915: 319; De Wildeman, 1929: 538; Exell, 1928: 94; Schellenberg, 1938: 52; Gossweiler \& Mendonça, 1939: 55; Troupin, 1952: 116; Exell \& Mendonça, 1954: 140; Hepper, 1958: 743. Type: Zaire, sin. loc., Cabra s.n. (holo: BR).
C. pynaertii De Wildeman, 1909: 98; 1929: 540; Schellenberg, 1938: 47; Troupin, 1952: 124. Type: Zaire, Lukolela, Pynaert 168 (holo: BR).
C. sapinii De Wildeman, 1909: 98; Schellenberg, 1938: 45; Troupin, 1952: 117. Type: Zaire, Sankuru, Sapin s.n. (holo: BR).
C. sapinii De Wild. var. claessensii (De Wild.) Troupin, 1952: 118. For type see under C. claessensii.
C. leucantha Gilg ex Schellenberg, 1910: 18; 1919: 439; 1938: 47. Type: Cameroun, Bipindi, Zenker 2157 (holo: B; iso: BM, E, G, K, L, MO, P, WAG, Z).
C. trichopoda Gilg ex Schellenberg, 1910: 18. Type: Cameroun, Bipindi Zenker 2335 (lecto: B, BM, BR, E, G, K, L, M, MO, P, WAG, Z).
C. claessensii De Wildeman, 1911a: 258; 1912: 406; 1929: 538; Schellenberg, 1938: 44. Type: Zaire, Lokandu, Claessens 473 (lecto: BR).
C. angolensis Schellenberg, 1915: 320 (nomen).
C. calantha Schellenberg, (1915: 320, nomen) 1919: 439; 1938: 47. Type: Cameroun, Grand Batanga, Dinklage 814 (holo: $\mathrm{B} \dagger$; lecto: P).
C. cinnabarina Schellenberg, 1919: 438; 1938: 46; Hepper, 1958: 743. Type: Cameroun, Bipindi, Zenker 1944 (holo: B $\dagger$; lecto: G; iso: BM, E, K).
C. dinklagei Schellenberg, 1919: 437; 1938: 45; Hepper, 1958: 743. Type: Liberia, Monrovia, Dinklage 2412 (holo: B). See note 5.
C. gabunensis Schellenberg, 1919: 440; Exell, 1928: 94; De Wildeman, 1929: 539; Schellenberg, 1938: 48; Gossweiler \& Mendonça, 1939: 55; Troupin, 1952: 120; Exell \& Mendonça, 1954: 139. Type: Gabon, Libreville, Sibange, Soyaux 143 (holo: $\mathrm{B} \dagger$; lecto: Z ; iso: GOET, $\mathrm{K}, \mathrm{P}$ ).
C. longiflora Schellenberg, 1919: 438; 1938: 46; Hepper, 1958: 743; Irvine, 1961: 572. Type: Nigeria, Lagos, Amuge, Dawodu 194 (holo: B $\dagger$; lecto: K).
C. zenkeri Schellenberg, (1915: 320, nomen) 1919: 441. Type: Cameroun, Bipindi, Zenker 2060 (holo: B $\dagger$; lecto: WAG; iso: E, G, K, L, MO, P, Z).
C. prehensilis Chevalier, 1920: 167 (nomen).
C. leucanthoides Pellegrin, 1923: 109. Type: Gabon, Tchibanga, Le Testu 1037 (holo: P).
C. agelaeoides Schellenberg, 1938: 52. Type: Gabon, near Libreville, Klaine 3508 (holo: P).
C. gimbiensis Troupin, 1951: 371; 1952: 125. Type: Zaire, Bas-Congo, Gimbi Valley, Toussaint 790 (holo: BR).
C. hirsuta Troupin, 1951: 368; 1952: 117. Type: Zaire, Yangambi, J. Louis $4286 a$ (lecto: BR). See note 6.
C. mullendersii Troupin, 1951: 370; 1952: 124. Type: Zaire, Bas-Katanga, Tshibonde, Mullenders 2051 (holo: BR).
C. vanderystii Troupin, 1951: 123. Type: Zaire, Bas-Katange, Merode, Vanderyst 22988 (holo: BR).

Agelaea pruriens Solander, nomen in sched.; Planchon, 1850: 440 (in syn.).


Fig. 78. Cnestis corniculata: 1. flowering branch, $2 / 3 \times$; 2. flower partly, $10 \times$; 3. branch with immature follicles, $2 / 3 \times ; 4-6$. follicles, $1 \times(4$ former C. iomalla, 5 former C. lescrauwaetii, 6 former

Spondioides pruriens Smeathman, nomen in sched.; Lamarck, 1789: 23 (in syn.).

Liana, often small, sometimes up to 20 m long. Branches cylindric, branchlets often somewhat angular, brown- or yellow-pilose or more or less glabrous. Leaves 2-13(-18)-jugate; petiole $0.2-10(-18) \mathrm{cm}$, rachis $5-40 \mathrm{~cm}$ long, grey-, brown- or yellow-pubescent, later more or less glabrous, often except at base of petiole. Leaflets (stiffly) papery, lateral ones opposite or not, ovate to narrowly oblong, ( $0.5-) 1-15(-30) \times 0.5-7.5(-13) \mathrm{cm}$, rounded or (sub)cordate and usually unequal at base, terminal one (narrowly) ovate or obovate to (narrowly) elliptic, $4-15(-30) \times 1.5-7.5(-15) \mathrm{cm}$, rounded or somewhat cuneate at base; all leaflets acuminate or sometimes obtuse or rounded, glabrous or more or less pilose above, glabrous to densely pilose beneath, midrib impressed above, prominent beneath, with 5-15(-20) lateral nerves on each side; tertiary nerves reticulate, more or less distinct; petiolules $0-5 \mathrm{~mm}$ long, pilose or rarely glabrous. Inflorescences racemes or rarely panicles, 1-20 per leaf-axil on stem, old or young branches, $1-15(-25) \mathrm{cm}$ long, $5-40$-flowered, densely yellowish brown-pilose, rarely also with reddish brown glandular hairs. Bracts ovate to subulate, $1-2 \mathrm{~mm}$ long, curved. Pedicels articulated $0-2 \mathrm{~mm}$ below the calyx, densely pilose. Flowers heterodistylous. Sepals usually distinctly reflexed (sometimes not), valvate or narrowly imbricate in bud, ovate to subulate or (narrowly) oblong, $(2.0-) 2.5-6.0(-8.5) \times 0.5-1.0(-2.5) \mathrm{mm}$, acute, sometimes obtuse at top, densely pilose, sometimes also with glandular hairs outside, glabrous inside, often indistinctly up to 5(-10)-veined. Petals valvate or narrowly imbricate in bud, (narrowly) oblong to elliptic, sometimes almost linear, $3.0-9.5 \times 0.5-1.0(2.0) \mathrm{mm}$, rounded to cuneate at base, obtuse, rounded or retuse and often inflexed at top, glabrous, distinctly up to 3(-7)-veined. Stamens more or less united at base, usually distinctly differing in length in the two whorls, $0.5-5.0(-6.0) \mathrm{mm}$ long, anthers $0.2-0.3 \times 0.1-0.2 \mathrm{~mm}$. Pistils 1.0-5.0 (but rarely between 2.0 and 3.0) mm long; ovaries ca 0.5 mm long, golden brown-pilose; styles mostly straight, pilose at base; stigmata usually oblique, more or less distinctly 2-lobed. Follicles 1-2(-4) in fruit, (narrowly) ellipsoid, more or less oblique, 2.5-4.5(-5) $\times 0.5-1.2$ cm , cuneate, mostly with $5-10 \mathrm{~mm}$ long stipe; beak slender, straight or curved, $5-20(-30) \mathrm{mm}$ long; pericarp with very short, red, spinelike hairs and long, easily caducous, stinging hairs outside and with long, slender hairs inside. Seeds ovoid, $10-15(-17) \times 5-10 \mathrm{~mm}$, sarcotesta $5-8 \mathrm{~mm}$ long, ruminate. Seedling epigeal.

Distribution: Tropical Africa from S Senegal to E Tanzania, and south to N Angola.

Ecology: Rain forest, semi-deciduous forest, thickets. Flowering in West Africa mainly from May to November, in Cameroun from January to May, in Gabon from August to November, in Zaire during the whole year, but most often from December to February and from June to October, in Angola from December to April and in Tanzania from April to June.


Fig. 79. Cnestis corniculata: 1-6. leaflets beneath, $2 / 3 \times(1$ former $C$. agelaeoides, 2 former $C . g a b u-$ nensis, 3 former C. sapinii, 4 former C. pynaertii, 5 former C. cinnabarina); $7-8$. flowers, $6 \times(7$ s.n.; 4. Pynaert 168; 5. Zenker C. aurantiaca; 1. Klaine 3508; 2. Monteiro \& Murta 133; 3. Sapin s.n.; 4. Pynaert 168; 5. Zenker 1944; 6. d'Orey 386; 7. Leeuwenberg 4010; 8. Bos 6896 ).


Fig. 80. Distribution of Cnestis corniculata

Selection of the ca 600 specimens examined:
Senegal: Basse Casamance, Oussouye (fl. Nov.) Berhaut 6598 (M); sin. loc. (y.fr.) Heudelot 650 (G, P).
Guinea-Bissau: Cantanhez(fr. Apr.) d'Orey 386 (COI, LISC, LISU); Cacine (fl., fr. Sept.) Esperito Santo 636 (COI).
Guinea: Dyeke (fl. Oct.) Baldwin 9668 (K); near Macenta (fl. Sept.) Jacques-Félix 1245 (P).
Sierra Leone: sin. loc., Afzelius s.n. (BM); Freetown (fr. Mar.) Dalziel 1007 (K, P); Lester Peak (fr. Dec.) Scott Elliot 3831 (BM, K); sin. loc. (fr.) Smeathman s.n. (BM, P, type); Mamaha (fl.) N. Thomas 4527 (K).

Liberia: sin. loc. (fr. Feb.) Adam 20833 (K); Lamco (fl. Oct.) Adames 624 (K); Mecca (fr. Dec.) Baldwin 10796 (K); Brewersville (fl. June) Barker $1325(\mathrm{~K})$; Monrovia (fr. Jan.) Dinklage 2412 (B, type of C. dinklagei); Virginia (fl. May) Dinklage 2712 (B, Z); near Sasala, Gibi Mt (fr. Nov.) Jansen 1753 (WAG); Gbanga (fr. Sept.) Linder 652 (K, WAG); Peahtah (fl. Oct.) Linder 957 (K, WAG).
Ivory Coast: Bouroukrou (fr. Dec) Chevalier 16884 (K, P); Adiopodoumé, Banco F.R. (fr. Nov.) de Koning 2849 (WAG); 16 km NW of Sassandra (fl., y.fr. June) W. de Wilde 227 (WAG); Sassandra (fl. Apr.) Leeuwenberg 4010 (B, BR, WAG); Toumodi (fr Jan.) Roberty 13543 (G); 15 km N of Abidjan (fl. May) Versteegh \& den Outer 124 (BR, WAG).
Ghana: near Cape Coast (fr. Sept.) Hall 1573 (K, P); sin. loc. (fl.b. Apr.) Hall 2508 (K).
Benin: Porto Novo (fr. Jan.) Chevalier 22828 (P); Dogboe (fl. Sept.) Le Testu 201 (BM, P); 8 km S of Adjohon (fr. Dec.) van der Zon 296 (WAG).
Nigeria: Ibadan (fr. Feb.) Brenan \& Keay 8974 (BM, P); Lagos (fl., fr. Nov.) Dalziel 1155 (C, E, K, M); Lagos (fl.) Dawodu 194 (K, type of C. longiflora); Benin Prov., Gagbe (fl. Aug.) Hambler 396 (K); Ibadan (fl. Sept.) Tamajong FHI 20964 (K, P); Ibadan (fl. Sept.) Latilo FHI 7923 (K, P); Calabar Prov., Oban Distr., Orem (fl. Mar.) Onochie FHI 36476 (K); Oban (fl.) Talbot 507 (BM, K); Degema (fl.) Talbot s.n. (BM); Old Calabar (fl.) Thomson 90 (E, K, type of C. grisea); 13 km W of Ilugun (fr. Mar.) van Meer 670 (WAG).
Cameroun: Bitye, Yaoundé (fl.) Bates 901 (BM, MO); Kumba Distr., Banga F. R. (fl. Mar.) Binuyo \& Daramola FHI 35605 (K); 6 km S of Kribi (fr. Nov.) Bos 3216 (K, WAG); 9 km S of Kribi (fl. May) Bos 4456 (K, WAG); 13 km from Kribi (fr. Oct.) Bos 5509 (K, WAG); Kribi-Edea, Fifinda (fl. Apr.) Bos 6722 (K, WAG); Malimba (fr.) Braun 60 (BM, K); 70 km SW of Eséka (fr. July) W. de Wilde 2805 (B, BR, K, WAG); Gross Batanga (Dec.) Dinklage 814 (P, type of C. calantha); Goyoum-Kalbe (fl., fr. Feb.) Letouzey 3357 (P); S of Nyong (fr. July) Letouzey 7367 (P);

Molundu Distr. (fr. Jan.) Mildbraed 4281 (HBG); Yaoundé (fl.) Zenker \& Staudt 652 (BM, K, type of C. aurantiaca); Bipindi (fr.) Zenker 1944 (BM, E, G, K, type of C. cinnabarina); Bipindi (fl.) Zenker 2060 (E, G, K, L, M, MO, P, WAG, Z, type of C. zenkeri); Bipindi (fl.) Zenker 2157 (B, BM, E, G, K, L, M, MO, P, WAG, Z, type of C. leucantha); Bipindi (fl.) Zenker 2335 (B, BM, BR, E, G, K, L, M, MO, P, WAG, Z, type of C. trichopoda); Bipindi (fl.) Zenker 2810 (BM, BR, E, G, K, L, MO, WAG, Z).
Central African Republic: Mbaiki (fl. July) Tisserant 75 (BM).
Gabon: km 6 Moanda-Franceville (fl., fr. Sept.) Breteler 6404 (WAG); km 40 Mouila-Yeno (fr. Sept.) Breteler, Lemmens \& Nzabi 8154 (LBV, WAG); km 50 Mouila-Yeno (fr. Sept.) Breteler, Lemmens \& Nzabi 8265 (WAG); 25 km NW of Kango (fr. Oct.) Breteler \& Lemmens 8286 (LBV, WAG); km 15 Libreville-Kango (fl.b. Oct.) Breteler \& Lemmens 8355 (LBV, WAG); km 28 Libreville-Kango (fl., fr. Oct.) Breteler \& Lemmens 8420 (LBV, WAG); Belinga (fl. June) Hallé 3869 (P); Libreville (fl. Oct.) Klaine 233 (P); near Libreville (fl. Aug.) Klaine 1617 (P); (fl., y.fr.) Klaine 2028 (P); (fl.) Klaine 3508 (K, P, type of C. agelaeoides); Tchibanga (fl., fr. June) Le Testu 1037 (BM, BR, P, type of C. leucanthoides); (fl. Oct.) Le Testu 1184 (BM, BR, K); Lastoursville (fl.) Le Testu 7144 (P); (fl., y.fr. Apr.) Le Testu 7181 (BM); (fl. Oct.) Le Testu 7539 (BM, BR, P); Oyem (fl. July) Le Testu 9641 (BM, BR, P); SSW of Mougouma, Doussala (fr.) Reitsma, Breteler \& A. Louis 1010 (LBV, WAG); SW of Mitzic (fl. Sept.) Reitsma 1570 (LBV, WAG); S of Mougouma, Doussala (fr. Oct.) Reitsma 1748 (LBV, WAG); near Libreville, Sibange (fl., fr. Aug.) Soyaux 143 (GOET, K, P, Z, type of C. gabunensis).

Congo: Foulakari (fl. Oct.) Bouquet 606 (P); Chaillu, Komono (fl. Nov.) Sita 4054 (P); Nganchu (fr. June) Vermoesen 2430 (BR).

Zaire: Moanda (fr. Sept.) Bequaert 745 (BR); sin. loc. (fr.) Cabra s.n. (BR, type of C. congolana); Kisantu (fl. Feb.) Callens 159 (BR); Lokandu (fl.) Claessens 473 (BR, type of C. claessensii and C. sapinii var. claessensii); Boma (fl., fr. Dec.) Dacrémont 134 (BR, K); Stanley Pool (fl. Feb.) Demeuse 227 (BR, type of C. iomalla); Rive française (fl. Feb.) Dewèvre $715 b$ (BR, type of C. emarginata); Luki (fl. Jan.) Donis 2322 (B, BR); Luculla (fr.) Laurent s.n. (BR, type of C. setosa); Ubangi, Libenge-Zongo (fl., y.fr. Nov.) Lebrun 1607 (BR); Yangambi (fl. Aug.) A. Léonard 1051 (BR, WAG); Kamusuku (fr. Aug.) A. Léonard 5968 (BR, WAG); Madibi (fl.) Lescrauwaet 88 (BR; type of C. lescrauwaetii); (fr. June) Lescrauwaet 115 (BR, type of C. iomalla var. grandifoliolata); Yangambi (fl. June) J. Louis 4286 (BR, type of C. hirsuta); (fr. Jan.) J. Louis 13496 (BM, BR, K); 17 km S of Leopoldville (fl. Sept.) Mildbraed 3549 (HBG); Tshibonde-Haut Lomani (fl. Feb.) Mullenders 2051 (BR, type of C. mullendersii); Lukolela (fl. July) Pynaert 168 (BR, type of C. pynaertii); Kasai Distr., Sankuru (fr. Sept.) Sapin s.n. (BR, type of C. sapinii); Stanley Pool (fl. June) Schlechter 12545 (BM, G, K, Z); Gimbi (fl. Jan.) Toussaint 790 (BR, type of C. gimbiensis); Nkula V. (fl. Sept.) Toussaint 2032 (BR); Kikwit (fl. Jan.) Vanderyst 2892 (BR, type of C. polyantha); Ipamu (fl. Feb.) Vanderyst 8810 (BR); Bas-Katanga, Mérode (fr.) Vanderyst 22988 (BR, type of C. vanderystii); Congo des Lemba (fr.) Verschueren 761 (BR); Kizu (fl. Mar.) Wellens 247 (BR).
Angola: Lunda, Chicapa R. (fr. Aug.) Carisso \& Mendonça 145 (BM, COI); Cazengo Distr. (fl.b.) Gossweiler 569 (BM, K); Cabinda, Buco Zau (fl. Oct.) Gossweiler 6730 (BM, COI, LISU); Maiombe, Rio Lufo (fl. Jan.) Gossweiler 7743 (BM, BR, COI, K); Maiombe, Belize (fl. Apr.) Gossweiler 7976 (BM, BR, COI); Maiombe (fr. Dec.) Gossweiler 8162 (BM, COI, K); Lunda, valleys of Chicapa and Luachimo (fl.) Marques 266 (BM, COI, LISU, type of C. grandiflora); sin. loc. (fl.) Welwitsch 4633 (BM, COI, G, K).

Tanzania: Iringa Distr., Msolwa (fr. Sept.) Carmichael 126 (EA, K, type of C. riparia); Pemba I. (fr. Feb.) Greenway 1457 (K); Ulanga Distr., Funga (fl.) Haerdi 514/0 (BR, G, K, WAG, type of C. calocarpa); Dar es Salaam (fr. Sept.) Peter 44838 (B, type of C. confertiflora); near Manaki, Pugu Hills (fl., y.fr. Sept.) Vaughan 3139 (BM, EA); Pugu Hills F.R. (fl. Apr.) Wingfield \& Lucas 1949 (WAG, type of C. confertiflora f. macrophylla).

Cult.: Ivory Coast, Adiopodoumé (seedling) de Koning 5974 (WAG).
Notes: 1. C. corniculata is the most variable species of the genus. Already in 1910 Schellenberg concluded that several species, described by Gilg (i.e. $C$. aurantiaca, C. grandiflora, C. iomalla, C. polyantha and C. setosa) are conspecific


Fig. 81. Cnestis corniculata: follicles (van der Maesen 5590; phot. L.J.G. van der Maesen).
with C. corniculata: '...beim Vergleiche der einzelnen Arten Gilgs findet man allerhand Uebergänge, so dass es mir nicht zweifelhaft erscheint, dass bei noch reichlicherem Materiale jede Unterscheidung dieser Arten, die schon jetzt höchst unsicher ist, zur reinen Unmöglichkeit werden wird.' And further on he states: 'Sehr nahe mit Cn. corniculata verwandt und vielleicht ebenfalls nur Formen dieser Art sind die drei folgenden ostafrikanischen Arten...: C. confertiflora Gilg, C. calocarpa Gilg, C. riparia Gilg.' In 1938 Schellenberg revised his opinion and reinstated these species, except $C$. polyantha and $C$. setosa. In the Flora of Tropical East Africa, Hemsley (1956) united some East African species. He placed C. riparia Gilg in the synonymy of C. confertiflora Gilg and doubted whether $C$. calocarpa is really distinct from them. He also stated that it is difficult to separate material determined as $C$. lescrauwaetii De Wild. from Congo and Angola from C. confertiflora.

The most variable characters in C. corniculata are:

1. Size and number of leaflets: large and few versus small and numerous.
2. Indumentum of leaflets beneath and of young branches: glabrous or scarcely pilose versus pilose.
3. Length of petals in relation to sepal length: petals as long as or hardly longer than sepals versus much longer.


Fig. 82. Cnestis corniculata: follicles (Breteler \& Lemmens 8420; phot. R.H.M.J. Lemmens).

In the following table all combinations of these character-states that were observed, are listed together with the corresponding synonyms of C. corniculata.
a. Leaflets large and few, (almost) glabrous beneath; petals as long as sepals or hardly longer. C. agelaeoides, C. cinnabarina, C. congolana.
b. Leaflets large and few, (almost) glabrous beneath; petals much longer than sepals. C. sapinii.
c. Leaflets large and few, pilose beneath; petals hardly longer than sepals. C. gimbiensis.
d. Leaflets large and few, pilose beneath; petals much longer than sepals. $C$. gabunensis, C. grisea, C. longiflora, C. mullendersii, C. vanderystii.
e. Leaflets small and numerous, (almost) glabrous beneath; petals hardly longer than sepals. C. corniculata s.s.
f. Leaflets small and numerous, (almost) glabrous beneath; petals much longer than sepals. C. confertiflora (often few leaflets!), C. lescrauwaetii.
g. Leaflets small and numerous, pilose beneath; petals as long as sepals or hardly longer. C. aurantiaca, C. iomalla, C. leucantha, C. pynaertii.
h. Leaflets small and numerous, pilose beneath; petals much longer than sepals. C. grandiflora.

This shows that all possible combinations are represented, moreover the pertinent characters vary independently.
The number of leaflets per leaf varies from 5-27 (2-16-jugate), rarely more.


Fig. 83. Frequency distribution of the highest number of leaflets per leaf of 104 specimens of $C$. corniculata.

Fig. 83 shows the frequency distribution of the highest number of leaflets per leaf of 104 specimens.

The length ratio of petals and sepals varies from 0.8-3.5. Fig. 84 shows the frequency distribution of the length ratio, petal length expressed as percentage of sepal length, of 63 specimens.

Considering the entire variation and the way it is distributed, it is, in my opinion, not possible to distinguish separate taxa in C. corniculata. Although various populations show a certain uniformity, the characters vary gradually and independently: no sharply defined limits can be established.

The more extreme forms that may be summarized are:
A. 'C. congolana', characterized by few, large, glabrous leaflets, long inflorescences and broad sepals, about as long as petals. Central Africa (S Nigeria to N Angola).
B. 'C. grisea', different from 'C. congolana' by pilose leaflets and narrower sepals, shorter than petals. Central Africa (S Nigeria to N Angola).
C. 'C. grandiflora', different from 'C. grisea' by numerous, small leaflets and usually somewhat smaller flowers. Central Africa (Gabon, N Angola, Zaire).
D. 'C. sapinii', linking up to ' $C$. congolana' in the leaves, but to ' $C$. grisea' in the flowers. Central Zaire.
E. 'C. cinnabarina', characterized by small, glabrous leaflets and petals about as long as sepals. S Nigeria and S Cameroun.
F. 'C. aurantiaca', different from 'C. cinnabarina' in usually more numerous, small, pilose leaflets. Liberia to W Zaire.


Fig. 84. Frequency distribution of the length ratio, petal length expressed as percentage of sepal length, of 63 specimens of $C$. corniculata.
G. 'C. confertiflora', very close to 'C. grandiflora', but with very long petals. E Tanzania.
H. 'C. longiflora', resembling 'C. aurantiaca' in the leaves, but differing from this form in the petals being much longer than sepals. SW Nigeria.
I. 'C. corniculata s.s.', close to 'C. grandiflora', but differing in the smaller flowers with petals hardly longer than sepals. W Africa, from S Senegal to Ivory Coast
J. 'C. iomalla', differing from 'C. corniculata s.s.' in the leaflets being pilose above and in the young branches and leaf-rachis provided with numerous, long, yellowish hairs. Central Africa (Cameroun, S Central African Republic, Gabon, Zaire, N Angola).

It should be understood explicitely that I do not grant any status under ICBN to these forms as numerous specimens cannot be placed in any single form because they are intermediate between two or more of them. An example to illustrate this is the specimen Breteler, Lemmens \& Nzabi8154 collected in Gabon which shows leaves with numerous (29), small $(1.5-6.5 \times 1.0-2.0 \mathrm{~cm})$ leaflets as well as leaves with few (11), much larger ( $5.0-13.0 \times 3.0-4.5 \mathrm{~cm}$ ) leaflets. This learns that leaf variation within one single plant can be considerable.

A discriminant analysis has been made, using the SPSS $X$ computer programme. The numerical values of 10 variable characters have been scored for 50 specimens of the 10 extremes of C. corniculata (A-J), and for 5 specimens of C. mannii (X), used as a control (table 24). Six of these characters relate to the leaves, one to the inflorescences, and three to the flowers. C. corniculata is strongly variable particularly in the leaves and flowers, as discussed before.

Table 24. Numerical values of 10 characters in 50 specimens of Cnestis corniculata and 5 specimens of C. mannii.

| NO | MLL | MNL | MLF | MWF | HLA | HLB | MLI | MLS | MLP | SRE | GROU |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 30.0 | 11 | 12.0 | 4.2 | 0 | 0 | 5.0 | 2.8 | 6.6 | 1 | D |
| 2 | 35.0 | 9 | 12.5 | 6.0 | 0 | 0 | 6.5 | 2.7 | 5.0 | 1 | D |
| 3 | 21.5 | 13 | 5.3 | 2.6 | 0 | 1 | 3.5 | 2.3 | 7.7 | 1 | G |
| 4 | 24.0 | 13 | 8.6 | 3.1 | 0 | 1 | 3.7 | 2.2 | 5.5 | 1 | C |
| 5 | 21.0 | 7 | 10.0 | 2.2 | 0 | 1 | 2.1 | 4.2 | 4.6 | 1 | C |
| 6 | 22.6 | 11 | 9.0 | 4.0 | 0 | 1 | 2.5 | 3.2 | 8.4 | 1 | C |
| 7 | 34.5 | 15 | 9.8 | 3.8 | 0 | 1 | 2.0 | 3.3 | 5.9 | 1 | C |
| 8 | 39.0 | 21 | 9.2 | 2.7 | 0 | 0 | 2.3 | 3.4 | 5.0 | 1 | C |
| 9 | 18.5 | 13 | 4.6 | 2.8 | 0 | 0 | 8.0 | 4.6 | 7.7 | 1 | C |
| 10 | 21.5 | 13 | 5.3 | 2.6 | 0 | 1 | 3.5 | 2.3 | 7.7 | 1 | C |
| 11 | 15.0 | 13 | 3.6 | 2.1 | 0 | 0 | 2.5 | 3.0 | 5.0 | 1 | C |
| 12 | 26.5 | 15 | 7.1 | 2.8 | 0 | 1 | 3.0 | 2.1 | 7.3 | 1 | C |
| 13 | 20.0 | 15 | 5.5 | 2.5 | 0 | 0 | 3.0 | 2.3 | 3.1 | 1 | C |
| 14 | 23.0 | 15 | 7.0 | 2.5 | 0 | 0 | 3.0 | 2.2 | 3.0 | 0 | C |
| 15 | 31.5 | 17 | 8.0 | 4.1 | 0 | 1 | 5.3 | 2.9 | 4.0 | 0 | F |
| 16 | 25.5 | 13 | 5.8 | 3.4 | 0 | 1 | 3.0 | 2.7 | 3.4 | 0 | F |
| 17 | 28.4 | 13 | 7.2 | 3.6 | 0 | 1 | 5.0 | 4.4 | 4.8 | 0 | F |
| 18 | 24.5 | 11 | 8.7 | 4.0 | 0 | 1 | 3.2 | 3.9 | 3.9 | 0 | F |
| 19 | 38.0 | 23 | 8.4 | 3.6 | 0 | 1 | 4.0 | 4.0 | 3.9 | 0 | F |
| 20 | 28.5 | 27 | 7.2 | 2.4 | 0 | 1 | 7.5 | 3.9 | 4.0 | 0 | F |
| 21 | 28.5 | 13 | 10.5 | 4.0 | 0 | 0 | 3.8 | 2.6 | 2.8 | 0 | F |
| 22 | 34.5 | 13 | 11.5 | 5.4 | 0 | 1 | 8.2 | 4.1 | 4.1 | 1 | F |
| 23 | 40.0 | 17 | 13.8 | 7.2 | 0 | 1 | 4.5 | 3.6 | 3.5 | 0 | F |
| 24 | 30.0 | 23 | 8.5 | 3.5 | 0 | 1 | 4.5 | 4.5 | 4.9 | 1 | F |
| 25 | 40.0 | 27 | 8.5 | 2.6 | 0 | 1 | 6.0 | 4.6 | 5.2 | 1 | F |
| 26 | 44.0 | 41 | 8.5 | 2.5 | 0 | , | 4.0 | 2.8 | 3.0 | 1 | F |
| 27 | 34.5 | 23 | 8.5 | 3.0 | 0 | 1 | 5.0 | 3.0 | 3.3 | 0 | F |
| 28 | 42.5 | 21 | 7.5 | 2.5 | 0 | 1 | 3.0 | 2.8 | 2.6 | 1 | F |
| 29 | 28.0 | 15 | 6.5 | 3.0 | 0 | 1 | 2.0 | 4.0 | 4.0 | 0 | F |
| 30 | 22.5 | 19 | 5.2 | 2.2 | 0 | 1 | 2.7 | 2.8 | 3.6 | 1 | I |
| 31 | 18.0 | 17 | 4.8 | 2.3 | 0 | 0 | 4.2 | 3.0 | 3.9 | 1 | I |
| 32 | 30.5 | 17 | 7.0 | 2.5 | 1 | 1 | 3.0 | 2.6 | 3.4 | 1 | J |
| 33 | 29.5 | 23 | 5.0 | 2.3 | 1 | 1 | 2.5 | 3.7 | 3.8 | 1 | J |
| 34 | 35.0 | 21 | 7.5 | 2.7 | 1 | 1 | 2.5 | 2.8 | 3.2 | 1 | E |
| 35 | 28.0 | 11 | 10.5 | 4.5 | 0 | 0 | 3.5 | 3.0 | 3.3 | 1 | E |
| 36 | 24.0 | 11 | 6.5 | 3.0 | 0 | 1 | 5.0 | 2.8 | 6.5 | 1 | H |
| 37 | 37.5 | 11 | 15.5 | 7.2 | 0 | 0 | 9.5 | 6.4 | 6.0 | 0 | A |
| 38 | 37.0 | 9 | 17.5 | 11.5 | 0 | 0 | 9.0 | 7.0 | 7.2 | 0 | A |
| 39 | 44.0 | 7 | 17.0 | 8.5 | 0 | 0 | 20.0 | 3.3 | 3.5 | 1 | A |
| 40 | 37.5 | 5 | 15.0 | 10.0 | 0 | 0 | 8.0 | 3.3 | 3.6 | 1 | A |
| 41 | 32.0 | 5 | 14.5 | 10.5 | 0 | 0 | 8.5 | 4.9 | 4.2 8.5 | 0 | A |
| 42 | 35.5 | 9 | 14.0 | 8.0 | 0 | 0 | 18.0 9.0 | 8.0 4.5 | 8.5 5.7 | 0 | A |
| 43 | 47.0 | 9 | 17.0 | 7.5 | 0 | 1 | 9.0 | 4.5 4.6 | 8.7 7.6 | 1 | B |
| 44 | 34.0 | 9 | 11.5 | 7.0 | 1 | 1 | 7.5 | 4.6 | 7.6 | 1 | B |
| 45 | 50.0 | 9 | 18.0 | 8.5 | 0 | 1 | 9.0 | 4.2 | 7.2 | 1 | B |
| 46 | 62.5 | 11 | 23.5 | 7.5 | 0 | 1 | 6.5 | 4.0 3.9 | 7.0 4.9 | 1 | B |
| 47 | 29.5 | 11 | 7.5 | 3.0 | 0 | 1 | 4.0 | 3.9 5.5 | 7.9 7.2 | 1 | B |
| 48 | 50.0 | 9 | 25.0 | 12.5 | 0 | 1 | 7.5 4.0 | 5.5 4.3 | 7.2 5.5 | 1 | B |
| 49 | 74.0 | 7 | 27.5 | 13.0 | 0 | 1 | 4.0 | 4.3 | 5.5 | 1 | B |
| 50 | 59.0 | 13 | 17.5 | 9.0 | 1 | 1 | 11.0 | 4.5 | 7.2 | 1 | B |
| $193$ |  |  |  |  |  |  |  |  |  |  |  |

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Table 24 (Continued)

| NO | MLL | MNL | MLF | MWF | HLA | HLB | MLI | MLS | MLP | SRE | GROU |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 51 | 27.0 | 5 | 12.0 | 8.5 | 0 | 1 | 27.5 | 6.0 | 1.7 | 0 | X |
| 52 | 37.0 | 7 | 19.0 | 8.5 | 0 | 1 | 16.5 | 5.0 | 2.5 | 0 | X |
| 53 | 38.0 | 9 | 15.0 | 8.5 | 0 | 1 | 40.0 | 4.5 | 2.0 | 0 | X |
| 54 | 25.5 | 9 | 17.0 | 8.5 | 0 | 1 | 20.5 | 5.0 | 2.0 | 0 | X |
| 55 | 23.5 | 7 | 12.0 | 7.0 | 0 | 1 | 24.0 | 4.0 | 1.5 | 0 | X |
| NO = entry number |  |  |  |  |  |  |  |  |  |  |  |
| MLL = maximum length of leaf ( c |  |  |  |  |  |  |  |  |  |  |  |
| MNL = maximum number of leaflets per lea |  |  |  |  |  |  |  |  |  |  |  |
| MLF = maximum length of leaflet (cm) |  |  |  |  |  |  |  |  |  |  |  |
| MWF = maximum width of leaflet (cm) |  |  |  |  |  |  |  |  |  |  |  |
| HLA $\quad=$ hairiness of leaflet above ( $0=$ glabrous; $1=$ pilose $)$ |  |  |  |  |  |  |  |  |  |  |  |
| HLB $\quad=$ hairiness of leaflet beneath ( $0=$ glabrous; $1=$ pilos |  |  |  |  |  |  |  |  |  |  |  |
| MLI $\quad=$ maximum length of inflorescence (cm) |  |  |  |  |  |  |  |  |  |  |  |
| MLS = maximum length of sepal (mm) |  |  |  |  |  |  |  |  |  |  |  |
| MLP = maximum length of petal (mm) |  |  |  |  |  |  |  |  |  |  |  |
| SRE = condition of the sepals ( $0=$ not reflexed; $1=$ reflexed $)$ |  |  |  |  |  |  |  |  |  |  |  |
| GROU $=$ form of C. corniculata in which the specimen could be placed, as discussed in the |  |  |  |  |  |  |  |  |  |  |  |

Three of the characters are qualitative, seven quantitative. Fig. 85 shows the all-groups scatterplot of this analysis. The axes are the discriminant scores calculated from the first two discriminant functions extracted during analysis. The discriminant functions result from the 'direct method', in which all variables are entered simultaneously (see SPSS X User's Guide). The 5 specimens of $C$. mannii are clustered separately but the forms of C. corniculata are all found in a single cluster. The scatterplot shows that the 'C. congolana'-form (A) and 'C. iomalla'-form ( J ) are the most extreme forms.

As a whole, this extremely variable species is best characterized by its follicles, that are beaked and possess stinging hairs, in combination with the racemose inflorescences.
2. Lamarck described leaves and follicles. The specimen in the Lamarck herbarium consists of one leaflet only. Therefore the description is probably based on the Smeathman specimen with both leaves and fruits in the De Jussieu herbarium. Consequently, this is the lectotype.
3. Gilg (1895a) cited in the protologue of C. grandiflora the specimen Marques 268, probably a printing error as the type is Marques 266.
4. In the protologue of C. riparia, Gilg (1896) reports extremely long petiolules $(1 \mathrm{~cm})$. Probably 1 mm was intended as Schellenberg (1910 and 1938) does not mention long petiolules, and I have not seen any over 5 mm long.
5. In the protologue of C. dinklagei, Schellenberg (1919) cited the specimen Dinklage 2312. This is an error, because the type is Dinklage 2412.
6. J. Louis 4286, the type of C. hirsuta Troupin (1951), is a mixture of Rourea


Fig. 85. Scatterplot of 50 specimens of 10 extreme forms (A-J) in Cnestis corniculata and of 5 specimens of $C$. mannii (X), resulting from a discriminant analysis (SPSS X computer programme).
parviflora Gilg (leaves and young branches) and C. corniculata (flowers and stems). The specimen Pittery 274, also cited by Troupin is sterile and represents Rourea parviflora. The C. corniculata element is separated as J. Louis $4286 a$ and here designated as the lectotype of $C$. hirsuta Troupin.

Uses: According to Schellenberg (1938) and Troupin (1952) the leaves are used against blennorrhoea (Zaire), the stems as a rope to climb palm-trees.
C. ferruginea De Candolle, 1825: 87; G.Don, 1832: 91; Planchon, 1850: 440; Walpers, 1852: 306; Baillon, 1867: 241; Baker, 1868: 461; Gilg, 1891a: 68, fig.37; Dewèvre, 1894: 98; Gilg, 1895b: 192; Durand \& Schinz, 1896: 102; Hiern, 1896: 190; De Wildeman \& Durand, 1900a: 15; De Wildeman \& Durand, 1901b: 10; De Wildeman \& Durand, 1901a: 56; De Wildeman, 1905: 91; 1906:246; Durand \& Durand, 1909: 120; De Wildeman, 1910a: 294; De Wildeman, 1910b: 188; De Wildeman, 1910c: 142, 244; Schellenberg, 1910: 11; De Wildeman, 1911b: 217; Engler, 1911: 632, fig.540; De Wildeman, 1912: 407; De Wildeman, 1914: 83; Gilg, 1914: 229; Schellenberg, 1915:318; De Wildeman, 1916: 244; Chevalier, 1920: 166; Exell, 1928: 94; De Wildeman, 1929: 538; 1931: 235; Irvine, 1930: 113; Schellenberg, 1938: 30, fig.3; Andrews, 1952: 353, fig.132; Irvine, 1952: 128, fig.115; Troupin, 1952: 118; Exell \& Mendonça, 1954: 138; Mangenot, 1957: no.81; Hepper, 1958: 743, fig.201; Irvine, 1961: 570, fig.111; Adam, 1971: 868, fig.405; Berhaut, 1975: 27 + fig.; Liberato, 1980a: 7; 1980b: 6; Ern, 1984: 164. See note 2.

Type: Sierra Leone, Smeathman s.n. (holo: G; iso: BM, P).
C. ferruginea DC. var. fraterna Baker, 1868: 462. For type see under C. fraterna.
C. fraterna Planchon, 1850: 440; Walpers, 1852: 306. Type: Senegal, Nunez R., Heudelot 660 (lecto: P; iso: G).
C. oblongifolia Baker, 1868: 462; Durand \& Schinz, 1896: 102; De Wildeman \& Durand, 1901a: 56; De Wildeman, 1906: 248; 1909: 97; Durand \& Durand, 1909: 121; De Wildeman, 1910a: 294. Type: Cameroun, Cameroon R. (=Wouri R.), Mann 753 (lecto: K).
C. togoensis Gilg, 1896: 216. Type: Togo, Misahöhe, Baumann 526 (holo: B n.v., according to Ern (1984) collection in spirit).

Agelaea ferruginea Solander, nomen in sched.; Planchon, 1850: 440 (in syn.).
Spondioides ferruginea Smeathman, nomen in sched.; De Candolle, 1825: 87 (in syn.).

Liana or shrub. Branches cylindric, branchlets often somewhat angular, densely rusty brown-pubescent. Leaves 4-16(-19)-jugate; petiole 2-10 cm, rachis $12-27 \mathrm{~cm}$ long, densely rusty brown-pubescent. Leaflets papery, lateral ones more or less alternate or sometimes opposite, ovate to narrowly oblong, 2-13 $\times 1-5 \mathrm{~cm}$, rounded, truncate or subcordate and slightly or not unequal at base, terminal one elliptic or narrowly (ob)ovate, $4-10 \times 1.5-5 \mathrm{~cm}$, cuneate at base; all leaflets acuminate or obtuse, glabrous or rarely somewhat pilose above, densely pilose beneath, midrib impressed above, prominent beneath, with 5-12 lateral nerves on each side; tertiary nerves reticulate, usually not distinct; petiolules $1.5-3 \mathrm{~mm}$ long, densely brown-pilose. Inflorescences panicles or (pseudo-) racemes, $1-10$ per leaf-axil on young branches, often the supporting leaves reduced resulting in a compound pseudoterminal inflorescence, $5-20 \mathrm{~cm}$ long, up to 100 -flowered, densely rusty brown-pilose, also with short glandular hairs.


Fig. 86. Cnestis ferruginea: 1. flowering branch, $2 / 3 \times ; 2$. flower, $6 \times$; 3 . flower partly, showing pistils, $6 \times ; 4-5$. stamens, $24 \times ; 6$. follicles from above, $1 \times ; 7$. follicles, $2 / 3 \times ; 8$. seed, $1 \times$ (1-5. Leeuwenberg 2397; 6-8. Louis et al. 1186).

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Fig. 87. Distribution of Cnestis ferruginea

Bracts ovate to subulate, 1-1.5 mm long. Pedicels articulated 1-2.5 mm below the calyx, densely brown-pilose. Flowers almost homostylous. Sepals never reflexed, imbricate in bud, ovate to narrowly elliptic, 2.0-4.0 $\times 0.8-1.3 \mathrm{~mm}$, acute at top, densely brown-pilose, usually also with short glandular hairs outside, pubescent inside. Petals imbricate in bud, orbicular to broadly obovate, 1.0-2.0 $\times 1.0-1.5(-2.0) \mathrm{mm}$, rounded or truncate at base and at top, glabrous (rarely with some hairs outside), usually indistinctly veined. Stamens more or less united at base, subequal, $0.7-1.2 \mathrm{~mm}$ long, anthers ca $0.3 \times 0.2 \mathrm{~mm}$, with an appendix at the base. Pistils $0.5-1.5 \mathrm{~mm}$ long; ovaries ca 0.5 mm long, brown-pilose; styles often strongly curved towards anthers, pilose; stigmata oblique. Follicles 1-5 in fruit, often united at base, ovoid, more or less oblique, 2-4.5(-5) $\times 1-2.5 \mathrm{~cm}$, rounded or truncate at base; beak blunt and broad, $5-20 \mathrm{~mm}$ long, often indistinctly separated; pericarp with short, red hairs outside and with long brownish hairs inside. Seeds ovoid, 12-20 $\times 5-10 \mathrm{~mm}$, sarcotesta 3-7 mm long. Seedling epigeal.

Distribution: Tropical Africa, from Gambia to E Zaire and S Sudan, south to N Angola.
Ecology: Rain forest, in bushes in savanna, often in secondary regrowths on farm land, in fences, fringing lagoons and near the beach. Very common in many countries. C.ferruginea can be found flowering all the year round.

Selection of the ca 1000 specimens examined:
Gambia: Kotu stream swamp (fl., y.fr. May) Fox 101 (K); Abuko Nature R. (fr. July) Starin 12 (K).
Senegal: near Oussouye (fl. Aug.) Berhaut 6272 (BR); (fl. Nov.) Berhaut 6586 (BR); Nunez R. (fl., fr.) Heudelot 660 (G, P, type of C. fraterna and C. ferruginea var. fraterna); Nunez R. (fl.)

Perottet 69 (G); Basse-Casamance, Boukot (fl. Dec.) vanden Berghen 1495 (BR); Mankagne (fl. July) vanden Berghen 1940 (BR); Brin (fr. June) vanden Berghen 5741 (BR); Cap Skirring (fl., fr. Nov.) vanden Berghen 5936 (BR).
Guinea-Bissau: S Domingos-Sedengal (fl., fr. Jan.) Alves Pereira 1460 (LISC); Bafate-Bricama (fr. Mar.) Alves Pereira 1727 (LISC); Cacheu-Bianga (fr. Feb.) Alves Pereira 3713 (LISC); Bissau Biombo (fl., fr. Dec.) d'Ory 29 (COI, LISC, LISU); Susana (fl. Dec.) Raimundo \& Guerra 381 (LISC); Cacine (fl., fr. Jan.) Raimundo \& Guerra 733 (LISC).

Guinea: Kouria (fl.) Chevalier 14809 (BR); Conakry (fl. Oct.) Maclaud 29 (P); Iles de Los (fl. May) Pobéguin 1177 (P); Dar Salam (fr. Feb.) Roberty 10562 (G, Z).
Sierra Leone: Moyamba (fr. Jan.) Cole \& Jarr EAC 84 (WAG); Lungi Penins. (fl. Apr.) Morton SL 1232 (WAG); sin. loc. (fl.) Smeathman s.n. (BM, G, P, type).
Liberia: Tchien, Zwedru-Sinoe (fl. July) Blyden 925 (WAG); Loffa county, St.Paul R.-Zorzor (fl., fr. Dec.) Bos 2525 (WAG); Monrovia (fr. Dec.) Dinklage 2753 (B); King's Farm (fr. Jan.) Dinklage 2950 (Z); Bomi Hills (fl. Oct.) Jansen 2235 (WAG); Monrovia (fr.) Krause 12016 (B); Gbanga (fl., fr. Sept.) Linder 608 (WAG); Zleh-Monroviatown, Tappita-Tchien (fl. Jan.) van Harten 248 (WAG); 5 miles N of Ibadan (fl. Sept.) van Meer 870 (WAG).
Ivory Coast: Yapo F. (fr. Jan.) Bamps 1863 (BR); Duékoué-Buyo (fl. Mar.) Bamps 2161 (BR); Man (fr. Feb.) Declercq s.n. (BR); Sikensi-Agboville (fr. Jan.) de Koning 170 (WAG); 10 km N of Dabou (fl., fr. May) de Kruif E58 (WAG); 7 km E of Bouaké (fl. May) W. de Wilde 68 (WAG); E of Dabou (fl. Aug.) Geerling \& Bokdam 796 (BR, WAG); 17 km W of Abidjan (fl., fr. Nov.) Leeuwenberg 1919 (BR, WAG, Z).
Ghana: Aburi Scarp. (fl. Jan.) de Wit \& Morton A 2856 (WAG); sin. loc. (fl.) Isert s.n. (C); 4 km NE of Dodowa, NW of Aiyikuma (y.fr. Feb.) Leeuwenberg 11913 (WAG); N Swedru (fl., y.fr. Apr.) Morton A 501 (WAG); near Kwapon, 100 km WSW of Kumasi (fl., y.fr.) Oldeman 769 (BR, WAG); Achimoto, Kumasi (fr. Nov.) Roberty 12898 (G); sin. loc. (fl.) Thonning s.n.; Kpandu (fl. Dec.) Veldkamp 6097 (L)
Togo: near Palimo (fl. Dec.) Brunel 1201 (B); Brunel 4128 (B); Tsevie-Tokpli, Mono R. (fl.b., fr . Nov.) Ern 2400 (B); Akposso H., 1.5 km S of Kouniohou (fr, Apr.) Hakki, Leuenberger \& Schiers 557 (B); 5 km N of Atakpame (fl. Nov.) Lejoly s.n. (BR).
Benin: Porto Novo, Sakété-Pédjilé (fl.b. Feb.) Chevalier 22907 (BR); 8 km E of Adjohon (fl. Dec.) van der Zon 300 (WAG); Sogo, near Porto Novo (fr, Feb.) van der Zon 405 (WAG)
Nigeria: Gambari F. R. (fr. Mar.) Bernardi 8745 (G); Prov. Benin, Distr. Iyekuselu (fl. Jan.) Daramola \& Emwiogbo 32775 (BR); Lagos (fl. Dec.) Hagerup 767 (BR, C); Old Calabar (fl., fr. Jan.) Holland 16 (K); SE St., Distr. Ikom, Ajasso Village (fl. Feb.) Latilo \& Ogumtayo 67665 (WAG); Ibadan (fr, Feb.) Pilz 2267 (B, WAG); Western Prov., Gambari (fl., y.fr. Jan.) van Eijnatten 1082 (WAG).
Cameroun: Douala (fl., fr. Dec.) Baldwin 14002 (MO); Falls of Lobé R. (fr. Jan.) Bamps 1702 (BR); Batanga (fl. Mar.) Bates 124 (BR, E, G, Z); Kumba (fl., fr. Feb.) Binuyo \& Daramola 35571 (WAG); 1.5 km S of Kribi (fl., fr. Sept.) Bos 2952 (BR, WAG); Bertoua (fl. Nov.) Breteler 691 (BR, WAG); Nkoldjobe Hill, Mbaminkom Mts (fl. Dec.) Dang 778 (P); Dume Distr., GandimaGarga (fl. Nov.) Elbert 48 (B); near Londji (fl., fr. Apr.) Leeuwenberg 5639 (BR, WAG); Cameroon R. (fl., fr. Jan.) Mann 753 (K, type of C. oblongifolia); Bipindi (fl.) Zenker 1921 (E, G, L, MO, WAG, Z); (fr.) Zenker 3055 (BR, E, G, L, MO, WAG, Z).
Central African Republic: Snoussi Land (fl. Jan.) Chevalier 7272 (BR); Boukoko, Mbaiki (fl. Feb.) Le Testu 2469 (BR); Ouaka (Feb.) Tisserant $496 b$ (P).

Sudan: Bahr el Ghazal Prov., S of Benderi (fl. Mar.) Dandy 670 (BM); SW Equatorial Prov., Source Yubu (fl.) Hoyle 700 (K); Niam-Niamland (fl., fr.) Schweinfurth 2948 (K); Equatorial Prov., Li Yabongo (fr. Mar.) Wyld 34 (BM).
Equatorial Guinea: Nkolentangan (fl. Mar.) Tessmann 267 (K); Bebai (fl.b. Sept.) Tessmann 511 (K).

Sao Tomé \& Principé: Principé, sin. loc. (fl.) Mann s.n. (P).
Gabon: 15 km N of Kango (fr. Oct.) Breteler \& Lemmens 8303 (LBV, WAG); km 7 Lalara-Ndjolé, than 56 km N (fr. Sept.) Breteler \& J. de Wilde 487 (WAG); Booué (fl. Aug.) Davies 303 (P); Cap Lopez (fl.) Debeaux 389 (B); 10 km SW of Ndjolé (fl. May) Hallé 1986 (P); Lastoursville (fl. Apr.) Le Testu 7174 (P); near Achouka (fl., fr. Nov.) A. Louis, Breteler \& de Bruijn 573 (WAG); A. Louis,


Fig. 88. Cnestis ferruginea: flowering branch (Breteler, Lemmens \& Nzabi 7790; phot. R.H.M.J.
Lemmens).

Breteler \& de Bruijn 692 (LBV, WAG); near Mougouma, Doussala (fr.) Reitsma 1356, 1650, 1751 (WAG); Haute Ngounié, St.Martin (fl.b., fr. July) Walker s.n. (P).
Congo: Hamon (fr. Aug.) Bouquet 424 (P); Matoko, 10 km from Epéna (fr. Feb.) de Nere 1028 (P); near Fort Rousset, 26 km from Ewo (fl. July) Descoings 8422 (P); Brazzaville (fl. Dec.) Koechlin
2348 (P).

Zaire: Yaekama, Terr. Isangi (fl.b., fr. Feb.) Bamps 336 (BR); Kalima (fl.b. Jan.) Becquet 995 (BR); Lukula (fl. Sept.) Bequaert 656 (BR); Penghe (fr. Feb.) Bequaert 2276 (BR); Yangambi (fr. Sept.) Bolema 5 (BR); Nala, Duambo (fl. June) Boone 81 (BR); Bambesa (fl. Apr.) Bredo 4098
(BR); Kisantu (fl.) Callens 4149 (BR); Giorgi 966 (BR); Bangala (fl.) Demeu); Ikenge (fr.) Claessens 692 (BR); Dundusana (fl. June) De ungu, Mondombe (fl.b. Dec.) Evrard 5426 (BR); Coquilhatville (fr. Jan.) Dewèvre 633 (BR); YalikKabumbu, Lumuna-Nuangwe (fl. June) Germain); Bambesa (fl. Dec.) Gerard 3271 (BR, WAG);


Fig. 89. Cnestis ferruginea: fruiting branch (Breteler \& Lemmens 8303; phot. R.H.M.J. Lemmens).

Epulu, Mambasa (fl. Oct.) Hart 138 (BR); Bangala (fl. June) Hens 106 (G, L, Z); Bolima (fl., fr. Oct.) Hulstaert 429 (BR); Eala (fr. June) Laurent 854 (BR); Prov. Orientale, Distr. Haut Uele, Dungu (fl. Feb.) Leclercq 431 (BR, WAG); Madibi (fl. June) Lescrauwaet 90 (BR); Lubi R., Dibaya (fr. Oct.) Liben 1664 (BR); Bienge (fr. Oct.) Sapin s.n. (BR); Stanley Pool (fl. June) Schlechter 12550 (Z); lpamu (fl. May) Vanderyst 9401 (BR).

Angola: Cuanza Norte, Quiage (fr. Apr.) Cardoso 131 (COI); Cabinda, Damba (fl.) Dawe 149 (K); Cuanza Norte, Golungo (fl., fr.) Exell \& Mendonça 3205 (COI, LISC); Cabinda, sin. loc. (fl.) Gossweiler 4247 (K); Granja de S.Luiz, Cazengo (fl., fr.) Gossweiler 4411 (COI, K); Loco, Dundo (fl. May) Gossweiler 13968 (B, BM, K); Cabinda, Buco Zau (fl. Sept.) Monteiro, Santos \& Murta 329 (LISC); sin. loc. (fl., fr.) Welwitsch 4632 (COI, G, K, P).
Cult.: Wageningen, greenhouse (seedling) van Veldhuizen 984 (WAG).

Notes: 1. The variability of C. ferruginea is little, compared with other species with a large area of distribution. The flowers are not variable at all, the characteristic rusty brown indumentum of leaves and branchlets is always present, while the shape and size of the leaves and follicles show a slight variability.
2. A note in Martin Vahl's hand (see Junghans, 1961) is attached to the Isert specimen in C, giving a description and the name Cnestis ferruginea. Vahl died in 1804, and Cnestis ferruginea was not published before 1825 by De Candolle. In the De Candolle-Herbarium in G a specimen of C.ferruginea is found with a note: 'Vahl 1804'. Possibly Vahl suggested the name Cnestis ferruginea to De Candolle and sent a sheet to Geneva in 1804. De Candolle adopted and published this name more than 20 years later. It is remarkable that De Candolle did not cite any specimen collected by Isert or Thonning in Ghana, but only a Smeathman specimen from Sierra Leone. However, in my opinion the complete correct authority of Cnestis ferruginea is Vahl ex DC.

Uses: The roots are a remedy for dysentery, syphilis, gonorrhoea, migraine and snakebite, and are said to be purgative. A decoction is an aphrodisiac and prevents abortion and ovarian troubles in women. The powdered bark is rubbed on the gums against pyorrhoea (swellings) according to Ainslie (1937). The leaves can be used as a laxative and against fever. Rubbing with boiled leaves relieves childbirth pains, as well as other kinds of pain (Berhaut, 1975; Irvine, 1961). A leaf decoction is used as an abortive, to fight colds, and the leaf juice is applied as eye-drops in ophthalmia. In Zaire the crushed leaves are used to repare cracks in pots (Troupin, 1952). The fruits, that are said to be bitter and juicy and possibly poisonous (Kerharo, 1971), are used for tooth-brushing (external part) and, boiled in water, against bronchitis, hooping-cough, tuberculosis and wounds. Crushed with rum or palm-wine they are reported as a remedy for snakebite (Ainslie, 1937; Troupin, 1952). On the beaches in Cameroun they are used as bait in traps for cocos-crabs. According to Schellenberg (1938) Cephalophus maxwelli (a small antelope) likes to eat the fruits. Various parts of the plant can form part of magic mixtures (Mangenot, 1957).

## Cnestis macrantha Baill.

Fig. 90, 91
C. macrantha Baillon, 1867: 242; Baker, 1868: 462; Schellenberg, 1910: 13; 1938: 34; Hepper, 1958: 743.

Type: Gabon, sin. loc., Duparquet 53 (lecto design. by Schellenberg, 1938: P). See note 1 .

Liana or climbing shrub. Branches cylindric, branchlets often somewhat angular, densely yellowish brown-pilose. Leaves 10-17-jugate; petiole $0.5-4.5 \mathrm{~cm}$, rachis $11-22 \mathrm{~cm}$ long, densely yellowish brown-pilose. Leaflets thinly papery, lateral ones more or less opposite, elliptic or (narrowly) oblong, 1-5 $\times 1-1.5$ cm , rounded, truncate or rarely subcordate and slightly unequal at base, termi-


Fig. 90. Cnestis macrantha: 1. flowering branch, $2 / 3 \times$; 2 . flower, $6 \times$; 3 . flower partly, showing stamens and pistils, $6 \times$; 4 . sepal inside, $8 \times$; 5 . petal outside, $8 \times$; . follicles, $1 \times(1-4$. Binuyo 45402; 5. Duparquet 53; 6. D. Thomas 3326).

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Fig. 91. Distribution of Cnestis macrantha
nal one obovate, oblong or elliptic, $2.5-3.5 \times 1-1.5 \mathrm{~cm}$, rounded or cuneate at base; all leaflets obtuse or truncate, more rarely retuse or subacute, scattered pilose above, densely pilose with long hairs beneath, midrib impressed above, prominent and densely pilose beneath, with 5-8 lateral nerves on each side; tertiary nerves indistinct; petiolules very short, up to 1 mm long, pilose. Inflorescences racemes or panicles, single in leaf-axils on top of young branches, the supporting leaves often reduced or very young resulting in a compound pseudoterminal inflorescence, $5-24 \mathrm{~cm}$ long, up to 40 -flowered, densely yellowish brown-pilose, also with short, brown glandular hairs. Bracts subulate or lanceolate, 3-5 mm long, usually curved. Pedicels articulated 3-7 mm below the calyx, densely pilose. Sepals never reflexed, imbricate in bud, narrowly oblong or narrowly obovate, $5.0-6.5 \times 1.5-2.5 \mathrm{~mm}$, obtuse or rounded, densely pilose, with numerous glandular hairs outside, pubescent inside. Petals imbricate in bud, obovate or obcordate, $2.0-3.0 \times 1.3-2.0 \mathrm{~mm}$, cuneate at base, truncate or retuse at top, with a few hairs in lower half outside, glabrous inside, indistinctly veined. Stamens united at base, subequal, $1.5-2.2 \mathrm{~mm}$ long, anthers ca $0.4 \times 0.3 \mathrm{~mm}$. Pistils $4.0-5.0 \mathrm{~mm}$ long; ovaries ca 1 mm long, brown-pilose; styles straight or curved in upper part, pilose at base; stigmata oblique, more or less distinctly 2-lobed. Follicles 1-4 in fruit, narrowly ovoid or narrowly ellipsoid, somewhat oblique, $4-6 \times 1-1.5 \mathrm{~cm}$, rounded at base; beak blunt and broad, $15-20 \mathrm{~mm}$ long, indistinctly separated; pericarp with short, red hairs and some longer, yellowish hairs outside and with long yellowish hairs inside. Seeds ovoid, $10-20 \times 5-8 \mathrm{~mm}$, sarcotesta $2-5 \mathrm{~mm}$ long.

Distribution: SE Nigeria, W Cameroun, NW Gabon. Ecology: Secondary rain forest, thickets.

Specimens examined:
Nigeria: Calabar Prov., Oban Distr., Oban Group F.R. (fl. Nov.) Binuyo 45402 (K, P); mile 66-67 Calabar-Mamfe road (fl., fr. Feb.) Latilo 45810 (K, WAG); (fr. Mar.) Latilo \& Oguntayo 70569 (K, WAG); Old Calabar R. (fl.) Mann 2235 (K, P); Oban F.R., Orem, Mamfe road (fr, Feb.) Onochie FHI 36409 (K); Oban (fl.) Talbot 1279 (K); (fl.) Talbot 1299 (BM); (fl.) Talbot 1378 (K); (fr.) Talbot 1706 (BM, K, Z); (fr.) Talbot s.n. (BM, K); (f1.) Talbot s.n. (BM).

Cameroun: Mamfe (fl., fr. Apr.) Maitland 1149 (K); SW Prov., Korup National Park, Baro village (fr. Mar.) D. Thomas 3326 (MO, WAG, YA).

Gabon: near Libreville, Mondah F. (Oct.) Breteler \& Lemmens 8344 (WAG); sin. loc. (fl.) Duparquet 53 ( P, type).

Notes: 1. Attached to the sheet of Mann 2235 (P) is a small convolute containing parts of leaves and some flowers of a specimen of C. macrantha. On this convolute is written in Baillon's hand: Cnestis, Duparquet n.53, Gabon. Schellenberg (1938) selected Duparquet 53 as lectotype. He assumed that this specimen was collected in Calabar, Nigeria, probably because all the other specimens available to him, including Mann 2235, came from SE Nigeria. However, Duparquet never collected in Nigeria but in Gabon as correctly stated by Baillon. Breteler \& Lemmens 8344 provides additional evidence that C. macrantha occurs in Gabon.
2. It is not known whether heterostylous flowers occur in this species, as in the specimens examined only a single type of flowers is found.

Cnestis macrophylla Gilg ex Schellenb.
Fig. 92, 93
C. macrophylla Schellenberg, 1910: 18; 1919: 442; 1938: 51.

Type: Cameroun, Bipindi, Zenker 947 (holo: B $\dagger$; lecto: $G$; iso: BM, $\mathrm{K}, \mathrm{P}$ ).

Liana. Branches cylindric, branchlets often somewhat angular, brown-pubescent, soon glabrescent. Leaves 2-4-jugate; petiole with distinct, blackish articulation at base, $8-13.5 \mathrm{~cm}$, rachis $7.5-19 \mathrm{~cm}$ long, glabrous or minutely pubescent. Leaflets stiffly papery, lateral ones more or less opposite, elliptic or (narrowly) obovate, $7-19 \times 4-8 \mathrm{~cm}$, cuneate or rounded and slightly or not unequal at base, terminal one (narrowly) obovate, 11-19 $\times 4.5-8.5 \mathrm{~cm}$, cuneate at base; all leaflets acuminate, glabrous both sides, midrib impressed above, prominent beneath, with 6-8 lateral nerves on each side; tertiary nerves reticulate, distinct on both sides; petiolules $8-11 \mathrm{~mm}$ long, blackish when dry, glabrous or minutely pubescent. Inflorescences racemes, 3-5 together inserted on the stem (cauliflorous), up to 16.5 cm long, up to 30 -flowered, brown-pubescent. Bracts subulate, $1-2 \mathrm{~mm}$ long, curved. Pedicels articulated $0-2 \mathrm{~mm}$ below the calyx, pubescent. Sepals spreading or reflexed, narrowly oblong, 5.5-7.5 $\times 0.8-1.3 \mathrm{~mm}$, acute, pilose outside, glabrous inside, distinctly 3-5-veined. Petals narrowly oblong to linear, ca $8 \times 0.6-1 \mathrm{~mm}$, inflexed at top, glabrous, distinctly 1-3-veined. Stamens with ca 0.2 mm long anthers. Follicles 1-3 in fruit, (narrowly) ellipsoid, oblique,


Fig. 92. Cnestis macrophylla: 1. branch with leaf, showing leaflets beneath, $2 / 3 \times ; 2$. leaflet above, $2 / 3 \times$; 3 . infrutescences, $1 \times(1-2$. Gentry \& Pilz 32759; 3. Leroy s.n.).


Fig. 93. Distribution of Cnestis macrophylla
$3.5-4.4 \times 0.7-1.1 \mathrm{~cm}$, cuneate, with $7-10 \mathrm{~mm}$ long stipe at base; beak more or less slender, distinct, $4-20 \mathrm{~mm}$ long; pericarp with very short, red, spinelike hairs and long, easily caducous, stinging hairs outside and with long, slender, yellowis hairs inside. Seeds (ob )ovoid, ca $16 \times 8 \mathrm{~mm}$, sarcotesta ca 5 mm long.

## Distribution: SW Nigeria, W Cameroun and W Gabon.

Ecology: Rain forest.
Specimens examined:
Nigeria: Ogun State, Om F.R., near Oloji (June) Gentry \& Pill 32759 (MO, WAG).
Cameroun: Bipindi (y.fr.) Zenker 947 (BM, G, K, P, type).
Gabon: Ogooué (fr.) Leroy s.n. (P).

Note: This species differs from C. corniculata only in the very long ( $8-11 \mathrm{~mm}$ ) petiolules, that are almost black when dry. In C. corniculata the petiolule are up to 5 mm long. In other characters $C$. macrophylla fits comfortably within the wide range of variety of C. corniculata, particularly close to the congolana type. Only two fruiting specimens have been collected so far and flowers are incompletely known. Although this taxon is maintained here at species level, additional material when available may render it necessary to reduce it into a variety of C. corniculata.

Both fruiting specimens consist of separate leaves and fruits, which indicate that the plants are cauliflorous. It cannot be established with complete certainty that the leaves and fruits are collected from the same plant and that possible mixtures of two families are not involved. This is, however, not likely, because the stomata are of the same type as seen in other Cnestis species and it is unlikely
that in that case the same error would have been made twice by two separate collectors.

Cnestis mannii (Baker) Schellenb.
Fig. 94-96
C. mannii (Baker) Schellenberg, 1915: 318; 1919: 436; 1938: 34; Hepper, 1958: 743.

Basionym: Connarus mannii Baker, 1868: 459.
Type: Nigeria, Old Calabar, Mann 2264 (holo: K; iso: P).
C. pseudoracemosa (Gilg) Schellenberg, 1919: 436; 1938: 35. Basionym: Connarus pseudoracemosus Gilg, 1891b: 317. Type: Gabon, Libreville, Sibange Farm, Büttner 166 (holo: B $\dagger$; lecto: P).
C. grandifoliolata De Wildeman \& Durand, 1901: 746; Durand \& Durand, 1909: 121; Schellenberg, 1910: 13; 1915: 318; Exell, 1928: 94; 1938: 35; Troupin, 1952: 120; Exell \& Mendonça, 1954: 138. Type: Zaire, Kisantu, Gillet 1420 (holo: BR).
C. tomentosa Hepper, 1957: 112; 1958: 743. Type: Cameroun, Kumba Div., near Banga, S Bakundu F.R., Brenan, Jones, Onochie \& Richards 9328 (holo: K ; iso: $\mathrm{BM}, \mathrm{P}$ ).

Liana, up to 30 m long. Branches cylindric, branchlets somewhat angular, densely brown-pubescent, more rarely glabrous. Leaves 2-4(-5)-jugate; petiole $3-12 \mathrm{~cm}$, rachis $5-15 \mathrm{~cm}$ long, brown-pubescent, sometimes glabrous. Leaflets thickly papery or leathery, lateral ones opposite or not, (narrowly) ovate or elliptic, 4-18 $\times 2-9 \mathrm{~cm}$, rounded to subcordate, rarely cuneate, equal, rarely unequal at base, terminal one (ob)ovate or elliptic, 6-19 $\times 3-12 \mathrm{~cm}$, rounded or rarely cuneate at base; all leaflets acuminate or sometimes acute, glabrous above, brown-tomentose or pubescent, rarely glabrous beneath, midrib impressed above, prominent beneath, with 4-15 lateral nerves on each side; tertiary nerves reticulate, distinct on both sides; petiolules $2-5 \mathrm{~mm}$ long, pilose or more rarely glabrous. Inflorescences panicles, single in leaf-axils on top of young branches, the supporting leaves usually reduced or very young resulting in a compound pseudoterminal inflorescence, up to 40 cm long, many-flowered, densely yellowish brown-pubescent, sometimes also with short glandular hairs. Reduced leaves at base of inflorescences subulate or linear, up to 12 mm long, bracts very small, $0.5-1 \mathrm{~mm}$ long. Pedicels articulated 1-2.5 mm below the calyx, densely pubescent. Flowers heterodistylous. Sepals never reflexed, narrowly imbricate in bud, narrowly ovate or narrowly oblong, $4.0-6.0 \times 1.0-1.5 \mathrm{~mm}$, acute, margins inflexed, yellowish brown-pubescent, rarely with glandular hairs outside, puberulus inside. Petals very narrowly imbricate in bud, obovate or elliptic, $1.5-3.0 \times 1.0 \mathrm{~mm}$, cuneate at base, obtuse or subacute at top, with long hairs in lower half outside, glabrous inside, indistinctly veined. Stamens shortly united at base, subequal, $1.5-2.5$ or (4.0-) $5.0-6.0 \mathrm{~mm}$ long, anthers $0.5-0.6 \times$ 0.3-0.4 mm. Pistils 1.5-2.5 or 4.5-6.5 mm long; ovaries ca 0.5 mm long, yellowish


Fig. 94. Cnestis mannii: 1. branchlet with inflorescences, $2 / 3 \times ; 2$-4. leaflets beneath, $2 / 3 \times$ ( 2 former C. pseudoracem 5 flow partly, $8 \times ; 6-7$. follicles, $1 \times 8$. seed, $1 \times(1$. Onyeachusim \& Latilo 54021; 2. Le Testu 8378; 3,6,8. J. de Wilde et al. 253; 4,7. J. de Wilde et al. 549; 5. Vanderyst 25787).

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Fig. 95. Distribution of Cnestis mannii
pilose; styles straight or curved, pilose at lower half; stigmata more or less oblique, 2-lobed. Follicles 1, sometimes 2 in fruit, narrowly ovoid or narrowly ellipsoid, oblique, 3-6.5 $\times 1-2.5 \mathrm{~cm}$, cuneate, with $5-25 \mathrm{~mm}$ long, more or less distinct stipe at base; beak usually rather slender, $5-15(-20) \mathrm{cm}$ long, distinctly separated; pericarp with short, red hairs and some longer, yellowish hairs outside and with long, easily caducous, yellowish hairs inside. Seeds ovoid, $20-25 \times 10-15 \mathrm{~mm}$, sarcotesta $7-11 \mathrm{~mm}$ long, ruminate.

Distribution: S Nigeria, SW Cameroun, Gabon, SW Zaire, NW Angola.
Ecology: Rain forest, occasionally in farmland. Flowering in Nigeria and Cameroun mainly from January to May, in Gabon and Zaire from September to October.

## Specimens examined:

Nigeria: Ijebu Distr., Omo F.R. (y.fr.) Ade-Oni FHI 39585 (K); Omo F.R., near Oloji (June) Gentry \& Pilz 32785 (MO, WAG); Old Calabar R. (fl. Feb.) Mann 2264 (K, P, type); Ijebu-Ode, Ogun, Omo F.R. (y.fr. May) Odewo \& Adedeji 245 (WAG); mile 52-53 Calabar-Mamfe (fl. Feb.) Onyeachusim \& Latilo 54021 (K, WAG); Ogun, Omo F.R., 3 km S of Alveru (fl.) Pilz 2384 (K); Ijebu, Shasha F.R. (fl.) Ross 198 (BM, G); Oban (fl.) Talbot 1707 (BM, K, Z).
Cameroun: Kumba Distr., Mbalange, S Bakundu (fl. Jan.) Binuyo \& Daramola 35455 (K, P); near Banga, S Bakundu (fl. Mar.) Brenan, Jones, Onochie \& Richards 9328 (BM, K, P, type of C. tomentosa); SW Prov., Ejagam F.R. (fr.) Maruhashi 101 (YA); Johann-Albrechts H. (fl.) Staudt 916 (BM, G).
Gabon: Libreville, Sibange Farm (fl. Sept.) Büttner 166 (P, type of C.pseudoracemosa); Cristal Mts (fr. Jan.) J. de Wilde et al. 253 (LBV, WAG); (fr.) J. de Wilde et al. 549 (LBV, WAG); (fr.) J. de Wilde et al. s.n. (WAG, spirit); Ogoué-Ivindo, La Nké (fl. Oct.) Floret, A. Louis \& Moungazi 1733 (LBV); Libreville (fl.b. Sept.) Klaine 2364, 2365 (P); near Lastoursville (fl. Sept.) Le Testu 8378 (BM, BR, LISC, P).


Fig. 96. Cnestis mannii: follicles (J. de Wilde et al. 549; phot. J.C. Arends).

Zaire: Bas-Congo, Gimbi (fl. Sept.) Compère 393 (BR, K); Prov. Leopoldville, Thijsville, Kinganga (fl. Oct.) Compère 684 (BR, K); Mankayi (fl. Oct.) Devred 866 (BR, K); Kisantu (fl.) Gillet 1420 (BR, type of C. grandifoliolata); Kisantu (fl. Sept.) Vanderyst 25785, 25787 (BR); (fl.) Vanderyst $35531,35637(\mathrm{BR})$.
Angola: Cuanza Norte, Loanda (fr.) Gossweiler 750 (BM, K, P).
Note: The number of leaflets and their shape, size, venation and indumentum show a considerable variation. One form was described by Gilg (1891) as Connarus pseudoracemosus, based on a specimen collected in Gabon by Büttner. It is characterized by glabrous, comparatively small leaflets with few secondary nerves. Some other specimens from Gabon are close to this specimen in having glabrous, but larger leaflets (Klaine 2364, J. de Wilde et al. 253). Le Testu 8378,
collected near Lastoursville resembles Büttner 166 in size and shape of leaflets, but the leaflets are somewhat pubescent beneath. Another more or less extreme form was described by Hepper (1956) as C. tomentosa. It is characterized by the comparatively large number of leaflets (up to 11), which are softly tomentose beneath. In fact, in C. mannii the indumentum of the leaflets beneath can vary from glabrous to densely pilose, and the hairs can be short to long.

The flowers are quite uniform in comparison to other species.
Only 5 specimens with mature fruits have been collected: 3 in Gabon, one in Cameroun, and one in N Angola. Consequently, the variation in the fruits is insufficiently known. In the few fruiting specimens examined the variation in size and shape of the follicle is considerable.

Under these circumstances it is not possible to maintain the species proposed by Gilg and Hepper.

It is remarkable that this species is apparently rare everywhere in its comparatively large range of distribution; there is not much material available.

## Cnestis mildbraedii Gilg

Fig. 97, 98
C. mildbraedii Gilg, 1911: 229; Schellenberg, 1938: 43; Troupin, 1952: 122.

Type: Zaire, between Beni and Irumu, Mildbraed 2842 (holo: $\mathrm{B} \dagger$ ), neo: Sudan, Lotti Imatong Mts, A. Thomas 1759 (BM; iso: BR, K). See note 1 .
C. ugandensis Schellenberg, 1938: 44; Eggeling, 1952: 100; Hemsley, 1956: 2. Type: Uganda, Mengo Distr., Mabira F., Mulange, Dümmer 5422 (holo: K).

Large shrub or small tree. Branches cylindric, branchlets with longitudinal grooves, brown-pilose, later glabrescent. Leaves 12-18-jugate; petiole $4-8 \mathrm{~cm}$, rachis $26-31 \mathrm{~cm}$ long in full-grown leaves, yellowish brown-pubescent. Leaflets papery, lateral ones in basical part of leaf more or less opposite and often fullgrown long time before alternate leaflets in apical part, narrowly ovate or narrowly oblong, $3.5-14 \times 1.5-3 \mathrm{~cm}$, rounded and (very) unequal at base, terminal one narrowly obovate or narrowly elliptic, $4.5-8 \times 1.5-3 \mathrm{~cm}$, cuneate at base; all leaflets obtuse or shortly acuminate, when young pilose but often glabrescent above, rather densely pilose beneath, midrib impressed above, prominent beneath, with 7-12 lateral nerves on each side; tertiary nerves reticulate, indistinct; petiolules 2-2.5 mm long, pubescent. Inflorescences racemes or sometimes panicles, $1-20$ per leaf-axil on young and older branches, $7-17 \mathrm{~cm}$ long, 15-30-flowered, yellowish brown-pilose. Bracts subulate to linear, $2.5-3 \mathrm{~mm}$ long. Pedicels articulated $2-3 \mathrm{~mm}$ below the calyx, densely pilose. Sepals never reflexed, narrowly imbricate in bud, narrowly (ob)ovate or narrowly oblong, $5.0-6.0 \times 1.5-2.5 \mathrm{~mm}$, obtuse, flat, yellow-pilose outside, glabrous or sometimes minutely pubescent inside. Petals narrowly imbricate in bud, elliptic or (narrowly) oblong, $5.5-6.0 \times 2.0-3.0 \mathrm{~mm}$, cuneate at base, distinctly retuse at top, glabrous, indistinctly veined. Stamens free, distinctly differing in length in the two whorls, $1.0-5.0 \mathrm{~mm}$ long, anthers ca $0.4 \times 0.3 \mathrm{~mm}$. Pistils $1.0-5.2 \mathrm{~mm}$ long;

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Fig. 97. Cnestis mildbraedii: 1. branch with young leaf, $2 / 3 \times ; 2$. leaflets beneath of full-grown leaf, $2 / 3 \times ; 3$. branch with inflorescences, $2 / 3 \times$; 4. flower, $6 \times$; 5 . follicle, $1 \times(1-2,5$. A. Thomas 1759; 3-4. Eggeling 1553).


Fig. 98. Distribution of Cnestis mildbraedii
ovaries ca 0.7 mm long, yellowish-pilose; styles straight, pilose at lower half; stigmata oblique. Follicles 1 in fruit, (narrowly) ellipsoid, oblique, 3-3.5 $\times 1$ cm , cuneate, with ca 5 mm long stipe at base; beak slender, ca 10 mm long, distinctly separated; pericarp with rather short, scarlet hairs outside. Seeds not seen.

Distribution: S Sudan, NE Zaire, Uganda, W Kenya.
Ecology: Forest, 1000-2000 m altitude. Flowering from August to December.
Specimens examined:

Sudan: Equatoria, Torit, Lotti F. (fr. Feb.) Jackson 1020 (B); Lotti Imatong Mts (fr. Dec.) A. Thomas 1759 (BM, BR, K, type).
Uganda: Mengo Distr., Mabira F., Mulange (fl. Aug.) Dümmer 5422 (K, type of C. ugandensis); Bunyoro Distr., Budongo F. (fl. Dec.) Eggeling $1553(=1468)(\mathrm{BR}, \mathrm{K})$; Buganda, Infranga F. (July) Kertlands.n. (K).
Kenya: Kibiri Block, Kakamega F., S side of Yala R. (Jan.) Faden 70/29 (EA).
Notes: 1. The holotype of C. mildbraedii Gilg was destroyed in Berlin. This was the only specimen cited by Gilg and by Schellenberg. The description of C. mildbraedii fits that of C. ugandensis Schellenberg as well as the specimens examined. In my opinion, there is no doubt that C. mildbraedii and C. ugandensis are conspecific. The type locality of Mildbraed 2842, the holotype, is linked to the area of distribution of $C$. ugandensis as well.
2. The specimens Kertland s.n. (from Uganda) and Faden 70/29 (from Kenya) are sterile. The leaves of these specimens resemble the leaves of flowering and fruiting material to such an extent that they undoubtedly belong in C. mildbraedii. Faden $70 / 29$ is the first record from Kenya.
3. The flowers are probably heterodistylous, but this is not certain; only two flowering specimens were available.

Cnestis palala (Lour.) Merr.
Fig. 99
C. palala (Lour.) Merrill, 1922: 201; 1935: 184; Schellenberg, 1938: 36; Andreas \& Prop, 1954: 612; Leenhouts, 1958b: 499; Pancho, 1983: 397.

Basionym: Thysanus palala de Loureiro, 1790: 284 p.p. (excl. syn: Rumphius).
Type: S Vietnam, Tourane (Da Nang), Clemens 3805 (neo design. by Merrill, 1935: BM, K, P).
C. palala (Lour.) Merr. subsp. diffusa (Blanco) Andreas, 1954: 613; Leenhouts, 1958b: 499. For type see under C. diffusa.
C. diffusa Blanco, 1837:386; Schellenberg, 1938: 38. Type: Philippines, Luzon, Cuming 951 (neo design. by Schellenberg, 1938: K; iso: BM).
C. platantha Griffith, 1854: 434; Andreas \& Prop, 1954: 614; Leenhouts, 1958b: 499. Type: Malay Penins., Griffith 1256 (lecto design. by Andreas \& Prop, 1954: K).
C. annamensis Gagnepain, 1952: 207. Type: N Vietnam, Vinh, Chevalier 32450 (holo: P).
For complete synonymy and literature see Leenhouts (1958b).
Liana up to 25 m long, large shrub (often climbing) or small tree, up to 10 m high. Branches cylindric, branchlets often somewhat angular, densely brownpilose, later more or less glabrescent. Leaves 6-21-jugate; petiole 1-7 cm, rachis $7-30(-38) \mathrm{cm}$ long, densely brown-pilose. Leaflets papery, lateral ones opposite or more or less alternate, (narrowly) ovate or (narrowly) oblong, (1-)1.5-8 $\times$ $0.7-2.5 \mathrm{~cm}$, rounded, truncate or subcordate and unequal or not at base, terminal one (narrowly) elliptic or (narrowly) obovate, $3-8 \times 1-3 \mathrm{~cm}$, rounded or cuneate at base; all leaflets rounded to acuminate, pilose (especially when young) or glabrous above, densely pilose beneath, midrib impressed above, prominent and densely pilose beneath, with 5-15 often indistinct lateral nerves on each side; tertiary nerves reticulate, usually indistinct; petiolules $0.5-1.5 \mathrm{~mm}$ long, pilose. Inflorescences racemes or panicles, a few to many per leaf-axil on older branches, $2-8 \mathrm{~cm}$ long, $10-35$-flowered, densely yellowish brown-pilose, mostly also with glandular hairs. Bracts subulate, $0.5-2 \mathrm{~mm}$ long. Pedicels articulated $0-6 \mathrm{~mm}$ below the calyx, densely pilose, mostly also with glandular hairs. Flowers obscurely heterodistylous, often almost homostylous. Sepals never reflexed, narrowly imbricate or more or less valvate in bud, narrowly ovate or narrowly oblong, $2.0-5.0 \times 0.5-1.0(-1.3) \mathrm{mm}$, acute or obtuse, often inflexed at top, densely brown-pilose with usually also many glandular hairs outside, pubescent inside. Petals imbricate in bud, (ob)ovate or elliptic to narrowly oblong, $(0.6-) 2.0-4.0(-5.1) \times(0.5-) 0.8-1.5 \mathrm{~mm}$, cuneate or rounded at base, rounded, truncate or retuse at top, glabrous or with some long hairs in basal part outside, glabrous inside, indistinctly veined. Stamens free or very shortly united at base,


Fig. 99. Distribution of Cnestis palala
slightly differing in length in the two whorls, $0.5-2.0(-4.0) \mathrm{mm}$ long, anthers ca $0.2 \times 0.2 \mathrm{~mm}$. Pistils $1.0-2.0(-3.5) \mathrm{mm}$ long; ovaries ca 0.5 mm long, yellowish brown-pilose; styles straight or curved, often pilose in basical part; stigmata oblique or not, prominent or not, more or less 2-lobed. Follicles 1-3 in fruit, ellipsoid, obovoid or pyriform, more or less oblique, 2.5-6 $\times 1-2.5 \mathrm{~cm}$, cuneate, with short or long (up to 25 mm ) stipe at base; apex rounded or with up to $10(-15) \mathrm{mm}$ long, more or less distinctly separated beak; pericarp thick and firm, with fairly long, rather soft, red hairs outside and long yellowish hairs inside. Seeds ovoid, sometimes oblique, $15-30 \times 8-15 \mathrm{~mm}$, sarcotesta $5-15 \mathrm{~mm}$ long, ruminate.

Distribution: S Burma, Thailand, S Laos, Vietnam, N Philippines, Andaman

Islands, Malaysia and Indonesia (Sumatra, Borneo; also recorded by Leenhouts (1958b) from Celebes).

Ecology: Rain forest, primary or secondary; riverain or marsh, sometimes dry forest; occasionally also in thickets. Flowering in Burma, Thailand and Laos mainly from October to January, Vietnam February to October, Philippines mainly January to April, Andaman Islands November to May, Malay Peninsula mainly October to March, Sumatra February to April, Borneo April to September. Fruiting some months later.

Selection of the ca 175 specimens examined:
Burma: Tenasserim, Falconer 94 (L); (fr.) Falconer s.n. (K, L); sin. loc. (fl., fr.) Griffith 1254 (K, P); Pegu (fr.) Kurz 1990 (L); Myaungmya Distr. (fr.) Lace 2988 (K); Amherst Distr. (fr. Feb.) Lace 5697 (K); Rangoon (fl. Oct.) Maingay 510/2 (K); Syriam, Ale Ywa (fl. Nov.) McKee 5800 (K, P).
Thailand: Bangkok, Chak Jai-Sriracha F. (fl.b. Nov.) Collins 1701 (BM); Phangnga, Khlong nang yon (fr. Apr.) Geesink \& Santisuk 5027 (L); Prov. Rayong, Ban Phe (fl. Dec.) Geesink \& Hiepko 7867 (K, L); Penins. Ranong, Kapur (fl. Dec.) Indrapong \& Smitinand 99 (K, L, P); Doi Dui Dong (fr. Mar.) Kerr 3157 (BM); Rat Buri (fr. Mar.) Kerr 10633 (BM, K); Prov. Utai Thani, Ban Rai (fr. Feb.) van Beusekom \& Santisuk 2959 (L, P).
Laos: Attopeu (fl. Jan.) Harmand 30 (L, P); Central Laos, Mekong R. (fl.) Harmand s.n. (L); km 20 Savannakhet-Quangtri (fl., y.fr. Jan.) Polaine 11689 (K, L); (fl., y.fr.) Polaine 11862 (K, L).
Vietnam: Tongking, Kiên Khê (fl. Aug.) Bon 3021 (L); (fr. Dec.) Bon 4076 (L); Vinh (y.fr.) Chevalier 32450 (P, type of C. annamensis); Tourane (fl. July) Clemens 3805 (BM, K, P, type); Vinh (fr. May) Fleury 32450 (P, WAG); Tongking, Cho Ganh (fl. Oct.) Pètelot 1177 (K, L); (fl. Sept.) Pètelot 1447 (K, L); Gia Rai (fl. Feb.) Polaine 2519 (P).
Philippines: Luzon, Prov. Bataan, Lamao R. (fl. Feb.) Borden 290 (P); Burias I. (y.fr. June) Clark 20188 (K); Prov. Albay (f1.) Cuming 951 (BM, K, type of C. diffusa and C. palala subsp. diffusa); Prov. Tayabas (fl. Mar.) Edaño 26943 (BM, K); Prov. of Laguna, Los Baños (fr. Apr.) Elmer 8267 (K); Prov. Union, Bauang (fr.) Fenix 127 (K); Rizal Prov., Antipolo (fl. Jan.) Merrill 252 (BM, K, L, P); Rizal Prov., Tanay (fr. Mar.) Merrill 2341 (K); Prov. Bataan, Lamao R. (fr. May) Whitford 24037 (K).
Andaman Islands: Little Andaman, Hut Bay (fl. Jan.) Bhargava 3427 (L); S Andaman (fl. May) Heinig 640 (L); S Andaman, Corbye's Cove (fl. Feb.) King's Collector s.n. (BM); North Bay (fl. Jan.) King's Collector s.n. (K); Dhani Khari (fl. Nov.) King's Collector s.n. (L); Carbyns Cove (fr. Apr.) Nair 3656 (L).
Malaysia: Malay Penins.: Ulu Selangor, Semangkok F.R. (fr. May) Chan FRI 13313 (L); Penang (fl. Jan.) Curtis 145 (K); sin. loc. (fl. Feb.) Gaudichaud 89 (L, P); (fl. Feb.) Gaudichaud 93 (P); Selangor, -Kepong (fl. Feb.) Gerus KEP 99476 (L); sin. loc. (fl., fr.) Griffith 1254 (K, P); (fl.) Griffith 1256 (K, type of C. platantha); Kelantan, Temangan (fr. June) Khairuddin FRI 31792 (L); Penang (fl. July) King's Collector 1330 (L); Perak, Larut (fr. Jan.) King's Collector 3759 (BM, K); sin. loc. (fr.) Maingay 509 (BM, L); Kedah, Langkawi (fr. Feb.) Millard KL 1413 (K, L); Johore, Sungei Bantang (fr. May) Shah \& Samsuri MS 1738 (K, L); Perak, road to Cameron Highlands (fr. Aug.) Stone 7290 (L); Kedah, Langkawi (fr. Mar.) Stone 15037 (L); Penang (fl., fr.) Wallich 8529 (K, P).
Malaysia: Sabah (N.Borneo): Tawau, Kalumpang Balong (fr. June) Bakar Hussin SAN 18514 (L); Tawau (fl.) Elmer 20995 (BM, L, P); (fr.) Elmer 21482 (BM, L); Distr. Lamag, Ulu Sg. Pin (fl. Sept.) Madani \& Saigol SAN 90980 (K, L); Distr. Tawau, Kalabakan (fr. June) Meyer SAN 19251 (L); Distr. Ranau, Kg. Pinawantai (fr. May) Shea \& Aban SAN 76929 (L); Distr. Beaufort, Ulu Membakut (fr. Sept.) Talib Bidin \& Marsal SAN 86131 (K).
Malaysia: Sarawak (N.Borneo): Distr. Barau, Paku (fr. June) Anderson 4021 (L); Belaga (fl. Apr.) Ashton S 18270 (L); Distr. Bintulu, Simalajau (fr. Dec.) Paie S 15829 (K, L); Melinau, Kapit (fl.b. Aug.) Paie S 25812 (L); Limbang, Long Amok (fl. Sept.) Rena George S 43010 (K, L); Limbang (fr. Oct.) Wright \& Ismawi S 32393 (K, L).


Fig. 100. Comparative petal length, expressed as percentage of sepal length, of 41 specimens of C. palala, arranged according to increasing length ratio.

Brunei (N.Borneo): Puteh, Tutong (fr. July) Ashton BRUN 296 (L); Bangar, Temburong (fr. Sept.) Ashton BRUN 493 (L).
Indonesia: Sumatra: Simeulue I., Tapah (Feb.) Achmad 1695 (L); Atjeh, Ketambe, 35 km NW of Kutatjane (fr. July) W. de Wilde 13929 (K, L); (fl. Feb.) W. de Wilde 14512 (K, L); (fl. Feb.) W. de Wilde 14548 (K, L); 75 km WNW of Medan (fr.) W. de Wilde 19433 (K, L); Lampongs, Sepaetik (fr. Jan.) Gusdorf 157 (K, L); sin. loc. (fl.b.) Teysmann 4016 (K, L); sin. loc. (fr.) Teysmann 4455 (L); Atjeh, from Pendeng via Oreng to Gadjah (fr. Feb.) van Steenis 9337 (K, L).

Indonesia: Kalimantan (Borneo): S of Kwala Kwajan, S of Permantang (fr. Jan.) Alston 13338 (BM, L); East Kutei, Mahakam Estuary (fr. July) Kostermans 12509 (K, L); Berau (fr. Oct.) Kostermans 21303 (L, P); upper Samba R., $60-80 \mathrm{~km}$ NNW of Tumbang Samba (fr. Nov.) Mogea \& W. de Wilde 3564 (L).

Note: Within the area of distribution C. palala varies in appearance from the North-West to the South-East. The petals are comparatively long in specimens from Burma to the Malay Peninsula and the Philippines, but short in those from the Malay Peninsula, Sumatra and Borneo. The follicles are often comparatively small and beaked in plants from Burma to the Malay Peninsula, small and not or hardly beaked in the Philippines and large, while they are not or hardly beaked in the Malay Peninsula, Sumatra and Borneo. Leaves are often larger and have more leaflets in Sumatra and Borneo than elsewhere.
Schellenberg (1938) distinguished two species in Asia: C. palala and C. diffusa, the latter being restricted to the Philippines.
Andreas \& Prop (1954) and Leenhouts (1958b) reject Schellenberg's concept. They also propose a division in two species, but $C$. diffusa is merged with $C$. palala while C. platantha is considered to be different. This division is based on a discontinuity in the comparative length of petals (expressed as a percentage of sepal lenght).

Fig. 100 shows the distribution of this comparative petal length. The discontinuity between peaks (one at about 0.5 and one at about 1.0 ) is not as obvious


Fig. 101. Follicle and beak length of 42 specimens of C. palala, arranged according to increasing follicle length.
as suggested by Andreas \& Prop. The difference in comparative petal length is not clear in the Malay Peninsula, as Gaudichaud 89 and 93 are intermediate.
In his key, Leenhouts (1958b) additionally mentioned a difference in the inflorescences, these being racemose in C. palala and paniculate in C. platantha. In fact, the inflorescence is always paniculate, but sometimes reduced to a pseudoraceme, especially in specimens from the northern part of the area.
Andreas \& Prop divide C. palala into two subspecies, subsp. palala with small, beaked follicles from the northern part of the area and subsp. diffusa with not or hardly beaked follicles from the Philippines and S Malaya, usually large, but small in the Philippines. Leenhouts (1958b) stated that fruiting specimens of $C$. palala subsp. diffusa and $C$. platantha cannot be distinguished with certainty. In fact, shape and size of the follicles do not show any discontinuity (see fig. 101), while the geographical segregation of the different forms does not hold. Some specimens from Burma and Thailand show scarcely beaked follicles (e.g. Kurz 1990, Kerr 3157), some from the Malay Peninsula (e.g. Stone 15037, Maingay 509) and Borneo (Meyer SAN 19251, Mogea \& W. de Wilde 3564) have distinctly, however short, beaked follicles, while the fruiting specimens from the Philippines show small follicles lacking a distinct beak.

In my opinion this division of the Asiatic material into two species and one of these into two subspecies is not warranted and should not be maintained: it all belongs to one species, C. palala.
When compared to the African continent, where most species of Cnestis occur, a comparative variation in petal length is seen in C. corniculata, and to a lesser extent also in the shape of its fruits.

Uses: A decoction of the roots is drunk against stomach-ache, malaria and after childbirth; external it is used to cure sprains and (possibly) gonorrhoea
(Burkill, 1966). According to Leenhouts (1958b) seeds and possibly also fruits are eaten. But seeds have also been recorded to be poisonous to dogs (notes on herbarium sheets; possibly a confusion with Rourea $s p$. of which seeds are poisonous to carnivorous animals).

## Cnestis polyphylla Lam.

Fig. 102, 103
C. polyphylla Lamarck, 1789: 23, pl.387: fig.2; De Candolle, 1825: 87; G. Don, 1832: 91; Planchon, 1850: 440; Walpers, 1852: 306; Baillon, 1867: 243; Baker, 1877: 65; Baillon, 1882: 346; de Lanessan, 1886: 530; Drake del Castillo, 1902: 33; Palacky, 1907: 57; Schellenberg, 1910: 13; 1915: 318; 1938: 39; Keraudren, 1958: 20, fig.5(2-4); Irvine, 1961: 572.

Type: Madagascar, Commerson s.n. (lecto: herb. De Jussieu: P). See note 2.
C. polyphylla Lam. var. bullata Baillon, 1867: 243; 1882: 346. Type: Madagascar, St.Marie I., Boivin 1889 (lecto design. by Baillon, 1882: P).
C. glabra Lamarck, 1789: 23, pl.387: fig.1; De Candolle, 1825: 87; G. Don, 1832: 91; Planchon, 1850: 440; Walpers, 1852: 306; Baillon, 1867: 243; Baker, 1877: 64; Baillon, 1882: 346; de Lanessan, 1886: 530; Baillon, 1887: tab.16a; Drake del Castillo, 1902: 34; Palacky, 1907: 57; Schellenberg, 1910: 13; 1915: 318; 1938: 40; Keraudren, 1958: 22, fig.5(5-7). Type: Mauritius, Commerson 599 (lecto design. by Schellenberg, 1938: P; iso: L).
C. scandens Gmelin, 1791: 729. Homotypic synonym of C. glabra.
C. borbonensis Raeuschel, 1797: 132 (nomen).
C. madagascariensis Raeuschel, 1797: 132 (nomen).
C. natalensis (Hochstetter) Planchon ex Sonder, 1860: 528; Gilg, 1896: 215; Schellenberg, 1910: 14; Baker f., 1911: 50; Schellenberg, 1915: 318; Burtt Davy, 1932: 511; Schellenberg, 1938: 40; Wild, 1953: 65; Mendes, 1966: 616, fig.130; Mendes, 1969: 2. Basionym: Zanthoxylum natalense Hochstetter in Krauss, 1844: 304; Sonder, 1850: 24 ; Schellenberg, 1910: 14 (as Xanthoxylum natalense in syn.); 1938: 40 (as Xanthophyllum natalense in syn.). Type: S African Republic, Natal, between Umlaas R. and Port Natal (Durban), Krauss 60 (holo: K). See
note 3.
C. lurida Baillon, 1867: 244; 1882: 346; Drake del Castillo, 1902: 34; Palacky, 1907: 57; Schellenberg, 1910: 15; 1938: 40; Keraudren, 1958: 17, fig.4(6-10). Type: Madagascar, Nossi-Bé I., Boivin s.n. (holo: P).
C. bullata Baillon, 1886: pl.17. For type see under C. polyphylla var. bullata.
C. boiviniana Baillon (1882: 346, nomen) ex Schellenberg, 1938: 39; Keraudren, 1958: 18. Type: Madagascar, St.Marie I., Boivin s.n. (holo: P).

Omphalobium discolor Sonder, 1850: 24 (nomen, in syn.).
Sarmienta cauliflora Sieber, nomen in sched.; Baillon, 1867: 243 (in syn.).
Liana or shrub, usually climbing. Branches cylindric, usually distinctly lenticellate, branchlets cylindric, usually densely brown-, rarely grey-pilose, later more or less glabrescent. Leaves 4-14-jugate; petiole (0.3-)1-10 cm, rachis 4-25


Fig. 102. Cnestis polyphylla: 1. flowering branch, $2 / 3 \times ; 2-7$. leaflets beneath, $2 / 3 \times(2$ former C. lurida, 4 former C. boiviniana, 5 former C. glabra, 7 former C. natalensis); 8 . flower, $8 \times ; 9-12$. follicles, $2 \times(9$ former C. natalensis; 1. Humbert 17574; 2. Perrier de la Bathie 6319; 3. Humbert 5735; 4. Boivin s.n.; 5. Commerson s.n.; 6. Kokwaro 3920; 7. Jalpin 14610; 8. Rakstomama 5879; 9. Ward 2830; 10. Faden 72/68; 11-12. Bosser 17013).
cm long, brown- or grey-pilose, sometimes glabrescent. Leaflets papery or more or less leathery, lateral ones often alternate, (narrowly) ovate, elliptic or oblong, $1-14(-18) \times 0.7-4.5(-7.5) \mathrm{cm}$, cuneate or rounded, sometimes truncate and unequal or not at base, terminal one (narrowly) obovate or elliptic, 2-13(-15.5) $\times 1-4.5(-7.5) \mathrm{cm}$, cuneate or rounded at base; all leaflets acuminate, obtuse or retuse, glabrous or rarely somewhat pubescent above, glabrous or more or less densely white-, brown- or sometimes grey-pilose beneath, midrib impressed above, prominent beneath, mostly pilose on both sides, with 6-12 lateral nerves on each side; tertiary nerves reticulate, usually distinct on both sides; petiolules 1-6 mm long, glabrous or pilose. Inflorescences racemes or panicles, up to 15 per leaf-axil on older or young branches, more rarely the supporting leaves reduced resulting in a compound pseudoterminal inflorescence, $3-10 \mathrm{~cm}$ long, 5-30-flowered, brown-pilose. Bracts ovate to subulate, $1-2 \mathrm{~mm}$ long, frequently with long hairs at top. Pedicels articulated (0-)1-3(-5) mm below the calyx, pilose. Flowers heterostylous, possibly intermediate between heterodi- and heterotristylous. Sepals reflexed, imbricate in bud, narrowly ovate, $2.5-5.0 \times 1.0-2.0 \mathrm{~mm}$, acute, flat, brown-pilose outside, glabrous or pubescent outside. Petals valvate in bud, (narrowly) obovate, (1.5-)2.0-4.0(-4.5) $\times 0.5-1.5 \mathrm{~mm}$, cuneate at base, obtuse, truncate or retuse at top, glabrous or with some long hairs in basal part outside, glabrous inside, indistinctly veined. Stamens free, slightly differing in length in the two whorls, ( $1.0-$ ) $1.5-4.0 \mathrm{~mm}$ long, anthers $0.4-0.5 \times 0.3-0.4 \mathrm{~mm}$. Pistils $1.0-4.5 \mathrm{~mm}$ long; ovaries $0.5-1.0 \mathrm{~mm}$ long, yellowish pilose; styles straight or curved, pilose in basical part; stigmata more or less prominent, usually oblique, 2-lobed. Follicles $1(-5)$ in fruit, obovoid or ellipsoid, more or less oblique, (1-)1.5-2.5 $\times 0.7-1.0 \mathrm{~cm}$, cuneate or rounded at base; apex rounded, acute or mucronate, sometimes with a short beak up to 4 mm long; pericarp with short or fairly long, rather soft, red hairs outside and long, easily caducous, stinging, yellowish hairs inside. Seeds ovoid, 8-18 $\times(3-) 5-9 \mathrm{~mm}$, sarcotesta $3-9 \mathrm{~mm}$ long, ruminate.

Distribution: S Kenya, E Zimbabwe and adjacent Mozambique, the eastern part of the S African Republic, Madagascar, Reunion and Mauritius.

Ecology: Forests, also in shrubby vegetations on rocky slopes, both in wet and in dry places, from 0-2000 m. Flowering mainly from August to December, in Kenya from December to March.

Selection of the ca 150 specimens examined:

Kenya: Kwale Distr., Jadini F., 30 km S of Mombasa (fl., fr. Jan.) Faden \& Faden 72/68 (EA, K); Diani F., 30 km S of Mombasa (fl., fr. Mar.) Kibuwa 1207 (BR, EA, K); Ukunda-Jadini, 30 km S of Mombasa (fl., fr. Mar.) Kibuwa 1218 (BR, EA, K); Diani F. (fl. Dec.) Kokwaro 3920 (BR, EA, K); Jadini-Mombasa (fr.) Robertson 4366 (EA, K, WAG); (fl.b.) Robertson 5098 (EA, K, WAG).

Zimbabwe: Distr. Melsetter, Chisengu F. R. (fr. Dec.) Armitage 176 (SRGH); Distr. Chipinga (fl. Dec.) Goldsmith 52/65 (SRGH); Chirinda Outskirts (fl. Dec.) Swynnerton 166 (BM, K, Z); Msasa Kop (fl. Sept.) Taylor 1740 (E, SRGH); Chirinda (fr.) Wild 2079 (BR, K); Wild 2126 (BR, K, SRGH).


Fig. 103. Distribution of Cnestis polyphylla

Mozambique: Distr. Manica es Sofala, Mossurize, Espungabera (fl. Aug.) Pimenta 13 (K, LISC, SRGH); Mt Marruma (fl. Sept.) Swynnerton 1348 (BM, K).
S African Republic: Pondoland, Umfuta (fl.) Bachmann 548 (E); Natal, Ubombo (fr. Nov.) Botha \& van Wijk 1128 (PRE); Transvaal, Bourkes Luck Potholes (fr. Dec.) Burchmore LN 1149 (PRE); Swaziland, Piggs Peak (fl. Sept.) Compton 31560 (K, M, PRE); Natal, Etonjaneni (fl. Nov.) Edwards 2309 (K); Natal (fr.) Gerrard 1098 (BM, K); Port

- Natal (fl.) Gueinzius 54 (C, P); Transkei, N of Umtata (fr. Dec.) Hilliard \& Burtt 18781 (E); Bothas Hill (fl. Sept.) Hutchinson 4651 (K); Transvaal, Pilgrims Rest (fr. Dec.) Jalpin 14610 (PRE); Port Natal (fr.) Krauss 60 (K, type of C. natalensis); Natal, Mbombe area (fr. Nov.) Mthonti $1 b$ (PRE); Distr. Kentani (fl., fr. Sept.) Pegler 803 (PRE, Z); Transvaal, Haenertsburg (fr. Nov.) Pott 13389 (PRE); Natal, Maritzburg (fl.) Rehmann 7534 (Z); Natal, Alexandra (fl. Sept.) Rudatis 1119 (BM, K, L, P, WAG, Z); Transvaal, Distr. Letaba, Duivelskloof (fl. Sept.) Scheepers 997 (BM, BR, K, M, PRE); Prov. Cape, Distr. Pondoland, Egossa F. (fl. Aug.) Sim 2368 (PRE); Transkei, Mateku Waterfall (fr. Nov.) Strey 10160 (K, WAG); Transkei, 9.6 km SW of Lusikisiki-Port St.Johns (fl. Aug.) Venter \& Vorster 157 (C, K, PRE).
Madagascar: Central Madagascar (fr.) Baron 2403 (K); Cupania (fl. Aug.) Baron 6759 (K); (fl.) Baron 6761 (K); St.Marie I. (fr.) Boivin 1888 (P); Nossi-Bé (fr.) Boivin s.n. (P, type of C. lurida); St.Marie I. (fl., fr.) Boivin s.n. (BM); St.Marie I. (fl.) Boivin s.n. (P,
type of C. boiviniana); sin. loc. (fr.) Boivin 1889 (P, type of C. polyphylla var. bullata and C. bullata); Foulpointe (fl., fr. Dec.) Bosser 17013 (P); Nickelville (fr. Jan.) Capuron 104 (P); Mandena, N of Fort Dauphin (fr.) Capuron 370 (P); sin. loc. (fl., fr.) Commerson s.n. (P, type); Fenerive (fr. Nov.) Debray 1875 (P); Belavenoke, Fort Dauphin (fl. Sept.) Decary 10616 (P); 30 km N of Fort Dauphin (fr. Nov.) den Outer \& van Veenendaal 1182 (WAG); sin. loc. (fl.) du Petit Thouars s.n. (BM); sin. loc. (fl., y.fr.) du Petit Thouars s.n. (BM); SE of Alaotra L. (fl. Oct.) Humbert 17574 (P); near Sambava (fr.) Humbert \& Capuron 24439 (K); Ambohoabé, Soanierana (fr. Dec.) Lam \& Meeuse 5669 (L); near Moramanga (fl. Aug.) Perrier de la Bathie 18029 (K).

Reunion: Mare Longue, St.Philippe (fl.b. Oct.) Bernardi 14500 (K, P, Z); sin. loc. (fl.b.) Boivin 14101 (P); Dos d’Ane (fl. Dec.) Bosser 20984 (P); Mare Longue, St.Philippe (fl. Oct.) Cadet 4456
(P); sin. loc. (fl. Dec.) Commerson s.n. (P); St.Philippe (fl. Nov.) Friedmann 2529 (K, P); sin. loc. (fl.) Richard 37 (P); sin. loc. (fl., fr.) Richard 58 (P).

Mauritius: sin. loc. (fr. Feb.) Ayres s.n. (K); sin. loc. (fl.) Blackburn s.n. (K); sin. loc. (fl., y.fr.) Boivin 1562 (P); sin. loc. (fl. Aug.) Boivin s.n. (P); sin. loc. (fl.) Bouton s.n. (K, P); sin. loc. (fl., fr.) Carmichael s.n. (K); sin. loc. (fl., fr.) Commerson 599 (L, P, type of C. glabra); sin. loc. (fl.b.) Cunningham 364 (BM, K); near Mare aux Vacoas, Perrier Nature R. (fl. Oct.) Lorence 1840 (K, P); sin. loc. (fl.) Sieber Fl.M. 2 no. 285 (BR, C, K, L, P).

Notes: 1. C. polyphylla is distributed in three well separated areas: Madagascar (including Mauritius and Reunion), SE Kenya and SE Africa. Especially in Madagascar, the species is strongly variable in number, size, shape and indumentum of the leaflets, length of the petiolules and position of the inflorescences.

Material with few, large, glabrous leaflets, long petiolules and inflorescences situated on the old branches was considered by many authors (e.g. Schellenberg, 1938; Keraudren, 1958) to represent C. glabra, material with numerous, small leaflets pilose beneath, and inflorescences situated on old and young branches to represent $C$. polyphylla. Analysis of the specimens now available shows that these species cannot be upheld as there are too many intermediate specimens.
According to Baillon (1867), C. lurida differs in the rounded apex of the comparatively small, almost membranous leaflets, which are greyish beneath. However, size and shape of the leaflets are close to C. polyphylla. The grey colour of the leaflets beneath is remarkable, but not related to other characters and does not warrant a separate specific status.

The specimen Boivin s.n., type of C. boiviniana, fits also in C. polyphylla, although it is a fairly extreme form in having large obovate leaflets with a greyish indumentum beneath.

Material from SE Africa was described as C. natalensis. It differs from the material from Madagascar in the small, very oblique leaflets, relatively broad sepals often pilose inside, and an often somewhat larger follicle with a more or less distinct beak. Material from the isolated population in Kenya bridges the differences in characters of the leaflets, the sepals and the fruits between SE Africa and N Madagascar. This intermediate population makes it impossible to maintain the SE African taxon as distinct. See also chapter 2 on geographical distribution.
2. Lamarck described leaves, flowers and follicles. The specimen named $C$. polyphylla in the Lamarck herbarium consists of a single leaf. Commerson specimens named C. polyphylla by Lamarck in the De Jussieu herbarium and in the main collection in P are the only other elements still available. The Commerson specimen in the De Jussieu herbarium is chosen as lectotype.


Fig. 104. Cnestis racemosa: 1-2. flowering branches, $2 / 3 \times$; 3 . flower, $6 \times 4$. follicles, $1 \times 5$. follicle, $2 \times$ (1,3. Voorhoeve 737; 2. Jansen 2475; 4-5. Morton 1616).
3. Schellenberg (1938) cited Hochstetter s.n. as the type of C. natalensis. This is incorrect. The type is Krauss 60 , on which the description in the protologue is based. Krauss (1844) published the name in Flora, in the list of plants collected by him in South Africa, but he is not responsible for the description and validation (see Gunn \& Codd, 1981).

Uses: The vernacular names 'Liane des rats' and 'Mort des rats' refer to the poisonous effect of the fruits (and possibly also the roots) on rats. Drake del Castillo (1902) mentioned the use of the fruits to poison dogs on Madagascar. In animals the fruits produce paralysis of the limbs, convulsions, hypersecretion of the salivary and lachrymal glands and hyperglycaemia (excess of sugar in the blood) with glycosuria and albuminuria (abnormal amounts of sugar and albumen in urine). Death occurs after 60-70 hours. The not yet isolated poison is probably glycosidic (Kerharo \& Bouquet, 1950). Plants are also used to make baskets according to the vernacular name 'liane a paniers'.

## Cnestis racemosa Don

C. racemosa Don, 1832: 91; Planchon, 1850: 440; Walpers, 1852: 306; Baker, 1868: 463; Schellenberg, 1910: 15; Chevalier, 1920: 167; Irvine, 1930: 114; Schellenberg, 1938: 41; Hepper, 1958: 743; Adam, 1971: 868.

Type: Sierra Leone, Afzelius s.n. (lecto design. by Schellenberg, 1938: BM).
C. liberica Schellenberg, 1915: 318; 1919: 436. Type: Liberia, Crozierville, Dinklage 2449 (lecto: B).

Manotes racemosa (Don) Gilg, 1896: 215. Homotypic synonym of Cnestis racemosa.

Liana or straggling shrub. Branches cylindric, branchlets somewhat angular, more or less densely brown-pubescent, later glabrescent. Leaves 1-2(-3)-jugate; petiole (1.5-) $3-9 \mathrm{~cm}$, rachis $2-10 \mathrm{~cm}$ long, brown-pubescent. Leaflets papery, lateral ones usually opposite, circular, broadly elliptic or broadly ovate, 2-10 $\times 1.5-5 \mathrm{~cm}$, truncate or sometimes rounded or subcordate and not or slightly unequal at base, terminal one broadly elliptic, $5-11.5 \times 3.5-7.5 \mathrm{~cm}$, rounded at base; all leaflets acuminate (with obtuse or rarely acute apex), glabrous above, sparsely pilose or almost glabrous beneath, midrib impressed above, prominent and pilose beneath, with $2-5$ curved lateral nerves on each side; tertiary nerves reticulate, distinct on both sides; petiolules $3-5 \mathrm{~mm}$ long, sparsely pilose or glabrous. Inflorescences racemes or rarely panicles, 1-5 per leaf-axil on young branches, sometimes the supporting leaves reduced or very young resulting in a compound pseudoterminal inflorescence, 3-10 cm long, 15-30-flowered, yellowish brown-pubescent. Bracts subulate, very small, ca 1 mm long. Pedicels articulated $0.5-2 \mathrm{~mm}$ below the calyx, densely pubescent. Flowers heterostylous, possibly intermediate between heterodi- and heterotristylous. Sepals reflexed, narrowly imbricate in bud, (narrowly) ovate, $2.0-3.0 \times 1.0-1.5 \mathrm{~mm}$, acute, den-


Fig. 105. Distribution of Cnestis racemosa
sely brown-pilose outside, glabrous inside. Petals valvate or very narrowly imbricate in bud, narrowly obovate, $2.0-3.0(-3.5) \times 1.0 \mathrm{~mm}$, cuneate at base, truncate or indistinctly retuse at top, glabrous, indistinctly veined. Stamens free, subequal or differing in length in the two whorls, $1.5-3.5 \mathrm{~mm}$ long, anthers ca $0.5 \times 0.4 \mathrm{~mm}$. Pistils $1.0-3.5 \mathrm{~mm}$ long; ovaries ca 0.5 mm long, yellowish pilose; styles straight or curved at top, pilose at base; stigmata prominent or not and oblique or not, often 2-lobed. Follicles 1, sometimes 2 in fruit, (narrowly) obovoid, oblique, 1.7-3.0 $\times 0.8-1.0 \mathrm{~cm}$, cuneate with rather long stipe at base; apex obtuse, acute or mucronate; pericarp with rather short, soft hairs outside and with long, easily caducous, yellowish hairs inside. Seeds ovoid, $10-15 \times 6-8$ mm , testa often distinctly veined, sarcotesta $4-7 \mathrm{~mm}$ long.

Distribution: Sierra Leone, Liberia, western part of Ivory Coast,
Ecology: Secondary rain forest, bushes. Flowering mainly from October to January.

Specimens examined:
Sierra Leone: Mt Loma (Nov.) Adam 23522 (K); Nimba-Gangra (fl.b. Oct.) Adam 26217 (P); sin. loc. Afzelius s.n. (BM, type); Freetown, Heddles Farm (fr. Feb.) Dalziel 974 (K); Njala (fr. Jan.) Dalziel 8105 (K); near Hill Station (fl., fr. Jan.) Dalziel 8119 (E, K, P); Zimmi (fl., y.fr. Nov.) Deighton 382 (K); near Mattru (fl. Nov.) Deighton 2335 (K); near Faiama (fr. Jan.) Deighton 3875 (K); Kowama, Peri Chiefdom (fl. Nov.) Deighton 5249 (K); Gaura Chiefdom (fl., y.fr. Dec.) King $81 b$ (K); Havelock, Fourah Bay College (fl., fr. Jan.) Morton 1616 (WAG); Kanu, near Mesina (fr. Jan.) Morton \& Jarr SL 1682 (WAG); Guma Valley, Penins. (fr, Mar.) Morton \& Jarr SL 1745 (WAG); near Freetown (fr. Mar.) Nielsen 1662 (C); sin. loc. (fl.) N. Thomas 6334 (B); Kumsabai (fl.b. Dec.) N. Thomas 6739 (K); N. Thomas 6790 (K); (fl. Dec.) N. Thomas 6806 (K); N. Thomas 6809 (B); N. Thomas 6890 (B); (fr. Dec.) N. Thomas 6963 (K); (fl.b.) N. Thomas 6978 (B); Kenyema (fr. Jan.) N. Thomas 7756 (B); sin. loc. (fr.) N. Thomas 8688 (K).

Liberia: sin. loc. (fr. Feb.) Adam 20817 (K); Beacon Rho, Liberian-Guinea border (fl. Nov.) Adames 750 (B, K); Western Prov., Vonjama Distr., Wohmen (fl.b. Oct.) Baldwin 10017 (K); Kolahun Distr., Genna Loffa (fl.b. Nov.) Baldwin 10099 (K); Karmadhun (fl.b. Nov.) Baldwin 10226 (K); Boporo Distr., Zuie (fl.b. Nov.) Baldwin 10288 (K); Kle (y.fr. Dec.) Baldwin 10635 (K); Gonatown (fr. Dec.) Baldwin 10779 (K, WAG); Mecca (fr. Dec.) Baldwin 10793 (K); Brewersville (fr. Dec.) Baldwin 10969 (K); Harbel (fr. Dec.) Bequaert 16 (K); Loffa county, N of Zorzor (fl., y.fr. Dec.) Bos 2578 (WAG); Gongon (fl. Nov.) Bunting 62 (BM); Monrovia, Crozierville (fr. Feb.) Dinklage 2449 (B, type of C. liberica); sin. loc. (fr. Jan.) Dinklage 3347 (BM, BR); 4 km S of Kakata (fl. Nov.) Jansen 1017 (WAG); 10 miles S of Ganta (fr. Jan.) Jansen 1429 (WAG); Bendu, 10 miles N of Robertsport (fr. Jan.) Jansen 1767 (WAG); 20 miles N of Harper (fl. July) Jansen 2475 (WAG); Gbanga (fl.b. Sept.) Linder 650 (K); Medina, Bumtuma (fl.b. Oct.) Linder 1318 (K); Peahtah (fl. Oct.) Linder 1828 (K); Harbel Div. 33 (fr. Jan.) Stoop van de Kasteele 128 (WAG); (fl. Oct.) Stoop van de Kasteele 238 (WAG); Loma National F. (f1.) Voorhoeve 737 (WAG); sin. loc. (fr.) Warner 92 (K); Kaka Town (fl. Apr.) Whyte s.n. (K).
Ivory Coast: Cavally R., Tépo land, Caté (fl.b. Aug.) Chevalier 19800 (P); Dyolas Country, Sam-pleu-Ganhoué (fr. Apr.) Chevalier 21144 (P).

Note: Although widely separated, the West-African C. racemosa seems to be related to C. polyphylla from E Africa and Madagascar. It differs in having few, conspicuously broad leaflets with few, curved, lateral nerves. Flowers and fruits are both very similar to those of C. polyphylla. C. racemosa can be easily distinguished from other West-African species by the small fruits that are not beaked, and by the number and shape of the leaflets.

Cnestis uncata Lemmens, sp. nov.
Fig. 106-109
Frutex scandens vel liana ramulis juventute dense brunneo-pubescentibus demum glabrescentibus. Folia imparipinnata, 6-10-juga. Foliola crassi-chartacea, lateralia inferiora ovata, superiora anguste oblonga, ( 0.5 ) $1.5-7 \times 1-2.5 \mathrm{~cm}$, basis cordata, foliolum terminale (ob)ovatum vel ellipticum, 4.5-7.5 $\times 2$ 2-3.5 cm , basi rotundatum vel subcordatum; foliola supra glabra (costa pilosa), subtus dense pilosa. Inflorescentia fasciculata. Pedicelli non articulati, 3-7 mm longi. Sepala reflexa, subulata, 3.0-4.5 $\times 0.5-0.8 \mathrm{~mm}$, extra pilosa, intra glabra. Petala anguste oblonga, $5.0-7.0 \times 0.8-1.0 \mathrm{~mm}$, glabra. Stamina subaequalia. Folliculus $2.5-3 \times 1 \mathrm{~cm}$, uncatus rostro incurvato, extus intusque hispidus.

Type: Gabon, km 25 Libreville-Kango, Breteler \& Lemmens 8340 (holo: WAG; iso: LBV).

Liana or climbing shrub. Branches and branchlets cylindric, initially densely brown-pubescent, later glabrescent. Leaves 6-10-jugate; petiole $0.5-4 \mathrm{~cm}$, rachis $7.5-23 \mathrm{~cm}$ long, brown-pubescent, later more or less glabrescent. Leaflets thickly papery, lateral ones alternate or sometimes opposite, ovate to narrowly oblong, (0.5-)1.5-7 $\times(0.5-) 1-2.5 \mathrm{~cm}$, cordate and unequal or subequal at base, terminal one ovate, obovate or elliptic, 4.5-7.5 $\times 2-3.5 \mathrm{~cm}$, subcordate, rounded or somewhat cuneate at base; all leaflets obtuse or indistinctly acuminate, glabrous above (but midrib pilose), densely pilose with curled hairs beneath, midrib impressed above, prominent beneath, with 5-10 lateral nerves on each side; terti-


Fig. 106. Cnestis uncata: 1. branch with leaf, $2 / 3 \times$; 2. flower partly, $6 \times$; 3. branch with flowers and follicles, $2 / 3 \times \cdot 4$ follicles, $1 \times(1,3-4$. Breteler \& Lemmens $8340 ; 2$. Breteler \& Lemmens 8393).

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Fig. 107. Distribution of Cnestis uncata
ary nerves reticulate, prominent and distinct on both sides; petiolules $0-1 \mathrm{~mm}$ long, pilose. Flowers clustered in fascicles (rarely also some short racemes), 3-10 together on nodose thickenings on older branches, heterodistylous. Bracts ovate to subulate, $1-2 \mathrm{~mm}$ long, often partly grown together on the nodose thickenings. Pedicels not articulated, 3-7 mm long, densely pilose. Sepals reflexed, valvate in bud, subulate, narrowly oblong to sublinear, $3.0-4.5 \times 0.5-0.8 \mathrm{~mm}$, obtuse or acute, pilose outside, glabrous inside, distinctly 1-3-veined. Petals valvate or narrowly imbricate in bud, narrowly oblong to sublinear, 5.0-7.0 $\times 0.7-1.0$ mm , rounded or cuneate at base, obtuse or subacute at top, glabrous, usually distinctly 3 -veined. Stamens united at base, subequal or differing in length in the two whorls (long-staminate type of flowers), $1.0-1.6$ or $3.1-4.3 \mathrm{~mm}$ long, anthers ca $0.2 \times 0.2 \mathrm{~mm}$. Pistils ca 1.1 or $2.8-4.4 \mathrm{~mm}$ long; ovaries ca 0.5 mm long, yellowish brown-pilose; styles more or less straight, pilose at base; stigmata more or less prominent and oblique, 2-lobed. Follicles $1(-2)$ in fruit, hookshaped, $2-3 \times 1 \mathrm{~cm}$, cuneate with $5-10 \mathrm{~mm}$ long stipe at base; beak broad, strongly reflexed towards the ventral side of the follicle, $10-13 \mathrm{~mm}$ long; pericarp with very short, red, spinelike hairs and long, easily caducous, stinging hairs outside, with long, easily caducous, yellowish hairs inside. Seeds ovoid, ca 13 $\times 7 \mathrm{~mm}$, sarcotesta ca 6 mm long.

## Distribution: NW Gabon.

Ecology: Rain forest and secondary regrowths.
Specimens examined:

Gabon: Libreville-Kango, Nzogomitang (fr. Oct.) Breteler \& Lemmens 8304 (LBV, WAG); km 25 Libreville-Kango (fr. Oct.) Breteler \& Lemmens 8340 (LBV, WAG, type); km 10 (fl.b. Oct.) Bre-


Fig. 108. Cnestis uncata: stem with inflorescences off flowering and follicles (Breteler \& Lemmens 8393; phot. R.H.M.J. Lemmens).
teler \& Lemmens 8374 (WAG); km 20 (fr. Oct.) Breteler \& Lemmens 8393 (LBV, WAG); Komo R., Kango (fr. Oct.) Chevalier 26890 (P); Kango, near Komo R. (fr. Nov.) J. de Wilde, Arends \& de Bruijn 8925 (LBV, WAG); near Nkogo, banks of Ogooué R. (fr. Aug.) Fleury 26383 (P); 10 km SW of Ndjolé (fr. Apr.) Hallé 1804 (P); Donguila (fr.) Leroy 9 (P); near Lambaréné (fr. Nov.) van der Maesen 5318 (LBV, WAG).

Note: C. uncata has the flowers in fascicles, just as C. urens. It differs by having typical hook-shaped fruits (beak strongly reflexed) and fewer, larger leaflets, that are glabrous above. This difference in the leaves also permits the identification of flowering and sterile material.

## Cnestis urens Gilg

Fig. 110, 111
C. urens Gilg, 1891a: 67, fig.37; 1891b: 330; 1895b: 192; Durand \& Schinz, 1896: 102; Schellenberg, 1910: 17, 94; 1915: 319; De Wildeman, 1916: 244; 1929: 540; 1931: 236; Schellenberg, 1938: 43; Troupin, 1952: 121, fig.1a.

Type: Gabon, Libreville, Sibange Farm, Soyaux 255 (holo: B $\dagger$, lecto: Z; iso: K, P).
C. laurentii De Wildeman, 1909: 96, fig.19; 1911b: 217; Gilg, 1911: 229. Type: Zaire, Eala, Laurent 1639 (lecto: BR).


Fig. 109. Cnestis uncata: stem with follicles (van der Maesen 5318; phot. L.J.G. van der Maesen).

Liana or climbing shrub. Branches and branchlets cylindric, initially (yellowish) brown-pilose, later more or less glabrescent. Leaves 12-21-jugate; petiole $0.5-3 \mathrm{~cm}$, rachis $11-22 \mathrm{~cm}$ long, yellowish brown-pilose, often with many long hairs at base of petiole. Leaflets thickly papery, lateral ones opposite or not, (narrowly) oblong, $0.5-3.5 \times 0.5-1 \mathrm{~cm}$, cordate and equal or unequal at base, terminal one narrowly ( ob ) ovate or narrowly elliptic, 2-3 $\times 0.7-1 \mathrm{~cm}$, subcordate or rounded at base; all leaflets obtuse or rounded, scattered, sometimes sparsely, pilose above, densely pilose with erect hairs beneath, midrib impressed above, prominent beneath, pilose at both sides, with 5-7 lateral nerves on each side; tertiary nerves indistinct; petiolules $0-0.5 \mathrm{~mm}$ long, pilose. Flowers clustered in fascicles, 2-15 together on nodose thickenings in the leaf-axils of young and old branches, heterodistylous. Bracts subulate, $1-1.5 \mathrm{~mm}$ long, often partly grown together on the nodose thickenings. Pedicels not articulated, (2-) $3-7 \mathrm{~mm}$ long, densely pilose. Sepals reflexed, valvate or narrowly imbricate in bud, narrowly ovate or narrowly oblong, 3.0-4.5(-5.0) $\times 0.7-1.0 \mathrm{~mm}$, acute, pilose, rarely with glandular hairs outside, glabrous inside, distinctly or indistinctly up to 5 -veined. Petals valvate or narrowly imbricate in bud, narrowly elliptic or oblong to almost linear, (4.0-)5.0-6.5 $\times 0.8-1.2 \mathrm{~mm}$, rounded to cuneate at base, obtuse or rounded, rarely somewhat retuse and usually inflexed at top, glabrous, distinctly or indistinctly up to 5 -veined. Stamens free, distinctly differing in length in the two whorls, $0.5-1.0$ or $2.5-5.2 \mathrm{~mm}$ long, anthers ca $0.2 \times 0.2 \mathrm{~mm}$. Pistils 1.0-1.1 or 2.3-3.2 mm long; ovaries ca 0.5 mm long, yellowish brown-


Fig. 110. Cnestis urens: 1. branch with flowers, $2 / 3 \times$; 2 . branchlet with leaves, $2 / 3 \times$; 3 nodose thickening with flowers, $6 \times$; follicle, $1 \times(1$. Couteaux 393; 2. Boone 84; 3. Laurent 762; 4. Laurent 1639).

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Fig. 111. Distribution of Cnestis urens
pilose; styles straight or curved, pilose at base; stigmata oblique, indistinctly 2-lobed. Follicles $1(-3)$ in fruit, ellipsoid, oblique, $2.5-4(-5) \times 0.6-1.5 \mathrm{~cm}$, more or less cuneate with $7-15 \mathrm{~mm}$ long, broad and indistinct stipe at base; beak slender, curved or involute at apex, ( $8-$ - $12-30 \mathrm{~mm}$ long; pericarp with very short, red, spinelike hairs and numerous, long, easily caducous, stinging hairs outside and long, slender yellowish brown hairs inside. Seeds ovoid, $10-15 \times 5-10 \mathrm{~mm}$, sarcotesta $3-6 \mathrm{~mm}$ long.

Distribution: Southern part of Central African Republic, SW Sudan, Gabon, Congo, northern and central Zaire.

Ecology: Rain forest, semi-deciduous forest, regrowths. Flowering mainly from March to August, in central N Zaire usually in November to January.

Selection of the ca 100 specimens examined:
Central African Republic: Mako R., 20 km NW of Alindao (fl. June) Tisserant 2536 (BM, BR); Tisserant 2537 (P).

Sudan: Monbuttu land, Kussumbo (fr. Dec.) Schweinfurth 3203 (K, Z); Niam-Niamland (fr.) Schweinfurth s.n. (K); Equatorial Prov., Zandeland, Sakure (y.fr. Jan.) Wyld 672 (BM).

Gabon: Mouila-Yeno (Sept.) Breteler, Lemmens \& Nzabi 8095 (LBV, WAG); 10 km SW of Ndjolé (fl. Apr.) Hallé 1940 (P); 40 km SW of Ndendé (fr. Dec.) A. Louis, Breteler \& de Bruijn 1100 (LBV, WAG); Libreville, Sibange Farm (fl. Mar.) Soyaux 255 (K, P, Z, type).

Congo: Brazzaville (July) Sita 4880 (BR).
Zaire: Avakubi (y.fr. Jan.) Bequaert 2004 (BR, K); Ngene Ngene, 10 km NE of Kisangani (fl., y.fr. Aug.) Bokdam 4222 (WAG); Nala (fl.) Boone 84 (BR); Lisala (fl.) Bruneel s.n. (BR); Djilingi de Lilnote (fl.b., fr. May) Collart 91 (BR); Eala (fl. June) Corbisier Baland 1930 (BR, K); Prov. Orientale, Basoko, Mokaria (fl. Dec.) Croegaert 62 (BR, K, WAG); Bosodula, N Furu (fr.) de Bilderling 54 (BR); Likimi (fl. Dec.) de Giorgi 1548 (BR); Equateur, Coquilhatville, Mabali, Tumba L. (fl. Jan.) Deuse 222 (BR); Bas-Uele (fl. Dec.) Dewulf 457 (BR); Basankusu, Terr. Lulonga-Iko-


Fig. 112. Cnestis yangambiensis: 1. apical part of leaf beneath, $2 / 3 \times$; 2. follicle, $2 \times$; basal part of leaf, $2 / 3 \times(1-3$. J. Louis 13623).
lomba (fl. July) Dubois 499 (BR); Bambesa (y.fr. July) Dubois 565 (BR); Kwada L. (fr. Mar.) Evrard 540 (BR); Baringa, Maringa (fl., fr. Oct.) Evrard 5085 (BR, K); Bambesa (fl., fr Jan.) Gerard 4000 (BR); Bokote (fr.) Hulstaert 962 (BR, partly); Eala (fl., y.fr. Aug.) Laurent 1083 (BR); (fl., fr.) Laurent 1639 (BR, type of C. laurentii); Wamba-Gombari, Uele-Nepeko (fl. July) Lebrun 3302 (BR); Urega (fl., fr. July) Lebrun 5775 (BR, K); 15 km E of Kisangani (fl.b. Nov.) Lejoly 81/381 (BR); Elua I., Tumba L. (fr. Sept.) J. Léonard 655 (BR); near Kisangani (fr. Nov.) Lisowski 15167 (BR, K); Yangambi (fr. Dec.) J. Louis 2899 (BR, K); Wabondo, Buta (fr. Nov.) Mosango 424 (BR); Yangambi (fl.b. June) Yafunga 198 (BR, WAG).

Note: The flowers and fruits and, to a lesser extent, the leaves of $C$. urens resemble certain forms of $C$. corniculata. However, the two species differ in their inflorescences: fasciculate in C. urens and racemose or paniculate in C. corniculata.

See note under C. uncata for differences with that species.
Uses: In Zaire the seed, softly boiled with sugar-cane serves as a medicine for the stomach (Troupin, 1952). The ashes of the fruits are used against toothache. Hunters wear a twig on the head as a talisman.

Cnestis yangambiensis Louis ex Troupin
Fig. 112, 113
C. yangambiensis Troupin, 1951: 369; 1952: 122.

Type: Zaire, Haut-Zaire, Yangambi, Tutuku I., J. Louis 13623 (holo: BR; iso: K ).

Liana, sometimes small. Branches and branchlets cylindric, initially yellowish brown-pubescent, often also with long hairs, later more or less glabrescent. Leaves $13-20$-jugate; petiole $0-6 \mathrm{~cm}$, rachis $25-45 \mathrm{~cm}$ long, yellowish brownpubescent, densely at base of petiole. Leaflets papery, lateral ones more or less alternate, (narrowly) oblong, more rarely ovate, $1.5-9 \times 1-2.5 \mathrm{~cm}$, truncate or subcordate and unequal at base, terminal one narrowly ovate or narrowly elliptic, $6-8 \times 2.5-3 \mathrm{~cm}$, cuneate or rounded at base; all leaflets acuminate, glabrous above, pilose, especially on the nerves beneath, midrib impressed above, prominent beneath, with 8-12 lateral nerves on each side; tertiary nerves indistinct; petiolules $0.5-1 \mathrm{~mm}$ long, pilose. Inflorescences racemes, 1-10 per leaf-axil on stem or older branches, $3-7.5 \mathrm{~cm}$ long, $10-20$-flowered, densely yellowish brownpilose with curled hairs. Bracts ovate to subulate, $1.5-2 \mathrm{~mm}$ long, curved. Pedicels articulated $0-0.5 \mathrm{~mm}$ below the calyx, densely pilose with curled hairs. Flowers heterodistylous. Sepals reflexed, valvate or very narrowly imbricate in bud, narrowly ovate or narrowly oblong, 2.5-3.5 $\times 0.7-0.8 \mathrm{~mm}$, acute or obtuse, brown-pilose outside, glabrous inside, more or less distinctly 1 -veined. Petals valvate or very narrowly imbricate in bud, narrowly oblong, rarely narrowly obovate, $(2.7-$ )3.0-4.0 $\times 0.7-0.8 \mathrm{~mm}$, rounded or cuneate at base, somewhat retuse and often inflexed at top, glabrous, indistinctly veined. Stamens free or very shortly united at base, subequal in length, 2.2-3.7 mm long, anthers


Fig. 113. Distribution of Cnestis yangambiensis
ca $0.2 \times 0.1 \mathrm{~mm}$. Pistils $1.2-1.5$ or 2.7-3.2 mm long; ovaries ca 0.4 mm long, brown-pilose; styles curved at top, pilose at base; stigmata more or less prominent and oblique, 2-lobed. Follicles 1-3 in fruit, oblique-pyriform or obliqueobovate, 2-3(-3.2) $\times$ 1.2-1.6 cm, cuneate with indistinct, short stipe at base; apex obtuse or somewhat acute, lacking beak; pericarp with very short, red, spinelike hairs and long, easily caducous, stinging hairs outside (stinging hairs often almost completely fallen out in old fruits), with long, slender hairs inside. Seeds ovoid, 13-19 $\times 6-10 \mathrm{~mm}$, sarcotesta $7-10 \mathrm{~mm}$ long, ruminate.

Distribution: N Zaire, near Yangambi.
Ecology: Primary, sometimes secondary rain forest, often near rivers. Fruiting specimens have been found from September to May.

## Specimens examined:

Zaire: Haut-Zaire, Ngoli (Feb.) Ankei 79/1103 (BR); Ankei 79/1124 (BR); 7 km W of Kisangani (fr. Sept.) Bokdam 3228 (WAG); Yangambi, Tutuku I. (fr. Oct.) Germain 354 (BR); (fr.) Germain 394 (BR); Kisangani, Kongolo I. (Mar.) Lejoly 1137 (BR); Lejoly 1396 (BR); Lejoly 4557 (BR); Lubi, terr. Dibaya (May) Liben 2993 (BR, WAG); Kisangani, Kongolo I. of Lindi (fr. May) Lisowski 18471 (BR); 5 km upstream from Wanie-Rukula (fr. Nov.) Lisowski 85578 (BR, WAG); Yangambi, Tutuku I. (fl., fr. Dec.) J. Louis 12882 (BR, K); (fr. Feb.) J. Louis 13623 (BR, K, type); Kisangani, Kongolo I. (fr. Mar.) Mandango 1457 (BR); Kisangani (fr. Apr.) Szafranski 1165 (BR, WAG).

Note: Flowering and sterile material of C. yangambiensis cannot be identified with complete certainty because of the overlap in variation with $C$. corniculata. In general, C. yangambiensis has longer leaves with a larger number of leaflets. Fruiting specimens are unmistakable.

## Excluded species

Africa:
C. corniculata Bentham, 1849: 290, non Lam. = Manotes expansa Soland.
C. obliqua Palisot-de Beauvois, 1804:97; Bojer, 1837: 84 = Agelaea pentagyna (Lam.) Baill.
C. pinnata Palisot-de Beauvois, 1804: $98=$ Rourea thomsonii (Bak.) Jongkind
C. trifolia Lamarck, 1789: 24 = Agelaea pentagyna (Lam.) Baill.

Asia:
C. acuminata Wallich, no. 8533 (nomen nudum) $=$ Rourea minor (Gaertn.)

Alston
C. emarginata Jack, 1822: $42=$ Rourea emarginata (Jack) Jongkind
C. erecta Blanco, 1837:387 $=$ Rourea minor (Gaertn.) Alston
C. florida Jack, 1822: $43=$ Rourea minor (Gaertn.) Alston
C. glabra Blanco, 1837: 387, non Lam. = Rourea minor (Gaertn.) Alston
C. mimosoides (Vahl) Jack, 1822: $44=$ Rourea mimosoides (Vahl) Planch.
C. monadelpha Roxb. ex De Candolle, 1825: $87=$ Rourea minor (Gaertn.)

Alston
C. pentaphylla Spanoghe, 1841: $189=$ Connarus monocarpus L. ssp. malayensis Alston
C. stenopetala Griffith, 1854: $433=$ Rourea stenopetala (Griff.) Hook.f.
C. trifolia Blanco, 1845: $270=$ Rourea minor (Gaertn.) Alston
C. vestita Wallich, no. 8535 (nomen nudum) = Agelaea borneensis (Hook.f.)

Merr.
C. volubilis Blanco, 1837: 383 = probably no Connaraceae .

America:
C. americana Martius, nomen in sched.; Schellenberg, 1938: 196 (in syn.) = Rourea martiana Baker

## Connarus L.

by R.H.M.J. Lemmens

## History and subdivision of the genus

In 1753 Linnaeus published Connarus monocarpus. Lamarck (1786) proposed three species in the genus, one of which does not belong to Connarus (C. pentagynus $=$ Agelaea pentagyna), another is based on a Smeathman collection from Africa (C. africanus). In 1825 De Candolle described a number of African, Asiatic and American species in the genus Omphalobium Gaertner. Planchon (1850) reduced Omphalobium into the synonymy of Connarus and treated almost 40 species. In his monograph on Connaraceae Schellenberg (1938) recognized 121 species in Connarus. Leenhouts (1958b) made a revision of the genus for Asia. In comparison with Schellenberg he reduced the number of species considerably. The revision of Connarus for tropical America by Forero (1983) however, resulted in an extension of the number of recognized species.
Schellenberg (1938) divided Connarus into 3 subgenera: Connarellus, Neoconnarus and Euconnarus, based on the dehiscence of the follicle. His subgenera are divided into 10 sections. In agreement with Leenhouts (1958b) and Forero (1983) this division is considered to be dubious and not reflecting the natural relationships. Because only a limited part of the genus, i.e. the African species, have been studied in detail, no new subdivision is presented here.

## Description of the genus

Connarus Linnaeus, 1753: 675; 1754: 305; Lamarck, 1786: 94; Cavanilles, 1790: 375; Willdenow, 1800: 691; Planchon, 1850: 424; Baker, 1868: 456; Schellenberg, 1938: 216; Troupin, 1952: 128; Hemsley, 1956: 22; Leenhouts, 1958b: 525; Liberato, 1980a: 15; 1980b: 12; Forero, 1983: 36.

Type species: C. monocarpus L. See note.
Tapomana Adanson, 1763: 343. Nom. illeg.
Omphalobium Gaertner, 1788: 217; De Candolle, 1825: 85; G. Don, 1832: 90. Type species: $O$. indicum Gaertner ( $=$ Connarus monocarpus L. ssp. monocarpus).

Erythrostigma Hasskarl, 1842: 45. Type species: E. diversifolia Hassk. (= probably Connarus semidecandrus Jack).
Anisostemon Turczaninow, 1847: 152. Type species: A. trifoliatus Turcz. (= Connarus grandis Jack).

Tricholobus Blume, 1850: 236. Type species: T. fulvus Bl. (lecto; = Connarus villosus Jack).

Lianas, shrubs or small trees. Branches cylindric. Leaves trifoliolate or impari-
pinnate, rarely upper leaves unifoliolate; leaflets opposite or not, often acuminate, often glandular punctate. Inflorescence an axillary panicle, often appearing terminal and more compound by a reduced development of the leaves. Flowers bisexual, pentamerous, heterostylous. Pedicels with a distinct joint. Sepals connate at the base, imbricate or valvate in bud, thick and fleshy or thin, usually glandular punctate. Petals longer than sepals, free or coherent, usually white, imbricate in bud, pilose or rarely almost glabrous outside, often with glandular hairs inside. Stamens 10, episepalous ones fertile, epipetalous ones shorter and fertile, sterile, or rudimentary; filaments united at base, longer ones usually with stipitate glands, shorter ones often lacking glands; anthers sometimes with glandular hairs on the apex. Carpel 1 ; style often pilose and with stipitate glands. Follicle red, opening lengthwise along the ventral suture, sometimes also along the dorsal suture, initially pubescent outside, but often glabrescent, glabrous or pilose and often with glands inside, often stipitate, usually with a short mucro apically. Seed solitary, attached to the ventral side of the follicle, ovoid or slightly kidney-shaped; testa shining black, yellow and fleshy (sarcotesta) below the hilum; endosperm absent; hilum lateral; radicle apical, dorsal or almost in the centre of the seed between the cotyledons; cotyledons thick, planoconvex.

A circumtropical genus. According to Schellenberg (1938) comprising about 120 species. In accordance with Leenhouts (1958b) I consider this number excessive. The combined number of species from Asia (Leenhouts), tropical America (Forero), and Africa is 77 species. They are generally confined to rain forest.

Note: Forero (1983) mentions C. macrocarpus L. as the type species. This is probably a printing error for C. monocarpus, as the combination C. macrocarpus has never been proposed so far.

Relations between the African, Asiatic and American species
When the African species are compared to the Asiatic ones, there is a remarkable resemblance between some species.
C. thonningii and C. longistipitatus are very closely related to the Asiatic, polymorphic C. semidecandrus Jack. The latter species only differs from C. longistipitatus in the always glabrous petals that are fimbriate at apex, and from C. thonningii in the usually less glandular-punctate sepals, petals and stamens, and often apparently fertile short stamens.
C. paniculatus Roxb. is very close to C. griffonianus, but unlike this species it has 10 fertile stamens.

The Asiatic C. monocarpus L. ssp. monocarpus is closely related to C. africanus. It differs in the often pinnate leaves, in the pericarp lacking glands inside and in the radicle, that is placed almost at the apex of the seed. C. monocarpus L. ssp. malayensis Leenhouts is related to C. congolanus and C.gabonensis, differing from the first in the usually pinnate leaves, the smaller follicle and in the exserted radicle, and from the latter in the smaller follicle.

Some South American species also show considerable resemblance to African species, e.g. C. beyrichii Planch. resembles C. longistipitatus and C. punctatus Planch. resembles C. thonningii. In Asiatic as well as in South American species usually all stamens are fertile. Only in a number of specimens of some American species sterile stamens are found, but in these plants all stamens are sterile, indicating functionally female plants. In some Asiatic species specimens can be found with sterile or rudimentary short stamens, but in most of these species 10 apparently fertile stamens is the more common situation. In Africa several species (nearly) always have sterile epipetalous stamens.
Only a worldwide revision of the genus can bring more lucidity in the relations of the species.

Keys to the species
Three keys are presented here. Specimens are best identified when complete material, i.e. with flowers and fruits, is available. Material with flowers only is sometimes difficult to identify.
A. Key to specimens with flowers and fruits

1a Follicle oblique-pyriform, up to 3.5 cm long, mucro lateral, rarely almost apical; radicle in seed apical
b Follicle ellipsoid, ovoid or (narrowly) obovoid, longer than 3.5 cm , not or only slightly oblique, mucro apical; radicle in seed dorsal or almost in the centre of the seed
2a All stamens (apparently) fertile, rarely short stamens rudimentary; follicle with a $5-10 \mathrm{~mm}$ long stipe, pericarp pilose inside
C. Iongistipitatus
b Short stamens rudimentary, rarely (apparently) fertile; follicle with a 2-5 mm long stipe, pericarp glabrous or sparingly pubescent inside
3a Sepals valvate in bud, more or less fleshy; petals densely pubescent outside; follicle with small, stipitate glands inside. Nigeria to Zaire C. griffonianus
b Sepals imbricate in bud, thin; petals (almost) glabrous outside; follicle glabrous and lacking glands inside. Ivory Coast to Togo
C. thonningii

4a Leaves (uni-)trifoliolate
5
b Leaves pinnate, with at least 5 leaflets
6
5a Sepals valvate or slightly imbricate in bud, fleshy; lateral margins of petals quite free; follicle not distinctly stipitate, pilose and without glands inside; radicle almost in the centre of the seed . . . . . . . . . . . C. congolanus
b Sepals imbricate in bud, thin or somewhat fleshy at base only; margin of petals usually connate for a short distance; follicle with $2-5 \mathrm{~mm}$ long stipe, glabrous and glandular inside; radicle dorsal . . . . . . . . C. africanus
6a Leaflets papery, distinctly acuminate, with 3-5 lateral nerves on each side of the midrib; follicle glabrous inside
C. staudtii b Leaflets leathery, acute or hardly acuminate, with 5-7 lateral nerves on each side of the midrib; follicle pilose inside .

## B. Key to flowering specimens

1a All stamens (apparently) fertile ..... 2
b Short stamens distinctly rudimentary, anthers minute ..... 4
2a Leaflets 5 or more, but often with few trifoliolate upper leavesC. longistipitatus (see note 2)
b All leaves trifoliolate, rarely uppermost leaves unifoliolate ..... 3
3a Nodes often produced into a distinct process at the base of the petiole;leaflets leathery, acute or acuminate; sepals valvate or slightly imbricatein bud, fleshy; margin of petals quite freeC. congolanus
b Nodes without a distinct process at the base of the petiole; leaflets paperyor thinly leathery, long-acuminate; sepals imbricate in bud, thin or some-what fleshy at base only; margin of petals usually connate for a short dis-tanceC. africanus4a Base of the petiole provided with a black pulvinus; petiolules (3-) 5-8 mmlong, blackish; leaflets distinctly acuminate with long and slender apex,with 3-5 strongly curved lateral nerves on each side of the midrib
C. staudtii
b Pulvinus at base of the petiole not blackish, usually indistinct; petiolulesup to 6 mm long, not blackish; leaflets broadly acuminate to obtuse, with(4-)5-12 not strongly curved lateral nerves on each side of the midrib . 5
5 a Sepals valvate in bud, more or less fleshy; petals densely pubescent outside;sepals and petals rather sparingly glandular punctate; long stamens with sti-pitate glands, short stamens lacking glands; reduced leaves at base of inflores-cences up to 13 mm long; Nigeria to Zaire . . . . C. griffonianus (see note 2)
b Sepals imbricate in bud, thin, petals to quite glabrous outside; sepals andpetals rather densely glandular punctate; long and short stamens with stipi-tate glands; reduced leaves at base of inflorescences minute, up to 1.5 mmlong. Ivory Coast to Togo
C. thonningii

Notes: 1. C. gabonensis is not included in this key because flowers are unknown.
2. C. longistipitatus very rarely has flowers with rudimentary short stamens, and C. griffonianus rarely with apparently fertile short stamens. C. longistipitatus has imbricate, thin sepals, longer than 3 mm and broader than 1.2 mm and coherent petals, pubescent outside. C. griffonianus has valvate, more or less fleshy sepals, up to $3 \times 1.2 \mathrm{~mm}$, and free petals, densely pilose outside.

## C. Key to fruiting specimens

1a Follicle oblique-pyriform, up to 3.5 cm long, mucro lateral, rarely almost
apical; radicle in seed apical . . . . . . . . . . . . . . . . . . . . . 2
b Follicle ellipsoid, ovoid or (narrowly) obovoid, longer than 3.5 cm , not or only slightly oblique, mucro apical; radicle in seed dorsal or almost in the centre of the seed
2a Follicle with $5-10 \mathrm{~mm}$ long stipe, pilose inside C. Iongistipitatus
b Follicle with 2-5 mm long stipe, glabrous or sparingly pubescent inside ..... 3
3a Follicle glabrous and without glands inside; leaves glabrous. Ivory Coastto TogoC. thonningii
b Follicle with small, stipitate glands and with some or without normal hairsinside; rachis and leaflets beneath pilose or glabrous. Nigeria to Zaire
C. griffonianus
4a Leaves trifoliolate, rarely uppermost leaves unifoliolate ..... 5
b Leaves pinnate, with at least 5 leaflets ..... 65a Follicle with 2-5 mm long stipe; pericarp rather thin, glabrous but withsmall glands inside; radicle in seed dorsal; sepals thin, deciduous; leafletspapery or thinly leathery, long-acuminate; nodes without a distinct processat the base of the petioleC. africanusb Follicle rounded or cuneate at base, not distinctly stipitate; pericarp thick,woody, pilose but lacking glands inside; radicle almost in the centre of theseed; sepals thick and stiff, persistent in fruit; leaflets leathery, acute oracuminate; nodes often produced into a distinct process at the base of thepetiole
C. congolanus
6a Follicle not distinctly veined, but somewhat striate outside, glabrous inside; leaflets papery, distinctly acuminate, with 3-5 strongly curved lateral nerves on each side of the midrib
C. staudtii
b Follicle distinctly veined outside, pilose inside; leaflets leathery, acute or hardly acuminate, with 5-7 slightly curved lateral nerves on each side of the midrib
C. gabonensis

## Connarus africanus Lam.

Fig. 114, 115
C. africanus Lamarck, 1786: 95; Cavanilles, 1789: 375, tab. 221; Vahl, 1794: 86; Willdenow, 1800: 691; Richard, 1831: 156; Hooker, 1849: 290; Planchon, 1850: 426; Walpers, 1852: 300; Baker, 1868: 457; Henriques, 1892: 111; Chevalier, 1920: 165; Schellenberg, 1923: 223; 1938: 283; Exell, 1944: 151; Hepper, 1958: 748; Irvine, 1961: 572; Exell, 1973: 368; Liberato, 1980a: 15; 1980b: 13.

Type: Sierra Leone, Smeathman s.n. (lecto: herb. De Jussieu in P; iso: BM, herb. Lamarck in P). See note.
C. venosus De Candolle, 1825: 85 (nomen; in syn.).
C. nigrensis Gilg, 1891b: 317; Chevalier, 1920: 165. Type: Nigeria, Lagos, Barter 2143 (holo: $\mathrm{B} \dagger$; lecto: K ; iso: P ).
C. djalonensis Chevalier, 1920: 165. Type: Guinea, Fouta-Djalon, Chevalier 18056 (lecto: P).

Omphalobium africanum (Lam.) De Candolle, 1825: 85; G. Don, 1832: 90, fig.20. Homotypic synonym of C. africanus.
Tricholobus africanus Heckel, 1891: 16. Homotypic synonym of C. africanus.
Liana or lianescent shrub. Branches cylindric, lenticellate, branchlets brown-


Fig. 114. Connarus africanus: 1. flowering branch, $2 / 3 \times$; 2 flower partly, $6 \times ; 3$. follicle from dorsal side, $2 / 3 \times$; 4 . follicle, $1 \times$; 5 . seed in longitudinal section, $1 \times(1$. Bos 2574 ; 2. Bos 4896 ;
3-5. van Harten 359 .
pubescent, soon glabrescent. Leaves trifoliolate, rarely uppermost leaves unifoliolate; petiole $2.5-14 \mathrm{~cm}$, rachis $1.5-4 \mathrm{~cm}$ long, brown-pubescent when young. Leaflets papery; lateral ones opposite, ovate or elliptic, (4-)6.5-25 $\times 2-9.5 \mathrm{~cm}$, rounded at base, up to 3 cm long acuminate; glabrous both sides (sometimes somewhat pubescent when very young), midrib impressed above, prominent beneath with (3-)4-7 lateral nerves on each side, tertiary nerves reticulate, usually distinct on both sides; petiolules $5-7 \mathrm{~mm}$ long, often wrinkled, glabrous. Panicles up to 35 cm long, up to ca 50 -flowered, densely brown-pubescent. Bracts, as well as the reduced leaves at base of inflorescences, ovate, up to 1.5 mm long. Pedicels short, articulated $0-1.5 \mathrm{~mm}$ below the calyx, brown-pubescent. Sepals imbricate in bud, ovate, thin or somewhat fleshy at base, (2.1-)2.7-4.0 $\times$ (1.0-) 1.2-2.0 mm, obtuse or rounded, rarely acute at top, more or less plane, brown-pilose outside, glabrous or pubescent inside, glandular punctate, often indistinctly up to 7 -veined. Petals usually coherent (rarely completely free), imbricate in bud, narrowly elliptic to narrowly obovate, 5.3-7.5(-8.0) $\times 1.0-2.0$ mm , cuneate at base, obtuse or rounded at top, glabrous or sparingly pubescent outside, glabrous or with glandular hairs inside, usually glandular punctate near the top, 3-7-veined, sometimes indistinctly so. Stamens $0.5-1.2 \mathrm{~mm}$ united at base; long ones $2.6-3.9 \mathrm{~mm}$ or $5.0-7.9 \mathrm{~mm}$ long, filaments with stipitate glands, anthers $0.3-0.5 \times 0.2-0.3 \mathrm{~mm}$; short ones $1.2-2.7 \mathrm{~mm}$ long, filaments lacking glands, anthers usually somewhat smaller, but apparently fertile. Pistil 2.5-3.9 mm or $5.0-7.0 \mathrm{~mm}$ long; ovary $1.0-1.5 \mathrm{~mm}$ long, brown-pilose; style pilose at base and with stipitate glands; stigma oblique, more or less 2-lobed, occasionally distinctly papillate. Follicle narrowly obovoid, slightly oblique, hardly compressed, 4.3-6.2 $\times(1.2-) 1.5-2.4 \mathrm{~cm}$, stipe (2-)3-5(-7) mm long; apex acute or with up to 2 mm long erect mucro; pericarp fairly thin, glabrous and lacking distinct veins, but slightly striate outside, glandular inside. Seed (ob)ovoid, 17-28 $\times$ $10-16 \times 7-10 \mathrm{~mm}$, sarcotesta $10-18 \mathrm{~mm}$ long, enveloping the basal part of the seed; radicle dorsal, 1/4-1/2 of length from top of seed. Seedling hypogeal.

Distribution: From southern Senegal to Cameroun, Equatorial Guinea and Sao Tomé.
Ecology: Rain forest, often near rivers; sometimes in thickets in savanna. Flowering in Senegal to Benin mainly from December to April, in Nigeria and Cameroun mainly from June to September and on Sao Tomé about December. Fruiting a few months later.

Selection of the ca 150 specimens examined:
Senegal: Casamance, Teudoux (May) Adam 13571 (P); Oussouye, Okout (fr. Apr.) Berhaut 5753 (M, P); (fl., y.fr. Apr.) Berhaut 5789 (M, P); Bignona (fl. Mar.) Berhaut 7185 (BR, M, P); Floup Fedyan (fr. Jan.) Chevalier 2975 (P); sin. loc. (fl., fr.) Heudelot 594 (B, P); (fl.) Heudelot s.n. (B, P); Casamance (fr. May) Leprieur s.n. (P); sin. loc. (fl.) Perrottet 147 (BM, G); Perrottet s.n. (P); (fr.) Perrottet s.n. (P).
Guinea-Bissau: Bedanda-Cantanhez (fr. Sept.) Alves Pereira 3139 (LISC); Pecixe (fr. Nov.) Alves Pereira 3453 (LISC); Cantanhez (fl., y.fr. Apr.) d'Orey 368 (LISJC); Fulacunda (fl., fr. July) Esperito


Fig. 115. Distribution of Connarus africanus

Santo 585 (COI, LISJC); Biombo (fl., y.fr. Feb.) Esperito Santo 1792 (COI, K, LISC, P, WAG); Prabis (fl. Mar.) Esperito Santo 1848 (COI, K, LISC, P, WAG); Cantanhez, Catio (fr. June) Esperito Santo 2999 (COI, LISC, LISJC, P, WAG).

Guinea: Dalaba (fl. Apr.) Adam 11839 (K); Kaba-Mamou (fr. Apr.) Chevalier 12765 (P); Fouta Djalon, Bilima Kante (fl. Mar.) Chevalier 18056 (P, type of C. djalonensis); Kouria-Irebéleya (fr. Sept.) Chevalier 18263 (P); Fruiguiagbé, Bingaya (fl. Feb.) Chillou 3625 (P); Konakry (fr. Oct.) Dybowski 51 (P); near Mamou (fl. Feb.) Jacques Félix 772 (P); Mamou R. (fl.) Pobéguin 1441 (P); Fouta Djalon (fr. Jan.) Pobéguin 1907 (P).
Sierra Leone: sin. loc. (fl.) Afzelius s.n. (BM); Njala (fl. Mar.) Deighton 1092 (BM); Musaia (fr. Mar.) Deighton 5453 (K); sin. loc. (fl., fr.) Don s.n. (K); Northern Prov., Makump (fl. Jan.) Glanville 140 (K); Lake Sonfon (fl. Feb.) Gledhill 262 (K, WAG); W Loma (fr. Sept.) Jaeger 7352 (K); (fl. Dec.) Jaeger 8998 (K); Bagroo R. (fl., fr.) Mann 863 (K, P); Tiama (fl. Feb.) Morton SL 873 (WAG); Songo Penins. (fl. Jan.) Morton SL 1659 (K); sin. loc. (fl., fr.) Scott Elliot 4698, 5603 (K); sin. loc. (fl. fr.) Smeathman s.n. (BM, P, type); (fl.) Smeathman s.n. (BM); Kennema (fl. Jan.) N. Thomas 1494 (K).
Liberia: Central Prov., Gbarnga (fr. Sept.) Baldwin 13228 (K); N of Zorzor (fl., fr. Dec.) Bos 2574 (K, WAG); NE of Gbanga (fr. June) Daniel 342 (BR, P); Fishtown, Gran Bassa (fr. Aug.) Dinklage 1978 (B); 10 km from Monrovia, Elwa (fr. Mar.) van Harten 359 (L, WAG); Bomi HillsMaho R. (fl. Feb.) van Meer 369 (WAG); Monrovia (fr. Sept.) Voorhoeve 460 (WAG); Bomi Hills (fl.b. Feb.) Voorhoeve 838 (WAG).
Ivory Coast: Banco (fr.) Aubreville 467 (BR); Abidjan, Dabou (fr.) Chevalier 15163 (BR, K, P); Guébo (fl. Feb.) Chevalier 17127 (P); Assinie, Sanvi (fl. Apr.) Chevalier 17864 (P); Chevalier 17906 (P); Banco F.R. (fl., y.fr. Feb.) de Koning 1161 (WAG); (fl., fr. Mar.) de Koning 5541 (WAG); Port Bouet (fr. July) Maire s.n. (P); Abidjan-Gd.Bassam (fr. Dec.) Oldeman 723 (BR, P, WAG); Vridi (fr. Dec.) Roberty 15729 (G).

Benin: Pobé (Sept.) Adjanohoun 70 (P); Ouja (fl., fr. Dec.) Le Testu 196 (BM, BR, K, P).
Nigeria: Lagos (fl., y.fr.) Barter 2143 (K, P, type of C. nigrensis); Lagos (fl. Sept.) Dalziel 1022 (K); Kabba Prov., Kotonkarifi (fr. Feb.) Daramola \& Binuyo FHI 61265 (K); N Nigeria, Gurara R. (fl. June) Elliott 179 (K); Kabba Prov., Igala, Ibaji Ojoku F.R. (fr. Feb.) Latilo FHI 47107 (K); Eket Distr. (fl.) Talbot 3242 (BM).
Cameroun: Lobé R. (fl., y.fr. Feb.) Bos 4001 (K, P, WAG); Kribi (fl. June) Bos 4896 (K, P, WAG); 8 km S of Kribi (fl. Sept.) Bos 5347 (WAG); S of Badjob, SW of Eseka (fr. Jan.) W. de Wilde 1740 (B, BR, K, MO, P, WAG, Z); Bulu-Last Banana, Ndian R. (fl. July) Thomas 2361
(WAG); Bipindi (fl., fr.) Zenker 1538 (B, BR, E, G, GOET, K, L, M, MO, P, WAG, Z); (fr.) Zenker 1675 (E, G, GOET, K, L, M, P, Z); (fl.) Zenker 4642 (B, BR, G, GOET, K, L, M, MO, P, Z). Equatorial Guinea: near Bata (fr. May) Trilles 64 (P).
Sao Tomé \& Principé: Sao Tomé, Juliana de Sousa (fr. July) Esperito Santo 3972 (LISJC); Sao Tomé (fl. Dec.) Quintas 135 (K).

Cult.: Ivory Coast, Adiopodoumé (seedlings) de Koning 5180 (WAG).

Note: Schellenberg (1938) cited the specimen Heudelot 594 as the type of $C$. africanus. This is incorrect. Lamarck (1786) only cites material collected by Smeathman in Sierra Leone. He cannot have seen material from Heudelot, who collected in Senegambia about 1837. Lamarck described both flowers and fruits. The specimen in the Lamarck herbarium shows flowers only. Consequently the Smeathman-specimen in the De Jussieu herbarium with flowers and fruits is chosen as lectotype.

Uses: According to de Lanessan (1886) a decoction of the bark is used as an astringent for wounds in Senegal. The seeds are used as a purge and vermifuge. They are especially effective against tapeworm, taken in the form of a decoction or with boiled rice; the effect is attributed to tannin (Dalziel, 1936). In Nigeria seeds are said to be used to bait hooks for fishing.

## Connarus congolanus Schellenb.

Fig. 116, 117
C. congolanus Schellenberg, 1938: 289 (as C. sapinii on p. 284; see note); Troupin, 1952: 135, fig. 2 B,C.

Type: Zaire, Dilolo, Sapin s.n. (holo: BR).
Liana or lianescent shrub. Branches cylindric, lenticellate, branchlets occasionally somewhat angular, brown-pubescent, soon glabrescent. Leaves trifoliolate; petiole $2.5-17 \mathrm{~cm}$ long, usually with a distinct process on the branchlet beneath attachment, rachis $0.5-4.5 \mathrm{~cm}$ long, brown-pubescent when young. Leaflets leathery, lateral ones more or less opposite, ovate or elliptic, $5-25 \times 3-10.5 \mathrm{~cm}$, rounded (lateral leaflets) or cuneate (terminal one) at base, acute or up to 2.5 cm long acuminate; glabrous both sides, midrib strongly impressed above, prominent beneath with 4-9 lateral nerves on each side, tertiary nerves reticulate, more or less distinct on both sides; petiolules $5-6(-9) \mathrm{mm}$ long, wrinkled, glabrous. Panicles up to 27 cm long, up to ca 50 -flowered, densely brown-pubescent. Bracts, as well as the reduced leaves at base of inflorescences, ovate, 0.5-1 mm long (reduced leaves sometimes subulate and up to 10 mm long). Pedicels short, articulated $0-1.5 \mathrm{~mm}$ below the calyx, brown-pubescent. Sepals valvate or narrowly imbricate in bud, (narrowly) ovate or triangular, fleshy, persistent at follicles, $2.5-3.6 \times 1.0-1.7 \mathrm{~mm}$, acute or obtuse at top, plane or somewhat keeled, brown-pilose outside, glabrous inside, glandular punctate, indistinctly up to 5 -veined. Petals free, valvate or narrowly imbricate in bud, narrowly elliptic, narrowly obovate to almost linear, (5.5-)6.5-8.1 $\times 1.0-1.7 \mathrm{~mm}$, cuneate at


Fig. 116. Connarus congolanus: 1. branch with leaf, $2 / 3 \times$; 2. leaflet beneath, $2 / 3 \times$; 3. flower partly, $6 \times$; 4. pistil, $8 \times$; 5. follicle, $1 \times$; 6 . seed in longitudinal section, $1 \times(1-4$. Leeuwenberg 5091; 5-6. Stoop v.d. Kasteele 335).


Fig. 117. Distribution of Connarus congolanus
base, obtuse at top, glabrous, rarely sparingly pubescent outside, glabrous or rarely with some glandular hairs inside, usually glandular punctate near the top, more or less distinctly up to 5(-7)-veined. Stamens $1.0-1.5 \mathrm{~mm}$ united at base; long ones $4.2-4.4 \mathrm{~mm}$ or $6.0-7.0 \mathrm{~mm}$ long, filaments with stipitate glands, anthers ca $0.3 \times 0.2 \mathrm{~mm}$; short ones $2.0-3.0 \mathrm{~mm}$ long, filaments lacking glands, anthers usually somewhat smaller, but apparently fertile. Pistil 3.4-4.1 mm or 7.9-9.7 mm long; ovary $1.0-1.5 \mathrm{~mm}$ long, brown-pilose; style pilose at base and with stipitate glands; stigma oblique, more or less 2-lobed, often distinctly papillate. Follicle ellipsoid, ovoid or obovoid, not or hardly oblique, 5.0-7.3 $\times 2.0-3.0$ cm , rounded or cuneate but not stiped at base, obtuse or acute at apex; pericarp thick, woody, glabrous and distinctly veined outside, densely pilose inside. Seed obovoid, ca $34 \times 25 \times 20 \mathrm{~mm}$, sarcotesta ca 10 mm long, enveloping the basal part of the seed at the ventral side only; radicle almost in the centre of the seed, between the cotyledons.

## Distribution: Liberia, Nigeria to South and Central Zaire.

Ecology: Primary or secondairy rain forest, often near rivers. Flowering in Cameroun and Gabon mainly in March and April, in Zaire from January to September. Fruiting a few months later.

## Specimens examined:

[^3]MO, P, WAG); Bulu-Last Banana, Ndian R. (fr. July) D. Thomas 2344 (MO, WAG, YA); Bipindi (fl.b.) Zenker 4895 (BR, G, GOET, K, L, M, MO, P, Z).

Gabon: near Libreville (fl., fr. June) Klaine 36 (B, K, P); (fr.) Klaine 445 (P); (fl.) Klaine 447 (P); Mbigou (fl. Apr.) Le Testu 5412 (BM, P); Epambwa (fl. Mar.) Le Testu s.n. (BM); S of Ekouk (fl., fr. Nov.) A. Louis, Breteler \& de Bruijn 299 (LBV, WAG). Congo: km 10 Mossendjo-Mayoko (fr. May) Bouquet 1323 (P).
Zaire: Katako-Kombe (fl. Jan.) Claessens 435 (BR); Kahemba, Kwango (fl. Mar.) Devred 2997 (BR); Ikela (fl. Sept.) Dubois 833 (BR); near Panzi (fr. Dec.) Renier 12 (BR); Dilolo (fr. June) Sapin s.n. (BR, type).

Note: Schellenberg (1938) named the species, based on the specimen Sapin s.n. from Zaire, C. sapinii. Later he realized this name was already used by De Wildeman (1909) for another species, now a synonym of C. griffonianus. Consequently, in the appendix of his monograph on Connaraceae he changed the name into C. congolanus.

## Connarus gabonensis Lemmens, sp. nov.

Fig. 118, 119
Liana. Folia imparipinnata, 3-4-juga. Foliola coriacea, lateralia anguste elliptica, $6-11 \times 3-5 \mathrm{~cm}$, basis rotundata, terminale anguste elliptica, $11-12 \times 4.5$ cm , basi rotundatum vel cuneatum; foliola acuta vel paulo acuminata, glabra. Inflorescentia grandis, laxa. Sepala circa $2 \times 1 \mathrm{~mm}$. Folliculus 5.5-7.5 $\times 2-2.5$ cm , lignosus, extus nervatus, intus pilosus.
Type: Gabon, 15 km N of km 10 Lalara-Makokou, Okano R., Breteler \& J. de Wilde 494 (holo: WAG).

Liana. Branches cylindric or somewhat angular, lenticellate, branchlets soon glabrescent. Leaves $3-4$-jugate; petiole $8-14 \mathrm{~cm}$, rachis $7.5-12.5 \mathrm{~cm}$ long, soon glabrous. Leaflets leathery, lateral ones alternate, narrowly elliptic, 6-11 $\times 3$-5 cm , rounded at base, terminal one narrowly elliptic, $11-12 \times 4.5 \mathrm{~cm}$, rounded or somewhat cuneate at base; leaflets acute or indistinctly acuminate, glabrous both sides, midrib impressed above, prominent beneath, with 5-7 lateral nerves on each side; tertiary nerves reticulate, distinct beneath, indistinct above; petiolules 5-7 mm long, wrinkled, glabrous. Panicles very large, up to 70 cm long, many-flowered, brown-pubescent. Bracts triangular or ovate, very small, up to 1 mm long. Sepals at base of follicle ovate to triangular, thick and stiff, ca 2.0 $\times 1.0 \mathrm{~mm}$, acute at top, pilose outside, glabrous inside. Follicle ellipsoid, somewhat triangular in cross section, not oblique, $5.5-7.5 \times 2-2.5 \mathrm{~cm}$, cuneate but not stiped at base, obtuse at top; pericarp thick, woody, initially brown-pubescent but soon glabrescent and distinctly veined outside, densely pilose inside. Seed immature.

Distribution: Central Gabon; only known from the type. Ecology: Found in riverbank vegetation in rain forest.


Fig. 118. Connarus gabonensis: 1. branch with leaf, $2 / 3 \times ; 2$. follicle from ventral side, $1 \times ; 3$. detail inner side of follicle, $24 \times(1-3$. Breteler \& J. de Wilde 494).

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Fig. 119. Distribution of Connarus gabonensis
Specimen examined:

Gabon: 15 km N of km 10 Lalara-Makokou, Okano R. (fr. Oct.) Breteler \& J. de Wilde 494 (WAG, type).

Note: This species differs from the closely related trifoliolate C. congolanus by having pinnate leaves. Various flower parts are not or insufficiently known.

## Connarus griffonianus Baill.

Fig. 120, 121
C. griffonianus Baillon, 1867: 235; Schellenberg, 1923: 225; De Wildeman, 1929: 551; 1931: 239; Schellenberg, 1938: 269; Exell, 1944: 151; Troupin, 1952: 132; Hepper, 1958: 748; Exell, 1973: 368; Liberato, 1980b: 14.

Type: Gabon, Griffon du Bellay 183 (lecto design. by Schellenberg, 1938: P).
C. griffonianus Baill. var. subsericeus (Schellenb.) Troupin, 1952: 134. Basionym: C. subsericeus Schellenberg, 1923: 227; Exell, 1928: 98; De Wildeman, 1929: 551; 1931: 239 (as C. sericeus); Schellenberg, 1938:272; Gossweiler \& Mendonça, 1939: 55, 145; Exell \& Mendonça, 1954: 154. Type: Angola, Pungo Andongo, Mechow 87 (lecto design. by Schellenberg, 1938: B $\dagger$; lecto: BR; iso: Z).
C. englerianus Gilg, 1891b: 316; Durand \& Schinz, 1896: 101; Durand \& Durand, 1909: 119; Gilg, 1911: 232; Schellenberg, 1923: 225; 1938: 272; Troupin, 1952: 134. Type: Zaire, Kasai Distr., Mukenge, Pogge 752 (holo: $\mathrm{B} \dagger$ ), neo: Zaire, Kakenge, Bakuba, Gillardin 273 (BR).
C. luluensis Gilg, 1895b: 64; Durand \& Durand, 1909: 119; Schellenberg, 1923: 225. Type: Zaire, Kasai, Lulua R., Pogge 741 (holo: B $\dagger$ ), neo: Zaire, Kazumba, Miao R., Liben 3422 (BR).
C. florulentus Hiern, 1896: 189. Type: Angola, Pungo Adongo, near Quiem-
bongo and Mata de Cabondo, Welwitsch 614 (lecto: BM; iso: K).
C. villosiflorus Gilg, 1896: 209; Schellenberg, 1923: 225; 1938: 272. Type: Cameroun, Yaoundé, Zenker 92 (holo: $\mathrm{B} \dagger$ ), neo: Cameroun, Bipindi (fl.) Zenker 2878 (B, BR, E, G, GOET, K, L, M, MO, WAG, Z).
C. sapinii De Wildeman, 1909: 89 (as C. sapini); 1910a: 292. Type: Zaire, Madibi, Sapin s.n. (holo: BR).
C. macrothyrsus Gilg ex Schellenberg, 1910: 19. Homotypic synonym of Manotes staudtii.
C. incurvatus Schellenberg, 1923: 228; 1938: 273. Type: Central African Republic, Boro, Chevalier 7688 (holo: B $\dagger$; lecto: P).
C. obovatus Schellenberg, 1923: 229; 1938: 273. Type: Central African Republic, Bondjo Land, Chevalier 6033 bis (holo: $\mathrm{B} \dagger$; lecto: P ).
C. orientalis Schellenberg, 1923: 228; 1938: 273; Troupin, 1952: 135. Type: Zaire, Mawambi-Kasanga, Mildbraed 3085 (holo: $\mathrm{B} \dagger$ ), neo: Zaire, 7 km W of Kisangani, Bokdam 3199 (WAG).
C. puberulus Schellenberg, 1923: 226; 1938: 271. Type: Cameroun, Tibati, Ledermann 2324 (lecto design. by Schellenberg, 1938: B $\dagger$ ), lecto: Cameroun, Yaoundé-Dendeng, Mildbraed 8341 (K).
C. triangularis Schellenberg, 1923: 226; 1938: 271. Type: Cameroun, Lomie Distr., Assobam, Bunda R., Mildbraed 5064 (holo: B $\dagger$ ), neo: Cameroun, 14 km WSW of Kinsassa, 65 km NNE of Moloundou, Letouzey \& Villiers 10513 (BR, P). See note 1 .
C. fernandesianus Exell \& Mendonça, 1952: 234, fig.14; 1954: 154, fig. 34. Type: Angola, Lunda, near Vila Henrique de Carvalho, Exell \& Mendonça 935 (holo: COI; iso: BM, BR).

Manotes staudtii Gilg, 1895b: 71. Type: Cameroun, Yaoundé, Zenker \& Staudt 122 (holo: B $\dagger$; lecto: K; iso: BM).

Liana or lianescent shrub. Branches cylindric, often with shallow longitudinal grooves, lenticellate, branchlets densely brown-pubescent, later glabrescent. Leaves (2-)3-5-jugate; petiole (3-) $5-12 \mathrm{~cm}$, rachis $4-16 \mathrm{~cm}$ long, brown-pubescent when young. Leaflets papery to leathery, lateral ones opposite or not, (narrowly) elliptic or (narrowly) obovate, $5-22 \times 2-7 \mathrm{~cm}$, rounded or cuneate at base, terminal one narrowly elliptic or narrowly obovate, $9-21 \times 3-8 \mathrm{~cm}$, more or less cuneate at base; all leaflets acuminate, glabrous above, densely brown-pubescent to glabrous beneath, midrib impressed above, prominent beneath, with (5-)6-12 lateral nerves on each side; tertiary nerves reticulate, distinct beneath, usually indistinct above; petiolules $4-7 \mathrm{~mm}$ long, often wrinkled, pilose or glabrous. Panicles up to 35 cm long, up to ca 50 -flowered, densely brown-pubescent. Reduced leaves at base of inflorescences linear, up to 13 mm long, more rarely ovate and small, bracts ovate, ca 1 mm long. Pedicels very short, articulated $0-1.5 \mathrm{~mm}$ below the calyx, brown-pubescent. Sepals often rather distinctly spirally arranged, valvate in bud, triangular to ovate, somewhat fleshy, $(1.7-) 2.0-2.5(-3.0) \times 0.7-1.2 \mathrm{~mm}$, acute or obtuse at top, more or less convex, brown-pilose outside, glabrous inside, glandular punctate with up to 15 glands,


Fig. 120. Connarus griffonianus: 1. branch with leaf, $2 / 3 \times ; 2$. branchlet with inflorescences, $2 / 3$ $x$; 3. detail leaflet beneath, $10 \times$; 4. flower, $6 \times$; 5 . flower partly, showing stamens and pistil, $6 \times$; 6. fertile and rudimentary stamen, $12 \times ; 7$. follicle, $1 \times ; 8$. detail inner side of follicle, 20 $\times$; 9 . seed, $1 \times ; 10$. seed in longitudinal section, $1 \times(1-6$. Breteler \& J. de Wilde 625; 7-10. Devred 2531).


Fig. 121. Distribution of Connarus griffonianus
up to 3 -veined. Petals free, imbricate in bud, narrowly elliptic to narrowly obovate, $4.5-6.5 \times 1.0-1.5 \mathrm{~mm}$, cuneate at base, obtuse or rounded at top, densely pilose outside, with some glandular hairs or sometimes glabrous inside, usually glandular punctate with some glands near the top, indistinctly up to 5 -veined. Stamens $0.5-1 \mathrm{~mm}$ united at base; long ones $2.0-3.0 \mathrm{~mm}$ or $4.2-6.0 \mathrm{~mm}$ long, filaments mostly with stipitate glands, anthers ca $0.3 \times 0.2 \mathrm{~mm}$, usually lacking glands; short ones $1-1.7 \mathrm{~mm}$ long, rudimentary and sterile with slender filaments and very small anthers, exceptionally apparently fertile (see note 2 ), lacking glands. Pistil $2.1-2.8 \mathrm{~mm}$ or 4.2-6.0 mm long; ovary $1-1.5 \mathrm{~mm}$ long, brownpilose; style pilose at base, with stipitate glands; stigma oblique, more or less 2-lobed. Follicle oblique-pyriform, compressed, $1.5-2.5 \times 1.3-1.8 \mathrm{~cm}$, stipe 2-4 mm long; apex with ca 1 mm long lateral mucro; pericarp thin, initially brownpubescent but often glabrescent outside, with a few hairs and many glands inside. Seed (narrowly) ovoid, 10-15 $\times 4-7 \times 4-6 \mathrm{~mm}$, sarcotesta $5-7 \mathrm{~mm}$ long, enveloping the basal part of the seed; radicle apical.

Distribution: Central Africa, from Nigeria to E Zaire and south to N Angola.
Ecology: Rain forest, usually in lowland, under 1000 m altitude (see note 2 under C. longistipitatus). Flowering in Nigeria, Cameroun, Central African Republic and Gabon mainly from September to March, in Zaire it can be found flowering all the year round.

Selection of the ca 250 specimens examined:
Nigeria: Benin Div., Uyere-Oke, Owam F.R. (fl. Feb.) Brenan \& Onochie 8984 (BM, K); Benin Div., Okomu F.R. (fr. Feb.) Brenan, Onochie, Jones \& Richards 9071 (K); Mambilla Div., GashakaGidan Kwano (fr. May) Chapman 4487 (K); Vogel Peak (fl. Feb.) Chapman 4742 (K); Sapoba (fl.)

Kennedy 2088 (BR, K, P); Udi Plateau (fl. Dec.) MacGregor 372 (K); Ogoja Prov., Sonkwala (fl. Dec.) Savory \& Keay FHI 25160 (K); Oban (fr.) Talbot 1765 (BM, K, Z).

Cameroun: Nola (fl., fr. Nov.) Aubreville 256 (P); Bitye (fl.) Bates 1609 (MO); Kumba Distr. (fl., fr. Feb.) Binuyo \& Daramola FHI 35529 (K); 5 km E of Bertoua (fr. Dec.) Breteler 846 (BR, K, P, WAG); km 6 Bertoua-Batouri (fr. Mar.) Breteler 1193 (BR, K, P, WAG); 6 km E of Bertoua (fl. Sept.) Breteler 1850 (BR, K, P, WAG); N of Nyassosso (fl. Apr.) Etuge \& D. Thomas 15 (MO, WAG); Gounso (fl. Feb.) Jacques Félix 3187 (P); Mai Idoanu, Mbaw R. (fl., y.fr. Feb.) Latilo \& Daramola FHI 34463 (B, K, MO, P); 14 km WSW of Kinsassa, 65 km NNE of Moloundou (fr. Mar.) Letouzey \& Villiers 10513 (BR, P, type of C. triangularis); Letouzey \& Villiers 10553 (BR, P); Molundu, Lokomo-Bumba (fl., y.fr. Jan.) Mildbraed 4343 (HBG); Yaoundé-Dendeng (fr. Feb.) Mildbraed 8341 (K, type of C. puberulus); Bipindi (fl.) Zenker 105 (B, C, U); Yaoundé (fl.) Zenker \& Staudt 122 (BM, K, type of Manotes staudtii and C. macrothyrsus); Bipindi (fl.) Zenker 2878 (B, BR, E, G, GOET, K, L, M, MO, WAG, Z, type of C. villosiflorus); (fr.) Zenker 3578 (BR, E, G, GOET, K, L, M); (fr.) Zenker 3617 (BR, E, G, GOET, K, L, M, MO, P, Z).

Central African Republic: km 17 Mbaiki-Boda, Bomangou F. (fr. Dec.) Badré 333 (P, WAG); near Mbaiki (fr. Dec.) Breyne 1304 (BR); Bembo (fl.b. Dec.) Breyne 1378 (BR); Krébédjé (fl. Oct.) Chevalier 6004 (G, L, P); sin. loc. (fl. Oct.) Chevalier 6033 bis (P, type of C. obovatus); Snoussi Land (fr. Mar.) Chevalier 7688 (P, type of C. incurvatus); 2 km S of Carnot, Mambéré R. (fl., fr. Dec.) Leeuwenberg 7252 (B, BR, K, MO, P, WAG); Yalinga Region (fr. May) Le Testu 4710 (BR, P); Molo-Mondoko, Lissongo (fl. Sept.) Tisserant 1586 (P, WAG).

Equatorial Guinea: Fernando Po (fl.) Mann 7 (K); (fr.) Mann 427 (K, P).
Sao Tomé \& Principé: Principé, Ogue Pipi (fr. Dec.) Exell 502 (BM); Pico Papagaio (fl.b. Dec.) Exell 679 (BM).

Gabon: km 40 Lalara-Makokou (fl. Sept.) Breteler \& J. de Wilde 523 (WAG); Ivindo R. (fl. Sept.) Breteler \& J. de Wilde 625 (WAG); sin. loc. (fl., fr.) Griffon du Bellay 183 (P, type); Griffon du Bellay 274 (P); Bélinga (fr. July) Hallé \& Le Thomas 120 (P); (fr. June) Hallé 3973 (P); near Libreville (fl.) Klaine 3011 bis (B, K, P); Lopé-Okanda (fr. Nov.) Leeuwenberg 12451 (LBV, WAG); Ogooué (fl.) Leroy s.n. (P); Mayumba (fl. Mar.) Le Testu 1002 (BR, K, P); Nyanga Region (fl.) Le Testu 1772 (BM, BR, P); Gaboon R. (fl.) Mann 980 (K, P); Sibange Farm near Libreville (fl. July) Soyaux 298 (K, Z).
Congo: Mboté R. (fr. Sept.) Bouquet 517 (P); near Brazzaville (fl. Aug.) Chevalier 27734 (P); (fr. Aug.) Chevalier 27744 (P); 15 km from Brazzaville (fl.b. Aug.) de Néré 1705 (P); km 39 EdouBoundji (fl. July) Descoings 8077 (P); 25 km W of Sibiti, Mudongo (fr. Aug.) Farron 4417 (P); Kimpanzou, Foulakari R. (fr. Nov.) Lejoly 86/148 (BR); Ouesso (fl., fr. Mar.) Pobéguin 131 (P); Alima R. (fr. Mar.) Thollon 916 (BR, P).
Zaire: Leopoldville (fl. Sept.) Achten 1231 (BR); Stanleyville (fl. Feb.) Bequaert 6926 (BR); 7 km W of Kisangani (fl. Sept.) Bokdam 3199 (WAG, type of C. orientalis); Yangambi (fl., fr. Oct.) Bolema 98 (BR); Momfinu, Maluku (fl., fr. May) Breyne 2200 (BR); Kimbuya-Kingedi, Lukula (fr. Aug.) Compere 150 (BR, K); Eala (fl. Aug.) Corbisier-Baland 1648 (BR, K); Leopoldville (fl. Aug.) Couteaux 1098 (BR, G, K, L, WAG); Kiyaka, Kwango, Bunga F. (fr. Sept.) Devred 2669 (BR, K); Luki (fr. Sept.) Donis 2016 (BM, BR, P); Ndeke, Basankusu (fl., fr. Sept.) Evrard 4892 (BR); Madabu (fl., fr. Mar.) Gerard 2776 (BR); km 62 Boma-Matadi, Kimpelo (fr. June) Germain 2319 (BR, K); Kakenge, Bakuba (fl. Nov.) Gillardin 273 (BR, type of C. englerianus); Gombe, Congo R. (fl., fr. Apr.) Jans 452 (BR); near Coquilhatville (fl., fr. July) Lebrun 818 (BR, G, P); Yangambi (fl. July) A. Léonard 864 (BR, K, M); Kazumba, Miao R. (fr. July) Liben 3422 (BR, type of C. luluensis); Yangambi (fr. Nov.) J. Louis 12773 (BM, BR, K, P); Kinkasi Benga, Popokabaka (fr. Oct.) Pauwels 152 (BR); Bombimba (fl. Aug.) Pynaert 320 (BR); Madibi (fr. June) Sapin s.n. (BR, type of C. sapinii); Ipamu (fr. Aug.) Vanderyst 10304 (BR).

Angola: Lunda, Vila Henrique de Carvalho (fl. Apr.) Exell \& Mendonça 935 (BM, BR, COI, type of C. fernandesianus); Pango Manga, Maiombe (fl., y.fr.) Gossweiler 6163 (BM, COI, LISU); Loco, Sumba, Peco (fl. June) Gossweiler 9140 (K); Pungo-Andongo (f1.) Mechow 87 (BR, Z, type of C. subsericeus and C. griffonianus var. subsericeus); Cuanza Norte, Camabatela (fl., fr. Feb.) Teixeira et al. 12070 (LISC); Pungo Adongo (fl., fr.) Welwitsch 614 (BM, K, type of C.florulentus).

Notes: 1. The holotype of C. triangularis, the only specimen cited by Schellenberg, was destroyed in B. According to Schellenberg, it is characterized by the triangular follicle and the leaflets, cordate at base. This description fits $C$. griffonianus. A specimen from Cameroun, Letouzey \& Villiers 10553, is chosen as neotype. Its follicles are more or less triangular in outline, and the leaflets have a somewhat cordate base.
2. In C. griffonianus flowers with 10 apparently fertile stamens are found rarely, but then the anthers of the short stamens are distinctly smaller than those of the long stamens. This was found in only 3 specimens (Le Testu 1002 from Gabon, Jans 452 and Gilbert 14202 from Zaire) out of the 68 flowering specimens studied. The plants from Zaire have fruits and there is no doubt that they belong to C. griffonianus. The specimen from Gabon has no fruits, but the narrow, thick sepals and the collecting locality agree with C. griffonianus rather than C. longistipitatus. For that reason it is identified as C.griffonianus.

## Connarus longistipitatus Gilg

Fig. 122, 123
C. longistipitatus Gilg, 1895b: 191; 1911: 232; Exell, 1928: 98; De Wildeman, 1931: 239 (as C. longestipitatus); Schellenberg, 1938: 268, fig. 46 (as C. longestipitatus); Gossweiler \& Mendonça, 1939: 90 (as C. longistipulatus); Troupin, 1952: 130 (as C. longestipitatus); Exell \& Mendonça, 1954: 152 (as C. longestipitatus); Hemsley, 1956: 24, fig.9.
Type: Tanzania, Bukoba, Stuhlmann 3831 (holo: B $\dagger$ ), neo: Tanzania, Bukoba, Minziro F.R., Watkins 532 (EA).
C. stuhlmannianus Gilg, 1895b: 192; Schellenberg, 1938: 268. Type: Tanzania, Bukoba, Stuhlmann 1128 (lecto: B $\dagger$ ), neo: Tanzania, Bukoba Distr., Kiziba, Ford 54 (EA).
C. mildbraedii Schellenberg, 1923: 224; 1938: 267; Troupin, 1952: 129. Type: Cameroun, Lomie Distr., Mokumelos, Mildbraed 5272 (holo: $\mathrm{B} \dagger$ ), neo design. by Troupin, 1952: Zaire, Lubutu-Kirundu, Bequaert 6814 (BR).
C. vrydaghii Troupin, 1951: 372; 1952: 131, fig.2A. Type: Zaire, Bambesa, Vrydagh 416 (holo: BR).

Liana or lianescent shrub. Branches cylindric, sometimes somewhat angular or with shallow longitudinal grooves, mostly lenticellate, branchlets initially brown-pubescent, soon glabrescent. Leaves (1-)2-4-jugate; petiole 3-11 cm, rachis (2-)4.5-17 cm long, brown-pubescent when young. Leaflets papery, rarely thinly leathery, lateral ones opposite or not, (narrowly) elliptic or (narrowly) ovate, $6-20 \times 3-9 \mathrm{~cm}$, rounded or cuneate at base, terminal one 7-20 $\times 4-11$ cm , cuneate or sometimes rounded at base; all leaflets acuminate, glabrous both sides (very young sometimes sparsely pubescent), midrib impressed above, prominent beneath, with 4-7 lateral nerves on each side; tertiary nerves reticulate, distinct beneath, usually indistinct above; petiolules $4-6 \mathrm{~mm}$ long, wrinkled, soon glabrous. Panicles 3-20 cm long, up to ca 50 -flowered, densely brown-



Fig. 123. Distribution of Connarus longistipitatus
pubescent. Reduced leaves at base of inflorescences as well as bracts triangular to (narrowly) ovate, 1-2 mm long (reduced leaves rarely longer). Pedicels very short, articulated $0-1 \mathrm{~mm}$ below the calyx, brown-pubescent. Sepals imbricate in bud, (broadly) ovate to obovate, rather thin (not fleshy), 3.0-4.5 $\times 1.3-2.0$ mm , obtuse or rounded at top, more or less plane, brown-pilose outside, pubescent inside, glandular punctate with up to 25 glands, usually indistinctly up to 5 -veined. Petals cohering at ca $1 / 3$ from the base, imbricate in bud, narrowly elliptic to narrowly obovate, $5.5-8.0 \times 1.5-2.0 \mathrm{~mm}$, cuneate at base, obtuse at top, pubescent outside, with glandular hairs inside, glandular punctate near the top with some to rather numerous glands, usually indistinctly up to 5 -veined. Stamens ca 1 mm united at base; long ones $3.3-4.2 \mathrm{~mm}$ or $6.0-7.5 \mathrm{~mm}$ long, filaments with stipitate glands, anthers ca $0.3 \times 0.2 \mathrm{~mm}$, usually lacking glands; short ones $2.0-2.6 \mathrm{~mm}$ long, apparently fertile, anthers mostly somewhat smaller than those of the long stamens, exceptionally rudimentary and sterile (see note 1), lacking glands. Pistil $3.3-4.0 \mathrm{~mm}$ or $5.1-6.5 \mathrm{~mm}$ long; ovary $1-1.5 \mathrm{~mm}$ long, brown-pilose; style pilose and with stipitate glands; stigma usually oblique, more or less 2-lobed. Follicle oblique-pyriform, somewhat compressed, 2.5-3.5 $\times$ $1.1-1.7 \mathrm{~cm}$, stipe $5-10 \mathrm{~mm}$ long; apex with up to 2 mm long lateral mucro, rarely mucro almost apical; pericarp rather thin, brown-pubescent when young, but soon glabrous outside, pilose and lacking glands (very rarely with some glands) inside. Seed obovoid, 12-17 $\times 6-8 \times 4-6 \mathrm{~mm}$, sarcotesta $5-9 \mathrm{~mm}$ long, enveloping the basal part of the seed; radicle apical.

Distribution: E Zaire, Burundi, S Kenya, N Tanzania; once collected in Nigeria, twice in Cameroun, once in NW Zaire and once in N Angola.

Ecology: Usually in submontane or montane forests, above 1000 m (see note 2); sometimes in thickets in savanna. Flowering in E Zaire, Uganda and N Tanzania mainly from May to July or from November to January.

## Specimens examined:

Nigeria: Obudu Cattle Ranch (fr.) van Meer 1822 (WAG).
Cameroun: Meuban, 24 km S of Djoum (fl. Nov.) Letouzey 8345 (P, WAG).
Zaire: Masisi-Walikale (fl. July) Bequaert 6448 (BR); Lubutu-Kirundu (fr. Feb.) Bequaert 6814 (BR, type of C. mildhraedii); Nala (fl.) Boone s.n. (BR); Mahagi, Kibali R. (fr. Apr.) Deville 320 (BR); Mbongo (fr. Scpt.) Evrard 1750 (BR); Kishanga, Walikale (fr. June) Gutzwiller 1073 (BR); Mutongo, Walikale (fr. May) Gutzwiller 2760 (BR); Gutzwiller 2827 (BR); Luamisole, (fl. May) Hendrick.x 378 (BR); Mushuva R. (fl. May) Hendrickx 379 (WAG); Kinene, Masisi (fr. Dec.) A. Léonard 1999 (BR); Kitshanga, Walikale (fl., fr. Jan.) A. Léonard 2429 (BR); (fr. Feb.) A. Léonard 2816 (BR); Bitale, km 48 Kavumu-Buniakiri (fl.b. Apr.) Pierlot 135 (BR, K); km 123 Sake road. Walikale (fr. May) Picrlot 2097 (BR); km 48.5 Kavumu-Walikale (fl., fr. June) Pierlot 3149 (BR); Bushangania (fl. Jan.) Rossignol 183 (BR); km 110 Kavumu-Walikale (fl.b. Apr.) Troupin 3167 (BR, K); Bambesa (fr. Apr.) Vrydagh 416 (BR, K, type of C. vrydaghii).

Angola: Cuanza sul, Amboim, Novo Redondo (fl., fr.) Gossweiler 4482 (BM, COI, K).
Burundi: Kigamba, Cankuzo-Muhinga (fr. Oct.) Auquier 4324 (BR); Urundi, Kitega (fr. Jan.) van der Ben 1842 (BR, K); (fl.) van der Ben 1849 (BR).

Uganda: N of Kagera (y.fr. Feb.) Bagshawe 158 (BM); near Entebbe, Mengo Distr., Busiro (fl., fr. Nov.) Dawkins 666 (EA, K); Makimo F. (fl. Dec.) Dümmer 536 (BM); Mengo Distr., Kivuvu (fl., y.fr. Nov.) Dümmer 1248 (BM, K); (fl. May) Dümmer 2614 (BM, K); Budongo F. (fl. Dec.) Eggeling 1470 (BM, BR, K); Eggeling 1556 (K); Entebbe (fl. July) Eggeling 4411 (K); near Kyanga, Kalinzu F. (fl.b., fr. Dec.) Gibson 387 (BR, K); Entebbe, Nubi village (fl. Dec.) Godman 40 (BM); Masaka Distr., Kyotera county (fr. Dec.) Katende 1417 (EA); Budongo F. (Nov.) Loveridge 127a (K); Mabira F. (fl. Dec.) Maitland 327 (K); Kanoni (fl., fr. July) Maitland 641 (K); Kigezi Distr., Kayonza F.R. (fr. Aug.) Paulo 642 (BR, EA, K); Budongo F. (fl.b. Mar.) Sangster 111 (K); Mabira F. (fr.) Ussher 94 (BM, K).

Kenya: Kwale (fl.b.) Graham 1695 (EA, K); Shimba Hills, Longo Magandi (fr. Feb.) Magogo \& Glover 192 (EA); Trans-Nzoia Distr., Kapretwa near Kitale (fr.) Thorold s.n. (BM).

Tanzania: Kiziba, Kagera basin (fr. July) Ford 54 (EA, type of C. stuhlmannianus); Bukoba, Kikongoro F.R. (II.b. Dec.) Kanywa 32 (EA); Bukoba (fl., y.fr.) Proctor 835 (K); (fr.) Proctor 1028 (K); (fl. Jan.) Proctor 1109 (K); Msolwa F. (fl. Nov.) Vollesen 4158 (C, EA); Bukoba, Minziro F.R. (fr. Sept.) W'atkins 532 (EA, type).

Notes: 1. In a single specimen, Vollesen 4158 from Kenya, rudimentary short stamens are found, a character common in C. griffonianus. However, the broad, thin sepals are characteristic for C. Iongistipitatus. Moreover C. griffonianus has never been collected in Kenya.
2. C. Iongistipitatus is usually found above 1000 m altitude, but in E Africa it is also present in the lowland. The Central African specimens with known altitude are all collected in the mountains, above 1000 m . The closely related C. griffoniamus is mainly restricted to lowland areas, and is rarely found in the mountains. According to the labels, only 5 specimens of the latter species were collected from above 1000 m . In the area, where both species occur, C. Iongistipitatus is usually restricted to the mountains, and C. griffonianus is found at lower altitudes.

Fig. 124, 125
C. staudtuii Gilg, 1896: 208; Schellenberg, 1923: 224; Exell, 1928: 98; De Wildeman, 1929: 551; Schellenberg, 1938: 286, fig.48; Gossweiler \& Mendonça, 1939:


Fig. 124. Connarus staudtii: 1. branch with leaf, $23 \times ; 2$. fower partly. shouing stamens and pistil. $6 \times$; follicle, $1 \times ; 4$. seed in longitudinal section. $1 \times 5$. seed in longitudinal section. Ievia removed, $1 \times$ (1. Paunels 6205; 2. Claessens 91: 3. Talbot 1427:4-5. Klaine 1461).

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55; Troupin, 1952: 136, fig.2B; Exell \& Mendonça, 1954: 154; Hepper, 1958: 748.
Type: Cameroun, Lolodorf, Staudt 271 (holo: B $\dagger$; lecto: G; iso: K, P).
C. macrourus Gilg, nomen in herb. Zenker; Schellenberg, 1938: 286 (in syn.).
C. odoratissimus Gilg, nomen in herb. Zenker; Schellenberg, 1938: 286 (in syn.).

Liana or lianescent shrub. Branches cylindric, lenticellate, branchlets often somewhat angular, brown-pubescent, soon glabrescent. Leaves 2-5-jugate; petiole with distinct, blackish articulation at base, $1.5-12 \mathrm{~cm}$ long, rachis $3.5-31$ cm long, brown-pubescent when young, soon becoming glabrous. Leaflets (stiffly) papery, lateral ones alternate or more or less opposite, (narrowly) ovate or (narrowly) elliptic, $3.5-14 \times 2.5-5.5 \mathrm{~cm}$, rounded or cuneate and not or hardly unequal at base, terminal one elliptic, $7-16 \times 4-5.5 \mathrm{~cm}$, cuneate at base; all leaflets $1.6-3.2 \mathrm{~cm}$ long acuminate, brown-pubescent when very young, soon becoming glabrous, midrib impressed above, prominent beneath, with 3-5 curved lateral nerves on each side; tertiary nerves indistinct on both sides; petiolules (3-)5-8 mm long, wrinkled, blackish, glabrous. Panicles $6-17 \mathrm{~cm}$ long, up to ca 50 -flowered, brown-pubescent. Bracts, as well as the reduced leaves at base of inflorescences, triangular or ovate, ca 1 mm long. Pedicels very short, articulated $0-0.5$ mm below the calyx, brown-pubescent. Sepals valvate in bud, (narrowly) triangular or ovate, thin or somewhat fleshy at base, $1.8-2.3 \times 0.5-0.9 \mathrm{~mm}$, acute or sometimes obtuse at top, plane or more or less convex, brown-pubescent outside, glabrous inside, glandular punctate with ca 12 glands, without distinct veins. Petals usually coherent, imbricate in bud, narrowly elliptic or narrowly oblong, (4.2-)5.0-6.9(-7.8) $\times(0.8-) 1.0-1.3(-1.5) \mathrm{mm}$, cuneate at base, obtuse or rounded and often inflexed at top, yellowish brown-pubescent outside, with glandular hairs inside, glandular punctate near the top, indistinctly (0-)3-5-veined. Stamens $0.3-0.6(-0.8) \mathrm{mm}$ united at base; long ones $2.4-3.3 \mathrm{~mm}$ or 4.5-6.5 mm long, filaments with stipitate glands, anthers ca $0.3 \times 0.2 \mathrm{~mm}$; short ones 1.1-1.6(-1.8) mm long, rudimentary, lacking anthers or anthers extremely small. Pistil $2.4-3.2 \mathrm{~mm}$ or 4.2-6.4 mm long; ovary $0.8-1.2 \mathrm{~mm}$ long, brownpilose; style usually pilose and with stipitate glands; stigma usually oblique, more or less 2-lobed. Follicle ellipsoid or obovoid, not or hardly oblique, 3.6-6.8 $\times$ $2.1-3.2 \times 1.6-2.6 \mathrm{~cm}$, cuneate with often indistinct, up to 7 mm long stipe at base; apex with up to 1.5 mm long mucro; pericarp rather thick, opening along the ventral and dorsal suture, glabrous both sides, lacking distinct veins, but somewhat striate. Seed (ob)ovoid or somewhat kidney-shaped, 22-32 $\times 10-22$ $\times 10-17 \mathrm{~mm}$, sarcotesta ca 5 mm long, partly enveloping the basal part of the seed, ruminate; radicle almost in the centre of the seed, between the cotyledons.

Distribution: SE Nigeria, W Cameroun, Gabon, S Congo, W Zaire, N Angola (Cabinda).

Ecology: Rain forest, often along rivers. Flowering in Cameroun in April and May, in Gabon and Congo about September, in Zaire from June to September. Fruiting a few months later.


Fig. 125. Distribution of Connarus staudtii

## Specimens examined:

Nigeria: Ngwugwo, Yalu road (fr. Dec.) Ariwaodo 876, FHI 58005 (K, P); Oban (fl.b.) Talbot 1297 (BM); (fr.) Talbot 1427 (BM, K, Z); Eket Distr. (fl.) Talbot s.n. (BM).
Cameroun: 65 km SSW of Eséka (fr. June) W. de Wilde 2759 (BR, K, MO, P, WAG); Ebea, 26 km N of Kribi (fl. Apr.) Leeuwenberg 5622 (WAG); km 58 Edea-Kribi (fl. May) Leeuwenberg 5674 (B, BR, C, K, MO, P, WAG); Fenda, 58 km E of Kribi (fl.) Mildbraed 5949 (HBG); Lolodorf (fl.) Staudt 271 (G, K, P, type); Bipindi (fl. Apr.) Zenker 541 (B, BR, C, G, MO, P); (fl.) Zenker 2066 (BM, E, G, GOET, K, P, Z); (fr.) Zenker 2769 (BM, BR, E, G, GOET, K, L, M, MO, P, WAG, Z); (fl. y.fr.) Zenker 2960 (BM, BR, E, G, GOET, K, L, M, P, Z); (fl.) Zenker 3061 (B, BM, BR, E, G, GOET, K, L, M, MO, P, WAG, Z); (fr.) Zenker 3858 (BM, E, G, GOET, K, MO); Zenker 3964 (BM, E, G, K); (fl.b.) Zenker $4985 a$ (BM, K, MO).
Gabon: 42 km N of km 10 Lalara-Makokou (fl., fr. Sept.) Breteler \& J. de Wilde 442 (WAG); km 35 Mouila-Yeno (fl., fr. Sept.) Breteler, Lemmens \& Nzabi 8232 (LBV, WAG); near Libreville (fr.) Klaine 1961 (B, BR, K, P, WAG); (fr. June) Klaine 2228 (P); (fr. Oct.) Klaine 3092 (P).
Congo: Djoumouna (fl. Sept.) Bitsindou s.n. (P); Taba-Mandzakala (y.fr. Oct.) Sita 2650 (P).
Zaire: Sabuka (fl.) Claessens 91 (BR); Luki (fl. Sept.) Donis 2005 (BR, K); Lukaya, Ngafula (fr. Nov.) Pauwels 6029 (BR, WAG); (fl., fr. June) Pauwels 6205 (BR).
Angola: Belize, Maiombe (fr.) Gossweiler 6984 (BM, COI, LISU).

Connarus thonningii (DC.) Schellenb.
Fig. 126, 127
C. thonningii (DC.) Schellenberg, 1923: 224; 1938: 280; Hepper, 1958: 748; Irvine, 1961: 573; Ern, 1984: 165.
Basionym: Omphalobium thonningii De Candolle, 1825: 86; Don, 1832: 90.
Type: Ghana, Töffri, Thonning s.n. (holo: herb. De Candolle in G; iso: C).
See note.
C. florulentus Thonning, nomen in sched.; De Candolle, 1825: 86 (in syn.).
C. floribundus Thonning ex Schumacher, 1827: 73; Walpers, 1842: 561; Plan-


Fig. 126. Connarus thonningii: 1. flowering branch, $2 / 3 \times$; detail leaflet beneath, $10 \times$; 3 . flower, $6 \times$; 4. flower partly, showing stamens and pistil, $6 \times$; 5. fertile and rudimentary stamen, $12 \times$; 6. follicle, $1 \times ; 7$. detail inner side of follicle, $10 \times$; 8 . seed, $1 \times ; 9$. seed in longitudinal section, $1 \times$ (1-2. Geerling \& Bokdam 427; 3-5. Hall 2707; 6-9. Aké Assi 7191).
chon, 1850: 426; Walpers, 1852: 300; Baker, 1868: 457. Type: Ghana, Töffri, Thonning 339 (holo: C). See note.
C. nemorosus Vahl ex Schumacher, 1827: 73 (nomen).

Liana or lianescent shrub. Branches cylindric, often with shallow longitudinal grooves, mostly lenticellate, branchlets glabrous, sometimes initially pubescent but very soon glabrescent. Leaves 1-3(-4)-jugate; petiole $2-5 \mathrm{~cm}$, rachis $0.5-8$ cm long, brown-pubescent when young. Leaflets papery, lateral ones opposite or not, elliptic, $4.5-10 \times 2.5-5 \mathrm{~cm}$, rounded at base, terminal one elliptic or obovate, $6.5-9.5 \times 3-4.5 \mathrm{~cm}$, rounded or somewhat cuneate at base; all leaflets obtuse or shortly acuminate, glabrous both sides, sometimes puckered, midrib impressed above, prominent beneath, with 5-8 lateral nerves on each side; tertiary nerves reticulate, mostly distinct on both sides; petiolules $3-4 \mathrm{~mm}$ long, wrinkled, glabrous. Panicles $4-15 \mathrm{~cm}$ long, up to 50 -flowered (sometimes more), densely brown-pubescent. Bracts, as well as the reduced leaves at base of inflorescences triangular or ovate, $1-1.5 \mathrm{~mm}$ long. Pedicels short, articulated $1-2 \mathrm{~mm}$ below the calyx, brown-pubescent. Sepals narrowly imbricate in bud, (narrowly) ovate, rather thin (at least near the top), $2.5-3.3 \times 1-1.5 \mathrm{~mm}$, obtuse at top, more or less convex, brown-pilose outside, glabrous inside, usually strongly glandular punctate, up to 5 -veined. Petals free, imbricate in bud, very narrowly elliptic to almost linear, 5.5-7.7 $\times 0.8-1.7 \mathrm{~mm}$, cuneate at base, obtuse at top, sparingly pilose to almost glabrous outside, with some glandular hairs inside, strongly glandular punctate, especially near the top, indistinctly up to 5-veined. Stamens ca 1 mm united at base; long ones $2.8-5.3 \mathrm{~mm}$ or $6.1-9.0 \mathrm{~mm}$ long, filaments with many stipitate glands, anthers ca $0.5 \times 0.3 \mathrm{~mm}$, mostly with glands at the top; short ones $1.5-2.3 \mathrm{~mm}$ long, rudimentary and sterile with rather slender filaments and very small anthers, filaments and mostly also anthers with glands. Pistil $3.8-4.5 \mathrm{~mm}$ or 5.3-8.3 mm long; ovary 1-1.5 mm long, yellowish brown-pilose; style pilose at base, with many stipitate glands; stigma usually oblique, more or less 2 -lobed. Follicle oblique-pyriform, somewhat compressed, $2.2-2.5 \times 1.0-1.3 \mathrm{~cm}$, stipe $2-5 \mathrm{~mm}$ long; apex with an up to 2 mm long lateral mucro; pericarp thin, initially brown-pubescent but very soon glabrous and sometimes with glands outside, glabrous, glossy and lacking glands inside. Seed ovoid, ca $13 \times 7 \times 5 \mathrm{~mm}$, sarcotesta ca 6 mm long, enveloping the basal part of the seed; radicle apical.

## Distribution: W Africa: Ivory Coast, S Ghana, S Togo.

Ecology: Thickets in savanna, remnants of forests, usually near rivers. Flowering from June to October, fruiting a few months later.

## Specimens examined:

Ivory Coast: Séguela-Mankono (fr. Dec.) Aké Assi 7191 (K, P); Soubré, Sassandra (fl. June) Chevalier 19111 (P); Gawi-Seyey, Iringou R. (fl. July) Geerling \& Bokdam 182 (B, BR, WAG); Bouna-Ferkessedougou, Comou R. (fl. Aug.) Geerling \& Bokdam 427 (B, BR, WAG); BouakéDabakala (fr. Jan.) Roberty 690 (G).


Fig. 127. Distribution of Connarus thonningii

Ghana: Cape Coast (y.fr.) Brass s.n. (BM); Ahkaful F.R., near Cape Coast (fr. Feb.) Hall 1717 (P); Cape Coast (fl., fr. Oct.) Hall 2707 (K); Töffri (fl.) Thonning 339 (C, type of C. floribundus); Thonning s.n. (G, type).
Togo: near Lome (fl., fr.) Warnecke 446 (BM, K, P).
Note: Four sheets with flowering branchlets of C. thonningii, collected by Thonning, are kept in C (Copenhagen). Likely these are four duplicates of Thonning 339 , which number is noted on one of the sheets only. The Thonning-specimen in Herb. De Candolle (G) is then possibly another duplicate, while the material in C is an isotype of C. thonningii, as suggested by Hepper (1970, note on one of the sheets).

## Doubtful species

Connarus smeathmannii (DC.) Planchon, 1850: 436; Baillon, 1867: 235; Baker, 1868: 458; De Wildeman, 1904: 124; 1906: 246; 1909: 90; 1910a: 293; 1916: 241; Schellenberg, 1923: 225; Hepper, 1958: 748.

Basionym: Omphalobium smeathmannii De Candolle, 1825: 86; G. Don, 1832: 91.

De Candolle cites a collection from Sierra Leone by Smeathman. In the description he designates $3-5$ leaflets per leaf. Most likely he did not see any material, since he did not add '(v.s.)', like he did with the other Omphalobium species. Planchon (1850) cited Connarus smeathmannii under 'species dubia'. Baillon (1867, in note) did not exclude that Connarus griffonianus Baill. is identical with C. smeathmannii (DC.) Planch., but Schellenberg (1923) excluded this possibility. None of these authors were able to find any material that fits the description
given by De Candolle and that was collected by Smeathman in Sierra Leone.
The only species found in Sierra Leone is the invariably trifoliolate C. africanus. It must be noted however, that some species, usually found in Central and East Africa, are occasionally collected in West Africa, i.e. C. congolanus and C. longistipitatus.

I agree with Schellenberg that C. smeathmannii (DC.) Planch. must be considered as a nomen dubium and should not be used.

## Excluded species (Africa)

C. duparquetianus Baillon, 1867: 237 = Jollydora duparquetiana (Baill.) Pierre
C. libericus Stapf, 1906: $93=$ Rourea thomsonii (Baker) Jongkind
C. mannii Baker, 1868: $459=$ Cnestis mannii (Baker) Schellenb.
C. pentagynus Lamarck, 1786:95 = Agelaea pentagyna (Lam.) Baill.
C. pseudoracemosus Gilg, 1891b: $317=$ Cnestis mannii (Baker) Schellenb.
C. pubescens Baker, 1868: $458=$ Rourea thomsonii (Baker) Jongkind
C. punctulatus Hiern, 1896: $189=$ Agelaea pentagyna (Lam.) Baill. (flowers only; leaves not Connaraceous)
C. reynoldsii Stapf, 1906: $94=$ Rourea solanderi Baker
C. thomsonii Baker, 1868: $458=$ Rourea thomsonii (Baker) Jongkind

# Ellipanthus Hook.f. 

by R.H.M.J. Lemmens

History and subdivision of the genus
For a long time Ellipanthus has been considered as an exclusively Asiatic genus. Not until 1947 the first species from Africa was described, E. hemandradenioides. In 1958 Keraudren correctly placed Hemandradenia madagascariensis Schellenberg, proposed in 1938, in Ellipanthus as well.

Schellenberg (1922) has separated Pseudellipanthus from Ellipanthus, mainly based on the flowers, being 4 -merous and unisexual in the former, and 5-merous and bisexual in the latter. These characters however, are not constant. In several Asiatic species a single specimen may show 4-merous as well as 5 -merous flowers, while unisexual flowers are not restricted to Ellipanthus beccarii Pierre (syn. Pseudellipanthus beccarii (Pierre) Schellenb.). Consequently and in accordance with Leenhouts (1958b), Pseudellipanthus is returned into the synonymy of Ellipanthus.

Leenhouts also reduced Hemandradenia Stapf into the synonymy of Ellipanthus, but did not make the necessary new combinations. I agree with Eimunjeze (1976) that Hemandradenia is a distinct genus, differing from Ellipanthus especially in the follicles and seeds (see also under Hemandradenia).

## Description of the genus

Ellipanthus Hooker f., 1862: 434; Schellenberg, 1938: 181; Hemsley, 1956: 22; Leenhouts, 1958b: 520; Keraudren, 1958: 20.

Type species: E. unifoliolatus (Thwaites) Thwaites.
Pseudellipanthus Schellenberg, 1922: 314; 1938: 189. Type species: P. beccarii (Pierre) Schellenb. ( = Ellipanthus beccarii Pierre)

Large shrubs or small trees. Branches cylindric. Leaves unifoliolate; leaflets acuminate. Inflorescences axillary. Flowers in small panicles, bisexual or unisexual, pentamerous or tetramerous, heterodistylous. Pedicels with a distinct joint. Sepals connate at the base, valvate or very narrowly imbricate in bud. Petals longer than sepals, free, usually white, imbricate in bud, pilose outside and usually also inside. Episepalous stamens fertile, epipetalous ones rudimentary; filaments united at base, pilose. Carpel 1; style pilose. Follicle brown, yellow or red, pericarp woody, opening lengthwise along the ventral suture, densely tomentose outside, glabrous inside, more or less stipitate. Seed solitary, rarely two seeds per follicle, attached to the ventral side of the follicle, ovoid or ellipsoid, basal part with a yellow or orange sarcotesta, inserted below the hilum, testa shining black; endosperm thin; hilum lateral; radicle apical; cotyledons thick.

A genus of about seven species occurring in Asia and E Africa, mainly restricted to rain forest.

## Relations between the African and Asiatic species

The differences between all species of Ellipanthus are extremely subtile, and often the species are not entirely separable, as the differential characters show some overlap.

The Malesian species $E$. beccarii Pierre and E. tomentosus Kurz usually have 4-merous unisexual flowers, and 5-merous bisexual flowers, respectively. But exceptions are found in both species. The type species, E. unifoliolatus (Thwaites) Thwaites from Ceylon, has been collected only twice. The type specimen apparently has unisexual flowers which seems to be the only differential character with the African species. The descriptions of E. calophyllus Kurz and E. glabrifolius Merr. by Schellenberg do not offer a clear delimitation towards neither the African nor the remaining Asiatic species.

The African species are very close to each other and differ only somewhat in the leaves. (See also note under E. madagascariensis). They both have (narrowly) ovate leaflets, while the Asiatic species have (narrowly) elliptic or obovate, only rarely ovate leaflets. Other distinguishing characters seem to be absent.

In my opinion it is quite possible that a more comprehensive study of all the Ellipanthus-species would lead to the conclusion, that there is only a single species in the genus. However, a complete revision of Ellipanthus is beyond the scope of this present work.

Key to the species
Leaflets papery or thinly leathery, ovate to narrowly ovate; lateral nerves not or hardly impressed above; tertiary nerves distinct on both sides; African continent

Leaflets leathery, narrowly ovate; lateral nerves strongly impressed above; tertiary nerves not distinct above; Madagascar
E. madagascariensis

## Ellipanthus hemandradenioides Brenan

Fig. 128, 129
E. hemandradenioides Brenan, 1947: tab.3452; Hemsley, 1956: 22. Type: Kenya, Malindi Distr., Mida, Dale 3876 (holo: K; iso: BR).

Shrub or small tree, up to 10 m high. Branches cylindric, usually lenticellate, branchlets often somewhat angular, pubescent, soon glabrescent. Petiole 3-7 mm long, initially pubescent but soon glabrous. Leaflet (stiffly) papery or sometimes thinly leathery, ovate or narrowly ovate, 3-11.5(-16.5) $\times 2-5(-8) \mathrm{cm}$,


Fig. 128. Ellipanthus hemandradenioides: 1. flowering branch, $2 / 3 \times ; 2$. flower partly, showing stamens and pistil, $6 \times$; 3 . follicle, $2 \times$; 4 . seed, $2 \times$; 5. fertile and rudimentary stamen, $6 \times$; (1-2,5. Faulkner 2158; 3-4. Reitsma \& J. de Wilde 143).


Fig. 129. Distribution of Ellipanthus hemandradenioides
cuneate to rounded at base, rarely peltate, more or less distinctly acuminate; glabrous both sides (sometimes some hairs on midrib), midrib impressed above, prominent beneath with 3-6(-7) lateral nerves on each side, tertiary nerves finely reticulate, distinct on both sides; petiolule $2-3.5 \mathrm{~mm}$ long, wrinkled, glabrous or somewhat pubescent. Panicles axillary, 1, rarely 2 per axil, $1-3(-5) \mathrm{cm}$ long, up to ca 15-flowered, densely brown-pubescent. Bracts ovate to subulate, 0.5-1.5 mm long, curved. Pedicels articulated $0.5-1.5 \mathrm{~mm}$ below the calyx, densely yerlowish brown-pubescent. Sepals valvate or narrowly imbricate in bud, ovate, $1.9-2.1 \times$ 1.1-1.2 mm, acute or obtuse, more or less plane, brown-pilose outside, glabrous inside. Petals imbricate in bud, narrowly oblong, 5.6-8.2 $\times 1.2-2.0$ mm , rounded at base and at top, pilose outside, pubescent inside, indistinctly $0-3$-veined. Stamens $0.8-1.0 \mathrm{~mm}$ united at base, tube glabrous outside, pilose or glabrous inside; episepalous ones 4.5-7.2 mm long, filaments pilose in lower half, anthers $1.0-1.2 \times 0.6-0.8 \mathrm{~mm}$; epipetalous ones rudimentary, $2.1-2.8 \mathrm{~mm}$ long, filaments pilose, anthers lacking. Pistil $3.5-4.7 \mathrm{~mm}$ or $6.2-8.2 \mathrm{~mm}$ long; ovary ca 1.5 mm long, yellowish brown-pilose; style pilose; stigma prominent, lobed. Follicle oblique-ellipsoid, 2.2-2.8 $\times 0.8-1.1 \times 0.8-1.0 \mathrm{~cm}$, stipe distinct or indistinct, up to 8 mm long; apex acute or with up to 3 mm long mucro; pericarp somewhat woody, densely golden-yellow or orange-brown tomentose outside, glabrous inside. Seed ovoid or ellipsoid, 11-18 $\times(5-) 8-10 \times 5-8 \mathrm{~mm}$, sarcotesta (3-)6-7 mm long, enveloping the basal part of the seed; radicle almost apical but somewhat dorsal; cotyledons thick; endosperm thin or rudimentary.

## Distribution: E Kenya and E Tanzania, along the coast.

Ecology: Lowland rain forest, sometimes in bushes in savanna. Flowering from July to October and around March, fruiting a few months later.

Specimens examined:
Kenya: Kilifi Distr., Arabuko-Sokoke F.R. (fl. Sept.) Beentje 2314 (WAG); Malindi Distr., Mida (fl. Oct.) Dale 3573 (EA, K); (fr. Apr.) Dale 3876 (BR, K, type); Kwale Distr., Buda Mafisini F., 8 miles WSW of Gazi (fr. Aug.) Drummond \& Hemsley 3954 (B, BR, K); Kwale Distr., Buda F. (fr. Mar.) Faden 74/292 (EA, K, WAG); Lamu Distr., Witu F. (Feb.) Faden 77/570 (BR); Kwale Distr., Muhaka F. (Mar.) Faden 77/602 (BR, K); Kilifi Distr., Gede F. (fr. Oct.) Gachathi 200/82 (EA); Lamu Distr., Witu F. (fr. Nov.) Gathii 125 (EA); Malindi Distr. (Jan.) Greenway EAH 12580 (EA); Lamu Distr., 5 km N of Klitu Ranger F. Post (Feb.) Katende 1750 (EA); Kwale Distr., Shimba F. (fl.b. Jan.) Katende \& Lye 4797 (EA, K); Kilifi Distr., Arabuko N.F. (fl. Mar.) Padwa B 910 (BR, EA); Kilifi Distr., S of Jilore F. Station (fr. Nov.) Perdue \& Kibuwa 10056 (BR, EA); 9 km E of Bamba, Ganze road (fr. Nov.) Reitsma \& J. de Wilde 143 (WAG); Kwale Distr., Muhaka F. (Feb.) Robertson \& Luke 4558 (WAG); Gedi (fr. Mar.) Trump 103 (EA, K).

Tanzania: Tanga Distr., Nyamaku (y.fr. July) Faulkner 2009 (EA, K); (fr. Dec.) Faulkner 2109 (B, BR, K); (ff. Jan.) Faulkner 2118 (B, BR, K); (fl. July) Faulkner 2158 (B, BR, EA, K, LISC); Utete Distr., Ngubuluni F.R., Kibiti (fr. Dec.) Shabani 291 (EA).

Note: Two accessions of this species show peltate leaflets (Greenway EAH 12580, Robertson \& Luke 4558, both sterile). There is no reason to keep these specimens apart on any taxonomic ground, as two Asiatic species ( $E$. beccarii and $E$. tomentosus) also show peltate leaflets in some specimens.

## Ellipanthus madagascariensis (Schellenb.) Capuron ex Keraudren

Fig. 130
E. madagascariensis (Schellenb.) Keraudren, 1958: 2.

Basionym: Hemandradenia madagascariensis Schellenberg, 1938: 65. Type: Madagascar, probably NW, Baron 5626 (holo: K).

Shrub or small tree. Branches cylindric, lenticellate, branchlets somewhat angular, glabrous. Petiole 2-4 mm long, glabrous. Leaflet leathery, narrowly ovate, $8-13.5 \times 3-5 \mathrm{~cm}$, rounded to almost truncate at base, obscurely acuminate; glabrous both sides, midrib strongly impressed above, prominent beneath, with 5-7 lateral nerves, that are impressed above, on each side, tertiary nerves very finely reticulate, distinct beneath, not above; petiolule $1.5-2 \mathrm{~mm}$ long, wrinkled, glabrous. Panicles axillary, 1 or 2 per axil, $1.5-3 \mathrm{~cm}$ long, up to ca 25 -flowered, brown-pubescent. Bracts ovate to subulate, 0.5-2 mm long, curved. Pedicels articulated $1-1.5 \mathrm{~mm}$ below the calyx, densely yellowish brown-pubescent. Sepals valvate or narrowly imbricate in bud, ovate, $1.8 \times 1.1 \mathrm{~mm}$, acute, somewhat convex or more or less plane, brown-pilose outside, glabrous inside. Petals imbricate in bud, oblong, $4.0-4.3 \times 1.6-1.7 \mathrm{~mm}$, rounded at base and at top, pilose outside and inside, but inside glabrous at base, not distinctly veined. Stamens ca 0.8 mm united at base, tube glabrous outside, pilose inside; episepalous
ones 2.8 mm long, filaments pilose in ones 2.8 mm long, filaments pilose in lower half, anthers $1.0 \times 0.5 \mathrm{~mm}$; epipetalous ones rudimentary, 1.8 mm long, filaments pilose in lower half, anthers lacking. Pistil 3.4 mm long; ovary 1.5 mm long, yellowish brown-pilose; style pilose; stigma prominent, lobed. Follicle and seed unknown.


Fig. 130. Ellipanthus madagascariensis: 1. flowering branch, $2 / 3 \times$; 2 . inflorescence, $2 / 3 \times$; 3. leaflet beneath, $2 / 3 \times ; 4$. detail leaflet beneath, $6 \times$; 5 . flower bud, $6 \times$; 6 . flower bud partly, showing stamens and pistil, $6 \times$; 7. fertile and rudimentary stamen, $12 \times(1-7$. Baron 5626$)$.

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Distribution: NW Madagascar; only known from the type, collected a century ago.

Specimen examined:
Madagascar: probably NW (fl.b.) Baron 5626 (K, type).
Note: Ellipanthus madagascariensis is very similar to E. hemandradenioides. It differs only by the more leathery, narrower leaflets, with more impressed secondary nerves and indistinct tertiary nerves above. The two species may be conspecific, but are maintained here due to scarcity of material, and and as follicles of E. madagascariensis are still unknown.

# Hemandradenia Stapf 

by V.E. Eimunjeze

Reprint from 1976 with additional information on new collections by F.J. Breteler

History and delimitation of the genus
Hemandradenia is characterized by unifoliolate leaves and non-stipitate, indehiscent fruits.
Stapf (1908) described it on the basis of two different specimens collected in Ivory Coast and Equatorial Guinea and expressed some doubt whether his new genus was sufficiently distinct from the formerly Asiatic genus Ellipanthus Hook.f. He, however, clearly indicated the main differences between the two genera as found in the fruits and seeds. He described two species based on the material at his disposal as $H$. mannii and H.chevalieri.

Schellenberg (1938) selected $H$. mannii as the type species and described a third one: H. madagascariensis. As the latter species had no fruits, he could not vouch for its true identity in Hemandradenia.

Leenhouts (1958-b) reduced Hemandradenia to a synonym of Ellipanthus, but did not make the necessary new combinations.

In the same year Aubréville and Pellegrin described a fourth species from Ivory Coast: H. glomerata. Capuron in Keraudren's revision of the family for Madagascar (1958) transferred Schellenberg's species to Ellipanthus.

The genera Hemandradenia and Ellipanthus are indeed closely related, in that both share unifoliolate leaves, flowers with mostly 5 stamens and 5 staminodes, and a single carpel. The carpel, however, is stipitate in Ellipanthus and sessile in Hemandradenia, which makes it possible to distinguish between the two genera with flowering material only. The fruits of the former are true follicles, but indehiscent in the latter. The sarcotesta present in both genera, is restricted to a part of the seed in Ellipanthus, whereas in Hemandradenia the entire outer layer of the seed coat is fleshy.

The main distinguishing characters of the two genera may be summarized thus:

## Hemandradenia

Carpel not stipitate.
Fruit indehiscent.
Fruit wall thinly crustaceous.
Seed coat completely fleshy.

## Ellipanthus

Carpel stipitate.
Fruit dehiscent (true follicle).
Fruit wall woody.
Seed coat partly fleshy.

In view of these differences Hemandradenia is maintained here as a distinct genus within the Connaraceae.

Description of the genus
Hemandradenia Stapf, 1908: 288; Schellenberg, 1910: 21, 103; 1938: 64; Thonner, 1915: 244; Leenhouts, 1958b: 520; Aubréville, 1959: 194; Hutchinson, 1964: 168; Dickison, 1973a: 121-138.

Type species: H. mannii Stapf.
Shrubs or small trees. Leaves alternate, entire, unifoliolate. Petiole terete and jointed to a petiolule, each with a pulvinus. Inflorescences axillary, glomerate or paniculate. Bracts minute, subtriangular. Flowers small, subsessile, predominantly 5 -merous, bisexual. Sepals 5 , basally connate, slightly imbricate to valvate. Petals 5, shortly coherent in the lower part to completely free, valvate to slightly imbricate. Stamens usually 5 fertile, opposite the sepals, alternating with 5 staminodes opposite the petals, both shortly connate at the base into a ring. Pistil 1; ovary sessile, ovoid to ellipsoid, with 2 collateral ovules; style short and fairly stout or long and filiform; stigma capitate to lobulate. Fruits ellipsoid, ovoid or obovoid, indehiscent, tomentose, yellow to brownish when ripe. Calyx persistent in fruit. Fruit wall thinly crustaceous. Seed 1, outer layer of seed coat fleshy (sarcotesta), inner layer thin; endosperm thin to copious; embryo with flat cotyledons. Germination epigeous.

Distribution: 2 species in West and Central Africa.
Note: The endosperm is very thick in $H$. mannii (Fig. 133:16) and the cotyledons are thin and narrow, whereas in $H$. chevalieri the figure shows that the endosperm is thin and cotyledons are very thick. This discrepancy may be attributed to differences in state of maturity of the seeds. $H$. mannii seeds as shown are probably less mature than $H$. chevalieri seeds, although the former had, at collecting time, already the colour of mature fruits.

Key to the species
Leaf margin not revolute; flowers in panicles, axillary and subterminal; sepals 1-2 mm long; petals free; fruits obovoid . . . . . . . . . . . . . . H. chevalieri Leaf margin revolute near base; flowers in axillary glomerules; sepals 3-4.5 mm long; petals coherent in lower part; fruits ellipsoid or ovoid . . . H. mannii

The seedlings of the two species can easily be distinguished as follows (see Fig. 27):

Hypocotyl shorter than epicotyl; cotyledons completely glabrous; first leaves cordate at base
H. chevalieri

Hypocotyl longer than epicotyl; cotyledons hairy at inner base; first leaves obtuse at base


Fig. 131. Hemandradenia chevalieri: 1. flowering branch, $2 / 3 \times$; 2. leaf base beneath, $2 \times$; 3. detail of venation, $4 \times$; 4. stamen-dominant flower, $4 \times$; 5 . long stamens with staminodes, $8 \times$; short pistil, $8 \times ; 7$. pistil-dominant flower, $4 \times$; 8 . short stamens with staminodes, $8 \times ; 9$. long pistil, $8 \times$; 10 . fruit, $2 / 3 \times$; 11. seed, $2 / 3 \times$; 12. cross section seed, $2 \times$. (1, 3-6. Chevalier 19968; 2. de Wit 9020; 7-9. Aubréville 1495; 10-12. de Koning 6169).

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H. chevalieri Stapf, 1908: 289; Schellenberg, 1938: 65; Hepper, 1958: 749; Aubréville, 1959: 194.
Type: Ivory Coast, basin of Cavally R., shore between Tabou and Béréby, Chevalier 19943 (holo: P).

Shrub or small tree. Branches dark-brown, with few scattered or many lenticels. Branchlets pale-brown tomentose, soon glabrescent. Leaves: petiole $5-7 \mathrm{~mm}$ long, terete pale-brown tomentose, glabrescent; petiolule terete, sometimes grooved above, $2.5-3 \mathrm{~mm}$ long, pale-brown tomentose, glabrescent; blade thinly coriaceous, oblong-elliptic, sometimes narrowly so, (7.5-)9-14(-18) cm long, (2-)3-6 cm broad; glabrous above, sparsely appressed-pubescent beneath; usually rounded, rarely broadly cuneate and subpeltate at base, apex acuminate; acumen c. 0.5-1.3(-2) cm long, with rounded or rarely truncate tip; leaf margin thickened, very slightly undulate; midrib prominent beneath with 5-9(-10) rather prominent lateral nerves; areolation large (see Fig. 131). Inflorescences paniculate, many-flowered, subterminal and/or in the axils of the upper leaves, c . $2-7(-10) \mathrm{cm}$ long; peduncles up to 4 cm long, pale-brown tomentose. Flowers $5(-7)$-merous, $5-8 \mathrm{~mm}$ long, subsessile; pedicel up to 1.5 mm long, pale-brown tomentose. Sepals slightly spreading or erect, triangular, c. 1.5 mm long, shortly connate at base, valvate, pale-brown tomentose outside, glabrous inside, apex acute. Petals free, imbricate, erect or slightly spreading and finally reflexed and once or twice coiled, narrowly elliptic, $5-5.5 \mathrm{~mm}$ long, c. 1 mm broad, finely tomentose both sides, apex acute. Stamens $3.5-7 \mathrm{~mm}$ long; filaments filiform, pubescent up to c. 1 mm below anther. Anthers cordate, c. 1 mm long. Staminodes 5 , narrowly ovate to narrowly elliptic, c. 1.5 mm long, glabrous, entire or shortly dichotomously branched and slightly beaked. Staminal ring usually puberulous inside, sometimes glabrous, generally glabrous outside. Pistil 3.5-7 mm long; stigma capitate to lobulate, exserted or not; style appressed-pubescent, occasionally only lower half and then upper half puberulous to glabrous; ovary ellipsoid, densely hirsute. Fruit obovoid, $2.6-2.9 \mathrm{~cm}$ long, $1.5-1.8 \mathrm{~cm}$ in diameter, densely tomentose, yellowish to brownish when ripe. Seed obovoid, 1.8-2.4 cm long, $0.9-1.2 \mathrm{~cm}$ in diameter; inner seed coat thin and brittle; endosperm cartilaginous; radicle short and stout, 3 mm long, 2 mm in diameter, protruding at the micropylar end, slightly beyond the endosperm; cotyledons obovoid, cream coloured, turning reddish-brown on exposure, up to 2.3 cm long, 1.0 cm broad, c. 6 mm thick, rather mealy.

Seedling: Viable seeds germinate in 2-3 weeks. Primary root well developed. Hypocotyl (2-)3-5.6 cm long, pale-brown appressed-pubescent. Cotyledons obovate, c. $2.4 \times 1.1 \mathrm{~cm}$, equal, opposite, horizontally spread, very shortly petiolate, swollen at inner base, glabrous, red outside, greenish-yellow inside, soon completely reddish. Epicotyl7-9.7(-11) cm long, terete, pale-brown appressed-pubescent. First leaves opposite, unifoliolate; petiole and petiolule together $1-1.6 \mathrm{~cm}$ long, pale-brown appressed-pubescent. Blade ovate, $4.5-7 \times 3.9-5.1 \mathrm{~cm}$, top


Fig. 132. Distribution of Hemandradenia chevalieri
acuminate to subcaudate, cordate at base, glabrous above, sparsely appressedpubescent beneath, more densely so on the midrib and main lateral nerves. Sub sequent leaves alternate, both petiole and petiolule 2-2.8 cm long; blade ovate to elliptic, 5.8-6.5 $\times 4-4.3 \mathrm{~cm}$, obtuse at base; otherwise similar to the first leaves.

Distribution: Ivory Coast.
Ecology: Rain forest and semi-deciduous forest.

## Specimens examined:

Ivory Coast: Port-Bouët, Aubréville 1495 (BR, P); (fr. April) 1636 (P); Embouchure du Sassandra (fr. April) Aubréville 2803 (BR, P); between Tabou and Béréby (fl. Aug.) Chevalier 19943 (P, type); (fl. Aug.) 19968 (BR, P); Banco Forest, Cremers 395 (BR); 445 (P); (fr. Nov.) De Koning 6169 (WAG); (fr. Jan.) De Wit 9020 (WAG); Toilliez 334 (BR); 347 (BR).
Cult. Wageningen: Eimunjeze s.n. (motherplant De Koning 6169) (WAG, seedling); De Wit et De Bruijn We 28 (WAG, seedling).

Note: Herbarium records show that this species has been collected in Banco forest reserve. This is not shown on the distribution map, because according to Mr. J. de Koning, H. chevalieri does not occur naturally in the Banco forest reserve, but it is present only in cultivation in the Banco forest Arboretum.

## Hemandradenia mannii Stapf

Fig. 133, 134
H. mannii Stapf, 1908: 288; Schellenberg, 1910: 21, 103; 1938: 64; Hepper, 1958: 749; Dickison, 1973a: 121-138.
Type: Equatorial Guinea, Muni river, Mann 1763 (holo: K).
H. glomerata Aubréville et Pellegrin, 1958: 35; Aubréville, 1959: 194. Type: Ivory Coast, Haute-Niouniourou, Aubréville 4123 (holo: P; iso: WAG).


Fig. 133. Hemandradenia mannii: 1 . flowering branch, $2 / 3 \times ; 2$. leaf beneath, $2 / 3 \times$; 3. revolute leaf base, beneath, $2 \times$; 4 . detail of venation, $4 \times$; stamen-dominant flower, $4 \times ; 6$. pistil-dominant flower, $4 \times$; 7 . corolla, $4 \times$; 8 . stamens and staminodes, $6 \times$; 9 long pistil, $6 \times$; 10. detail staminode pistil-dominant flower, $12 \times$; 11. staminodes stamen-dominant flower, $6 \times$; 12. short pistil, $6 \times$; 13. detail staminode stamen-dominant flower, $12 \times$; 14. fruiting branchlet, $2 / 3 \times ; 15$. Tisserant 316; 2. J. Léonard 583; seed, $2 \times$; 17. detail of seed-coat, $10 \times$ (1, 3-5, 11-13. Equipe

Shrub or small tree $3-15 \mathrm{~m}$ tall and up to 8 cm in diameter. Branchlets terete, pale-brown appressed-pubescent, glabrescent. Leaves: petiole (3- )4-7 mm long, petiolule $2-3.5 \mathrm{~mm}$ long, both usually terete, sometimes grooved above, mostly pale-brown appressed-pubescent in young leaves and puberulous or glabrescent in older ones; blade thinly coriaceous, narrowly elliptic or elliptic, $7-18.5 \mathrm{~cm}$ long, $1.5-6.5 \mathrm{~cm}$ broad, glabrous above, pale-brown appressed-pubescent and finally glabrescent beneath; obtuse to cuneate at base, slightly caudate to acuminate at apex; margin thickened, slightly undulate, revolute in the basal part; acumen c. (0.2)0.4-1.8 cm long, usually rounded, very rarely faintly emarginate at the tip; main lateral nerves $6-10(-11)$ pairs, areolation small and distinct (see Fig. 133). Inflorescences glomerate, few to many-flowered, pale-brown appressed-pubescent. Flowers (4-)5-merous, subsessile, pedicel up to 1 mm long, appressed-pubescent. Sepals erect or slightly spreading, slightly imbricate or valvate, narrowly triangular, 3-4.5 mm long, c. 1 mm broad, pale-brown appressed-pubescent outside, glabrous inside, apex acute. Petals slightly spreading, narrowly ovate to narrowly obovate or narrowly elliptic, ( $5-$ ) $6-8 \mathrm{~mm}$ long, coherent in the lower part for 2-3 mm length, apical part erect or reflexed and once or twice coiled, pale-brown appressed-pubescent outside, inside glabrous or tomentulose to puberulous or partly so. Corolla often detaching as a unit at the end of anthesis. Stamens usually 5 fertile, $5-9(-10.5) \mathrm{mm}$ long, filaments filiform, variously partly pubescent, rarely completely pubescent or glabrous. Staminodes $5,1-1.5(-3.5) \mathrm{mm}$ long, usually triangular, rarely oblong and beaked, or occasionally with broad base and upper half filiform and beaked, in the latter case thickened glands between the stamens and staminodes may be observed. Anthers yellow c. 1 mm long, usually ovate, rarely elliptic, occasionally the base and/or connective pilose. Pistil 3.5-6.5(-11) mm long, stigma capitate to lobulate, exserted in long-styled flowers; style short and fairly stout in short-styled flowers, long and filiform in long-styled flowers, pale-brown appressed-pubescent, often sparsely so in the upper half; ovary ovoid to obovoid, densely hirsute, rarely appressed-pubescent. Fruits ellipsoid or ovoid, 3.3 cm long, 2 cm in diameter, densely tomentose, yellowish-brown when ripe. Fruit wall crustaceous, 1.5 mm thick, glabrous inside. Sced ellipsoid or ovoid, c. 2.3 cm long, c. 1.3 cm in diameter; sarcotesta greyish-violet or cream; endosperm very hard. Radicle short and stout, 3.5 mm long, 2.5 mm in diameter, cotyledons thin, flat and narrow, 17 mm long, 7 mm broad.

Seedlings: Primary root well developed. Hypocotyl $7.5-8 \mathrm{~cm}$ long, terete, densely pale-brown appressed-pubescent. Cotyledons elliptic, c. $1.3 \times 0.8 \mathrm{~cm}$, horizontally spread, equal, opposite, fleshy, very shortly petiolate, hirsute at inner base. Epicotyl c. 4.5 cm long, terete, densely pale-brown appressed-pubescent. First leaves opposite, unifoliolate, petiole and petiolule together $0.7-1 \mathrm{~cm}$ long, densely pale-brown appressed-pubescent. Blade elliptic, c. $7.5 \times 5 \mathrm{~cm}$, obtuse at base, caudate at apex, glabrous above, appressed-pubescent beneath, more densely so on the midrib and main lateral nerves.

Distribution: Ivory Coast, Nigeria, Cameroun, Central African Republic, Equatorial Guinea, Gabon and Zaïre.


Fig. 134. Distribution of Hemandradenia mannii

Ecology: Rain forests and semi-deciduous forests at low and medium altitudes.

## Specimens examined:

Ivory Coast: Haute-Niouniourou (fl. Feb.) Aubréville 4123 (P, WAG, type of H. glomerata); 38 km N.E. of Sassandra (fr. Nov.) Breteler 6116 (WAG).

Nigeria: Benin, Okomu F.R. (fr. Dec.) Brenan 8561 (BM, BR, FHI, K); 9160 (FHI); (fr. Feb.) Brenan and Onochie 9026 (FHI, K); Obudu, Okwangwo F.R. (fl. May) Latilo FHI 30960 (K); Eluji, Shasha F.R. (fl. April) Ross 193 (BM, BR); Calabar, Ikoromo (fr. July) Ujor FHI 31629 (FHI).

Cameroun: Bitye nr. R. Dja (fl. Sept.) Bates 1881 (BR, K); Akonekye, 15 km N.W. d'Ambam (fr. March) Letouzey 10206 (P).

Central African Republic: Mbaiki and Boukoko Region (fl. Oct.) Tisserant (Equipe) 316 (P); (fl. Oct.) 1157 (P); (fl. Sept.) 1891 (P); (fr. Jan.) 2337 (P).

Equatorial Guinea: River Muni, Mann 1763 (K, type).
Gabon: Monts de Cristal, River Sanga (fr. Feb.) Hallé and Villiers 5287 (P); Lastoursville (fl. June) Le Testu 8867 (BM, P).
Zaïre: Binga, Croegaert 46 (BR); Ikela (fr. May) Dubois 823 (BR); Tumba Lake, Elema Isl. (fl. March) Evrard 3779 (BR, K); 3786 (BR); Kimbili Mts, Flamigni 10446 (BR); between Yafela and Yandjali (fl. and fr. Dec.) Germain 4559 (BR); Yabibi, towards Basoko (fr. Oct.) Germain 4637 (BR); Yandjali, between Isangi and Ligasa, Germain 4924 (BR); Ikela, (fl. June) Germain 7413 (BR); R. Lukenzu, Ikela (fl. June) Germain 7450 (BR); Yangambi, Gilbert 7869 (BR); 8255 (BR); Mpotia, Tumba Lake (fl., fr. Sept.) Léonard 583 (BR, L, WAG); Basukutu, nr. Lubilu (fl. Nov.) Léonard 1547 (BR); Dundusana, Mortehan 504 (BR); (fl. Dec.) 877 (BR); Gimbi, Fuka Valley (fl. Feb.) Toussaint 842 (BR); Inéac, Gimbi (fl. Jan.) Wagemans 466 (BR); (fr. Jan.) 467 (BR, WAG).
Cult. Wageningen: De Bruijn 2038 (WAG, seedling of Breteler 6116).
Additional material examined:
Cameroun: km 26 Ipono-Dipikar I., bank of Northern Ntem R. (fl., fr. June) J.J. de Wilde 8321 (WAG); near Akonetye, S of Ebolowa (fr. Aug.) Koufani 153 (WAG, YA); 26 km NW NGuti (fr. June) Letouzey 13815 (WAG); N of Banda (fr. Apr.) J. \& A. Raynal 10751 (YA).

Gabon: near Koumameyong (fl., fr.juv. Apr.) Breteler et al. 8980 (WAG); Lara R. near Mitzic-
édouneu Rd (fr. Nov.) Louis et al. 475 (LBV, WAG); 40 km N of Lébamba (fr. Nov.) Louis et al. 1042 (LBV, WAG).
Zaïre: La Kulu (fl.b.) Van den Brande 239 (BR); ibid. (fl. Sept.), Van den Brande 696 (BR); Gimbi (fr. July) Wagemans 1543 (BR).

Note: Comparative studies of the holotype and isotype of H.glomerata (Aubréville 4123) with material of $H$. mannii showed that the former only represents a short-styled (stamen-dominant) specimen of H. mannii, and in conjunction with other characters, perfectly fits into the variability of $H$. mannii.

Additional Note: The material from Cameroun and Gabon is slightly aberrant in having distinctly apiculate to beaked fruits. J.J. de Wilde 8321 from the former country is also differing by its large oblong leaves (up to $25 \times 8 \mathrm{~cm}$ ) which are densely brown-floccose beneath when young.

## Excluded species

Hemandradenia madagascariensis Schellenberg (1938) = Ellipanthus madagascariensis (Schellenb.)Capuron (1958).

Note: Examination of the type material (Baron 5626) preserved in the Kew Herbarium leaves no doubt that this material belongs in Ellipanthus.

# Jollydora Pierre 

by F.J. Breteler \& H.W. van Ziel

## History of the genus

The type species of this genus was first described by Baillon (1867: 236) as Connarus duparquetianus, named after the type collector, the R. P. Duparquet. When Pierre studied this species in 1895, on the basis of flowering material collected in Old Calabar by Mann (no 2307) and fruiting material from Gabon collected by Jolly (no 111), he concluded that C. duparquetianus was to be placed in a new genus. This was named Jollydora: gift of Jolly. An interesting detail is the fact that Pierre published his new genus by means of a very detailed drawing, made by Delpy and based on the two specimens cited above. This drawing was multiplied and distributed as 'indelible autograph' e.g. to the botanical museum in Berlin (see Gilg 1896: 217). This constitutes valid publication of a monotypic new genus.

In 1896 (l.c.) Gilg published a second species which he named J. pierrei. Pierre had labelled some material from the same area as J. ellimabouro. Schellenberg (1910: 70) compared this material with the type of J. pierrei and concluded that it belonged to this species. A third species was described by Schellenberg in 1919 from the Victoria area in Cameroun and named J.glandulosa. In 1930 Mildbraed published $J$. pedunculosa from the same area, based on two collections made by himself. Hepper's (1958: 749) presumption that Mildbraed's species (cited by him as $J$. peduncula) is synonymous with $J$. glandulosa is confirmed. Schellenberg overlooked Mildbraed's name completely.
Since Pierre published it in 1895 the genus Jollydora has never been disputed. It is very well delimitated within the Connaraceae by its habit, its pinnate leaves, and its unicarpellate flowers producing indehiscent, $1-2$-seeded fruits. Its rather isolated position was illustrated by Gilg and followed by Schellenberg in placing it in a separate subfamily the Jollydoroideae.

That it differs considerably from 'common' Connaraceae is illustrated by names given to Jollydora specimens which were published in really different families, e.g. Anthagathis by Harms (1897: 195) who placed it in the Leguminosae and Ebandoua by Pellegrin (1955: 331) who considered it to be Anacardiaceous. When material is not carefully studied it is easily mistaken for a species of the Sapindaceae.

Gilg (1896: 217) stated that Pierre had been asked to set the genus apart from the other Connaraceae and to classify it in the Simaroubaceae.
Description of the genus
Jollydora Pierre, 1895 (unprinted drawing); 1896: 1233; Gilg, 1896: 217;

1897b: 189; Schellenberg, 1910: 69; 1919: 455; 1938: 24; Hutchinson, 1964: 167.
Type species: Jollydora duparquetiana (Baill.) Pierre.
Anthagathis Harms, 1897: 195. Type species: Anthagathis monadelphia Harms (= J. duparquetiana (Baill.) Pierre).

Ebandoua Pellegrin, 1955: 331. Type species: Ebandoua cauliflora Pellegrin (= J.duparquetiana (Baill.) Pierre).

Small, evergreen, usually unbranched treelets, up to ca 8 m high, showing the architectural model of Corner. Young parts covered with a reddish to lightbrown woolly, silky or tomentose indumentum. Leaves pinnate, usually crowded at the top. Petiole somewhat thickened at base, usually shorter than rachis. Leaflets opposite to alternate, even or odd in number, the rachis as a rule terminated by a leaflet; petiolule short, somewhat thickened. Inflorescence a raceme, clustered on the stem or in the leaf-axils. Pedicel jointed. Flowers 5-merous, heterotristylous. Sepals imbricate, free, unequal, the two outer smaller. Petals imbricate, free or somewhat coherent. Stamens 10 , united at base into a more or less conspicuous cup partly enclosing the ovary. Pistil 1; ovary ellipsoid, ovules nearly basally attached; stigma simple or somewhat lobed. Fruit 1-2-seeded, indehiscent. Seed with almost completely fleshy seedcoat. Endosperm absent. Cotyledons thick and almost horny, radical apical.

Distribution: 3 species in tropical Africa, from E Nigeria to Angola (Cabinda). Ecology: Rainforest, up to ca 1000 m altitude.

Key to the species
1a Vegetative parts and sepals with aglandular hairs only; fruits obovoid-ellipsoid to almost globose, always shortly but distinctly stipitate (whole area) J. duparquetiana
b Leaflets with scattered glandular hairs along midrib both sides; sepals with glandular hairs, at least partly so; fruits either not stipitate or stipitate but then narrowly (sub)ellipsoid
2a Sepals with a mixture of glandular and aglandular hairs; fruits narrowly (sub)ellipsoid, tapering both ends (Gabon)
J. pierrei
b Sepals predominantly with glandular hairs; fruits ellipsoid, not stipitate (S E Nigeria, W Cameroun)
J. glandulosa

## Jollydora duparquetiana (Baill.)Pierre

Fig. 18, 135-137
J. duparquetiana (Baillon)Pierre, 1895 (unprinted drawing); 1896: 1233; Gilg, 1896: 218; Schellenberg, 1910: 71; 1919: 456; 1938: 26; Hepper, 1958: 749.
Basionym: Connarus duparquetianus Baillon, 1867: 236.
Type: Gabon, sin.loc., Duparquet 54 (holo: P, see note).
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Fig. 135. Jollydora species: sepals with indumentum outside $(15 \times$ ) and fruitshape $(1 \times), 1,4$. J. duparquetiana; 2,5. J. pierrei; 3,6. J. glandulosa. (1. Breteler 9001; 2. Klaine 2335; 3. Letouzey 13416; 4. J.J. de Wilde 309; 5. Jolly 77; 6. Latilo FHI 30923).
J. rufobarbata Gilg ex Schellenberg, 1910: 71. Type: Cameroun, Bipindi, Zenker 1685 (lecto: K ; iso: BM, Z).
J. acuta Schellenberg, nomen in herb. Zenker
J. cinnabarina Gilg, nomen in herb. Zenker
J. gigantophylla Gilg, nomen in herb. Zenker
J. gilgiana Schellenberg, nomen in herb. Zenker
J. villosissima Gilg, nomen in herb. Zenker

Anthagathis monadelphia Harms, 1897: 196. Type: Gabon, Mondah forest, Breteler \& J.J. de Wilde 387 (neo: WAG, see note).
Ebandoua cauliflora Pellegrin, 1955: 331. Type: Gabon, Haute Ngounié, Ebandou Dicobi, Le Testu 6307 (holo: P).

Small, usually unbranched treelet to ca 8 m tall and ca 5 cm diameter. Bark of stem brown-red to grey-yellow, rather smooth. Wood reddish to pale-brown. Petiole $4.5-22 \mathrm{~cm}$ long, yellow to red-brown, often becoming greyish, pulvinus up to 2 cm long and 12 mm thick. Rachis $7-45 \mathrm{~cm}$ long, 2-5 mm thick. Leaflets 5-11, papery to coriaceous, elliptic to obovate or oblong, 10-47 $\times 3-13(17) \mathrm{cm}$, cuneate at base, up to 2.5 cm long acuminate, petiolule $3-10 \mathrm{~mm}$ long; midrib slightly prominent above, lateral nerves 7-18 pairs. Inflorescence cauliflorous, usually consisting of one to several, up to 7-flowered, clustered racemes, very rarely axillary, reddish tomentose; rachis up to ca 2 cm long. Pedicel articulate, with a small bract (up to 1 mm long) and two opposite bracteoles of ca 0.5 mm long, the upper part less than 1 mm long. Sepals ovate-elliptic to oblong, $2-5 \times 1-3 \mathrm{~mm}$, obtuse to acute at apex, appressed-short-hairy outside, glabrous inside. Petals coherent in the middle, otherwise free, oblong, $5-9 \times 0.8-2 \mathrm{~mm}$, apex rounded, glabrous both sides. Stamens 10 , rarely one missing, the long ones 2-5.5 or 4.5-6.3 mm long, the short ones 1-2.5 or 2.5-5.5 mm long; filaments glabrous; anthers 0.6 mm long. Pistil $1-7 \mathrm{~mm}$ long; ovary $0.7-1.3 \mathrm{~mm}$ long, pubescent; style $0-0.5,1.5-2.5$, or 2.5-5.5 mm long, glabrous or with a few hairs; stigma somewhat lobed or not. Fruit obovoid-ellipsoid to subglobose $2-4 \mathrm{~cm}$ long, 1-2.2 cm diameter, mucronate or not, shortly but distinctly stipitate, yellow to orange or scarlet at maturity; pericarp shining outside, $0.5-1 \mathrm{~mm}$ thick, glabrous or glabrescent. Seeds 1-2 per fruit; testa almost completely fleshy, except in a narrow zone on the preraphal side, $0.5-1.5 \mathrm{~mm}$ thick, whitish when fleshy, brown when not; cotyledons thick and almost horny, radicle minute.

## Distribution: From eastern Nigeria to Angola (Cabinda).

Ecology: Primary or old secondary forest, often recorded from rather wet habitats.

## Specimens examined:

Nigeria: Calabar R. (fl. March) Latilo FHI 41338 (K); Old Calabar R. (fl.fr. Febr.) Mann 2307 (K); (fl. Febr.) Mann 2309 (P) (most likely a duplicate of Mann 2307, see note); 20 km ENE of Calabar (fr. April) Van Meer 1144 (WAG); Oban (fl.) Talbot 1708 (BM).
Cameroun: Near Grand Batanga (fr. Jan.) Bos 3758 (WAG); 8 km S . of Kribi (fr. Febr.) Bos 3985 (WAG); ca 18 km Kribi-Lolodorf (fl. March) Bos 4061 (WAG); (fl. March) Bos 4122 (WAG); 28 km Kribi-Lolodorf (fl. April) Bos 4325 (WAG); 12 km Kribi-Ebolowa (fr. April) Bos 4438 (WAG); 20 km Kribi-Lolodorf (fr. Dec.) Bos 5817 (WAG); 8 km W of Bipindi (fl. Febr.) Bos 6360 (WAG); km 28 Kribi-Lolodorf (fl. March) Bos 6614 (WAG); 15 km SE of Kribi (fl. March) Bos 6644 (WAG); ca 40 km Kribi-Edea (fl. April) Bos 6730 (WAG); 40 km S of Kribi (fl. Aug.) Bos \& Breteler 7276 (WAG); S Bakundu F.R. (fl. March) Brenan 9407 (BM, BR, K, P); (fl. March)


Fig. 136. Jollydora duparquetiana: 1. habit, ca $1 / 40 ; 2$. leaflet beneath, $2 / 3 \times ; 3$. inflorescence, $2 / 3$ $\times ; 4-5$. flowers, $4 \times ; 6$. flower, one sepal and petals removed, $4 \times ; 7$. fruits, $2 / 3 \times ; 8$. two-seeded fruit in transverse section, $1 \times ; 9$. one-seeded fruit in transverse section, $1 \times ; 10$. seed with sarcotesta, ventral side with hilum, $1 \times$. (2. Louis et al. 1256; 3. J.J. de Wilde et al. 7850; 4-6. Breteler et al. 9001; 7,8. J.J. de Wilde et al. 309; 9,10. J.J. de Wilde 8301).


Fig. 137. Distribution of Jollydora duparquetiana

Brenan 9411 (BM, BR, K, P); 39 km E. of Douala (fl. Febr.) Breteler c.s. 2601 (C, P, WAG); 25 km Ebolowa-Kribi (fl. Dec.) J.J. de Wilde 7850 (WAG); Nkoemvone (fl. Dec.) J.J. de Wilde 8005 (WAG); 16 km Kribi-Ebolowa (fr. June) J.J. de Wilde 8301 (WAG); 50 km NW of Eséka (fl. Nov.) W. de Wilde 1254 (BR, K, P, WAG); 40 km NW of Eséka (fl. Dec.) W. de Wilde 1436 (WAG); 60 km NW of Eséka (fr. Febr.) W. de Wilde 1767 (WAG); 60 km SW of Eséka (fl. March) W. de Wilde 2139 (BR, K, MO, WAG); (fr. March) W. de Wilde 2139B (WAG); W of Limbe (Victoria) (fr. Nov.) Gentry \& Thomas 52850 (WAG); Elephant Mt near Kribi (March) Huber 1052 (YA); Kumba (fl. Jan.) Keay FHI 37369 (K, P, WAG); 60 km SW of Eséka (fl. March) Leeuwenberg 5039 (BR, K, P, WAG); km 11 Loum-Yabassi (fl. March) Leeuwenberg 9481 (WAG); near Bella (fr. Jan.) Letouzey 4168 (P); 50 km SE of Kribi (fr. March) Letouzey 9009 (BR, P); 40 km SE Kribi (fl. March) Letouzey 9091 (HBG, P); km 81 Kribi-Ebolowa (fl. April) Letouzey 9449 (BR, P, WAG); 20 km SW of Ambam (fl. March) Letouzey 10163 (P); 20 km N of Eséka (fr. Dec.) Letouzey 12321 (P); 35 km SW of Edea (fl. Jan.) Letouzey 12659 (P); 25 km NNE of Bipindi (fl. Jan) Letouzey 12826 (P); Baduma Forest (fr. June) Nemba \& Thomas 117 (WAG); Kumba (fr. May) Olorunfemi FYI 30576 (K); Dipikar I. (fr. Dec.) Satabié 498 (P, YA); Limb (Victoria) (fl. May) Winkler 40b (Z); Bipindi (fl.) Zenker 1685 (BM, E, G, K, P, Z, type of J. rufobarbata); (fr.) Zenker 1980 (BM, G, K); (fl.) Zenker 1995 (BM, E, G, GOET, K, L, P, Z); (fr.) Zenker 2510 (BM, BR, E, G, K, P); (fl.) Zenker 2744 (BM, E, G, K); (fl.) Zenker 3438 (BM, BR, E, G, GOET, K, L, M, MO, P); (fl.) Zenker 3754 (BM, BR, E, G, K, MO); (fl.) Zenker 3756 (BM, BR, E, G, GOES, K, MO).

Gabon: Libreville (fr.) Autran (Heckel) 15 (P); 25 km NW Libreville (fr. Aug.) Breteler \& de Wilde 387 (WAG, type of Anthagathis monadelphia); near La Lara (fl. Sept.) Breteler \& de Wilde 443 (WAG); (fr. Sept.) Breteler \& de Wilde 447 (WAG); 34 km Mouila-Yeno (fr. Sept.) Breteler css. 8121 (LBV, WAG); 5-10 km W of Koumémayong (fl. April) Breteler css. 9001 (LBV, WAG); 9003 (LBV, WAG); 15 km N of Doussala (fr. March) de Wilde \& Jongkind 9462 (WAG); Cap Estérias (fr. Jan.) J.J. de Wilde c.s. 309 (LBV, WAG); sin.loc. (fl.) Duparquet 54 (P, type, see note); Bélinga (fr. March) Florence 688 (P); Makokou (fr. March) N. Hallé 1503 (P); 1504 (P); (f.) N. Hallé 2647 (P); Bélinga (fr. June) N. Hallé 3934 (P); 4054 (P); N. Hallé \& Le Thomas 173 (P); 7 km SW Makokou (fr. April) Hladik 2067 (P); Mondah Forest (fr. Feb.) INEF s.n. (P); Libreville (fr. April) Jolly 111 (P); (fr. May) Klaine 186-2 (P); (fl. Sept.) Elaine 359 (P); (fr. Jan.) Klaine 395 (P); (fr. June) Klaine 470 (P); (fl. Aug.) Klaine 532 (P); (fr. Feb.) Klaine 716 bis (P); SE Sindara (fl. Sept.) Leeuwenberg \& Persoon 13633 (LBV, WAG); Ebandou Dicobi (fl. Sept.) Le Testu 6307 (BM, BR, P, type of Ebandoua cauliflora); Matoro (fl. Oct.) Le Test 7495 (BM, P); Lastoursville (fl. Oct.) Le Testu 7519 bis (BM, BR, P); Coumamala (fl.fr. Sept.) Le Test 8342 (BM, P); 8343
(BM, P); Oveng (fr. Nov.) Louis c.s. 395 (LBV, WAG); 20 km N of Lastoursville (fr. Nov.) Louis c.s. 805 (WAG); 32 km SE Sindara (fr. Dec.) Louis c.s. 1256 (LBV, WAG); 1332 (LBV, WAG); Oveng (fr. May) Reitsma c.s. 901 (LBV, WAG); (fl. May) Reitsma c.s. 903 (LBV, WAG); 30 km SW of Doussala (fl. Aug.) Reitsma 1430 (WAG); 40 km NW of Oveng (fl. Sept.) Reitsma 1514 (WAG); 30 km SW of Doussala (fr. Febr.) Reitsma 1961 (WAG); 25 km WSW of Mitzic (fr. Nov.) Reitsma 2577 (WAG); Sibang (fl. June) Soyaux 10 (K, Z); Sibang (fr. July) Thomas \& Wilks 6344 (WAG); 32 km SE of Sindara (fr. Feb.) Wilks 1224 (WAG).
Congo: Moufouma (fr. Aug.) Farron 4293 (P); Djoumouna (fl.Oct.) Farron 4662 (P); (fl. Nov.) F. Hallé 1480 (P); Mantaba (fr. Sept.) Koechlin 3121 (P); Banza N’Dounga (Sept.) Koechlin 5274 (P); sin.loc. (fl.) Sita 2629 (P).

Zaire: Lusanga Sundi (fr. Sept.) Donis 1452 (BR); Luki (fr. March) Donis 1754 (BR); (fr. May) Wagemans 1521 (BR); (fr. Aug.) Wagemans 1621 (BR); Gimbi (fr. Feb.) Wagemans 2203 (BR)
Angola: Belize (fr.) Gossweiler 8011 (BM, LISU).

Notes: Baillon (1867: 236) cites Duparquet 55 as the type. This is an error. By personal communication of N. Hallé and J.C. Jolinon from the Paris herbarium attention was drawn to a note attached to Mann 2309 ( P ,see below). This note from the hand of Pierre proves that no 55 is a misprint and should read no 54. Schellenberg (1938: 26) cites both numbers 54 and 55! Duparquet 54 is also cited (l.c.: 58) by him under Manotes griffoniana.

The Paris specimen of the Mann collection referred to as Mann 2309 should most likely read Mann 2307. The figure 7 on the original label of this Mann duplicate can be mistaken for a 9 as did Delpy when he made the detailed drawing, based on Mann 2307 and Jolly 111, on which this genus was founded.

Harms (1897: 196) did not cite a specimen when publishing Anthagathis monadelphia, but cited Gabon as its origin. Not any material could be traced which might possibly be accepted as type of this monotypic genus. Therefore a neotype has been designated.

Jollydora glandulosa Schellenb.
Fig. 135, 138
J. glandulosa Schellenberg, 1919: 455; 1938: 25; Hepper, 1958: 749.

Type: Cameroun, between Joh. Albrechtshöhe and Ediki, Winkler 1042 (holo: $\mathrm{B} \dagger$; lecto: Z ).
J. pedunculosa Mildbraed, 1930: 971. Type: Cameroun, 15-35 km NE of Limbe (Victoria), Likomba Pflanzung, Mildbraed 10607 (lecto: K).
J. peduncula Mildbraed, nomen on Mildbraed 10607.

Treelet up to ca 5 m tall, usually unbrached. Petiole $15-18 \mathrm{~cm}$ long, up to 10 mm thick at base, rachis $10-45 \mathrm{~cm}$ long. Leaflets up to 13, opposite to subopposite, papyraceous, oblong to obovate-elliptic, $8-43 \times 2.5-10.5 \mathrm{~cm}$, up to 1.5 cm long acuminate, cuneate at base; petiolule $4-10 \mathrm{~cm}$ long; midrib prominent both sides, lateral nerves 6-13 on each side. Inflorescence of clustered racemes, axillary or just below the leaves; each raceme up to 9 mm long, 1-3 flowered, with mixture of appressed and red glandular hairs. Pedicel jointed, $0.5-7 \mathrm{~mm}$ long. Bracts and bracteoles up to 0.7 mm long. Sepals ovate-triangular or


Fig. 138. Distribution of Jollydora glandulosa
oblong, 2-6 $\times 1.5-3 \mathrm{~mm}$, rounded to acute at apex, outside with appressed aglandular and red glandular hairs, glabrous inside. Petals coherent in the middle, otherwise free, oblong, $9-11 \times 1.2-1.5 \mathrm{~mm}$, top rounded, glabrous both sides. Stamens 10 , the long ones 5-6.5 or up to 10 mm long, the short ones $1.5-3$ or $5-6.5 \mathrm{~mm}$ long; filaments glabrous, anthers ca 0.6 mm long. Pistil $1,4.5$ or 10 mm long; ovary ca 1.5 mm long, pubescent, hairs ca 2.5 mm long; style glabrous; stigma distinct, subentire. Fruit $1(-2$ ?)seeded, ovoid-ellipsoid, up to $4 \times 2.5 \mathrm{~cm}$, yellow, glabrous or glabrescent. Seeds ovoid-ellipsoid, $15-18 \times 10-13 \mathrm{~mm}$.

## Distribution: SE Nigeria, W Cameroun. <br> Ecology: Rain forest.

Specimens examined:
Nigeria: Obudu, Boshi-Okwangwo F.R. (fr. May) Latilo FHI 30923 (K).
Cameroun: Near Obang, 18 km S of Wum (fl. Dec.) Letouzey 13416 (P); $15-35 \mathrm{~km}$ NE of Limbe (Victoria)(fl.Nov.) Mildbraed 10607 (K, type of J. pedunculosa); between Joh. Albrechtshöhe and Ediki (fl. Dec.) Winkler 1042 (Z, type).

Notes: The characters of the type specimen of this species were already discussed by Schellenberg in 1910 (p. 70). At that moment he classified it with some doubt as J. pierrei, because of insufficient knowledge of the flowers of J. pierrei. In 1919 (l.c.) this doubt had disappeared as result of a misuse of the conformity in leaf indumentum between J. duparquetiana (Zenker 2744 \& 3756) and J. pierrei (Jolly 77, Soyaux 186). The leaf indumentum being the same in the two $J$. pierrei specimens and in Zenker 2744, the latter is no longer considered to represent $J$. duparquetiana but $J$. pierrei. This Zenker material has an aglandular calyx, so $J$. pierrei has a calyx without glands. As a result J. glandulosa can be distinguished from J. pierrei by its glandular calyx.

A character which might be useful to distinguish sterile material of this species from $J$. duparquetiana and $J$. pierrei is found in the angle between the midrib and its main laterals. This angle is $45^{\circ}$ in J . glandulosa and usually $50^{\circ}-70^{\circ}$ in the other two species.

Jollydora pierrei Gilg
Fig. 135, 139
Jollydora pierrei Gilg, 1896: 218; Schellenberg, 1910: 69; 1919: 456; 1938: 26, p.p. (except material from Cameroun, see note under J. glandulosa).

Type: Gabon, Sibang, Soyaux 186 (holo: B $\dagger$ ); neotype: Gabon, near Libreville, Klaine 1596 (P).
J. ellimabouro Pierre, nomen in herb. Klaine 390; Gilg, 1896: 218 (as J. elimaboura); Schellenberg, 1910: 70.

Treelet up to 5 m tall, usually unbranched. Petiole $7-13 \mathrm{~cm}$ long, rachis 4-9 cm long. Leaflets 3-7, opposite or alternate, papyraceous, narrowly (obovate-) elliptic, $11-22 \times 3.5-8 \mathrm{~cm}$, cuneate at base, rather abruptly acuminate apically, acumen 5-15(20) mm long, slender; midrib and the $10-16$ main laterals on each side prominent both sides as well as the tertiary, reticulate venation; petiolule 3-8 mm long. Inflorescence of clustered racemes, cauliflorous; raceme ca 7flowered, up to 1.5 cm long. Pedicel jointed; bracts and bracteoles $0.5-1 \mathrm{~mm}$ long, tomentose. Sepals elliptic to ovate-triangular, 2-4.5 $\times 1-1.5 \mathrm{~mm}$, rounded to acute at top, outside with appressed and erect glandular hairs, glabrous inside. Petals usually partly coherent, free at base and apically, oblong, $7-9 \times 0.8 \mathrm{~mm}$, top rounded, glabrous both sides. Stamens 10 , the long ones $5-6.5$ or $5-8 \mathrm{~mm}$ long, the short ones ca 1.5 mm or $3-5 \mathrm{~mm}$ long; filaments glabrous; anthers


Fig. 139. Distribution of Jollydora pierrei
0.6 mm long. Pistil $1.2-8 \mathrm{~mm}$ long; ovary ca 1 mm long, woolly; style 1 or 7 mm long, with a few hairs; stigma lobed. Fruit narrowly ellipsoid, tapering both ends, $4.5-6 \mathrm{~cm}$ long (up to 9 cm long in Schellenberg 1938: 28), 0.9-1.7 cm diam., $1(-2)$ seeded. Pericarp smooth, glossy, glabrous or glabrescent. Seed narrowly ellipsoid, 2-3 cm long, $6-10 \mathrm{~mm}$ diam.

Distribution: Gabon, only collected near Libreville.
Ecology: Rain forest.
Specimens examined:
Gabon: Libreville (fr. Febr.) Jolly 77 (P); near Libreville (fl. Oct.) Klaine 390 (P); (fl.fr. July) Klaine 1596 (P,type); (fl. July) Klaine 1903 (P); (fl. July) Klaine 2335 (P); (fr. Dec.) Klaine 2564 (P); (fr. May) Klaine 2884 (P).

Note: Schellenberg (1938: 26) described the fruits as being up to 9 cm long and Gilg (1896: 218), the author of this species, as up to 8 cm long. This is much longer than measured in the material examined for this revision. The specimen seen by both these authors and not examined now is Jolly 186, the type, which was lost in Berlin.

# Manotes Sol. ex Planchon 

by C. C. H. Jongkind

## History of the genus

Manotes was described by Planchon in 1850 with a single species: M. expansa. In 1867 Baillon proposed a second species, M. griffoniana. Many new species, mostly based on minor differences in indumentum and/or leafshape, were added in the following decennia. In 1897 Gilg described the genus Dinklagea with the only species $D$. macrantha. In 1910 Schellenberg published his thesis 'Beitrage zur vergleichenden Anatomie und zur Systematik der Connaraceen' in which Connaraceae were critically reviewed but not formally revised. In this work Schellenberg reduced Dinklagea to a section of Manotes and so Dinklagea macrantha became Manotes macrantha. The formal revision was completed much later and published in 1938. In his revision Schellenberg did not apply most of his critical remarks made in 1910. His species concept is very narrow and resulted in as many as ten Manotes species. The present revision maintains only three of them. Together with M. lomamiensis described by Troupin in 1951, the total number of species recognized here in the genus Manotes becomes four. M. soyauxii which Schellenberg in 1938 considered to be a synonym of M. pruinosa ( $=$ M. expansa) was described by him in 1919 from W Congo. In this revision it is considered to be a hybrid between M. expansa and M. griffoniana. The present revision is based on many recent collections and on ca $75 \%$ of the herbarium material seen by Schellenberg, the remainder being destroyed in Berlin.

Delimitation of the genus
Manotes is distinctly delimitated within Connaraceae not only by generative characters but also by a vegetative one.

Among the genera with 5-carpellate flowers Manotes is the only genus with a short but distinct androgynophore. Manotes is also the only genus of this group where inner and outer pericarp split apart at maturity.

When sterile, Manotes can be distinguished from other material with pinnate leaves by its typical pattern of the ultimate veinlets (see fig. 147.4).

Some other characters can be added when delimitation against some particular taxon is concerned but the above mentioned characters are always sufficient in distinguishing Manotes from other genera of Connaraceae.

## Indumentum

In Manotes there are three kinds of hairs on the vegetative and generative


Fig. 140. The three hair types of Manotes.
parts. These three types are termed here glandular hairs, globular hairs and long hairs (fig. 140) and they are described as follows.

The glandular hairs are one-celled and have a small globular top on which, when dry, often tiny cristals can be observed. These hairs are usually erect and up to 0.15 mm long.
The globular hairs are many-celled in the shape of a stalked globe. The globe is in every direction more than one-celled in diameter and it is usually strikingly coloured. Its stalk is a few cells long and one cell wide. They can be up to 1 mm long, but usually they are shorter.

The long hairs are not glandular, they are one-celled and have a sharp end. They are usually appressed or subappressed and up to 1.5 mm long.

The presence or absence of these different hair types on the pistil and on the fruit is the most decisive character to distinguish most species of Manotes. The indumentum of the other generative parts and the vegetative parts may vary between collecting localities especially in M. expansa that has a large geographical distribution. M. lomamiensis on the other hand, with a restricted area of distribution, is much more constant in its indumentum.

Description of the genus
Manotes Solander ex Planchon, 1850: 438; Bentham \& Hooker, 1862: 433; Baker, 1868: 451,459; Gilg, 1890: 67; Schellenberg, 1910: 18,97; 1938: 54; Thonner, 1915: 244; Aubréville, 1959: 193; Troupin, 1952: 70; Exell, 1954: 140; Hutchinson, 1964: 169.

Type species: M. expansa Solander ex Planchon.
Dinklagea Gilg, 1897a: 242; 1897b:190. Type species: D. macrantha Gilg (= M. macrantha (Gilg) Schellenberg).


Fig. 141. The indumentum of the pistil and the fruit of Manotes section Manotes (see fig. 140 for the symbols of the different indumentum types).

Lianas or scandent shrubs. Branches cylindric or very slightly lobed; wood presumably always without interxylary phloem. Leaves imparipinnate. Leaflets opposite or subopposite, entire, symmetric or nearly so; the nervation ending in a dense pattern of very fine parallel veinlets. Flowers in axillary, paniculate or racemose inflorescences, pentamerous, hetero-tristylous or hetero-distylous, reddish to yellow. Sepals connate at the base, valvate in bud. Petals longer than sepals, free, imbricate in bud. Androgynophore short but distinct. Stamens in two whorls, free, the five stamens opposite the sepals longer than the five stamens opposite the petals. Pistils five, free. Fruit a follicle, one to five per flower, constricted at base, beaked or not, glabrous inside, dehiscing by a ventral suture exposing the pendulous seed; inner pericarp separating from exocarp at maturity. Calyx persistent and usually accrescent in fruit. Seed solitary, subovoid, attached to the ventral suture; testa shiny and completely fleshy (sarcotesta) or with a thin part on the dorsal side, sarcotesta with a threadlike appendix attaching the seed to the base of the follicle; hilum ventral; radicle apical; embryo with thin flat distinctly nerved cotyledons completely enclosed by abundant endosperm. Seedling as far as known epigeal with a strongly elongated hypocotyl.

A genus of four species and one putative hybrid of humid tropical Africa, extending from Guinea to E Zaire and from the Central African Republic to the North of Angola. In drier regions confined to gallery forest.

Note: In his monograph of the Connaraceae Schellenberg (1938) distinguished the two sections of Manotes on the character of axillary inflorescences in section Dinklagea (M. macrantha) versus terminal inflorescences in section Manotes, all other species). This character is not tenable to distinguish the two sections, as explained in the paragraph on inflorescences. The characters used to distinguish the two sections in this revision are the ones mentioned in the key.

Key to the sections and species
1a Petals with two lateral lobes (fig. 147.6). Stamens of a single flower all about the same length, pistils unequal to them (hetero-distyly). Leaflets coriaceous. Dimensions of the flower bud when the calyx lobes are about to open 3-3.5 $\times 2-2.5 \mathrm{~mm}$. . section Dinklagea, only species: M. macrantha
b Petals without such lateral lobes. Stamens in two whorls of clearly different length, pistils unequal to either whorl (hetero-tristyly). Leaflets papery. Dimensions of the flower bud when the calyx lobes are about to open 1-2.7

$$
\times 1-1.8 \mathrm{~mm} . . . . . . . . . . . . . . . . . . \text { section Manotes }-2
$$

2a Pistil in bud as well as in open flower with globular hairs all over the style and with a dense cover of long hairs on the ovary. Fruit always with long ( $>0.3 \mathrm{~mm}$ ) hairs, more or less distinctly mixed with glandular and globular hairs (fig. 141). Flower bud with full-grown, closed calyx (nearly) globose.
M. griffoniana
b Pistil with a different indumentum, style in bud without globular hairs. Fruit often without long hairs. Flower bud with full-grown, closed calyx ovoid, ca 1.5 times as long as wide. . . . . . . . . . . . . . . . . . . . . -3
3a Fruit with short glandular hairs only, lacking both globular and long hairs. West and Central Africa. . . . . . . . . . . . . . . . . . . . . M. expansa
b Developing ( $>2.5 \mathrm{~mm}$ ) and mature fruit with globular hairs as well as long hairs, short glandular hairs not in evidence. S Zaire. . . M. Iomamiensis

Note: Within the area where M. expansa and M. griffoniana occur together, some hybrid specimens may be found that do not fit in this key (see M. soyauxii).

Manotes expansa Sol.ex Planch.
Fig. 141-143
M. expansa Solander ex Planchon, 1850: 439; Baker, 1868: 459; Schellenberg, 1910: 20; 1938: 59; Hepper, 1958: 747; Burkill, 1985: 524.

Type: Sierra Leone, sin. loc., Afzelius s.n. (holo: BM).
M. longiflora Baker, 1868: 460; Hutchinson, 1928: 517; Schellenberg, 1938: 56; Mangenot, 1957: 1; Hepper, 1958: 747: Aubréville, 1959: 193; Irvine, 1961: 573; de Koning, 1983: 277,288; Burkill, 1985: 524. Type: Nigeria, Eppah, Barter 3283 (holo: K).
M. pruinosa Gilg, 1891b: 332; De Wildeman, 1912: 407; Schellenberg, 1938: 59 p.p. except Le Testu 1049 and 1061 (see note under M. soyauxii), Tilman 79 and Verschueren 28 (see under M. griffoniana); Troupin, 1952: 72; Exell \& Mendonça, 1954: 140. Type: Zaire, Lulua, Pogge 724 (holo: B $\dagger$; lecto: K).
M. sanguineo-arillata Gilg, 1891b: 333; De Wildeman, 1905: 91; 1912: 407. Type: Zaire, Mukenge, Pogge 749 (holo: $\mathrm{B} \dagger$; lecto: K).
M. aschersoniana Gilg, 1891b: 334. Type: Zaire, Mukenge, Pogge 751 (holo: $\mathrm{B} \dagger$; lecto: K).
M. brevistyla Gilg, 1891b: 334; Schellenberg, 1910: 18,19. Type: Zaire, Musumba, Pogge 532 (syn: $\mathrm{B} \dagger$ ), Lulua, Pogge $739 b$ (syn: $\mathrm{B} \dagger$ ). Neotype: Zaire, Kaskama, Kananga ( = Luluabourg), Gillardin 263 (holo: BR).
M. cabrae De Wildeman \& Durant, 1900c: 62; Schellenberg, 1910: 20. Type: Zaire, Mayombe, Cabra 30 (holo: BR).
M. moandensis De Wildeman, 1909: 106. Type: Zaire, near Moanda, Gillet 3989 (holo: BR).
M. leptothyrsa Gilg, nomen in herbarium Dinklage 1735 (B, P), 1842 (B, BR, BM, P, Z), and 2011 (B); Schellenberg, 1910: 20, nomen.
M. griffoniana auct. non Baillon, Schellenberg, 1938: 58 p.p.: Dewèvre 434, Gossweiler 7792, 7805, and 8109, and Thollon 974 (see note under M. griffoniana).

Cnestis corniculata auct. non Lamarck, Bentham, 1849: 290.
Branchlets with a dense indumentum of long hairs; older branches glabrous or with a few hairs and lenticellate. Petiole 2-4.5(-7.5) cm long; rachis 4-15.5


Fig. 142. Manotes griffoniana: 1-2. flowering branchlet (with interruption), $2 / 3 \times$; 4 . detail of leaflet (see $\times$ in 1.), $4 \times ; 5$. flower, $4 \times$; 6 . petal, $4 \times$; 7. flower partly, showing androgynophore, 4 $\times ; 8$. flower bud, $4 \times$; 9 . follicles, $2 / 3 \times$; 11. length section of follicle, showing seed and flat cotyledons, $2 \times ; 12-13$. seed, showing partly fleshy testa (dark part), $2 \times$.

Manotes expansa: 3. leaflet $1.5 \times ; 10$. follicle dehiscing by a ventral suture, $2 / 3 \times$. (1-2. Troupin 4500; 3. A. Louis et al. 731; 4. Troupin 4500; 5-7. A.Louis et al. 1389; 8. Bos 3243; 9. A.Louis et al. 184; 10. Carlier 29; 11-13. A.Louis et al. 184).

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cm long, pubescent to glabrous; petiolules $1-4 \mathrm{~mm}$ long; leaflets $7-13$, ovate to elliptic, pubescent or glabrous, base cordate to acute; apex acuminate; young leaflets pink; terminal leaflet $3.8-15.5 \times 1.4-6.8 \mathrm{~cm}$; lateral leaflets 2.3-15 $\times$ $1.1-6.5 \mathrm{~cm}$. Inflorescence up to 40 cm long, pubescent to glabrous. Pedicel above the joint $1-3 \mathrm{~mm}$ long. Flower bud when the calyx lobes are about to open (1.5-)1.8-2.2(-2.7) $\times(1-) 1.2-1.5(-1.8) \mathrm{mm}$. Sepals lanceolate (1.7-)2.5-3.5(-4) $\times$ $0.8-1.5 \mathrm{~mm}$, greenish-white to dark red but usually pink. Petals narrowly elliptic 5.5-7.5(-11) $\times 0.8-1.2(-2) \mathrm{mm}$, reflexed, first white often with pink, later yellow. Sepals and petals frequently with all three kinds of hairs. Long stamens $3-6 \mathrm{~mm}$; short stamens $1.5-4 \mathrm{~mm}$ long; filaments white, with glandular hairs and sometimes with globular hairs as well; anthers yellow. Pistil $2-5.5 \mathrm{~mm}$ long, unequal to the stamens, white to pink with glandular hairs and sometimes with long hairs at the base of the ovary. Follicles 1-5, up to $20 \times 10 \mathrm{~mm}$, orange to red, minutely velutinous (glandular hairs), beaked. Seed ca $10 \times 5 \mathrm{~mm}$; testa partly fleshy and red, dorsal partly thin and black. Seedling epigeal; hypocotyl strongly elongated and densely pubescent; first leaves opposite.

Distribution: From Guinea to Zaire and from the Central African Republic to N Angola.

Ecology: Rain forest and gallery forest, observed and collected particularly in the forest edges. From sea level up to 600 m alt.

Selection of more than 500 specimens examined:
Guinea: N'Zérékoré (fl. Dec.) Adam 7824 (P); Diéké (fl. Oct.) Baldwin 9661 (K, P); Friguiagbé (fr.) Chillon 2423 (C); Macenta (fl. July) Jacques-Félix 1012 (P).
Sierra Leone: Freetown (fl., fr. Dec.) Dalziel 955 (K, P); Njala (fl. Nov.) Deighton 1787 (BM, K); Kokoru (fl. Oct.) Deighton 5197 (K, P); Korombai (fl. Dec.) N.W.Thomas 6922 (K).

Liberia: Mt Bele Rd (fl. Nov.) Adam 754 (K, P); Nyaake (fr. June) Baldwin jr. 6218 (K, P); Brewersville (fl. Sept.) Barker 1076 (K, P); N of Zorzor (fl. July) Bos 2222 (BR, K, WAG); Chien (fl., fr. Jan.) Bos 2847 (BR, K, P, WAG); Grand Bassa, Fishtown (fl., fr. Oct.) Dinklage 1842 (B, BM, BR, G, P, Z); NE of Suacoca (fl. Oct.) Traub 293 (BM, BR, C, G, K).

Ivory Coast: Toulepleu (fl. Sept.) Adam 6329 (P); between Grabo and Taté (fl. Aug.) Chevalier 19760 (P); between Taté and Tabou (fl. Aug.) Chevalier 19816 (P); Banco F.R. (fl. June) de Koning 6984 (WAG); 17 km W of Abidjan (fl., fr. June) W.de Wilde 299 (BR, P, WAG, Z); Adiopodoumé (fl., fr. July) Geerling \& Bokdam 323 (B, BR, WAG); Sassandra (fl., fr. Dec.) Leeuwenberg 2244 (K, L, P, WAG); 18 km W of Abidjan (fl., fr. Sept.) Oldeman 442 (B, BR, P, WAG); Adiopodoumé (fl., fr. Sept.) Roberty 12161 (G, K, Z); San Pedro (fl., fr. Aug.) Thoiré 323 (BR, K, P).

Ghana: Bibiana (fl., fr. May) Darko 872 (K, P); Ananji (fl., fr. Oct.) Howes 973 (K, P); near mouth of Ankobra R. (fl. April) J.K.Morton 6590 (K, WAG).

Nigeria: Eppah (fl.) Barter 3283 (K, type of M. longiflora); Jesse (fl. Sept.) Butler Cole 21 (BR, K, P); Lagos (fl.) Dalziel 1023 (C, K, M); Enuga (fr.) Hepper 2230 (K, P); Old Calabar (fl.) Mann 2256 (K, P); Ijebu-Ode (fl., fr. Jan.) Onochie FHI 19687 (K, P, WAG); Eket (fl.) Talbot 3112 (BM, K, Z).

Cameroun: 15 km N of Kribi (fl. Feb.) Bos 3830 (BR, K, P, WAG); 20 km NE of Ngambe (fl. Jan.) Letouzey 11060 (P).

Central African Republic: 10 km from M’Poko bridge (fl. March) Descoings 10088 (P); Yalinga region (fl. Aug.) Le Testu 3072 (BM, P); Waka region (fl. Nov.) Tisserant 1688 (P); Boukoko (fl., fr. Nov.) Equipe Tisserant 1254 (BM, P).

Equatorial Guinea: Sanje, Benito R. (fl. Sept.) Bates 571 (L, P).


Fig. 143. Distribution of Manotes expansa

Gabon: Moanda-Franceville Rd (fl., fr. Sept.) Breteler 6241 (LBV, WAG); 25 km NE of Assok (fl. Aug.) Breteler \& de Wilde 107 (LBV, WAG); Mouila (fl., y.fr.) Le Testu 5051 (BM, P); Moubana (fl. Aug.) Le Testu 5482 (BM, BR, P); 35 km SW of Doussala (fl., fr. May) Reitsma et al. 1021 (LBV, WAG).
Congo: Moutampa (fl. June) Bouquet 165 (P); Brazzaville (fl.) Chevalier 4008 (P); Batéké plateau (fr. Nov.) Descoings 9837 (P); between Maya and Loukakou (fr. Nov.) Descoings 11385 (P); Niari region (fl., fr.) Thollon 974 (P).

Zaire: Kinshasa (fl. May) Bequaert 7552 (BR, K); Kimuenza-Lukaya (fl. Dec.) Breyne 14 (BR, K); Mayombe (fl.) Cabra 30 (BR, type M. cabrae); Kiama (fr. April) Callens 1701 (BR, K); Nyangwe (fl. Jan.) Claessens 111 (BR, K); Bokote (fl. Dec.) Dubois 315 (BM, BR, K); Lulonga (fl. July) Dubois 511 (BR, K); Yalikungu (fl. Jan.) Evrard 5472 (BR, K); Kwango-Wamba (fr. Aug.) Germain 2569 (BR, K); 10 km Bengamisa Rd (fl. March) Gilbert 2143 (BM, BR, K); Kakenge (fl. Dec.) Gillardin 323 (BR, K); Sangaie (fl. Feb.) Gillardin 501 (BR, K); Bosako (fl.) Hulstaert 1031 (BR, K, WAG); Libenge (fl. Oct.) Lebrun 1551 (BR, P); Gemena-Karaiva (fl. Dec.) Lebrun 1882 (BR, K, P); Buta-Titule (fl. April) Lebrun 2660 (BR, P); Niangara-Wamba (fl. June) Lebrun 3217 (BR, P); Urenga (fl., fr. July) Lebrun 5750 (BR, K); Kindu-Katakokbe (fl. Aug.) Lebrun 6083 (BM, BR, K); Yangambi (f1., fr. Jan.) Louis 945, (fl., fr. Sept.) Louis 2570 , (fl., fr. June) Louis 4242 (fl., fr. Nov.) Louis 6779 (fl. June) Louis 10109 (fl. Nov.) Louis 12816 (BM, BR, K, P); Mukenge ( fr. Jan.) Pogge 718; fl. June) Pogge 724, (fr. Sept.) Pogge 751 (K); Moand (fl. Aug.) Schouteden 97 (BM, BR); Hemptinne St.Benoit (fr.) Vanderyst 23637 (BR); (y.fr.) Vanderyst 23682 (BR).

Angola: Saurimo ( = Vila Henrique de Carvalho) (fl. April) Exell \& Mendonça 937 (BM, COI); Cabinda, Caio, Hombe, Lufu R. (fl., fr. Feb.) Gossweiler 7792 (BM, COI, K, LISU); (fl. March) Gossweiler 7805 (BM, BR, K); Cabinda, Chiluango R. (fl., fr. June) Gossweiler 8109 (BM, COI, K); Congo, Zombo, Beie (fl. Feb.) Gossweiler 13394 (LISC); Lunda, Dundo (fr. Oct.) Gossweiler 13691 (13699?) ( B, BM, K, P); (fl., fr. May) Gossweiler 14013 (K, LISC, P); Cabinda, Buca ZauChiaca (fl., fr. Aug.) Monteira et al. 209 (BM, COI, LISC); (fl. Aug.) Raimundo et al. 227 (LISC); Uige, Quimbele e Icoca (fr. Aug.) Raimundo et al. 827 (BR, LISC).

Cult.: Seedlings, de Koning 5453 (WAG).
Note: M. expansa has the largest distribution and also the greatest variation of all species of Manotes. The variation in the indumentum of most parts of the plant throughout the area is remarkable. The farther from the equator the
plant grows, the more hairy it usually is. The synonym $M$. longiflora for example represents the hairy types at the north side of the distribution area of M. expansa from Ivory Coast to the Central African Republic. At the south side this tendency is less clear, but there M. expansa meets its hairy relative M. lomamiensis. Striking differences are observed in different areas, in W Africa there is less variation between plants from Sierra Leone and Nigeria than there may be between two plants from nearby localities within Zaire or Gabon.

## Manotes griffoniana Baill.

Fig. 15, 141, 142, 144, 145
M. griffoniana Baillon, 1867: 244; Baker, 1868: 460; Schellenberg, 1910: 19; 1938: 58 p.p. except Dewèvre 434, Gossweiler 7792,7805, and 8109, and Thollon 974 (see under M. expansa) and Thollon 895 and 1278 (see note under $M$. soyauxii); Troupin, 1952: 74 p.p. except De Giorgi 219 and Gillardin 213 (see note under M. lomamiensis); Exell, 1954: 140.

Type: Gabon, Pyrat, Griffon 292 (holo: P).
M. tomentosa Gilg, 1891b: 331; Schellenberg, 1910: 19. Type: Gabon, Sibange, near Libreville, Soyaux 432 (holo: B $\dagger$; lecto: K; iso: Z).
M. laurentii De Wildeman, 1905: 90; Schellenberg, 1938: 57 p.p. (except De Giorgi 219 see M. lomamiensis). Type: Zaire, border of Pioka R., Laurent s.n. (holo: BR).
M. tessmannii Schellenberg, 1919: 443; 1938: 56. Type: Cameroun, Akonangi in Campo area, Tessmann s.n. (holo: B $\dagger$ ); Cameroun, near Zingui, 20 km WSW of Ebolowa, Letouzey 10290 (neo: P).
M. zenkeri Gilg ex Schellenberg, 1910: 19; 1919: 444; Hutchinson, 1928: 517; Schellenberg, 1938: 57; Hepper, 1958: 747; Burkill, 1985: 524. Type: Cameroun, Bipindi, Zenker 896 (lecto: GOET; iso: E, P).
M. rosea Schellenberg, 1919: 445; 1938: 58. Type: Cameroun, Bebai in Campo area, Tessmann 652 (holo: $\mathrm{B} \dagger$; lecto: K).
M. rubiginosa Schellenberg, 1919: 445; 1938: 57. Type: Angola, Cazengo, Gossweiler 659 (holo: B $\dagger$; lecto: K ; iso: BM, P).
M. altiscandens Gilg, nomen in herbarium Zenker (896, GOET).
M. pruinosa auct.non Gilg, Schellenberg, 1938: 59 p.p.: Tilman 79 and Verschueren 28.

Branchlets with a usually dense indumentum of long hairs, lenticellate. Petiole $2.5-8.5 \mathrm{~cm}$ long; rachis $4-14 \mathrm{~cm}$ long, pubescent; petiolules $1-4 \mathrm{~mm}$ long; leaflets $7-13$, ovate to elliptic, pubescent, base cordate to acute; apex acuminate; young leaflets pink; terminal leaflet 4.3-12 $\times 1.5-5 \mathrm{~cm}$; lateral leaflets $1.9-12 \times 0.9-4$ cm . Inflorescence up to 40 cm long, pubescent. Flower buds with closed calyx at most 1-1.2(-1.7) $\times 1-1.2(-1.5) \mathrm{mm}$. Pedicel above the joint $0.5-2 \mathrm{~mm}$ long. Sepals (1.3-)1.7-2(-2.5) $\times(0.7-) 1-1.2 \mathrm{~mm}$, lanceolate, from greenish-white to dark red but usually pink. Petals 5.5-7.5 $\times 0.8-1.3 \mathrm{~mm}$, reflexed, first white sometimes with with pink, later yellow. Sepals and petals with all three kinds


Fig. 144. Manotes griffoniana: flowers (de Wilde \& Jongkind 9589; phot. C.C.H. Jongkind).
of hairs. Long stamens $3-6.5 \mathrm{~mm}$, short stamens $1.5-4 \mathrm{~mm}$ long; filaments with glandular hairs and usually with globular hairs as well. Pistil $2-5.5 \mathrm{~mm}$ long, unequal to the stamens, ovary entirely covered with long hairs, style with glandular and globular hairs (already present in bud!). Follicles $1-5$, up to $20 \times 10$ mm , orange-brown to red-brown, with long hairs, globular hairs and sometimes with glandular hairs as well. Seed ca $10 \times 5 \mathrm{~mm}$; testa for the greater part fleshy and red, dorsal partly thin and black; endosperm dirty-white. Seedling epigeal; hypocotyl strongly elongated and densely pubescent; first pair of leaves opposite and often unifoliolate, membranaceous.

Distribution: From Nigeria eastward to Zaire and southward to Angola.
Ecology: Rain forest and gallery forest, observed and collected particularly at forest edges. From sea level up to 900 m alt.

Selection of the nearly 200 examined specimens:
Nigeria: Calabar (fl., fr. July) Daramola 55183 (BR, K); Oban-Osomba (fl. March) Latilo \& Oguntayo 70551 (K, WAG); Bonny R. (fl., fr. Oct.) Mann 508 (K, P); Calabar near Uquo (fl., fr. May) Onochie 33155 (K, WAG); Eket distr. (fl.) Talbot \& Talbot 3125 (BM, K); Port Harcourt (fl., fr. July) Timmerman 13 (L, WAG).
Cameroun: Bitye (fl.) Bates 1077 (BM, MO, Z); Kribi (fl. Nov.) Bos 3243 (BR, K, P, WAG); Longii (fl. March) Bos 4104 (BR, K, P, WAG); Bertoua (fl. March) Breteler 1190 (BR, K, M, P, WAG, Z), (fl., fr. July) Breteler 1677 (BR, K, M, P, WAG); Bimba (fl. April) Breteler 2814 (BR,


Fig. 145. Distribution of Manotes griffoniana

K, P, WAG); 65 km SSW of Eséka, Nyong R. (fl., fr. June) W.de Wilde 2747 (BR, P, WAG); (fr. July) W.de Wilde 2850 (B, BR, K, MO, WAG); Bipindi (fl., fr.) Zenker 1169 (BM, G, GOET, K, L, M, P, WAG, Z); (fl.) Zenker 2996 (BM, BR, GOET, K, L, M, P, WAG, Z); (fl.) Zenker 3106 (B, BM, BR, GOET, K, L, M, WAG, Z); (fr.) Zenker 3198 (BM, BR, GOET, K, L, M, P, WAG, Z).

Central African Republic: Obo region, Zemio Rd (fl. Dec.) Descoings 12251 (P); Sangha R. (fl. July) Thomas \& Fay 7271 (MO, WAG).

Equatorial Guinea: Bebai, Campo (fl. Nov.) Tessmann 652 (K, type M. rosea).
Gabon: Gamba (fl. Sept.) Breteler 5616 (WAG); near Libreville, 25 km on road to Kango (fr. Nov.) Breteler 8537 (LBV, WAG); Ndendé (fl., fr. Dec.) Descoings 6400 (P); Kerellé, Denis, Pyrat (fl.) Griffon du Bellay 292 (P, type); near Libreville (fl., fr.) Klaine $28 b$ (BM, K, P); 32 km SE of Sindara (fl., fr. Dec.) Louis et al. 1299 (LBV, WAG); (fl. Dec.) Louis et al. 1389 (LBV, WAG); Sibange, near Libreville (fl., fr. April) Soyaux 432 (B, BR, K, P); Cap Esterias (fr. Sept.) Villiers 323 (P).

Congo: Boko region (fr. Aug.) de Neré 507 (P); Brazzaville-la Foulakari (fr. Feb.) Descoings 9608 (P); Kitabi (fl.) Lecomte s.n. (P); Ogooué (fl.) Leroy s.n. (P).

Zaire: Lukengo (fr. Jan.) Compère 1232 (BR, K); M’Vuazi (fl. Sept.) Devred 321 (BR, K, P); Bikoro-Inongo (fl. Oct.) Evrard 2671 (BR, K); Eala (fl., fr. Oct.) J.Léonard 877 (BR, M, K); Eala (fl., fr. May) Louis 1986 (BR, K, P); Mabali (fl. Oct.) Thonnet 22 (BR, K); Kavumu-Walikale (fl. Sept.) Troupin 4407 (BR, K, WAG); (fl., fr. Oct.) Troupin 4500 (BR, K, WAG); (fl. Sept.) Troupin 4540 (BR, K); (fl., fr. Nov.) Troupin 4702 (BR, K, WAG); Kangu (fl. Oct.) Vanderyst 26081 (BR).
Angola: Cuanza Norte, Quiage (fr. Feb.) F.J.Cardoso 82 (COI); Cuanza Norte, Cazengo (fr.) Gossweiler 659 (BM, K, P, type M. rubiginosa); Cabinda, Bélize (fl., fr. Nov.) Gossweiler 7569 (BM, BR, COI, K, LISU); Golungo Alto, Mata de Quisucula (fl. Aug.) Welwitsch 4639 (BM, COI, G).
Cult.: Seedlings, Jongkind 688 (WAG), from seeds collected in Gabon, Breteler 8537.

## M. lomamiensis Troupin, 1951: 366; 1952: 76.

Type: Zaire, district du Bas-Katanga, Kaniama, Mullenders 2182 (holo: BR). M. laurentii auct.non De Wildeman \& Durand, Schellenberg, 1938: 57 p.p.: De Giorgi 219.


Fig. 146. Distribution of Manotes lomamiensis
M. griffoniana auct.non Baillon, Troupin, 1952: 74 p.p.: De Giorgi 219 and Gillardin 213.

Branchlets with a dense indumentum of long hairs. Petiole $1.5-5.5 \mathrm{~cm}$ long; rachis $7-11 \mathrm{~cm}$ long, hairy; petiolules $1-4 \mathrm{~mm}$ long; leaflets $9-13$, ovate to elliptic, pubescent, base cordate to acute, apex acuminate; terminal leaflet 6-9.5 $\times 1.8-4$ cm ; lateral leaflets 2.9-8.5 $\times 1.8-4 \mathrm{~cm}$. Inflorescence up to 35 cm long, pubescent. Flower buds with closed calyx up to $1.7-2.3 \times 1.5 \mathrm{~mm}$. Pedicel above the joint $1-3 \mathrm{~mm}$ long. Sepals lanceolate, (1.5-)2-3 $\times 0.8-1.2 \mathrm{~mm}$. Petals narrowly elliptic, $7.5-8.5 \times 0.8-1.2 \mathrm{~mm}$. Sepals and petals frequently with all three kinds of hairs. Long stamens $3-6 \mathrm{~mm}$, short stamens $1.5-4 \mathrm{~mm}$ long; filaments with glandular hairs and usually with globular hairs. Pistil 2-5.5 mm long, unequal to the stamens, with glandular hairs and, on the ovary, also with long hairs; ovary soon after fertilization covered with many globular hairs. Follicles $1-5$, up to $20 \times$ 10 mm , beaked, covered with a mixture of all three kinds of hairs. Seed ca 10 $\times 5 \mathrm{~mm}$.

Distribution: S Zaire.
Ecology: Gallery forest.
Specimens examined
Zaire: Lukelenge (fl. Oct.) De Giorgi 219 (BR); Yambo forest, E of Kaniama (fr. July) Delvaux 341 (BR); 75 km of Kaniama, Kaniama-Bukama Rd (fr. July) Delvaux 370 (BR); Kabalo Terr., Tendy (fr. July) Delvaux 429 (BR); Kasai, Gandajika (fl. March) Devred 3984 (BR); Bilala (fl., fr. Feb.) Gillardin 213 (BR); Yamba (fl. May) Herman 2323 (BR); Kaniama, Haut Lomami (fr. Sept.) Mullenders 1072 (BR, M, P); (fr. Aug.) Mullenders 2182 (BR, type); Sentery Terr., Sangwa (fl. June) Risopoulos 1095 (BR); Nakariba, Kabongo-Kongolo (fl. April) Schmitz 1642 (BR).
M. macrantha (Gilg) Schellenberg, 1910: 18; Hutchinson, 1928: 517; Schellenberg, 1938: 62; Hepper, 1958: 747.

Basionym: Dinklagea macrantha Gilg, 1897: 242.
Type: Liberia, Grand Bassa, Fishtown, Dinklage 1633 (holo: B; iso: BM, BR, E, G, Z).

Liana, mainly climbing by leaves modified to strong woody hooks. Branchlets velutinous, soon glabrescent. Petiole $5.5-10.5 \mathrm{~cm}$ long; rachis $4.5-11 \mathrm{~cm}$ long, almost glabrous; petiolules $2-5 \mathrm{~mm}$ long; leaflets $5-9$, ovate to elliptic, cordate to subcordate at base, coriaceus, slightly hairy beneath, glabrous above; apex acuminate; terminal leaflet $10-18 \times 3.5-6 \mathrm{~cm}$; lateral leaflet $5.5-16.5 \times 2.5-6$ cm . Inflorescence up to 10 cm long, pubescent or glabrous, frequently in the axil of a hook-like modified leaf. Flower bud when the calyx lobes are about to open 3-3.5 $\times$ 2-2.5 mm. Pedicel above the joint 1-4 mm long. Sepals lanceolate, $4-5 \times 1.5-2 \mathrm{~mm}$, red, frequently with all three kinds of hairs. Petals with two lateral (glandular?) lobes, $5.5-8 \times 1.5-1.7 \mathrm{~mm}$, yellow, covered on both sides with glandular hairs. Stamens $3-6 \mathrm{~mm}$ long; filaments covered with glandular hairs. Short pistils ca 2 mm , long pistils ca 6 mm long, with short glandular hairs only. Follicles $1-5$, up to $20 \times 10 \mathrm{~mm}$, thinly woody, minutely velutinous with short glandular hairs only, beaked. Sepals in fruit 8-10 $\times 2-4 \mathrm{~mm}$, dark red. Seed ca $10 \times 7 \mathrm{~mm}$; testa totally fleshy and red.

Distribution: Liberia, W Ivory Coast and Gabon.
Ecology: Rain forest and gallery forest, observed and collected particularly in forest edges.

## Specimens examined

Liberia: Ganta (fr. Nov.) Adam 30188 (K); Sinoe Co: Duo (fl. March) Baldwin jr. 11360 (K, WAG); Duport (fr. April) Bos 1888 (BR, K, P, WAG); Monrovia (fr. April) Cooper 73 (K); Devilsbush, 15 km E of Monrovia (fl. March) de Wilde \& Voorhoeve 3624 (B, BR, K, P, WAG); Grand Bassa, Fishtown (fl., fr. April) Dinklage 1633 (B, BM, BR, E, G, Z, type); (fr. Aug.) Dinklage 1747 (B); Grand Bassa, Dinklage 1804 (B); (fl., fr. July) Dinklage 1965 (G, K, P); Monrovia (fl., fr. April) Dinklage 2812 (B, HBG, P, WAG); 20 km NW of Harper (fl., fr. Aug.) Hall 45560 (K); Sinoe to Port (fl. Jan.) Jansen 1128 (WAG); 20 mls N of Buchanan (fl. Feb.) Jansen 1902 (WAG); 7 mls N of Harper (fr. July) Jansen 2400 (WAG); Devilsbush, near Payesville (fr. Aug.) Leeuwenberg \& Voorhoeve 4909 (B, BR, HBG, P, WAG); Porobush, Duport area (fl. March) van Harten 360 (HBG, WAG); Devilsbush, Payesville (fr. July) Voorhoeve 342 (WAG).

Ivory Coast: 50 km E of Sassandra (fr. April) Leeuwenberg 4054 (B, BR, HBG, WAG).
Gabon: near Djidji, W of Koumameyoung, Breteler et al. 8715 (LBV, WAG); Lopé Reserve (fr. Nov.) Breteler 9012 (WAG, alc.!); Doudou Mts, W of Doussala (old fr. March) de Wilde \& Jongkind 9330 (LBV, WAG); Ogouoé-Ivindo Fauna Res. (fr. Nov.) Louis 64 (LBV, WAG); near entrance Lopé Reserve, Jongkind 702 (LBV, WAG); 45 km SW of Doussala (fr. Oct.) Reitsma 1728 (WAG); Lopé Reserve (fr. Nov.) Reitsma 2642 (WAG); NW of Mouila on road to Fougamou (y.fr. July) Thomas 6507 (MO, WAG); St. Martin (fr. March) A.Walker s.n. (P, WAG).


Fig. 147. Manotes macrantha: 1. flowering branchlet, $2 / 3 \times$; 2 . leaflet, $2 / 3 \times$; 3 . detail of leaflet (see $\times$ in 2), $4 \times$. flower, $4 \times$; 5 . flower partly, showing androgynophore, stamens, and pistils of a short-styled flower, $4 \times$; 6 . petal, showing two lateral lobes, $4 \times$; 7. branchlet with fruits, $2 / 3 \times$; 8 . fruit, $2 \times$. (1,4-6. de Wilde 3624; 2,3. Leeuwenberg 4909; 7,8. Bos 1888).

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Fig. 148. Distribution of Manotes macrantha

Manotes soyauxii Schellenb.
Fig. 141, 149
M. soyauxii Schellenberg, 1919: 446.

Type: Congo, Loango near Nanga, Soyaux 120 (holo: $\mathrm{B} \dagger$; lecto: K)
M.griffoniana auct. non Baillon, Schellenberg, 1938: 58p.p.: Thollon 895 and 1278.
M. pruinosa auct. non Gilg, Schellenberg, 1938: 59 p.p.: Le Testu 1049 and 1061, and Soyaux 120.

Branchlets with a long indumentum of long hairs. Petiole ca 4 cm long; rachis $7-12 \mathrm{~cm}$, glabrous; petiolules $1-4 \mathrm{~mm}$ long; leaflets $9-13$, ovate to elliptic, slightly pubescent or glabrous, base cordate to acute, apex acuminate; terminal leaflet $5-8.5 \times 2-3.2 \mathrm{~cm}$; lateral leaflet 1.1-7.5 $\times 0.8-2.5 \mathrm{~cm}$. Inflorescence up to 27 cm long, pubescent to glabrous. Flower bud with closed calyx up to 2-2.5 $\times$ $1.5-1.7 \mathrm{~mm}$. Pedicel above the joint $1.5-6 \mathrm{~mm}$ long. Sepals lanceolate $2.5-3 \times$ 1 mm . Petals narrowly elliptic $7.5-9 \times 1.2-1.4 \mathrm{~mm}$. Sepals and petals frequently with all three types of hairs. Long stamens $3-6 \mathrm{~mm}$; short stamens $1.5-4 \mathrm{~mm}$ long; filaments with glandular hairs and globular hairs as well. Pistil 2-5.5 mm long, unequal to the stamens, ovary with (short) glandular hairs and long hairs only or with globular hairs as well, style sith glandular hairs only. Follices with all three types of hairs.

Distribution: Cameroun, Gabon, Congo, and Zaire.
Specimens examined:
Cameroun: 13 km SW of Eséka (fl. March) Leeuwenberg 5163 (B, BR, C, EA, K, LISC, MO,
P, SRGH, WAG, YA).


Fig. 149. Distribution of Manotes soyauxii

Gabon: Tchibanga (fl. July) Le Testu 1049 (BM, P); (fl., y.fr. July) Le Testu 1061 (BM, P); (fl., y.fr.) Le Test 2332 (BM).

Congo: Loango near Manga (fl. Sept.) Soyaux 120 (K, type); Alima R. (fl.) Cholon 895 (P); Loango (fl., fr. Oct.) Cholon 1278 (P).
Zaire: Basankusu-Bokakote Rd (fl., fr. Sept.) Evrard 4812 (BR, K)
Note: The 8 specimens of $M$. soyauxii cited here all originate from an area where M. expansa and M. griffoniana occur together, and are all in one way or another intermediate between these species. It is felt that M. soyauxii is a hybrid between $M$. expansa and $M$. griffoniana. The fact that the specimens differ to such an extent from each other could be explained when they represent different hybridisation levels, e.g. F1, F2 and stages still farther away from the original species. The specimens of putative hybrid origin are outnumbered in the same area by the size of M. expansa and M. griffoniana populations.

## Excluded species

Manotes asiatica Gagnepain, 1951:207 = Eurycoma longifolia Jack (Simaroubaceae).

Manotes macrophylla Hern, 1896: $190=$ Ostryoderris lucid (Welw. ex Baker) Dak. f. (Papilionoideae).

Manotes palisotii Planchon, 1850: 439 (ill. name) $=$ Rourea thomsonii (Baker) Jongkind.

Manotes racemosa (Don) Gilg, 1896: 215 = Cnestis racemosa Don.
Manotes staudtii Gilg, 1895b: 71 = Connarus griffonianus Ball.

# Rourea Aublet 

by C. C. H. Jongkind

History of the genus
Rourea was published in 1775 by Aublet with R.frutescens as the only species. Another three Rourea species were described prior to the publication of a short revision of the Connaraceae by Planchon in 1850. In this work Planchon added 24 new species or combinations from America, Asia, and Africa.

In 1867-1870 Baillon combined Planchon's genera Roureopsis and Bernardinia, and the genus Byrsocarpus of Schumacher with Rourea. This concept of Rourea is almost the same as that of the present revision. In treating Rourea in this large sense Baillon was followed by most taxonomists e.g. Baker, Hiern, De Wildeman, and initially also Gilg.

Later on Gilg, followed by Schellenberg, employed a much more narrow generic concept resulting in many new genera notably Jaundea, Paxia, Santaloides, Santaloidella, and Spiropetalum, all within the circumscription of Rourea sensu Baillon. In consequence of this, and because of the reinstalment of Byrsocarpus and Roureopsis, the name Rourea vanished from Africa and Asia. All these genera with narrow and unreliable generic delimitations caused confusion to such an extent that Schellenberg (1938) referred flowering material of Rourea parviflora to Byrsocarpus parviflorus (Gilg) Schellenberg and fruiting material of the same species to Santaloidella gilletii Schellenberg. This unsatisfactory situation culminated in the publication of the Connaraceae in Das Pflanzenreich in 1938 by Schellenberg.

In 1958 when Leenhouts treated the Connaraceae for Flora Malesiana he rejected many of the new genera and he accommodated the pertinent Asiatic species once more to the genus Rourea. Keraudren (1958) acted along the same lines for Madagascar in treating the former Byrsocarpus orientalis and Santaloides gudjuana as species of Rourea.

The main difference in the delimitation of Rourea between the present treatment, in accordance with Baillon, and that of Leenhouts, is that the latter work recognizes Roureopsis as a distinct genus.

## Delimitation of the genus

Among Connaraceae with five-carpellate flowers Rourea is delimitated by the combination of the following characters: pinnate leaves (but occasional branches with exclusively unifoliolate- or trifoliolate- leaves may occur), no androgynophore, follicles rounded at base, not stipitate, glabrous inside, and seeds without endosperm.

## Description of the genus

Rourea Aublet, 1775: 467 (nom. conserv.); Planchon, 1850: 413; Bentham \& Hooker, 1862: 432; Baillon, 1867: 228; Baker, 1868: 455; Baillon, 1870: 18; Gilg, 1891a: 66; Schellenberg, 1910: 34, 37, 55; 1938: 194; Keraudren, 1958: 3; Leenhouts, 1958a: 143; 1958b: 510; Hutchinson, 1964: 166; Forero, 1976: 1; 1983: 138.

Type species: R. frutescens Aublet.
Byrsocarpus Thonning ex Schumacher, 1827: 246; Bentham \& Hooker, 1862: 431; Baillon, 1867: 228; Baker, 1868: 451; Gilg, 1890: 66; Schellenberg, 1910: 34, 39, 117; 1938: 146; Troupin, 1952: 88; Hemsley, 1956: 15; Keraudren, 1957: 525; Hutchinson, 1964: 166; Mendes, 1966: 622; Mendes, 1969: 5; Liberato, 1980a: 12. Type species: B. coccineus Thonn. ex Schum. ( $=$ Rourea coccinea (Thonn. ex Schum.) Benth.).

Bernardinia Planchon, 1850: 412; Bentham \& Hooker, 1862: 431; Gilg, 1891a: 65; Schellenberg, 1910: 57, 126; 1938: 100; Hutchinson, 1964: 165; Forero, 1983: 25. Type species: B. fluminensis (Gardn.) Planch. ( $=$ Rourea fluminensis (Gardn.) Jongkind).

Roureopsis Planchon, 1850: 432; Gilg, 1891a: 66; Schellenberg, 1910: 24-27, 105; 1938: 107; Troupin, 1952: 77; Hutchinson, 1964: 165; Leenhouts, 1958b: 505. Type species: R.pubinervis Planch. (= Rourea emarginata (Jack) Jongkind).

Taeniochlaena Hooker f., 1862: 433; Gilg, 1891a: 68; Schellenberg, 1938: 167. Type species: T. griffithii Hook.f. ( $=$ Rourea acutipetala Miquel).

Paxia Gilg, 1891a: 70; 1891b: 320; Schellenberg, 1910: 30, 111; 1938: 114; Troupin, 1952: 79; Hutchinson, 1964: 165. Type species: P. scandens Gilg (= Rourea myriantha Baill.).
Spiropetalum Gilg, 1891a: 70; 1891b: 335; Schellenberg, 1910: 31, 114; 1938: 103; Troupin, 1952: 127; Hutchinson, 1964: 169; Liberato, 1980a: 9. Type species: S. odoratum Gilg ( $=$ Rourea solanderi Baker).

Santalodes O.Kuntze, 1891: 154 nom.rej., see Hemsley \& Bullock, 1956: 57.
Jaundea Gilg, 1894: 388; 1895b: 66; Schellenberg, 1910: 43; 1919: 457; 1938: 161; Troupin, 1952: 83; Hemsley, 1956: 19; Hutchinson, 1964: 166; Mendes, 1966: 627; Liberato, 1980a: 13. Type species: J.zenkeri Gilg ( $=$ Rourea thomsonii (Baker) Jongkind).

Santaloides Schellenberg, 1910: 35-37, 46-54, 119 (nom. conserv.); 1912: 246; 1938: 119; Hemsley, 1956: 13; Hemsley \& Bullock, 1956: 57; Hutchinson, 1964: 166; Mendes, 1966: 622; Mendes, 1969: 8; Liberato, 1980a: 10. Type species: S. minus (Gaertn.) Schellenberg ( $=$ Rourea minor (Gaertn.) Alston).

Santaloidella Schellenberg, 1938: 118; Troupin, 1952: 80; Hutchinson 1964: 167. Type species: S. gilletii Schellenberg ( $=$ Rourea parviflora Gilg) .

Lianas, shrubs or small trees. Branches cylindric or clearly lobed, often ending in a tendrilloid tip; wood of some species frequently with interxylary phloem. Leaves imparipinnate, occasionally with one leaflet only; leaflets opposite or subopposite, entire, symmetric or asymmetric, often mucronate. Inflorescences
axillary, paniculate or racemose sometimes nearly globose, frequently more than one per axil of the sometimes rudimentary leaf, sometimes one or more together at the end of a leafy branch and resembling a terminal inflorescence. Flowers pentamerous, heterodistylous, sweet-scented; pedicel always with a distinct joint. Sepals free or almost completely connate, imbricate in bud, persistent and usually accrescent, sometimes strongly so, accrescent soon after pollination when the fruit is still very small. Petals as long as to much longer than the sepals, free or connivent near base, often lorate and inrolled or folded, white often with a trace of yellow or red, glabrous or with a few hairs apical. Stamens in two whorls, slightly united at base, the five stamens opposite the sepals longer than the five opposite the petals; filaments glabrous. Carpels five, free, glabrous to pilose. Follicles one to five per flower, ovate to elliptic with a rounded to acute apex or beaked, glabrous inside, glabrous or velutinous, and/or with glandular hairs outside, orange to red or (rarely) white, dehiscing by a ventral suture or more or less circumscissile at base. Seed solitary, rarely two per follicel, subovoid to ellipsoid; testa partly to almost totally fleshy, this part yellow to red; other part of the testa dark brown to black (sometimes red?) and shiny; hilum basal; endosperm absent in mature seed; cotyledons planoconvex, glabrous; radicle apical to ventral. Seedlings epigeal or hypogeal.

A circumtropical genus with forty to seventy species of forests and savannas. Most species are restricted to the tropical rain forest.

Note: The genera Rourea and Roureopsis sensu Leenhouts are here united. The main differences used to distinguish Roureopsis from the former were inrolled petals and sepals not imbricate in fruit. However, these characters are not exclusive. Inrolled petals are also found in Rourea thomsonii (the former Jaundea species) and the sepals of the fruiting calyx are not imbricate in many American species and often also not in Rourea cassioides (formely Byrsocarpus cassioides).

Leenhouts united the Asiatic Taeniochlaena with Roureopsis. His diagnosis for the combined genera needed only minor adjustments in order to accommodate the African Spiropetalum and Paxia as well. Hence these genera are also united with Rourea in the present paper.

Generic adjustments would have been necessary anyway, due to the discovery of the fruits of Paxia calophylla and Paxia calophylloides (Rourea calophylla and Rourea calophylloides). These fruits turned out to have a velutinous and a powdery indumentum respectively, while the other species of Paxia have glabrous fruits. The possession of glabrous fruits was one of the two characters separating Paxia and Spiropetalum.

Sectional arrangment
The subgenera and sections that were made for previous taxonomic treatments are not upheld in this revision because the genus concept changed much
and also because they were often based on artificial characters (e.g. see note on $R$. minor pag. 341).
In this revision the genus is divided into five sections. They are described below and their species are enumerated. They are synonymous with one or more of the genera in Schellenberg's revision of 1938.

These sections are not very sharply delimitated one against the other but it is felt that they are rather natural entities which structure the variation in the important characters within the genus.

For the clustering of the American species see page 368.
Section Bernardinia (Planchon) Jongkind comb. \& stat. nov.
Basionym: Bernardinia Planchon as genus.
Type species: B. fluminensis (Gardn.) Planch. (= Rourea fluminensis (Gardn.) Jongkind).

Small stomatal vestibule. Petals never inrolled. Fruit glabrous, usually more than one developed follicle per flower. Sepals in fruit only slightly accrescent and often reflexed. Testa fleshy for about $1 / 4$. Radicle apical.

Species: R. fluminensis.
Distribution: America.
Section Byrsocarpus (Thonn. ex Schum.) Jongkind comb. \& stat. nov.
Basionym: Byrsocarpus Thonning ex Schumacher as genus.
Type species: B. coccineus Thonn. ex Schum. ( $=$ Rourea coccinea (Thonn. ex Schum.) Benth.).

Synonym: Jaundea Gilg.
Small stomatal vestibule. Petals sometimes inrolled. Fruit glabrous, usually only one but sometimes two developed follicles per flower rarely more. Sepals clasping the base of the fruit, slightly accrescent. Testa in one species, R. coccinea, variable, for $1 / 4$ to nearly entirely fleshy. In the other species always nearly entirely fleshy. Radicle apical or ventral.

Species: R. cassioides, R. coccinea, R. orientalis, R. thomsonii.
Distribution: Africa.

## Section Rourea

Synonym: Santaloidella Schellenberg.
Small stomatal vestibule. Petals never inrolled. Fruit glabrous or sparsely hairy, usually only one developed follicle per flower. Sepals clasping the base of the fruit, slightly to strongly accrescent. Testa fleshy for about $1 / 4$. Radicle apical.

Species: R. accrescens, R. acropetala R. camptoneura cluster, R. frutescens cluster, R. gardneriana cluster, R. induta cluster, R. krukovii, R. martiana cluster, R. parviflora, R. pinnata, R. prancei, R. pubescens, R. revoluta cluster, R. suerrensis cluster.

## Distribution: Africa, America, Asia.

Section Roureopsis (Planchon) Jongkind comb. \& stat. nov.
Basionym: Roureopsis Planchon as genus.
Type species: Roureopsis pubinervis Planch. (= Rourea emarginata (Jack) Jongkind).

Synonym: Taeniochleana Hook. f.; Paxia Gilg; Spiropetalum Gilg.
Large stomatal vestibule. Petals inrolled. Fruit glabrous, velutinous, or with an indumentum of glandular hairs only. One or one to five follicles per flower. Sepals not clasping the fruit, often strongly accrescent. Testa for about $1 / 4$ fleshy. Radicle apical or ventral.

Species: R. acutipetala, R. asplenifolia, R. calophylla, R. calophylloides, R.confundens, R. dictyophylla, R. emarginata, R. erythrocalyx, R. myriantha, R. obliquifoliolata, R. solanderi, R. stenopetala.

Distribution: Africa, Asia.
Section Santaloides (Schellenb.) Jongkind comb. \& stat. nov.
Basionym: Santaloides Schellenberg.
Type species: Santaloides minus (Gaertn.) Schellenb. (=Rourea minor (Gaertn.) Alston).

Synonym: Rourea subg. Palliatus Leenh.
Small stomatal vestibule. Petals never inrolled. Fruit glabrous, usually one developed follicle per flower. Sepals clasping the base of the fruit, slightly accrescent. Seed entirely enveloped by the sarcotesta which is for the greater part free from the seed. Radicle more or less apical.

Species: R. balansea, R. fulgens, R. harmandiana, R. minor, R. mimosoides, R. prainiana, R. radlkoferiana, R. rugosa.

Distribution: Africa, Asia.
General key for the African species mainly based on fruiting material.
1a Fruit velutinous. $-2$
b Fruit glabrous or nearly so or with a powdery indumentum of glandular hairs only.
$-3$
2a Calyx lobes 1-1.5 times as long as wide, unequal in shape. . R. solanderi
b Calyx lobes 2-4 times as long as wide, equal in shape. . . R. calophylloides
3a Fruit covered with a powdery indumentum of glandular hairs
R. calophylla
b Fruit glabrous or nearly so. . . . . . . . . . . . . . . . . . . . . . . . -4
4a Radicle more or less apical. . . . . . . . . . . . . . . . . . . . . . . . . . . -5
b Radicle distinctly ventral. . . . . . . . . . . . . . . . . . . . . . . . . -8
5a Testa for ca one third fleshy, yellow to scarlet, other two third thin, maroon to almost black and shiny.
R. parviflora
b Testa almost completely fleshy, yellow to scarlet, if not then the thin darkcoloured part almost completely covered by the free part of the sarcotesta. $-6$
6a Sarcotesta for an important part free from the seed. . . . . . . R. minor
b Sarcotesta completely united with the seed.
$-7$
7a Branches without lenticells or distinct cork layer. Leaflets asymmetrical at base. Inflorescences on a leafy branch.
R. cassioides
b Branches with lenticells and/or distinct cork layer. Leaflets symmetrical at base. Inflorescences usually in the axil of deciduous leaves. R. orientalis
8a Petiole $0-0,5 \mathrm{~cm}$. Leaves pinnate
R. obliquifoliolata
b Petiole distinctly longer, or leaves unifoliolate.
9a Sepals 6-12 mm long, not appressed in fruit.
b Sepals 2-4 mm long, clasping base of fruit (not always appressed when dry). $-11$
10a Inflorescence up to 5 cm long. Apex of the leaflets long-acuminate; acumen emarginate (e.g. fig. 161.1).
R. erythrocalyx
b Inflorescence usually longer than 5 cm . Apex of the leaflets acuminate; acumen retuse to mucronate (fig. 165.2-165.4).
R. myriantha

11a Apex of lateral leaflets acute to emarginate.
R. coccinea subsp. coccinea var. coccinea
b Apex of lateral leaflets acuminate, or leaves unifoliolate.
$-12$
12a Petals distinctly folded inward in bud, not imbricate. Leaflets in West and Central Africa with a prominent parallel tertiary nervation. In East Africa only in mountain forest ( $1200-3500 \mathrm{~m}$ alt.).
R. thomsonii
b Petals imbricate in bud, at most slightly folded. Leaflets never with a pronounced parallel tertiary nervation. In East Africa only at low altitudes. $-13$

13a Deciduous, sometimes scandent, shrub. East Africa.
R. coccinea subsp. boiviniana
b Usually evergreen liana or scandent shrub. Central and Eastern W Africa.
R. coccinea subsp. coccinea var. viridis

Key to the African species based on flowering material
1a Petals lorate and inrolled particularly so in bud, not imbricate (fig. 167.3).
b Petals only slightly folding inward in bud, imbricate.
R. obliquifoliolata

2a Petiole $0-0,5 \mathrm{~cm}$ long. Leaves pinnate.
$-3$
b Petiole distinctly longer, or leaves unifoliolate.
3a Inflorescence and sepals outside covered by (sometimes small) multicellular glandular hairs
b Inflorescence and sepals with an indumentum of ordinary hairs rarely mixed with a few glandular hairs.
4a Flower buds globose. Inflorescence densely covered by glandular hairs, obscuring its epidermis from view.
b Flower buds ellipsoid or ovoid. The glandular hairs on the inflorescence too small to cover its epidermis from view. R. calophylloides
5a Sepals distinctly hairy inside, at anthesis some of them for more than $2 / 3$
R. solanderiof their length connate.
b Sepals (almost) glabrous inside, free to connate for less than $1 / 3$ ..... $-6$
6a At least some leaves with more than twelve leaflets. Branches without lenti-cells.R. cassioides
b All leaves with less than twelve leaflets. Branches usually lenticellate. . -7
7a Leaflets with a long acuminate apex; acumen emarginate. (fig. 161.1).Inflorescence up to 5 cm . Pedicel very short, with a joint close to calyx.
R. erythrocalyx
b Leaflets often shortly acuminate; acumen retuse to mucronate. Inflores-cence often longer than 5 cm . Pedicel with a joint removed from the calyx.
8a Sepals elliptic-ovate, apex rounded-acute. Petals spiral in flower and bud.Filaments curved inwards (fig. 165.6).R. myriantha
b Sepals triangular-ovate, apex acute to acuminate. Petals usually only once folded inwards. Filaments straight or curved outwards (fig. 177.7).
R. thomsonii
9a Carpels only hairy on their adaxial side. Leaflets (long) acuminate.
R. minor
b Carpels hairy all around. Apex of leaflets acuminate or not. ..... -10
10a At least some leaves with more than twelve leaflets. ..... $-11$
b All leaves with less than twelve leaflets. ..... $-14$
11a Leaflets with an acuminate apex; acumen usually emarginate. Inflorescence up to 2 cm long. Old branches deeply furrowed. In rain forest. R. parviflora
b Apex of the leaflets emarginate to acuminate. Inflorescence often longer than2 cm . Old branches never deeply furrowed. In forest and savanna.$-12$
12a Branches without lenticells or cork layer. Inflorescences on immature leafy branches. R. cassioides
b Branches with lenticells and/or a distinct cork layer. Inflorescences on older branches. ..... $-13$
13a Plant from Southern Africa, East Africa south of the equator, or Madagas- car. Petals connivent near their base. Leaflets nearly symmetrical at base.R. orientalis
b Plant from all parts of tropical Africa except Madagascar. If from the samearea as $R$. orientalis than petals not connivent and leaflets usually asymme-trical at base.R. coccinea subsp. coccinea var. coccinea
14a Lateral leaflets with an acute to emarginate apex.
R. coccinea subsp. coccinea var. coccinea
b Lateral leaflets acuminate ..... $-15$
15a Decidous shrub (sometimes scandent). E Africa.
R. coccinea subsp. boiviniana
b Liana or scandent shrub, usually evergreen. Central and Eastern W Africa.$-16$

16a Leaves with 5-19 leaflets; acumen usually emarginate. Inflorescence up to 2 cm long. Old branches deeply furrowed. . . . . . . . . . . R. parviflora
b Leaves with 1-7 leaflets; acumen never emarginate. Inflorescence sometimes longer. Old branches never deeply furrowed.
R. coccinea subsp. coccinea var. viridis

## Rourea calophylla (Gilg ex Schellenberg) Jongkind comb.nov. <br> Fig. 150, 151

Basionym: Paxia calophylla Gilg ex Schellenberg, 1910: 31; 1919: 447; 1938: 115.

Type: Cameroun, Bipindi, Zenker 1963 (holo: B; iso: BM, BR, G, E, GOET, K, L, M, MO, P, WAG, Z).

Large liana or shrub. Petiole up to 11 cm long; rachis up to 12 cm long; petiolules 2-6 mm long; leaflets 3-7, ovate to elliptic, usually with three to five long arching lateral nerves, glabrous, thinly coriaceous, acuminate at apex; terminal leaflet $8-22 \times 3-10.5 \mathrm{~cm}$; lateral leaflets nearly symmetrical, $5-19 \times 3-10 \mathrm{~cm}$. Inflorescence up to 20 cm long, with many striking reddish, glandular hairs. Flower buds globose. Pedicel above the joint 1-3 mm. Sepals 3-4 $\times 1-2 \mathrm{~mm}$, outside covered with glandular hairs, inside with ordinary hairs. Petals 7-10 $\times$ 2-2.5 mm, lorate, inrolled in bud, free. Long stamens $1.8-5.5 \mathrm{~mm}$ long, short stamens $1-3.5 \mathrm{~mm}$ long; filaments curving inwards. Pistil $1.2-4.5 \mathrm{~mm}$ long; style glabrous or with some hairs; ovary pilose. Follicles one or two per flower, rarely more, ca $30 \times 15 \mathrm{~mm}$, beaked, covered with many reddish glandular hairs, dehiscing by a ventral suture. Sepals $5-7 \times 3-4.5 \mathrm{~mm}$ in fruit, coriaceous. Seedcoat for ca one third fleshy; thin part of the testa probably very dark red and shining. Radicle ventral.

Distribution: E Nigeria, Cameroun, Gabon, Angola (Cabinda).
Ecology: Lowland rain forest.

## Specimens examined:

Nigeria: S Bakundu N.A.F.R. (fl. Jan.) Binuyo \& Daramola FHI 35065 (K, P).
Cameroun: 60 km SW Eseka (y.fr. March) Leeuwenberg 5101 (K, MO, P, WAG); Tisongo Lake (fl.b. Feb.) Struhsaker 24 (K); Bipindi (fl.) Zenker 1963 (B, BM, BR,G, GOET, K, L, M, MO, P, WAG, Z, type); (fl.) Zenker 2177 (WAG); Bipindi (fl.) Zenker 150 (C, L, U).

Gabon: Lalara-Makokou Road (fl. Sept.) Breteler \& de Wilde 490 (LBV, WAG); ca 24 km N of Koumameyoung, Breteler et al. 8634 (LBV, WAG); near Djidji, W of Koumameyoung (fr. April) Breteler et al. 8975 (LBV, WAG); Libreville, Klaine 3319 (P); S of Medouneu, (fl. Sept.) Leeuwenberg \& Persoon 13576 (LBV, WAG); 40 km E S.E.F., Crystal Mts (fl., y.fr. Sept.) Leeuwenberg \& Persoon 13583 (LBV, WAG); Gwagnya (fl. March) Le Testu 6415 (BM, BR, P, WAG); Kemboma (fl. Sept.) Le Testu 8919 (BM, BR, P); near Oveng (fr. June) Reitsma 1245 (WAG); (fr. Sept.) Reitsma 1472 (WAG).

Congo: between N'Gongo and crossing Maamar (y.fr. May) Sita 3764 (P).
Angola: Cabinda, Buca Zau, Chiaca (fl.b. June) Monteiro \& Murta 27 (LISC).


Fig. 150. Rourea calophylla: 1. flowering branchlet, $2 / 3 \times$; 2 . flower, $4 \times$; 3. stamens and pistils of a short-styled flower, $6 \times$; 4. fruit, $1 \times$; 5 . seed, $1 \times ; 6$. cotyledon inside with ventral radicle, $1 \times$; 7. cotyledon outside, $1 \times$. (1. Zenker 1963; 2-3. Binuyo \& Daramola FHI 35095; 4-7. Reitsma et al. 1472)


Fig. 151. Distribution of Rourea calophylla

Rourea calophylloides (Schellenberg) Jongkind comb.nov.
Fig. 152, 153

Basionym: Paxia calophylloides Schellenberg, 1938: 115.
Type: Gabon, Tchibanga, Le Testu 1735 (holo: BM; iso: P).
Large liana. Petiole up to 12 cm long; rachis up to 30 cm long; petiolules 2-6 mm long; leaflets 3-7, elliptic to obovate, glabrous, thinly coriaceous; apex acuminate; terminal leaflet $18-19 \times 10-12 \mathrm{~cm}$; lateral ones $10-12 \times 6-10 \mathrm{~cm}$. Inflorescence up to 10 cm long, with many small glandular hairs, often cauliflorous or subcauliflorous. Flower bud oblong. Pedicel above the joint $3-5 \mathrm{~mm}$ long. Sepals $5-9 \times 2-3 \mathrm{~mm}$, both sides with ordinary hairs, only outside with many small glandular hairs. Petals 12-13 $\times 1.5-2 \mathrm{~mm}$, lorate, coherent near base, inrolled in bud, glabrous. Long stamens $3.5-6 \mathrm{~mm}$ long; short ones 2-4 mm long. Pistil $2-7 \mathrm{~mm}$ long; style with many hairs; ovary pilose. Follicles velutinous, beaked, dehiscing by a ventral suture, often more than one per flower. Sepals in fruit 6-9 $\times 2.5-4 \mathrm{~mm}$, outside rather densely covered with glandular hairs. Testa for ca one fourth fleshy. Radicle ventral.

Distribution: S Gabon.
Ecology: Lowland rain forest.
Specimens examined.
Gabon: between Mouila and Yeno (fr. Sept.) Breteler \& Lemmens 8007 (LBV, WAG); 3 km along road from Moabi to Doussala (fr. Nov.) de Wilde et al. 8943 (WAG); Tchibanga (fl. May)


Fig. 152. Rourea calophylloides: 1. flowering branchlet, $2 / 3 \times$; 2. flower bud partly, showing the inrolled petals, $4 \times$; 3 . flower partly, showing the stamens and the pistils of a short-styled flower, $4 \times$; 4. branchlet with young fruits, $2 / 3 \times$; 5. young follicle, ventral side, $2 / 3 \times$; 6 . follicles, one showing seed, $2 / 3 \times ; 7$. empty follicles, $2 / 3 \times ; 8$. seed with sarcotesta (lower part), $2 \times ; 9$. cotyledon inside with the ventral radicle, $2 \times$. (1-3. Le Testu 6497; 4-5. Breteler et al. 8007; 6-9. J.de Wilde 8943).


Fig. 153. Distribution of Rourea calophylloides

Le Testu 1735 (BM, P, type); Mourombo (fl. May) Le Testu 5444 (BM, BR, LISC, P); Nzouna (fl. April) Le Testu 6497 (BM, BR, P).

Note: This is the only species of Rourea in Africa with a narrow distribution.

## Rourea cassioides Hiern

Fig. 154, 155
R. cassioides Hiern, 1896: 187.

Type: Angola, Cuanza Norte, Mt Queta, Welwitsch 4627 (holo: BM; iso: C, COI, G, K).

Byrsocarpus cassioides (Hiern) Schellenberg, 1910: 41; 1912: 243; 1938: 148; Troupin, 1952: 91; Exell \& Mendonça, 1954: 150.

Liana. Branches glabrous, never lenticellate; branchlets puberulous. Petiole $2.5-4 \mathrm{~cm}$ long; rachis 7-35 cm long; petiolules 1-2 mm long; leaflets 13-31, gla-
brous to puberulous, chartaceous, papillate beneath; apex rounded; terminal leaflet oblong-ovate to elliptic, 3-7 $\times 1-3 \mathrm{~cm}$; lateral ones strongly asymmetrical, elliptic to oblong, 1.4-7 $\times 0.8-2.5 \mathrm{~cm}$. Inflorescence up to 6 cm long, puberulous, in the axil of immature or reduced leaf on developing shoots. Pedicel above the joint $1-3.5 \mathrm{~mm}$ long. Sepals $3-4 \times 1.5-2.5 \mathrm{~mm}$, puberulous outside, nearly glabrous inside. Petals $5-8 \times 1.5-2 \mathrm{~mm}$, free, top in bud sometimes distinctly folded. Long stamens $3.5-5.5 \mathrm{~mm}$ long, short ones $2.8-4.5 \mathrm{~mm}$ long. Pistil $1.5-4$ mm long; style with some long hairs; ovary pilose. Follicles one per flower rarely more, 13-16 $\times 7-8 \mathrm{~mm}$, symmetrical, with rounded top, glabrous, dehiscing by a ventral suture. Sepals in fruit $4-5 \times 3-4 \mathrm{~mm}$, with some scattered hairs


Fig. 154. Rourea cassioides: 1. branchlet with flowers, $2 / 3 \times ; 2-4$. leaflets with nervation from beneath, $2 / 3 \times ; 5-6$. branchlet with fruits, one fruit showing seed, $2 / 3 \times ; 7$. seed testa partly removed, cotyledons visible, $2 \times$; 8-9. cotyledons with apical radicle, $4 \times$. (1. Breteler 1284; 2-4. Le Testu 4645; 5. Compere 1160; 6-9. W. de Wilde 2637).


Fig. 155. Distribution of Rourea cassioides
outside. Seed with the radicle emerging at the apical end; testa entirely fleshy.
Distribution: Central Africa.
Ecology: Lowland rain forest.

## Specimens examined:

Cameroun: 42 km SE Mbalmayo (fr. May) Asonganyi 46 (P, YA); 69 km SE Akonolinga (fr. June) Asonganyi 304 (P, YA); Bitye (f1.) Bates 1652 (BM, MO); Bertoua (fl. April) Breteler 1284 (BR, WAG); N’Kolbisson (fr. June) W.de Wilde et al. 2637 (BR, MO, WAG); Ngoekele (Etang); (fr. Oct.) Endengle 69 (P, YA); (fr. Nov.) Endengle 82 (P, YA); Mbanga (fr. July) Letouzey 2358 (P); 40 km E Mbalmayo (fr. March) Letouzey 11344 (BR, P, WAG); N Lom R. (fl. April) Mildbraed 8929 (K); Kongola-Mbussa (fl. April) Mildbraed 9060 (K).

Central African Republic: Yalinga (fl. April) Le Testu 4645 (BM, BR, P, WAG); Boukoko (fl. March) Equipe Tisserant 1407 (BR, P, WAG); (fr. July) Equipe Tisserant 1529 (P).

Equatorial Guinea: sin. loc. (fl. April) Tessmann 337 (K).
Gabon: 10 km S of Makokou, Florence 2018 (P); Lopé Reserve, Jongkind 707 (WAG); Moucwagnya (fl. April) Le Testu 8732 (P, WAG); Abam (fl.) Le Testu 9132 (BR, LISC, P).
Congo: Brazzaville, M.J.de Brazza 240 (P).
Zaire: Lubutu-Kirundu (fr. Feb.) Bequaert 6794 (BR); Songa (fl. Feb.) Compère 892 (BR); Dembo (fr. Jan.) Compère 1160 (BR); M’Vuazi (fl., fr. Sept.) Devred 768 (BR); Bas-Uele (fl. March) Dewulf 721 (BR); Bambesa (fr. June) Gérard 5225 (BR); Mt Hoyo (fr. Aug.) Lisowski 40462 (BR).

Angola: Cuanza Norte, Granja S.Luiz (fr.) Gossweiler 5250 (BM, COI); Cuanza Norte, Queta Mts (fr. Dec.) Welwitsch 4627 (BM, C, COI, G, K, type).

## Rourea coccinea (Thonn. ex Schum.) Bentham

Fig. 156-160

For literature, synonyms, and typification see under the subspecies and varieties.


Fig. 156. Rourea coccinea subsp. coccinea var. coccinea: 1.flowering branchlet, $2 / 3 \times ; 4-5$. branchlets with fruits, $2 / 3 \times$; seed, showing almost entirely fleshy testa, $4 \times$.

Rourea coccinea subsp. boiviniana: 2. flowering branchlet, $2 / 3 \times$; 3. leaflet, $2 / 3 \times$. (1. Latilo FHI 47131; 2. Jaasund 2625; 3. Torre \& Correira 17053; 4. Hiepko et al. 286; 5. W.de Wilde 336; 6. Hiepko et al. 286).

Liana or shrub. Branches lenticellate, cylindrical, sometimes with a distinct cork layer. Petiole $0.9-7.5 \mathrm{~cm}$ long; rachis $0-12 \mathrm{~cm}$ long; petiolules $0.5-5 \mathrm{~mm}$ long; leaflets 1-21, ovate to oblong or obovate, glabrous to pubescent, chartaceous to thinly coriaceous; apex emarginate to acuminate; terminal leaflet 1.6-15 $\times 1-8 \mathrm{~cm}$; lateral ones symmetrical to strikingly asymmetrical, $0.7-10 \times 0.6-5.5$ cm . Inflorescence up to 11 cm long, few flowered, glabrous to pubescent. Pedicel above the joint 1-10 ( -30 ) mm long. Sepals $1.5-4 \times 1.5-3 \mathrm{~mm}$, usually wider than long. Petals 6-11.5 $\times 1.5-3.5 \mathrm{~mm}$, often coherent near base, imbricate and not folded in bud, apex emarginate to acute, sometimes with a few apical hairs. Long stamens 1.8-7 mm long, short ones 1.3-6 mm long. Pistil 1.7-9 mm long; style with a few to many hairs; ovary pilose. Follicles one or two per flower, rarely more, ellipsoid with a rounded or acute apex, $15-20 \times 7-10 \mathrm{~mm}$, glabrous, dehiscing by a ventral suture. Seed with the radicle ventral; testa for one quarter to entirely fleshy and orange to red, remaining part of testa if available black and shining; cotyledons green. Seedling hypogeal; hypocotyl not elongated, first two leaves opposite.

Distribution: West, Central, and East Africa, with a disjunction in East Africa. This disjunction separates subsp. coccinea in the West from subsp. boiviniana in the East (see fig. 160).

Key to the subspecies and varieties
1a Decidous (sometimes scandent) shrub, inflorescences and young foliage simultaneously on the bare shrub. Lateral leaflets 4-10, symmetrical or nearly so; apex acute to acuminate. East Africa. . R. coccinea subsp. boiviniana
b Decidous or evergreen shrub or liana. Lateral leaflets $0-20$, symmetric to strongly asymmetrical; apex emarginate to acuminate. West, Central, and East Africa.
R. coccinea ssp. coccinea -2

2a Lateral leaflets 0-6; apex acuminate
R. coccinea subsp. coccinea var. viridis
b Lateral leaflets 4-20; apex emarginate to acute.
R. coccinea subsp. coccinea var. coccinea

Rourea coccinea (Thonn. ex Schum.) Benth. subsp. coccinea var. coccinea Fig. 156, 157
R. coccinea (Thonn. ex Schum.) Bentham, 1849: 290; Hiern, 1896: 186.

Basionym: Byrsocarpus coccineus Thonning ex Schumacher, 1827: 227; Planchon, 1850: 412; Baker, 1868: 452; Schellenberg, 1938: 148; Troupin, 1952: 91; Exell \& Mendonça, 1954: 148; Hemsley, 1956: 17; Hepper, 1958:741; Aubréville, 1959: 13; Irvine, 1961: 568; Mendes, 1966: 624; Adam, 1971: 866,867; Berhaut, 1975: 20; Liberato, 1980a: 12; Hall \& Swaine, 1981: 139; de Koning, 1983: 279; Ern, 1984: 164; Burkill, 1985: 518.

Type: Ghana (Danish Guinea), sin. loc., Thonning 19 (holo: C).

Byrsocarpus coccineus var. parvifolius Planchon ex Schellenberg, 1910: 41; Baker, 1868: 452. Type: Liberia, Cestos R., Dinklage 1948 (holo: B).
R. inodora De Wildeman \& Durand, 1899c: 71, fig. 36; 1899a: 17. Type: Zaire, Kembo, Dewèvre 442 (holo: BR ).

Byrsocarpus puniceus Thonning ex Schumacher, 1827: 227; Planchon, 1850: 412. Type: Ghana (Danish Guinea), sin. loc., Thonning 14 (holo: C).

Byrsocarpus parvifolius Planchon, 1850: 412, nomen.
Byrsocarpus ledermannii Schellenberg, 1919: 451; 1938: 154. Type: Cameroun, Banjo, Ledermann 2232 (lecto: $\mathrm{B} \dagger$ ). Neotype: Cameroun, Mayo Banyo, Letouzey 8546 (holo: WAG; iso: P).

Byrsocarpus puberulus Schellenberg, 1938: 150. Type: Zaire, Kisantu, Kinanga, Oddon in Gillet 1876 (holo: BR).

Byrsocarpus tisserantii Aubréville \& Pellegrin, 1950: 59. Type: Central African Republic, Oubangui, Waka area, Tisserant 257 (holo: P; iso: BM).

Byrsocarpus tomentosus Schellenberg, 1938: 151 (pro parte: only Angolan material!); Exell \& Mendonça, 1954: 149.

Byrsocarpus astragalifolius A.Chevalier, nomen.
Shrub, rhizomatous shrublet or liana, often deciduous. Branchlets with lenticells in a contrasting colour, branches sometimes with a distinct cork layer. Leaflets 5-21, ovate to elliptic or angular-oblong; terminal leaflet $1.5-4 \times 1-3 \mathrm{~cm}$, with an emarginate to slightly acuminate apex; lateral leaflets symmetrical to strikingly asymmetrical, $0.5-4 \times 0.5-3 \mathrm{~cm}$, with an emarginate to acute (never acuminate) apex. Inflorescences up to 6 cm , in the axil of full-grown or deciduous leaves. Seed-coat partly to entirely fleshy.

Distribution: Most parts of Tropical Africa, but in E Africa only in W Tanzania.
Ecology: Savanna, savanna woodland, and secondary forest, from sea level up to 1250 m alt.

Selection of the more than 400 specimens examined:
Senegal: Niassia (fl. April) Berhaut 5738 (P); Boudié Forest (fl.b. July) Berhaut 6096 (P); Soutou (fr.) Berhaut 7355 (P); Djibelor (fr. Sept.) v.d. Berghen 6652 (BR).

Mali: near Kayes (fl., fr. May) Legagneux s.n. (L).
Guinea Bissau: Cacine (fr. Aug.) Espirito Santo 621 (COI, LISJC); Cacine R. (fl. June) Espirito
Santo 2948 (LISC, LISJC, P, WAG); Bedanda Catanhez (fr. Sept.) Alves Pereira 3159 (LISC).
Guinea: Macenta (fl. Feb.) Adam 3742 (P); N'Zerekoré (fr.) Adam 5222 (P); Dyeke (fr. Oct.)
Baldwin 9659 (K); Kaba valley (y.fr. May) Chevalier 13131 (P); Friguiagbé (y.fr. May) Chillon 392
(P); Benty (fl. June) Jacques-Félix 1726 (P); Boké (fl. April) Paroisse 53 (P); Konakry (fr. June)

Pobéguin 35 (P); Los isles (fr.) Pobéguin 1181 (P); Ziama Mts (fr. May) Schnell 2654 (P).
Sierra Leone: Taiama (fr. Aug.) Dawe 496 (K); Kowama (fr. Nov.) Deighton 5250 (K); Kortright, Freetown (fl. April) Gledhill 405 (B, K, WAG); Foria N.P. (fl. Feb.) Gledhill 415 (K); Juba Peninsula (fl. May) Morton SL1329 (K, WAG); Fourah Bay College, Freetown (fr. June) Morton \& Jarr SL2046 (K, WAG); Makéni (fl. April) Roberty 171276 (G).

Liberia: Mt Nimba (fr. July) Adam 28587 (WAG); Tubman bridge (fr. Sept.) Barker 1409 (K); Cestos R. (fr. May) Dinklage 1948 (B, type of Byrsocarpus coccineus var. parvifolius); Monrovia (fr. July) Dinklage 3075 (Z); E of Harper (fr. July) Jansen 2434 (WAG); Sinkor, Monrovia


Fig. 157. Distribution of Rourea coccinea subsp. coccinea var. coccinea
(fl. March) van Harten 363 (WAG); 2 km W of Tappeta (fl., fr. Feb.) van Meer 469 (WAG). Ivory Coast: near Tabou (fr. April) Breteler 7404 (WAG); km 116 on the Bouna-Bondoukou Rd (fl. March) de Wilde \& Leeuwenberg 3507 (B, BR, P, WAG); 17 km W of Abidjan (fl. Nov.) Leeuwenberg 1923 (BR, WAG, Z); E of Béyo (fl. March) Leeuwenberg 2930 (B, BR, L, P, WAG, Z); Mt Tonkoui (fl. March) Leeuwenberg 2952 (BR, P, U, WAG, Z).

Ghana: Achimoto (fr. May) Ankrah GC20173 (K); Kintampo N.P. (fr. July) Chipp 525 (K); Kumasi Town F.R. (fr. March) Cudjou 510 (H, WAG, Z); Tantara Hill near Dome Accra (y.fr. Feb.) Enti FE2115 (MO, WAG); Gambaga (fl. March) Hepper \& Morton A3136 (K); Salaga (fl. Oct.) Krause s.n. (K); 1 km N of Salt Pond (fl. March) Leeuwenberg 11162 (WAG); Konongo, Ashanti (fr. July) Obeng-Darko 8031 (WAG); Achimota (fr. Nov.) Roberty 12862 (G); Kpandu (fr.) Rodenburg 31 (L).
Togo: Avétonou (fr. Sept.) Breteler 7136 (B, WAG); Cacaveli (fl. Sept.) Ern et al. 133 (B); Fosse aux Lions savanna (fr. Oct.) Ern et al. 1702 (B); 3 km SW de Faille d'Aledjo (fr. Oct.) Ern et al. 1980 (B); Adétikopé (fr. Nov.) Ern $2361 a$ (B); Alédjo-Kadara (fl. Dec.) Ern 2786 (B); 26 km NE of Aného (fr. April) Hakkiet al. 112 (B); Basser (fr. April) Hakkiet al. 370 (B); 8 km NE of Atakpamé (fr. Sept.) Hiepko et al. 286 (B); 7 km E of Lomé (fr. May) Jansen 2612 (WAG); NW Palimé (fr. Sept.) Mathey et al. 129 (B).

Benin: Cotonou (fr. March) Chevalier 4446 (P); Tohoué village (fl., fr. Jan.) Chevalier $22798 b$ (P); Agouagou (fl. May) Chevalier 23532 (P).

Nigeria: 50 mls S of Yelwa (fr. July) Cook 313 (K); Wawagi F.R. (fl. May) Eimunjeze \& Adebusuyi FHI 69996 (K, WAG); Ibadan (fl. Feb.) Emwiogbon FHI 47152 (WAG); Milliken Hill (fl., fr. July) Latilo FHI 27610 (WAG); Nimbia F.R. (fl., y.fr. April) Latilo FHI 47131 (K, WAG); Lagos, Isolo (fl., fr. March) Leeuwenberg 11211 (WAG).

Cameroun: 10 km SW Ndemba (fr. May) Breteler 2931 (P, WAG); Hoséré Gode (fr. July) Fotius 2092 (K, P, YA); 7 km W of Yaounde (fr. Aug.) Leeuwenberg 6041 (P, WAG); 65 km NNE of Moloundou (fl. March) Letouzey \& Villiers 10536 (BR, HBG, P, WAG); Bundi (fl. March) Mildbraed 4682 (HBG, P).

Central African Republic: 35 km SE Boda (fr. June) Badré 95 (P, WAG); Ndouka and Kouti Tèlé terr. (fl. May) Chevalier 8247 (BR, G, L, P, WAG, Z); Ouadda area (fl. April) Descoings 11059 (P); Parc Manovo, Gounda (fr. July) Fay 7309 (BR, MO, P); Yalinga (fl.) Le Testu 3844 (BR, P); (fl. Feb.) Le Testu 4565 (BR, P); Waka area (fl., fr. Dec.) Tisserant 257 (BM, P, type Byrsocarpus tisserantii).

Gabon: km 30 Moanda-Bakoumba, Breteler 6749 (LBV, WAG); Corisco Bay (fl.) Mann 1848
(K, P); Oveng-Mitsic (fl. March) Reitsma 735 (WAG); 20 km NE of Oveng (fr. June) Reitsma 1226 (WAG); 30 km S of Doussala (fl. Oct.) Reitsma 1740 (WAG).

Congo: Djoumouna Forest (fr. Oct.) Bitsindou 6 (P); Brazzaville (fr. Dec.) de Wit 6010 (WAG).
Zaire: Kimbuba (fr. Dec.) Callens 3841 (BR, K); Nsafu Road (fr. Feb.) Devred 1532 (BR); Befale-
Tongote (fr. May) Evrard 4147 (BR, K); Bolombo Eala (fl. Aug.) Lebrun 1184 (BR, K); Banzyville (fl. Jan.) Lebrun 2095 (BR, K); Eala (fl.) Leemans 318 (B, BR); Tshibombo (fr. Nov.) Liben 1933 (BR, K); N Bondo near Baye (fr. July) Lisowski 50078 (BR, K); Yangambi (fl. April) Louis 14554 (BR, C, K); 40 km NNW Kolwezi (y.fr. Feb.) Malaisse \& Robbrecht $2295 b$ (BR).

Angola: Cuanza Norte, Pungo (fl. Aug.) da Silva 2129 (BR); Cazengo, Granja de S. Luis (fr.) Gossweiler 5248 (BM, COI, LISU); Cabinda, Panga Mungo (fl.) Gossweiler 6202 (BM, COI, LISU); Luanda, Musseque de Luanda (fl. Nov.) Gossweiler 10512 (BM, COI, K, M); Lunda, Dundo (fl. Oct.) Gossweiler 13699 (B, K); Cuanza Sul, Rosa Vianense-Calulo (fr. Jan.) Raimundo et al. 645 (BR, LISC); Cuanza Norte, Golungo Alto (fl. Dec.) Welwitsch 4624 (BM, COI, G); Lunda, Dundundo R. (fl.) Young 478 (BM, BR, COI, LISC); Lunda, Saurimo (fl. Aug.) Young 620 (BM, COI, LISC); Lunda, Alto Cuilo (fl. Sept.) Young 694 (BM, COI, LISC).

Burundi: Kigwena mission (fl. Sept.) Auquier 4132 (BR); Rumonge (fl. Jan.) Reekmans 8550 (BR, K, WAG); Gitwe (fr. Jan.) Reekmans 9572 (BR, K, WAG); Nyaunza (fl. Feb.) Shantz 697 (K).

Tanzania: Gombe stream N.P. (fl. Oct.) Morris Goodall 87 (EA); (fl. Oct.) Morris Goodall 101 (EA); (fl. Nov.) Morris Goodall 106 (EA); Uvinza, Malagarassi (fl.b. Feb.) Peter 36169 (B); Uvinza, W Lugufu (y.fr. Feb.) Peter 36572 (B); Kasakata (fr. March) Suzuki 208 (EA); Kasakela Res. (fr. Nov.) Verdcourt 3343 (BR, EA).

Zambia: S of Matonchi farm (fl. Nov.) Milne-Redhead 3145 (BR, K); N of Dambo, NE of Dobeka bridge (fr. Dec.) Milne-Redhead 3885 (BR, K).

Cult.: Seedlings, de Koning 3821, 5953 (WAG).

Rourea coccinea (Thonn.ex Schum.) Benth. subsp. coccinea var. viridis (Gilg) Jongkind comb.nov.

Fig. 158, 159
Basionym: R. viridis Gilg, 1891b: 327; De Wildeman, 1912: 406.
Type: Zaire, Mukenge, Pogge 750 (holo: B $\dagger$ ).
Neotype: Cameroun, Bipindi, Zenker 248 (holo: WAG; iso: B, C, G, MO).
R. mannii Gilg, 1891b: 323. Type: Equatorial Guinea, Muni R., Mann 1828 (holo: $\mathrm{B} \dagger$; lecto: K ).
R. poggeana Gilg, 1891b: 326. Type: Zaire, Mukenge, Pogge 748 (holo: $\mathrm{B} \dagger$; lecto: K).
R. unifoliolata Gilg, 1891b: 325. Type: Zaire, Mukenge, Pogge 1626 (holo: $\mathrm{B} \dagger$ ). Neotype: Cameroun, near Bamekok, Breteler 2831 ( $=$ Letouzey 4775) (holo: WAG; iso: B, HBG, K, P).
R. dinklagei Gilg, 1895b: 67. Type: Cameroun, Grand Batanga, Dinklage 908 (holo: $\mathrm{B} \dagger$ ). Neotype: Cameroun, 40 km NW of Bertoua, Breteler 2935 (holo: WAG, Z).
R. pallens Hiern, 1896: 188. Type: Angola, Cazengo, Cabondo, Welwitsch 4629 (holo: BM).
R. foenum-graecum De Wildeman \& Durand, 1899a: 18; 1899c: 75, fig. 38. Type: Zaire, Boma, Dewèvre 424 (holo: BR).
R. ealensis De Wildeman, 1909: 91. Type: Zaire, Eala, Pynaert 560 (holo: BR).
R. laurentii De Wildeman, 1909: 90, fig. 24. Type: Zaire, Bomange, M.Laurent 1634 (holo: BR).


Fig. 158. Rourea coccinea subsp. coccinea var. viridis: 1. flowering branchlet, $2 / 3 \times$; 2. acumen of leaflet from above, $8 \times ; 3$. acumen of leaflet from beneath, $8 \times ; 4$. petals (connivent near base), $12 \times ; 5$. flower petals removed, $8 \times ; 6$. stamens and pistils, $8 \times ; 7$. infructescence, $2 / 3 \times$; 8 . follicle opening by a ventral suture, $2 / 3 \times ; 9$. seed with an entirely fleshy testa, partly damaged (basal part accidently removed), $1 \times ; 10$. seed partly, one cotyledon partly removed, with dorsal radicle, $1 \times$; 11. cross section of seed, showing fleshy testa, $1 \times$. (1-6. Breteler \& de Wilde 691; 7. Bos 3291; 8. Breteler 2935; 9-11. A.Louis 1218).
R. coriacea De Wildeman, 1911a: 258; 1912: 404. Type: Zaire, LulongaCoquilhatville, Pynaert 746 (holo: BR).
$R$. zenkeri Gilg, nomen in herbarium Zenker.
Byrsocarpus viridis (Gilg) Schellenberg, 1910: 46; 1912: 245; 1938: 158; Troupin, 1952: 96; Exell \& Mendonça, 1954: 150; Hepper, 1958: 741; Burkill, 1985: 519. Basionym: R. viridis (see above).

Byrsocarpus poggeanus (Gilg) Schellenberg, 1910: 45; 1912: 245; 1919: 453; 1938: 154; Troupin, 1952: 93, fig. 7; Hepper, 1958: 741; Burkill, 1985: 519. Basionym: R. poggeana Gilg (see above).

Byrsocarpus dinklagei (Gilg) Schellenberg, 1929: 544; 1938: 157; Troupin, 1952: 94. Basionym: R. dinklagei Gilg (see above).

Byrsocarpus foenum-graecum (De Wild.) Schellenberg, 1910: 41; 1912: 244. Basionym: R. foenum-graecum De Wildeman (see above).

Byrsocarpus coriaceus (De Wild.) Schellenberg, 1912: 401. Basionym: R. coriacea De Wildeman (see above).

Byrsocarpus laurentii (De Wild.) Schellenberg, 1912: 401; 1938: 157. Basionym: R. laurentii De Wildeman (see above).

Byrsocarpus papillosus Schellenberg, 1919: 453; 1938: 154. Type: Cameroun, between Sangmelima and Dja R., Mildbraed 5507 (holo: B $\dagger$; lecto: HBG).

Large liana or shrub. Branches rarely with a (thin) cork layer, branchlets glabrous and often green. Leaflets 1-5(-7), ovate to obovate, (nearly) glabrous; apex acuminate; terminal leaflet 4-15 $\times 2-8 \mathrm{~cm}$; lateral ones 2-10 $\times 1.5-5.5 \mathrm{~cm}$, nearly symmetrical. Inflorescence ca 2 cm long, but sometimes up to 11 cm long, usually in the axil of a full-grown leaf; branches often green. Seedcoat nearly always entirely fleshy.

Distribution: From Nigeria eastward to Central African Republic, southward to Angola.

Ecology: Rain forest and gallery forest from sea level up to 870 m alt.
Selection of the ca 150 specimens examined:
Nigeria: Onogholo F.R. (fr. June) Eimunjeze \& Oguntayo FHI 72763 (K, WAG); Ikom farmland (fl. Oct.) Emwiogbon et al. FHI 87264 (WAG); Eket distr. (fl.) Talbot \& Talbot 3172 (G); 2 mls from Calabar (fl. May) van Meer 1514 (WAG).

Cameroun: 2 km S of Gr. Batanga (fr. Sept.) Bos 5355 (P, WAG); 30 km SW of Batouri (fr. April) Breteler 2831 (= Letouzey 4775) (B, HBG, K, P, WAG, type R. unifoliolata); 27 km SW of Bertoua (fr. May) Breteler 2961 (WAG); N'Kolbisson (fr. May) W.de Wilde 2611 (B, MO, WAG, Z); Barombi Kang (fl. Feb.) D.W.Thomas 4365 (MO, WAG); Nyong R. 2 km downstream of Akonolinga (fr. April) D.W.Thomas 6268 (MO, WAG); Bipindi (fr. March) Zenker 248 (B, C, G, MO, WAG, type R. viridis).

Central African Republic: 10 km N of Bambari (fl. March) Tisserant 1477 (P); Boukoko (fl. Dec.) Equipe Tisserant 1290 (P); (fl. March) Equipe Tisserant 1666 (BR).

Equatorial Guinea: Muni R. (fl.) Mann 1828 (K, type of R. mannii).
Gabon: km 5 Belinga-Makokou (fl. Sept.) Breteler \& de Wilde 691 (LBV, WAG); 15 km SSE of Pano (fr. Oct.) Breteler 6978 (LBV, WAG); km 15 Libreville-Kango Road (fr.) Breteler 8542 (WAG, alc.!); 9 km SSW of Makokou (fr. Nov.) Leeuwenberg 11426 (LBV, WAG); Pingo (fl. Sept.)


Fig. 159. Distribution of Rourea coccinea subsp. coccinea var. viridis (West and Central Africa) and Rourea coccinea subsp. boiviniana (East Africa).

Le Testu 6082 (BM, BR, P); 32 km SE of Sindara (fr. Dec.) Louis et al. 1325 (LBV, WAG).
Congo: M’Bamou, Bouenza (fr. Nov.) Bouquet 768 (P); Edou (fl. July) Descoings 7797 (P); between Meya and Loukakou (fr. Nov.) Descoings 11388 (P); M’Binda (fr. March) Sita 3543 (BR, P, WAG).
Zaire: Penge (fl. Jan.) Bequaert 2176 (BR); INEAC Bongabo (fr. June) Breyne 1676 (BR); Kinkosi (fr. Dec.) Callens 3874 (BR); Kiyaka-Kwango (fl. Sept.) Devred 2657 (BR); Luki (fr. Dec.) Donis 2265 (B, BR); Likati (fr. March) Gérard 2226 (BR); Tupkwo (fr. May) Gérard 4524 (BR); Bokoro (fr. Oct.) Jans 600 (BR); Bolongula (fr. 20 Nov. 1903) Laurent s.n. (BR); Tshondo (fr. Jan.) Liben 2200 (BR, WAG); (fr. June) Louis 9882 (B, BR); Bikoro (fl. March) Nsola 533 (BR).
Angola: Cuanza Norte, Queta, Gossweiler 5578 (BM, COI); Cabinda, Buca Zau (fl.) Gossweiler 6762 (BM, COI, LISU); Cabinda, Bélize (y.fr.) Gossweiler 7130 (BM, COI); Cuanza Norte, Cazengo (fr. June) Welwitsch 4629 (BM, type R. pallens).
Cult: Photograph in collection WAG of seedlings in greenhouse. Seedlings of Breteler 8542 from Gabon.

Note: In selecting neotypes for $R$. viridis and $R$. unifoliolata specimens that are well represented in many herbaria were preferred over those collected at Agric. Univ. Wageningen Papers 89-6 (1989)
the original localities, as specimens with characters exactly matching the protologues of both species have been collected all over Central Africa.

Rourea coccinea (Thonn.ex Schum.) Benth. subsp. boiviniana (Baill.) Jongkind comb.nov.

Fig. 156, 159
Basionym: R. boiviniana Baillon, 1867: 231.
Type: Kenya, Mombasa, Boivin s.n. (holo: P).
R. maxima (Baker) Gilg, 1895a: 192. Basionym: Byrsocarpus maximus Baker, 1868: 453; Schellenberg, 1919: 454; 1938: 155. Type: Tanzania, Rovuma R., Kirk s.n. (holo: K).
R. ovatifolia (Baker) Gilg, 1895a: 192. Basionym: Byrsocarpus ovatifolius Baker, 1868: 452. Type: Tanzania, Rovuma R., Meller s.n. (holo: K).
R. usaramensis Gilg, 1895a: 192. Type: Tanzania, Dunda, Stuhlmann 6420; Dilangilo, Stuhlmann 6641; Kikuli, Stuhlmann 6780; Magule, Stuhlmann 7091 (syn: $\mathrm{B}_{\dagger}$ ). Neotype: Tanzania: Pangani, Khuki-plateau, Goetze 99 (holo: K; iso: E).
R. goetzei Gilg, 1900: 394. Type: Tanzania, Khutu-Uhehe, Goetze 415 (holo: $\mathrm{B} \dagger$; lecto: K ; iso: E ).

Byrsocarpus boivinianus (Baill.) Schellenberg, 1938: 155; Hemsley, 1956: 16; Mendes, 1966: 625,626; Mendes, 1969: 7. Basionym: R. boiviniana Baillon (see above).

Byrsocarpus goetzei (Gilg) Greenway, 1940: 41. Basionym: R. goetzei Gilg (see above).

Byrsocarpus usaramensis (Gilg) Schellenberg, 1910: 43; 1912: 244. Basionym: R. usaramensis Gilg (see above).

Shrub, sometimes scandent. Branches often with a distinct corklayer, branchlets puberulous to glabrous. Leaflets 5-9(-11), terminal ones and lateral ones nearly identical in shape, ovate to elliptic, $1-10 \times 1-5 \mathrm{~cm}$, glabrous or sparsely hairy; apex acute to acuminate. Inflorescence up to 10 cm long; leaf- and flower buds are opening simultaneously on the bare shrub, during the flowering time there are no mature leaves present.

Distribution: Kenya, Tanzania, and Mozambique.
Ecology: Coastal bush and thicket edges in savanna, from sea level up to 700 m alt.

Specimens examined:
Kenya: Mombasa (fr.) Boivin s.n. (P, type); Arabuko-Sokoke Forest (fr. June) Dale 3775 (EA, P); Arabuko (fr. April) Donald 9 (EA, G, K); Mararani, Kucher 13484 (EA); Sokoke Forest, Moggridge 155 (EA); N of Sokoke For. Station (fr. June) Musyoki \& Hansen 1022 (C, EA, K).

Tanzania: Entebbe (fl. Oct.) Brown 341 (K); Kilosa (fr. Jan.) Burtt 74 (EA); sin.loc. (fl.) Busse 636 (EA, G); Makonde plateaux (fr.) Busse 1088 (B, EA, G); 30 km S Handeni (fl. March) Drummond


Fig. 160. Distribution of Rourea coccinea: subsp. coccinea (West) and subsp. boiviniana (East).
\& Hemsley 1467 (B, BR, K); Morogoro-Dar es Salaam, Furuya 10 (EA); Seedi (fl. Dec.) Gillman 1141 (EA); Mnima (fr. March) Gillman 1292 (EA); Pangani (fl.) Goetze 99 (E, K, type of R. usaramensis); Tondwa-Dawe Simba (fl. Oct.) Greenway 5383 (K); Funga (fr.) Heardi 177/OB (BR); Pande F.R. (fl. Nov.) Harris 3604 (EA); Kilwa Masoko (fl. Sept.) Jaasund 2625 (EA); Chidya (fl. Oct.) Jahl 167 (EA); Rovuma R. (fr.) Kirk s.n. (K, type of R. maxima); Ruva For. station (fr.) Magogo 751 (K); banks of the Rovuma R. (fr.) Meller s.n. (K, type of R. ovatifolia); Bana F.R. (fr. Jan.) Mfinange 12 (BR, EA, K); Bana F.R. (fr. Oct.) Mgaza 690 (BR, EA, K); (fl. Oct.) Mgaza 762 (fl. Oct.) Mgaza 763 (EA); Amboni-Gombero (fr. June) Peter $23956 a$ (B); Chiwata, Price 46 (EA); Banda F.R. (fr. Dec.) Proctor 2810 (K); Balenge (fl. Nov.) Rodgers 522 (EA); Selous Reserve (fr. Feb.) Rodgers 894 (EA); N Ruhudje R. (fl.) Schlieben 1353 (B, K); Lutamba Lake (fl. Oct.) Schlieben 5454 (B, G, HBG, P, Z); Mchinjiri (fr. Feb.) Semsei 659 (K); Kilosa (fr. 12 Jan. \& 13 Jan. 1922) Swynnerton s.n. (BM); Nakitala thicket (fl. Dec.) Vollesen 3076 (C, EA).
Mozambique: Mussoril (fl. 1884/85) Carvalho s.n. (COI); Nangororo Road (fr. March) Gomes e Sousa 4638 (COI, IIAM, PRE, WAG); 10 km W Palma (fr. March) Gomes e Sousa 4680 (COI, IIAM, PRE, WAG); Mocimboa-Mueda, Jansen 8107 (II,AM); Palma-Nangade (fl. Oct.) Mendonça 998 (COI, IIAM, LISC, SRGH); Eráti (fr. Dec.) Torre \& Paiva 9583 (COI, IIAM, LISC); 36 km de Vila da Maganja (y.fr. Jan.) Torre \& Correira 17053 (LISC); Praia-Logoa (fr. Jan.) Torre \& Correira 17356 (LISC); António Enes, Boila (fr. Jan.) Torre \& Correira 17372 (LISC).

Note: In Schellenberg's revision this species is segregated into ten different species of the genus Byrsocarpus. Schellenberg separated them on differences in leaf shape and indumentum, characters that are very variable and not suitable for the delimitation of species. The only constant character that separates Rourea coccinea from the other former Byrsocarpus species (R. cassioides, R. orientalis, and $R$. parviflorus) is the place of the radicle in seed. This differential character was not recognized as such by Schellenberg.

The leaf shape in $R$. coccinea ranges from leaves with 21 small leaflets with an emarginate apex, to leaves with one or three leaflets with an acuminate apex. Every possible number and shape between these extremes is found, but not in every possible combination. In the present revision these variants are considered to belong to one species with two subspecies and two varieties, in an attempt to bring order in at least part of this extensive variation. The number of intermediates is far too large to justify maintenance of taxa involved on species level. The subspecies coccinea and boiviniana are segregated by a disjunction in the species distribution in E Africa, as is made visible at the map of fig. 160.

Rourea erythrocalyx (Gilg ex Schellenb.) Jongkind comb.nov. Fig. 161, 162
Basionym: Roureopsis erythrocalyx Gilg ex Schellenberg, 1910: 27, 28 descr. in clavi.

Type: Gillet 2006 (holo: B $\dagger$; lecto: BR)
R. thonneri De Wildeman, 1911b: 215,tab.14. Type: Zaire, Ubangi, Gugo near Yakoma, Thonner 228 (holo: BR).

Paxia erythrocalyx Gilg, nomen on Gillet 2006 (BR).
Roureopsis thonneri (De Wild.) Schellenberg, 1919: 447; 1938: 111; Troupin, 1952: 78; Exell \& Mendonça, 1954: 145. Basionym: R. thonneri De Wildeman (see above).

Large liana up to 20 m long. Branchlets puberulous. Petiole $1-8 \mathrm{~cm}$ long; rachis $2.5-12 \mathrm{~cm}$ long; petiolules $1-3 \mathrm{~mm}$ long; leaflets $3-11$, ovate to elliptic, glabrous or puberulous beneath, many mucous cells in the upper surface, these show as small pits in herbarium specimens; apex acuminate; acumen emarginate; terminal leaflet $3.5-10 \times 1.5-6 \mathrm{~cm}$; lateral ones $2.5-9 \times 1.5-4.5 \mathrm{~cm}$, somewhat asymmetrical. Inflorescence up to 6 cm long, puberulous, bracteoles near the calyx. Pedicel jointed at the apex. Sepals 3-5 $\times 1.5 \mathrm{~mm}$, nearly glabrous inside. Petals $11-14 \times 1-1.5 \mathrm{~mm}$, free, inrolled at least in bud. Long stamens $1.5-4.5 \mathrm{~mm}$ long, short ones $1-3 \mathrm{~mm}$ long. Pistil $1.2-5 \mathrm{~mm}$ long, style sparsely hairy; ovary pilose. Follicles one to five per flower, $14-22 \times 6-8 \mathrm{~mm}$, glabrous, dehiscent by a ventral suture. Sepals in fruit 13-15 $\times 4-7 \mathrm{~mm}$, reddish, thinly coriaceous, sparsely hairy or glabrous outside. Seed coat for ca one fourth fleshy, other part of testa shining black. Radicle ventral.


Fig. 161. Rourea erythrocalyx: 1. leaves, $2 / 3 \times ; 2$. branchlet with flowers, $2 / 3 \times$; 3. opening bud, $6 \times$; 4. flower, $6 \times$; 5. young fruit, $2 \times$; 6 . empty follicle, $2 \times$; 7. seed, $2 \times$; 8. cotyledon inside with dorsal radicle, $2 \times$. (1. J.Louis 9536; 2-4. Le Testu 7651; 5. J.Gillet 2006; 6-8. Reitsma et al.. 1488)

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Fig. 162. Distribution of Rourea erythrocalyx

Distribution: Cameroun, Gabon, Angola (Cabinda), Zaire.
Ecology: Rain forest from sea level up to 500 m alt.

## Specimens examined:

Cameroun: Samat-Messimni (fl. Feb.) Letouzey 3400 (P); 5 km NW Ndikinimeki (fl. Dec.) Letouzey 10905 (P, WAG).

Gabon: Ndendé-Lébamba (fl. Aug.) Breteler 7696 (WAG); Ogooué (fr. July) Hallé 271 (P); IRET Makokou (fl.b. Sept.) Hladik 1385 (P); Hladik 1549 (P)); Ganda (fl.) Le Testu 6081 (BM, BR, P); Lastoursville (fl., fr.) Le Testu 7651 (BM, BR, P, WAG); 20 km NE Oveng (fl. Sept.) Reitsma 1488 (WAG.

Congo: Moutsene Batéké village, Bouba Road, Bouquet 1032 (P).
Zaire: 10 km E Kisangani (fl. Oct.) Bokdam \& de Wit 3340 (WAG); Amboko (y.fr. April) Claessens 449 (BR); Bas-Uele (fl. March) Dewulf 643 (BR); Singa valley (fr. Jan.) Donis 2311 (BR); INEAC Luki, Dubois 372 (BR, WAG); Bambesa (fr. May) Gérard 2922 (BR, WAG); (fl. Feb.) Gérard 3265 (BR, WAG); (fl. Jan.) Gérard 4348 (BR); (fr. April) Gérard 5113 (BR); (fr. May) Gérard 5470 (BR, WAG); sin.loc. (fr.) Gillet 2006 (BR, type); Banzyville-Yakoma (fl. Feb.) Lebrun 2206 (BR, P); Babobgié (fl. June) Lejoly 3832 (BR); Yangambi (fr. May) Louis 9536 (BR); (fl. July) Louis 10492 (BR, P, WAG); Louis 11789 (BR); Louis 15771 (BR); Luki (fr. Jan.) Madoux 277 (BR, WAG); Luki (fr. Jan.) Nsimundele 130 (BR); Gugo near Yakoma (fl. Feb.) Thonner 228 (BR, type R. thonneri); N'Kula valley (fr. Feb.) Toussaint 242 (BR).
Angola: Maiombe, Mungo (y.fr. Jan.) Gossweiler 6140 (COI); Maiombe, Buco-Zau (y.fr. Oct.) Gossweiler 6799 (COI, LISU).

Note: The specific epithet erythrocalyx that is cited simply as nomen by Schellenberg (1938: 111) and by Troupin (1952:78), was validly published by Schellenberg in 1910 with its description in the key on page 27, and citation of specimens on page 28 .
R. minor (Gaertn.) Alston, 1931: 67; Leenhouts, 1958: 514; Vidal, 1962: 34; Ramamoorthy, 1976: 363.

Basionym: Aegicerus minus Gaertner, 1788: 216,tab.46.
Type: Sri Lanka, König s.n. (holo: L).
R. santaloides (Vahl) Wight \& Arnott, 1834: 144; Baker, 1868: 455. Basionym: Connarus santaloides Vahl, 1794: 87. Type: Sri Lanka, Colombo, Wight cat.nr. 539 (lecto: K).
R. afzelii R.Brown ex Planchon, 1850: 418. Type: Sierra Leone, Afzelius s.n. (holo: BM).
R. platysepala Baker, 1886: 336; Keraudren, 1958: 8, fig. 4. Type: Madagascar, Baron 2528 (holo: K; iso: P).
R. gudjuana Gilg, 1891b: 323. Type: Sudan, Dar Fertit, Schweinfurth 229 (holo: $\mathrm{B} \dagger$; lecto: K ).
R. splendida Gilg, 1891b: 321. Type: Zaire, Mukenge, Pogge 744 (holo: B $\dagger$ ). Neotype: Angola, Luachimo R., Carisso \& Mendonça 130 (holo: COI; iso: BM).
R. chiliantha Gilg, 1896: 212. Type: Zaire, Mukenge, Pogge 727; 732; 739a; 745; 746; 747; 757 (syn: $\mathrm{B} \dagger$ ). Neotype: Zaire, Bamanga, Dewèvre 1146 (holo: BR).
R. bamangensis De Wildeman \& Durand, 1899b: 82. Type: Zaire, Bamanga, Dewèvre 1146 (holo: BR ).
R. striata De Wildeman, 1909: 94,tab.24. Type: Zaire, km 18 Grand Lacs railway. M.Laurent 1032 (holo: BR).
R. bipindensis Gilg, nomen; Schellenberg, 1910: 45.

Santaloides minus (Gaertn.) Schellenberg, 1924: 28; 1938: 126. Basionym: Aegicerus minus Gaertn. (see above).

Santaloides afzelii (R.Br. ex Planch.) Schellenberg, 1910: 53; 1912: 248; 1938: 138, fig. 24; Hepper, 1958: 746; Irvine, 1961: 573; Mendes, 1966: 622; Mendes, 1969: 9; Berhaut, 1975: 40; Liberato, 1980a: 11; Ern, 1984: 165; Burkill, 1985: 525; Caballé, 1986: 200, 226, 229. Basionym: R. afzelii R.Br. ex Planch. (see above).

Santaloides platysepalum (Baker) Schellenberg, 1938: 138. Basionym: R. platysepalum Baker (see above).

Santaloides gudjuanum (Gilg) Schellenberg, 1919: 454; 1938: 138; Andrews, 1952: 355; Aubréville, 1952: 13. Basionym: R. gudjuana Gilg (see above).
Santaloides splendidum (Gilg) Schellenberg, 1919: 455; 1938: 140; Troupin, 1952: 82, fig. 5; Exell \& Mendonça, 1954: 148; Hemsley, 1956: 13, fig. 5. Basionym: R. splendida Gilg (see above).

Santaloides bamangensis (De Wild. \& Dur.) Schellenberg, 1919: 455; 1938: 138. Basionym: R. bamangensis De Wildeman (see above).

Santaloides urophyllum Schellenberg, 1919: 454; 1938: 140; Exell \& Mendonça, 1954: 145. Type: Cameroun, Bipindi, Zenker 3421 (holo: B; iso: E, G, L, M, MO, Z).

Santaloides gossweileri Exell \& Mendonça, 1952: 233, tab.13a; 1954: 148, tab.33. Type: Angola, Moxico, Teixeira de Sousa, Gossweiler 12345 (holo: BM; iso: LISC).


Fig. 163. Rourea minor: 1. flowering branchlet, $2 / 3 \times$; 2. leaf with narrow leaflets, $2 / 3 \times$; 3 . long acuminate leaflet, $2 / 3 \times$; 4. leaflet with short apex, $2 / 3 \times ; 5$. young infructescence with accrescent calyx, $2 / 3 \times: 6$. fruits dehiscing by a ventral suture, $2 / 3 \times ; 7$. fruits dehiscing circumscissile at base and by a ventral suture, $2 / 3 \times ; 8$. fruits dehiscing circumscissile at base, $2 / 3 \times$. (1. Hart 330 ; 2. Rakotosou 16029; 3. Zenker 535; 4. Torre \& Pereira 12464; 5. Bos 4940; 6. Bosser 7528; 7. Espirito
Santo 2647; 8. Jans 760)

Small tree, shrub or large liana up to 26 m long and 15 cm diameter, evergreen. Branches glabrous, cylindrical to deeply furrowed, often with interxylary phloem; branchlets puberulous or glabrous. Petiole 2-9 cm long; rachis 0-17 cm long; petiolules 1-4 mm long; leaflets 1-11(-19), ovate to oblong-elliptic, chartaceous or thinly coriaceous, glabrous, often wax coated beneath; apex acuminate; acumen up to 2.5 cm , never mucronate, midrib usually fading away distally; terminal leaflet $1.5-12.5 \times 0.7-6 \mathrm{~cm}$; lateral ones $1.5-12 \times 0.5-6 \mathrm{~cm}$, nearly symmetrical to asymmetrical. Inflorescence up to 9 cm long, glabrous. Pedicel above the joint 3-7 mm long. Sepals $1.5-4 \times 1-3.5 \mathrm{~mm}$ (wider than long), margin ciliate, glabrous elsewhere. Petals 5-8 $\times 1.5-4 \mathrm{~mm}$, usually connivent near the base, imbricate in bud, apex rounded. Long stamens $3.5-6 \mathrm{~mm}$ long, short ones 2.5-4.5 mm long; anthers obcordate. Pistil $2-5 \mathrm{~mm}$ long; style sparsely hairy or glabrous; ovary sparsely hairy but only adaxially. Follicles one per flower, rarely more, $10-22 \times 5-12 \mathrm{~mm}$, ovate, finely longitudinally striate, dehiscing more or less circumscissile at base and/or rarely by a ventral suture, glabrous; apex acute or acuminate. Sepals in fruit ca $4 \times 3 \mathrm{~mm}$ (wider than long). Seed ovoid with an acute apex; sarcotesta for the larger part free from the other parts of the seed, covering the thin part of the testa almost entirely; radicle more or less apical. Seedling hypogeal; first two leaves opposite (de Vogel, 1980: 221).

Distribution: West, Central, and East Africa, Madagascar, and Asia. Ecology: From rain forest to savanna, from sea level up to 1500 m alt.

Selection of the more than 150 African specimens examined:
Senegal: Dinndefelou, Adam 19990 (P); Mt Assirik (fl. Nov.) Tutin 172 (K).
Mali: Sikasso (fl. Oct.) Demange 2666 (P); Doniéna (y.fr. Jan.) Demange 3381 (P); Fantarasso (y.fr. Dec.) Floret 1402 (BR, P).

Guinea Bissau: Bafata (fr. April) Alves Pereira 1799 (LISC); Bafata, Geba (fr. Feb.) Espirito Santo 2674 (BR, COI, LISC, LISJC, P, WAG); Bafata, Madina do Boé (fl. Jan.) Espirito Santo 2860 (COI, LISC, LISJC, P); Bissora-Massaba (y.fr. Jan.) d'Orey 65 (LISC).
Guinea: Sérédou (y.fr. Dec.) Camara et al. 16 (BR); Timbo (fl. Dec.) Chevalier 14637 (P); Kouroussa (fr. May) Chevalier 25842 (P); Dintinn (fl. Dec.) Jacques-Félix 608 (P); near Dabadou (fl. Jan.) Lisowski 10318 (BR, WAG); Labe-Tougue Road (fr. Feb.) Lisowski 51507 (BR); between Pita and Dalaba (fl. Dec.) Roberty 6527 (G); Petel (fl. Jan.) Roberty 16422 (G).

Sierra Leone: Gberia Fotombu (fl. Sept.) Small 283 (P).
Liberia: Karmadhun (fr. Nov.) Baldwin 10154 (K, WAG); Ganta (fr. Jan.) Harley 1471 (K).
Ivory Coast: Sonderegue (fr. March) Hudru 6472 (P); Tieman (fl. Oct.) de Kruif 455 (WAG); Sassandra (fl. Aug.) J.J.de Wilde 343 (WAG); Bonna N.P. (fl. Jan.) Oldeman 923 (B, WAG); N de Boundiala (fr. Jan.) Roberty 7017 (G, Z); 15 km NE of Korhogo (y.fr. July) Versteegh \& den Outer 468 (U, WAG).

Burkina Faso: Bobo-Dioulasso (y.fr. Oct.) Geerling \& Bokdam 1433 (WAG); (fl. Oct.) Geerling \& Bokdam 1458 (BR, WAG).

Ghana: Banda ravine, Wenhi (fl. Dec.) Morton 25130 (K); Atuna (fl.b. Dec.) Vigne 3530 (P).
Togo: Aledjo Kodoio (fl. Dec.) Brunel \& Heitz 1515 (B); Sokodé (fl. Dec.) Brunel 7121 (B); Aledjo (fl. Dec.) Ern 2616 (B, P); (fl., y.fr. Feb.) Ern 3023 (B); Sokodé-Bafilo (fr. April) Hakki et al. 259 (B).

Nigeria: Gangoro F.R. (y.fr. Feb.) Chapman 4157 (K); Kpashimi F.R. (fr. May) Eimunjeze et al. FHI 66325 (K, WAG); Vogel Peak area, Hepper 2772 (K); 11 mls SE of Kaduna (fl. Dec.) Jackson


Fig. 164. Distribution of Rourea minor in Africa

192 (K); Anara F.R. (fl.b. Oct.) Keay FHI 21124 (K); Jaguidi (fl. Nov.) Keay FHI 22270 (K); Nimbia F.R. (fr. April) Latilo FHI 47136 (K); Kan Gimi (fl. Nov.) Ogbeni \& Obiora FHI 21692 (K); Sang R. F.R. (fl. Dec.) Olorunfemi FHI 55667 (K, P); Jos (fl., fr. March) Tuley 2232 (K).

Cameroun: 15 km SE of Kribi (y.fr. June) Bos 4940 (P, WAG); 4 km S of Ngaoundéré (fl. Oct.) Breteler 585 (WAG); 7 km S of Poli (fr. July) Fotius 2166 (P, YA); Lac Mbella Assom (fl.b. Dec.) Letouzey 2478 (K, P); Guider (fl. Sept.) Meurillou 1451 (BR, P, YA); 70 km E Tibati (fl. Dec.) Satabié 560 (P, YA); Lake Tison (fl. Nov.) Satabié 778 (P, YA); 100 km N of Meiganga (fl.b. Nov.) W.de Wilde \& J.J.de Wilde 4145 (P, WAG); Bipindi (fr.) Zenker 2979 (G, GOET, L, M, MO, WAG, Z). Central African Republic: 15 km from Mbaika (fl. Dec.) Badré 329 (P, WAG); Krebedje (fl.) Chevalier 5690 (K, P); Kaga Pongourou (fl.b.) Chevalier 6559 (G, L); Kaga Dje, Kaga M’Bre (fl.b. Dec.) Chevalier 6623 (Z); Ndéllé (fr. April) Chevalier 8158 (P); Bouali (fr. March) Descoings 10190 (P); route de Bria (fr. April) Descoings 11002 (P); Ouadda-Djalle (fl. Oct.) Mazade 1643 (P); Yalinga (fl. Oct.) Le Testu 3311 (BM, P, WAG).

Sudan: Sakor R., Andrews 1543 (K); Abingo R. (fr. May) Andrews 1587 (K); Lado, Yei R. (fr. Nov.) Sillitoe 227 (K).

Gabon: 10 km SW of Ndjolé (fl.b. April) Hallé 1716 (P, WAG); Libreville (y.fr.) Klaine 2167 (BR); Coundou (fl. March) Le Testu 5876 (BM, BR, LISC, P); Moulounda (fl.) Le Testu 8038 (BM, BR, WAG); 50 km SW of Forestry Camp Doussala (fl. Feb.) Reitsma 1916 (WAG); ca 50 km SW of Doussala (y.fr. April) Reitsma 3339 (WAG).

Congo: forest near Makaba (fr. Dec.) Sita 4751 (BR, P, WAG).
Zaire: Yangambi (fr. July) Bolema 1227 (BR); Nakpudu (fl., fr. Oct.) De Graer 20/157 (BR); Panzi-Kwango (fl. June) Devred 2025 (BR, WAG); Lebo (y.fr. Oct.) Gérard 3482 (BR, WAG); Kurukwata (fl. Dec.) Gérard 3692 (B, WAG); Mpese mission (fl. April) Germain 2095 (P); Epulu (fl. Sept.) Hart 330 (BR); Ntolo (fl. May) Jans 689 (BR); Kabambare (y.fr. July) Luxen I86 (B, BR); Mingazi (fr. Sept.) Pierlot 840 (BR); Kaluke R. (fr. July) Quarré 5820 (BR); Dumba (fr. Aug.) Risopoulos 801 (BR, WAG).

Angola: Luachimo R. (fr. July) Carrisso \& Mendonça 130 (BM, COI, type of R. splendida); Moxico, Teixeira de Sousa (fr. July) Gossweiler 12342 (BM, LISC); (f1., fr. July) Gossweiler 12345 (BM, LISC, type of Santaloides gossweileri).

Burundi: Bururi Road (fl. June) Lewalle 902 (M, WAG); Bururi (fr. Dec.) Lewalle 5015 (G); Mutambara (fr. Oct.) Reekmans 1076 (BR); Gitwe (fr. May) Reekmans 6986 (WAG).

Uganda: Kobboko (fr. March) Eggeling 1835 (K); Amua Valley, f1. Dec.) Eggeling 5548 (EA); Otze (fl. Jan.) Oakley 25 (EA).

Tanzania: Nderema-Monga Road (fr.) Drummond \& Hemsley 3427 (B, BR, K); Amani, Peter 302 (B); (fr. May) Peter 10249 (B); NE of Kinole, Pocs \& Lungwecha 6881 (EA).

Zambia: Kawambwa (y.fr. Aug.) Fanshawe 3591 (BR, K).
Zimbabwe: Makurupini Forest, Mavi 1440 (SRGH); Makurupini Forest, Müller 2379 (SRGH). Mozambique: Gorongasa (fl., y.fr. Oct.) Torre \& Pereira 12464 (COI, LISC).
Madagascar: Nossi-Bé, Boivin s.n. (P); Morarano (fr. Dec.) Bosser 7528 (P); S of Moramange, Decary 18397 (P); Manampanihy valley near d'Ampasimena (fl.) Humbert 20582 (K); Antalaha (fr. Nov.) Perrier de la Bathie 2026 (P); Fort Dauphin (fr. Sept.) Rakotosou 16029 (P).

Note 1: The neotype for $R$. chiliantha was selected by Troupin in 1951 in the herbarium of Brussel. It is published here for the first time.

Note 2: This species is widely distributed and it shows a rather wide range of variation in its leaves.

In Schellenberg's revision of 1938 it is represented by six different specific names in his genus Santaloides, based on the almost free sarcotesta that can easily be removed. Leenhouts (1958) treated Santaloides as a synonym of Rourea. In my opinion the six species of Schellenberg have to be united as they represent a single variable species (see also Mendes, 1966:622), for which $R$. afzelii is the oldest name for Africa.

In Asia occurs a Rourea species from the former genus Santaloides that also has a very variable appearance and a wide distribution, from Sri Lanka to the Pacific Islands. Careful comparison of these two widely distributed species from Africa and from Asia respectively, undeniably shows that both represent a single species for which $R$. minor is the oldest name.

Previously the Asiatic and the African material was classified in different sections of Santaloides by Schellenberg, and Leenhouts placed them in different sections of Rourea. These two sections were distinguished on the dehiscence of the fruit: by a ventral suture for the Asiatic material and by a circumcission at the base in the African specimens. After carefull scrutiny of many specimens this difference in dehiscence proved not to be restricted to material of either continent. Some specimens from Africa, particularly from Madagascar, are clearly dehiscing by a ventral suture (e.g. Baron 6413 and Bosser 7528) and among the Asiatic material specimens occur that show, besides their ventral suture, at least partly a basal suture as well. As such no character remained to treat the African and Asiatic material as different entities, neither as sections, nor as species.
R. myriantha Baillon, 1867: 198; Baker, 1868: 455.

Type: Gabon, Griffon du Bellay s.n. (holo: P).
R. soyauxii Gilg, 1891b: 324. Type: Gabon, Sibange Farm, near Libreville, Soyaux 70 (holo: B $\dagger$; lecto: P ; iso: K, Z).

Santalodes myriantha (Baill.) O.Kuntze, 1891: 155. Basionym: R. myriantha Baill. (see above).

Paxia myriantha (Baill.) Pierre 1896: 1233; Schellenberg, 1919: 448; 1938: 115; Exell \& Mendonça, 1954: 145. Basionym: R. myriantha Baill. (see above).

Paxia scandens (Gilg, 1891b: 321. Type: Gabon, Sibange Farm, near Libreville, Soyaux 262 (lecto: K; B $\dagger$; iso: P, Z); Soyaux 380 (para: B $\dagger$; iso: P).

Paxia soyauxii (Gilg) Pierre ex Schellenberg, 1910: 31; 1938: 116; Troupin, 1952: 80. Basionym: R. soyauxii Gilg (see above).

Paxia liberosepala (Baker f.) Schellenberg, 1938: 115; Hepper, 1958: 740. Basionym: Spiropetalum liberosepalum Baker f., 1913: 24. Type: Nigeria, Oban, Talbot 1404 (holo: K; iso: BM, G).

Paxia cinnabarina Schellenberg, 1919: 449; 1938: 118; Hepper, 1958: 741. Type: Cameroun, Bipindi, Zenker 2791 (holo: B $\dagger$; lecto: K; iso: E, G, L, M, Z).

Paxia lancea Schellenberg, 1919: 450; 1938: 118. Type: Cameroun, Mimfia, Zenker 4553 (holo: B $\dagger$ ). Neotype: Gabon, Lastoursville region, Le Testu 7962 (holo: WAG; iso: E, BM, BR, P).

Paxia zenkeri Schellenberg, 1919: 448; 1938: 116. Type: Cameroun, Bipindi, Nkaumbe, Zenker 3337 (holo: B; iso: E, G, K, L, MO, P, Z).

Large liana up to 40 m long. Branches glabrous and often silvery grey; branchlets puberulous. Petiole $5-10 \mathrm{~cm}$ long; rachis $0-15 \mathrm{~cm}$ long; petiolules $1-5 \mathrm{~mm}$ long; leaflets $1-11$, very variable in shape, ovate, elliptic or oblong to oblongobovate, coriaceous or rarely chartaceous, nearly glabrous; apex acute to acuminate, mucronate; terminal leaflet 4-18 $\times 2-8.5 \mathrm{~cm}$; lateral ones 3-14 $\times 1.5-6.5$ cm , almost symmetrical. Inflorescence up to 15 cm long, puberulous or glabrous; bracts and bracteoles similar to small sepals. Pedicel above the joint $0-2 \mathrm{~mm}$ long. Flower bud globose. Sepals 3-4 $\times 1.5-2.5 \mathrm{~mm}$, puberulous outside, almost glabrous inside, the sun exposed sides red, the shaded parts white (often the two colours present in one flower); petals $10-15 \times 1-3 \mathrm{~mm}$, frequently coherent near the base, folded in bud. Long stamens $2-6 \mathrm{~mm}$ long, short ones $1.5-3 \mathrm{~mm}$ long, filaments curved inwards. Pistil $1.5-5 \mathrm{~mm}$ long; style with some hairs; ovary pilose. Follicles one per flower sometimes more, $25-45 \times 15-20 \mathrm{~mm}$, beaked, glabrous, frequently (pseudo?) lenticellate. Sepals in fruit $6-12 \times 4-6 \mathrm{~mm}$, coriaceous, nearly glabrous. Seed coat for one third fleshy, other part of testa thin, shining and very dark red to black. Radicle ventral.

Distribution: From Nigeria eastward to Zaire and southward to Angola.
Ecology: Rain forest from sea level up to 500 m alt.


Fig. 165. Rourea myriantha: 1. flowering branchlet, $2 / 3 \times ; 2-4$. leaflet apices, $2 \times, 2$. \& 4. from above, 3 . from below; 5 . flower $4 \times ; 6$. flower partly, showing stamens and pistils of a long-styled flower, $6 \times ; 7$. fruit, $2 / 3 \times ; 8$. seed, showing sarcotesta (dark part), $2 \times ; 9$. cotyledon inside with ventral radicle, $2 \times$. (1. J.de Wilde 8071; 2-3. Letouzey 12045; 4. Zenker 2933; 5-6. J.de Wilde et al. 511; 7. Farron 4607; 8-9. Zenker 2933).


Fig. 166. Distribution of Rourea myriantha

Selection of the 76 specimens examined:
Nigeria: Oban (fl.) Talbot 1404 (BM, G, K, type of Paxia liberosepala).
Cameroun: Kribi (fl. March) Bos 4121 (P, WAG); (fl. May) Bos 4496 (P, WAG); between Poute and Ebaka (fr.) Letouzey 2913 (P;WAG); 12 km E of Somalomo (fr. Feb.) Letouzey 4334 (P, WAG); near Mvangan (fl. March) Letouzey 10122 (BR, P, WAG); Mbalam (fl. Feb.) Letouzey 12045 (K, P, WAG); Bipindi (fr. April) Zenker 584 (B, C, G, MO, P, U, WAG).

Gabon: sin. loc. (fl.) Griffon du Bellay s.n. (P, type) Bélinga (fr. July) Hallé \& Le Thomas 75 (P); Libreville (fl. March) Klaine 3 (HBG, P); (fl. March) Klaine 2822 (G); Tchibanga (fr. Sept.) Le Testu 1631 (BM, P); Pounga (fl. Feb.) Le Testu 5242 (BM, BR, LISC, P, WAG); Haute Ngounié (fl. Feb.) Le Testu 6394 (BM, BR, P); Lastoursville (fl. March) Le Testu 7951 (BM, BR, LISC, P, WAG, type of Paxia lancea); Sibange Farm, near Libreville (fl. March) Soyaux 70 (K, P, Z, type of R. soyauxii); (y.fr. March) Soyaux 262 (K, P, Z, type of Paxia scandens).

Congo: between Kakamoeka and the Loundji (fl. March) Attims 84 (P); near Edou (fl.b. July) Descoings 7995 (P); 4 km W Grand-Bois (fr. Aug.) Farron 607 (P, WAG); Boungola (fl. Jan.) Farron 4876 (P, WAG).

Zaire: Yambata (fl. Oct.) De Giorgi 1377 (BR); (fl. Oct.) De Giorgi 1425 (BR); Gemena (fl. July) Evrard 1349 (BR); E of Basoko (fr. Feb.) Germain 4743 (BR); Mondjo (fr. Sept.) J.Léonard 524 (BR); Yangole (fr. Oct.) Louis 12097 (BR).
Angola: Cabinda, Panga Mungo (fl.) Gossweiler 6294 (COI, LISU) (fr. Aug.) Gossweiler 6590 (COI, LISU); Cabinda, Buco Zau (fr. Sept.) Gossweiler 6712 (COI).

Note 1: This species is in Schellenberg's revision segregated into six species of the former genus Paxia. They were delimited by him exclusively by the shape of the leaflets. It is often not hard to recognize two or more of those six species on separate sheets of a single herbarium accession, as $R$. myriantha is very variable in the shape of the leaflets. No relation between leaflet shape and geographical area was found.
Note 2: Because it was hard to find a collection that properly matches the first description of Paxia lancea properly, the neotype does not originate from the same area as the lost holotype.
R. obliquifoliolata Gilg 1891: 328.

Type: Zaire, Mukenge, Pogge 733 (holo: B $\dagger$ ).
Neotype: Cameroun, Bipindi, Zenker 2992 (holo: WAG; iso: B, BR, E, G, GOET, L, M, MO, Z).
R. fasciculata Gilg, 1891b: 329. Type: Zaire, Mukenge, Pogge 731 (holo: B $\dagger$ ). Neotype: Cameroun, Kribi, Bos 5363 (holo: WAG; iso: BR, K, P).
R. fasciculata Gilg var. flagelliflora Welwitsch ex Hiern, 1896: 187. Type: Angola, Cuanza Norte, Cazengo, Welwitsch 4628 (holo: BM; iso: COI, G, P).
R. adiantoides Gilg, 1896: 213. Type: Cameroun, Yaoundé, Zenker \& Staudt 402 (holo: $\mathrm{B} \dagger$; lecto: K).
R. ptaeroxyloides Gilg, nomen; Schellenberg, 1910: 28.

Roureopsis obliquifoliolata (Gilg) Schellenberg, 1910: 28; 1938: 108; Troupin, 1952: 77; Exell \& Mendonça, 1954: 145; Hepper, 1958: 740; Burkill, 1985: 524. Basionym: R. obliquifoliolata Gilg (see above).

Roureopsis fasciculata (Gilg) Schellenberg, 1910: 28. Basionym: R. fasciculata Gilg (see above).

Large liana up to 25 m long or shrub. Branchlets puberulous. Petiole 0-0.5 cm long; rachis $3.5-28 \mathrm{~cm}$ long, puberulous; petiolules $0.5-3 \mathrm{~mm}$ long; leaflets 13-41, ovate to elliptic or rhombic to kidney-shaped, puberulous beneath on the midrib or glabrous, chartaceous; apex rounded to subacuminate, mucronate; terminal leaflet $1.7-9 \times 1-5 \mathrm{~cm}$; lateral ones $0.7-8.5 \times 0.4-3.5 \mathrm{~cm}$, strikingly asymmetrical. Inflorescence up to 1.2 cm long, subglobose, often many together at the end of a leafy branch resembling a terminal inflorescence. Pedicel above the joint $0-1 \mathrm{~mm}$ long. Sepals 3-6 $\times 1.5-2.5 \mathrm{~mm}$, nearly glabrous inside. Petals $11-14 \times 1.5-2 \mathrm{~mm}$, lorate, free, inrolled in bud. Long stamens $2.5-7 \mathrm{~mm}$ long, short ones $1.5-5 \mathrm{~mm}$ long. Pistil $1.5-6 \mathrm{~mm}$ long; style with a few hairs; ovary with hairs only on surfaces facing adjacent carpels. Follicles one to five per flower, $15-24 \times 7-10 \mathrm{~mm}$, glabrous, dehiscing by a ventral suture. Sepals in fruit 6-8.5 $\times 2.5-3 \mathrm{~mm}$, reddish, chartaceous to coriaceous, almost glabrous. Seedcoat for ca one fourth fleshy, other part of testa thin, shining and black; radicle ventral.

Distribution: From Nigeria eastward to Zaire and southward to Angola. Ecology: Rain forest and gallery forest from sea level up to 1000 m alt.

Selection of the more than 150 specimens examined:
Nigeria: Calabar, Akor-Orem (fl. Jan.) Onochie FHI 36103 (K); Oban (fl.) Talbot 504 (Z).
Cameroun: Bukundu F.R., Binuyo \& Daramola FHI 35075 (P); Kribi (fl. Nov.) Bos 3344 (WAG); (fl., fr. Nov.) Bos 3356 (WAG); (fr. May) Bos 4556 (WAG); (fl. June) Bos 4823 (BR, MO, P, WAG); (fl., fr. Sept.) Bos 5363 (BR, P, WAG, type of R. fasciculata); Bertoua (fl., y.fr. Sept.) Breteler 239 (WAG); (fr. Dec.) Breteler 707 (BR, WAG); Yokodouma (fl. June) Breteler 1546 (BR, WAG); Mboro R. (fl. Jan.) J.J.de Wilde 7904 (WAG); S of Nkoulaze (fr. March) Letouzey 4546 (BR, P);


Fig. 167. Rourea obliquifoliolata: 1. flowering branchlet, $2 / 3 \times ; 2$, young flower from above, $4 \times$; 3. young flower partly, showing inrolled petals, $4 \times$; 4. flower, $4 \times$; stamens and pistils of a long-styled flower, $4 \times ; 6$. branchlet with fruits, $2 / 3 \times ; 7$. fruit, $2 / 3 \times ; 8$. seed from beneath, showing sarcotesta (dark part) and hilum, $2 \times ; 9$. seed partly (one cotyledon partly removed) showing cotyledon inside with ventral radicle, $2 \times$; 10. cotyledon with ventral radicle, $2 \times$ (1. Breteler 6240; 2-5. A.Louis et al. 938; 6. Reitsma et al. 1280; 7-9. A.Louis et al.515; 10. Reitsma et al. 1280).


Fig. 168. Distribution of Rourea obliquifoliolata

Banga (fl. April) Letouzey 4902 (BR, P); Bipindi (fl.) Zenker 2992 (B, BR, E, G, GOET, L, M, MO, WAG, Z, type).
Central African Republic: Bimbo (fl. Dec.) Breyne 1379 (BR); 35 km SW Bangui (fr. Dec.) Hepper 4114 (K); Sosa, W of Yandiba (fl. July) Leeuwenberg 6247 (BR, P, WAG); near Mbanza (fr. Nov.) Leeuwenberg 7137 (WAG); Yalinga (fl. July) Le Testu 4006 (BM, BR, P, WAG); (fr. Nov.) Le Testu 4289 (BR); Mbaiki (fl. June) Equipe Tisserant 3775 (BR).
Equatorial Guinea: Bebai, Tessmann 536 (K); sin. loc. (fl.) Tessmann 1008 (HBG, K).
Gabon: Mayibout 2 (fl., fr. Sept.) Breteler \& de Wilde 666 (LBV, WAG); Gamba (fr. Sept.) Breteler \& van Raalte 5644 (WAG); between Mouila and Yéno (fr. Sept.) Breteler \& Lemmens 8111 (LBV, WAG); Nkogo (fr. Aug.) Chevalier 26355 (P); Mbigou (fl. June) Le Testu 5968 (BM, BR, P); Oveng (fr. Nov.) Louis et al. 515 (LBV, WAG).
Congo: km 16 route Mouyondzi-Mayama, Bouquet 633 (P); Otende village (fl. June) Bouquet 1486 (P); Stanleypool (fl. Aug.) Fr.Hens 38 (Z); Ngandju Sedec (fl. June) Vermoesen 2450 (BR).
Zaire: Beonde (fr. April) Bamps 586 (BR); Panga (fl., fr. Dec.) Bequaert 1532 (BR); Panzi (fl. Feb.) Callens 3121 (BR); Kizulu (fr. Dec.) Compère 983 (BR); Mobwasa (fl. May) De Giorgi 836 (BR); Bokakata (fr. Feb.) Dewèvre 772 (BR); Mbolohu Road (fl. Sept.) J.de Wilde 383 (BR, WAG); Bankaie (fr. July) Gilbert 14355 (BR); Kapinga (fr. Nov.) M.Laurent s.n. (BR); Bunyakiri (fl., fr. Feb.) A.Léonard 2910 (BR, WAG); Bulungu (fr. April) Pauwels 5582 (BR).
Angola: Cabinda, Panga-Mungo (f1.) Gossweiler 6288 (COI); Cabinda, Buco Zau (fr.) Gossweiler 7322 (COI, LISU); Cabinda, Buco Zau (fl. Oct.) Monteiro et al. 382 (LISC); Cuanza Norte, Cazengo (fl., fr. June) Welwitsch 4628 (BM, COI, G, P, type R. fasciculata var flagelliflora).

Cult: Photograph in collection WAG of seedlings in greenhouse. Seedlings of Breteler s.n. 1961 from Cameroun.

Note 1: Although this species has been proposed as new on several occasions it is very uniform in comparison to other species of Rourea. Even Schellenberg found no reasons to segregate it into several taxa and in 1938 he treated it in the same manner as in the present revision.
Note 2: Because this species is uniform throughout its area, the neotypes have been selected by their availability in the herbaria, rather than by their origin in the vicinity of the original collecting localities.
R. orientalis Baillon, 1867: 230; Keraudren, 1958: 7, fig. 1.

Type: Kenya, Mombasa, Boivin s.n. (holo: P).
R. orientalis var. hirtella Keraudren, 1957: 527; 1958: 7. Type: Madagascar, Morondava-Bemaraha, Humbert 11367 (lecto: P); 11360 (para: P).
R. orientalis var. pubescens Keraudren, 1957: 527; 1958: 7. Type: Madagascar, Ankarafantsika, Reserves Naturelles 2005 (lecto: P); 2543 (para: P).
R. pervilleana Baillon, 1867: 232; 1887: tab.16; Drake de Castillo, 1902: 32. Type: Madagascar, Nossibé, Pervillé 755 (holo: P).
R. ovalifoliolata Gilg, 1891b: 327. Type: Kenya, Mombasa, Hildebrandt 1943 (holo: $\mathrm{B} \dagger$; lecto: K ).
R. macrantha Gilg, 1900: 393. Type: Tanzania, Uhehe, Ruahe, Goetze 417 (holo: $\mathrm{B} \dagger$; lecto: K ).
R. bussei Gilg, nomen on Busse 804.

Byrsocarpus orientalis (Baill.) Baker, 1868: 452; Schellenberg, 1919: 453; 1938: 151; Hemsley, 1956: 17, fig. 6; Mendes, 1966: 624; Mendes, 1969: 6. Basionym: R. orientalis Baill. (see above).

Byrsocarpus orientalis var. hirtella Keraudren, 1957: 527 (see R. orientalis var. hirtella Keraudren).

Byrsocarpus orientalis var. pubescens Keraudren, 1957: 527 (see $R$. orientalis var. pubescens Keraudren).

Byrsocarpus pervilleanus (Baill.) Schellenberg, 1938: 153. Basionym: R. pervilleana Baill. (see above).

Byrsocarpus baronii Baker, 1887: 462; Schellenberg, 1938: 151. Type: Madagascar, Baron 4922 (holo: K).

Byrsocarpus ovalifoliolatus (Gilg) Schellenberg, 1910: 42. Basionym: R. ovalifoliolata Gilg (see above).

Byrsocarpus tomentosus Schellenberg, 1919: 452; 1938: 151 (pro parte: Angolan material is excluded, it represents $R$. coccinea ssp. coccinea var. coccinea); Troupin, 1952: 92. Type: Tanzania, Ssongea, Busse 804 (holo: B; iso: EA, G, WAG).

Byrsocarpus usambaricus Schellenberg, 1938: 154. Type: Tanzania, E Usambara, Longusa-Sigital, Peter 40014 (holo: B).

Byrsocarpus baillonianus Gilg, nomen; Schellenberg, 1910: 40.
Shrub, rhizomatous shrublet, small tree or lianescent shrub, usually deciduous, often evergreen in SE Zaire. Branches strongly lenticellate, terete and often with a distinct cork layer; branchlets puberulous to tomentose. Petiole $1.5-7 \mathrm{~cm}$ long; rachis $6-30 \mathrm{~cm}$ long; petiolules $0.5-2 \mathrm{~mm}$ long; leaflets $13-33$, oblong to oblong-ovate, chartaceous to thinly coriaceous, glabrous to tomentose; apex rounded to acute; terminal leaflet 1-5.5 $\times 0.5-3 \mathrm{~cm}$, sometimes obovate; lateral ones $0.8-5 \times 0.3-2.5 \mathrm{~cm}$, nearly symmetrical. Inflorescence up to 7 cm long, glabrous to tomentose. Pedicel above the joint $1-5 \mathrm{~mm}$ long. Sepals 1.5-3 $\times$ 1.5-3 mm. Petals 7-12 $\times$ 3-4 mm, coherent near base, sometimes folded


Fig. 169. Rourea orientalis: 1. flowering branchlet, $2 / 3 \times ; 2$. opening flowerbud, $9 \times$; 3. stamens and pistils, long-styled flower, $4 \times$; $4-5$. fruits, some showing seed, $2 / 3 \times ; 6$. cotyledon with apical radicle, $2 \times$. (1-3. Mendonca 870; 4. Torre \& Paiva 9758; 5. Torre \& Paiva 9493; 6. Torre \& Paiva 9758).

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Fig. 170. Rourea orientalis: 1-4. leaves, $2 / 3 \times$. (1. Torre \& Paiva 9758; 2. Torre \& Paiva 9493; 3. Milne-Redhead 3660; 4. Lewis 174).


Fig. 171. Distribution of Rourea orientalis
at the top especially in bud. Long stamens $1.5-7 \mathrm{~mm}$ long, short ones $1-4.5 \mathrm{~mm}$ long. Pistil $1.5-4 \mathrm{~mm}$ long; style sparsely hairy; ovary pilose. Follicles one per flower rarely more, $15-23 \times 5-12 \mathrm{~mm}$, symmetrical, top rounded, dehiscing by a ventral suture, glabrous. Sepals in fruit 3.5-5 $\times 3-4 \mathrm{~mm}$, imbricate. Seed coat entirely fleshy and scarlet, the radicle is emerging from the sarcotesta at the apical end.

Distribution: E Africa, Southern-Central Africa, Southern Africa excluding the Republic of South Africa, and Madagascar.

Ecology: Thicket edges in savanna and semi-deciduous forest up to 2500 m alt., frequently on termite mounds.

Selection of the more than 300 specimens examined:
Zaire: Kina (fl. Oct.) Desenfans 4582 (BR); Niemba (fl. Oct.) De Saeger P3 (BR); 63 km NW of Kolwezi, Empain et al. 2316 (BR); Pweto (fr. Dec.) Lisowski 54242 (BR); Musoshi (fr. Dec.) Agric. Univ. Wageningen Papers 89-6 (1989)

Lisowski 54244 (BR); Kaniama (fr. Dec.) Mullenders 1748 (BR); Kisamamba (fr. Dec.) Symoens 6763 (BR).

Kenya: Pengo Hill (fl. Jan.) Bamps 6333 (BR, EA); Mombasa (fr.) Boivin s.n. (P, type); Mikongaga (fr. Dec.) Haerdi $177 / 0$ (EA); Mombasa (fl. March) Hildebrandt 1934 (BM, K); Sokoke (fl.) Jeffrey K166 (EA, G, K); 25 km NW of Kiunga shops, Muchiri 536 (EA); Shimba Forest (fl. April) Lucas et al. $245(\mathrm{~K})$

Tanzania: 8 km N Mpanda (fr. Feb.) Boaler 483 (EA); Lupa F.R. (fr. Dec.) Boaler 785 (K); Zanzibar, Kizimkazi (fr. March) Faulkner 2521 (B, BR, K); 19 km from Lukumburu to Songea (fl. Nov.) Gillet 17885 (EA); Univ.College Dar es Salaam (fr. Nov.) Harris 2604 (EA, WAG); Dabaga (fl.b. Feb.) Lynes D67 (K); Kidatu (fr. Jan.) Mhoro 211 (EA, K); Nahoro (fr. Dec.) Milne-Redhead \& Taylor 7612 (B, BR, EA, K); Amboni-Kiongwe (fr. June) Peter 23701 (B); Kombe (fr. Jan.) Peter 35443 (B).

Zambia: Mwinilunga (fl. Sept.) Angus 570 (BM, K); Mfuwe (fr. Nov.) Astle 4110 (K, SRGH); 15 km S of Broken Hill (fl. Sept.) Brenan \& Greenway 7859 (K, P); 25 mls S of Solwezi (fl. Sept.) Brenan \& Greenway 7987 (K, WAG); Chingola (fl. Oct.) Fanshawe 2536 (K); S of Matonchi Farm, fl. Oct.) Milne-Redhead 2726 (BM, BR, K); SW of Dobeka bridge (fr. Dec.) Milne-Redhead 3660 (BR, K); Kalambo Falls (fl. Nov.) Richards 18418 (BR, K); Mapanza W (fl. Sept.) Robinson 899 (K); near Chavuma (fr. Oct.) White 3499 (K).

Zimbabwe: Victoria Falls (fl. Nov.) Armitage 163/59 (SRGH); 4 km N of the confluence of the Muzirizwi R. and the Bwazi R. (fr. Jan.) Biegel et al. 4817 (K, PRE, SRGH); 12 km S of Kadoma, Burrows 1959 (SRGH); near top of Katombora Rapids (fr. Dec.) Gonde 400 (SRGH); Chipingabadfa Farm (fl. July) Jacobsen 1405 (PRE); Haroni R. (fr. Jan.) Mavi 804 (SRGH); S of Matonchi Farm (fl. Oct.) Milne-Redhead 2726 (BM, BR, K); km 8 Margula-Lions Den (fl. Oct.) Pope 798 (BM, K, PRE, SRGH).

Malawi: Mua Livulezi Forest (y.fr. Jan.) Adlard 535 (P, SRGH); 5 mls S of Monkey Bay (fl. Dec.) Eccles 208 (SRGH); 77 km N of Lilongwe (fl. Oct.) Gillet 17514 (L, SRGH, WAG); Kasungu N.P. (fl. Dec.) Hall-Martin 1037 (SRGH); Songwe N.P. (y.fr. Nov.) Hall-Martin 1134 (SRGH); Nkhata Bay (fr. Jan.) Pawek 5057 (SRGH); Salima (fr. Feb.) Robson 1614 (SRGH).

Mozambique: Namacurra (fr. May) Andrada 1530 (COI, LISC); Quissanga (fr. Oct.) Barbosa 2422 (IIAM, LISC, SRGH); Buzi Reserve (fl., fr. Oct.) Carvalho 672 (IIAM, PRE); Moatize (fr. Jan.) Correia 348 (COI, IIAM, LISC, SRGH); Gogoi Road (fr. Nov.) Laech \& Chase 10499 (COI, LISC, PRE, SRGH); Marrupa, Mahua (fl. Oct.) Mendonça 870 (COI, K, LISC, PRE); Erati, between Namapa and Nacaroa (fl. Oct.) Mendonça 1147 (COI, LISC, PRE); de Namina a Ribaue (fr. Dec.) Torre 1111 (COI); Lichinga (fl.b. March) Torre \& Paiva 11017 (LISC); km 34 from Catandice, Tete Road (fr. Dec.) Torre \& Correia 13551 (IIAM, LISC, M, WAG).

Namibia: E Caprivi strip, Chobe R. (fr. Jan.) Killick 3389 (M, PRE, SRGH); W Caprivi strip, Kwando Flood Plain margin (fl. Oct.) Tinley 1530 (L, M, PRE).

Botswana: Chobe distr. (fl. Oct.) Miller B/1099 (PRE); Kasane Rapids, Robertson \& Elffers 53 (K,PRE).

Madagascar: Nossi-Bé (y.fr. Dec.) Bernardi 11839 (L, P, Z); Sainte-Marie, Boivin 1887 (P); Maro-vato-Anketraka (fr. Jan.) Gilbert 5457 (P); Forest relicts SE of Morondava (fl. Oct.) Humbert 11367 (P, type of R. orientalis var hirtella); Tsiempihy Forest (fr. Dec.) Léandri et al. 2284 (P); Ambato Boeni (fl.) Saboureau 1113 (P).

Note 1: Flowers and foliage are usually produced simultaneously on the bare shrub.

Note 2: This species is in Schellenberg's revision represented by four different species in the former genus Byrsocarpus, all of them exclusively based on differences in leaf shape or leaf indumentum. These characters are too feeble to justify recognition of these taxa. Most of these forms are found throughout the entire area of the species.


Fig. 172. Rourea parviflora: 1. flowering branchlet, $2 / 3 \times$; 2. apex of leaflet, $1 \times$; 3 . flower, $8 \times$; 4. stamens, $8 \times ; 5$. pistils of a long styled flower, $8 \times ; 6$. branchlet with fruits, $2 / 3 \times$; 7. follicle showing seed, $2 / 3 \times ; 8$. empty follicles, $2 / 3 \times ; 9$. seed showing sarcotesta, $1 \times ; 10$. seed longitudinal
 section, showing the cotyledons and the apical , $\times$. 1 289; 9-10. Breteler 1649).
Zenker 2876; 6. J.Louis 15336; 7. J.Louis 2722; 8. A.Leonard 2879, 9-10. Breter
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R. parviflora Gilg, 1891b: 322.

Type: Cameroun, Mt John, E.Mann 1795 (holo: B $\dagger$; lecto: K; iso: P).
R. strigulosa Gilg, 1896: 211. Type: Cameroun, Yaoundé, Zenker \& Staudt 747 (holo: $\mathrm{B} \dagger$; lecto: K ; iso: $\mathrm{BM}, \mathrm{GOET}, \mathrm{M}, \mathrm{Z}$ ).

Byrsocarpus parviflorus (Gilg) Schellenberg, 1910: 45; 1912: 245; 1938: 157; Troupin, 1952: 97; Exell \& Mendonça, 1954: 150. Basionym: R. parviflora (see above).

Santaloidella gilletii Schellenberg, 1938: 119; Troupin, 1952: 81; Caballé, 1986: 198, 214. Type: Zaire, sin. loc., Gillet anno 1909 (holo: BR).

Large liana up to 35 m long and 15 cm diameter. Branches deeply furrowed, usually with interxylary phloem; branchlets puberulous to glabrous. Petiole $2.5-7 \mathrm{~cm}$ long; rachis $6-22 \mathrm{~cm}$ long; petiolules $1-2 \mathrm{~mm}$ long; leaflets $5-19$, ovate to oblong or oblong-obovate, nearly glabrous; apex usually acuminate; acumen often emarginate; terminal leaflet $5-15 \times 2-6 \mathrm{~cm}$; lateral ones $2-14 \times 1-5 \mathrm{~cm}$, asymmetrical to nearly symmetrical. Inflorescence up to 2 cm long, puberulous. Pedicel above the joint $1.5-4 \mathrm{~mm}$ long. Sepals $2 \times 1.5 \mathrm{~mm}$. Petals 5-6 $\times 1.5-2.5$ mm , connivent near base, imbricate and only slightly folded in bud. Long stamens $2.5-5 \mathrm{~mm}$ long, short ones $2-4 \mathrm{~mm}$ long. Pistil $2-5 \mathrm{~mm}$ long; style with some hairs; ovary pilose. Follicles one per flower rarely more, $25-32 \times 10-15$ mm , ovoid, acute at top, glabrous except for a few hairs at the top, dehiscing by a ventral suture. Sepals in fruit $4-6 \times 4-6 \mathrm{~mm}$. Seed up to $22 \times 12 \mathrm{~mm}$, testa for ca one thirth fleshy and yellow, other part of testa thin, very dark (red?) and shining, radicle apical, hypocotyl in seed already ca 1 mm long. Seedling epigeal; hypocotyl strongly elongated. Primary root absent. Cotyledons spreading, succulent. First leaves pinnate, (sub-) verticillate.

Distribution: Central Africa, and eastern W Africa.
Ecology: Rain forest from sea level up to 1000 m alt.
Specimens examined:
Nigeria: 11 mls from Ikot (fl. Jan.) Okafor \& Latilo FHI 56020 (K, P, WAG).
Cameroun: Bitye (fl.) Bates 1639 (BM, MO, Z); Bertoua, Breteler 1304 (P, WAG); (fr. July) Bre-
teler 1649 (M, P, WAG); 45 km E de Foumban (y.fr.) Letouzey 7702 (P); Tissongo (fr. Aug.) Mc
Key 6 (P, YA) \& seedlings (YA); Mt John (fl.) Mann 1795 (K, P, type); Mendoum (fr. Feb.) J.
\& A.Raynal 10073 (P, YA); Yaoundé (fl.b.) Zenker \& Staudt 747 (BM, GOET, K, M, Z, type R.
strigulosa); Bipindi (fl.) Zenker 2867 (E,G, GOET, L, M, MO, P, WAG); (fl.) Zenker 540 (C, G,
MO, P, U, WAG).
Central African Republic: Boukoko (fr. Aug.) Equipe Tisserant 1555 (BM, BR, P).
Gabon: Mouila-Yéno, Breteler \& Lemmens 8141 (LBV, WAG); $15 \mathrm{~km} \mathrm{~N} \mathrm{of} \mathrm{Doussala} \mathrm{(fr}. \mathrm{March)}$
de Wilde \& Jongkind9470 (LBV, WAG); Poupa (fl. Oct.) Le Testu8411 (BM, BR, P, WAG); Mouya-
nama-Mbigou (fr. April) Louis et al. 1497 (LBV, WAG).
Congo: Komono (fr. Jan.) Bouquet 2363 (P); Louvoulou (fr. Feb.) Farron 4969 (P).
Zaire: Bunyakiri (fr. Feb.) A.Léonard 2879 (BR, WAG); Yangambi (fr. Oct.) Louis 2722 (BR,


Fig. 173. Distribution of Rourea parviflora
G); Louis 4286 (BR); (fr. July) Louis 5684 (BR, C); Yangole, Louis 11925 (BR); 20 km NE Yamboa (fr. June) Louis 15336 (BR); Bambesa, Pittery 274 (BR); Yangambi (y.fr. Feb.) Toussaint 871 (BR, P); (y.fr. Feb.) Toussaint 872 and 873 (P); (y.fr. Feb.) Toussaint 874 (BR, P).

Angola: 5 km de Bula Atumba (fr. April) Cardoso 117 (COI); Maiombe, Buco Zau (fr. Jan.) Gossweiler 6929 (COI, LISC); sin.loc. (y.fr.) Gossweiler 7602 (COI, LISC).

Note 1: As already observed under History of the genus, this species was formely (Schellenberg 1938) known under two names i.e. Byrsocarpus parviflorus for flowering specimens and Santaloidella gilletii for fruiting specimens. For the former the fruits were supposed to be still wanting while for the latter the flowers needed yet to be collected. This case is very illustrative to show what results may be expected from excessive splitting.

Note 2: Many specimens are partly covered with long, flat, and tough hairs, which are often red- or black-coloured and can be found on the branches, leaf petiole, and rachis. These hairs are very peculiar and quite different from usual plant hairs, but they cannot be considered as artefacts as they are already present in the seedling stage (see pag. 21 and fig. 26.2).

Note 3: According to the amount of material collected this species seems to be rather rare. However, in view of the small and inconspicuous inflorescences and fruiting branches, and the frequency of the occurrence of seedlings observed in Gabon, it may be just undercollected.

## Rourea solanderi Baker

Fig. 174-176
R. solanderi Baker, 1868: 456.

Type: Sierra Leone, sin. loc., Afzelius s.n. (holo: BM).


Fig. 174. Rourea solanderi: flowers (phot. H.C.D. de Wit, Liberia)
R. heterophylla Baker, 1868: 456. Type: Sierra leone, sin. loc., Afzelius s.n. (holo: BM; iso: G).

Santalodes solanderi (Baker) O.Kuntze 1891: 155. Basionym: R. solanderi Baker (see above).

Santalodes bakeri O.Kuntze 1891: 155. Type: The same as for $R$. heterophylla Baker (see above).

Spiropetalum solanderi (Baker) Gilg, 1896: 214; Schellenberg, 1938: 104; Irvine, 1961: 574; Hall \& Swaine, 1981: 291; Burkill, 1985: 526. Basionym: R. solanderi Baker (see above).

Spiropetalum heterophyllum (Baker) Gilg, 1896: 214; Schellenberg, 1938: 106; Irvine, 1961: 573; Hall \& Swaine, 1981: 291; Burkill, 1985: 525. Basionym: $R$. heterophylla Baker (see above).

Spiropetalum odoratum Gilg, 1891b: 336; 1896: 214; Schellenberg, 1938: 105; Troupin, 1952: 127; Exell \& Mendonça, 1954: 144. Type: Gabon, Sibange Farm, near Libreville, Soyaux 249 (holo: B $\dagger$; lecto: P).

Spiropetalum polyanthum Gilg, 1895b: 69; 1896: 214; Schellenberg, 1919: 450. Type: Cameroun, Abo, Buchholz s.n. March 1874 (holo: B $\dagger$; lecto: P).

Spiropetalum triplinerve Stapf, 1906: 93; Schellenberg, 1938: 104. Type: Liberia, near Monrovia, Whyte s.n. (holo: K).

Spiropetalum reynoldsii (Stapf) Schellenberg, 1919: 450; de Koning, 1983: 291; Burkill, 1985: 525. Basionym: Connarus reynoldsii Stapf 1906: 94. Type: Liberia, near St. Paul's R., Reynolds s.n. (holo: K).


Fig. 175. Rourea solanderi: 1. flowering branchlet, left in bud, right in flower, $2 / 3 \times$; 2 . leaflet partly, $2 / 3 \times$; 3. flower buds, $2 \times$; 4. flower, $4 \times$; 5. stamens, $6 \times$; 6 . pistils of a long-styled flower, $6 \times$; 7. follicles, $2 / 3 \times$; 8. open follicle, $2 / 3 \times$; 9. lenght section follicle, showing the cotyledons, $2 / 3 \times$; 10. seed, $2 / 3 \times$; 11. cotyledon inside with ventral radicle, $2 / 3 \times$. (1-2. Leeuwenberg 4024; 3-6. Oldeman 174; 7. de koning 4579; 8. Bos 3089; 9. de koning 4579; 10-11. Bos 3089).

Spiropetalum calophyllum Gilg, nomen in herbarium Zenker. Spiropetalum erythrocarpum Gilg, nomen in herbarium Zenker. Spiropetalum erythrosepalum Gilg, nomen in herbarium Zenker. Spiropetalum klainianum Pierre, nomen in herbarium Klaine. Spiropetalum phaeseosepalum Gilg, nomen in herbarium Zenker.

Shrub to large liana. Branches glabrous, terete or furrowed; branchlets tomentose to glabrous. Petiole $1-13 \mathrm{~cm}$ long; rachis $0-15 \mathrm{~cm}$ long, glabrous to tomentose, sometimes with a few glandular hairs; petiolules 2-5 mm long; leaflets 1-9, ovate to elliptic, chartaceous to coriaceous, glabrous to tomentose, frequently with many mucous cells at the upper side, these show as small pits in herbarium specimens; apex acute to acuminate, mucronate; in developing leaves the mucronate tip is already full-grown when other parts of the leaflet are still small; terminal leaflet 2-18 $\times 1-9 \mathrm{~cm}$; lateral ones $1.5-18 \times 1-8 \mathrm{~cm}$, nearly symmetric. Inflorescence up to 7 cm long, puberulous to tomentose. Pedicel above the joint 0.5-6 mm long. Sepals partly united, some of them for $3 / 4$ connate, ca $5 \times 2.5 \mathrm{~mm}$, wider than long, velutinous on both sides. Petals $10-24 \times 1.5-3 \mathrm{~mm}$, lorate, sometimes connivent near base, folded inward in bud. Long stamens $2-7.5 \mathrm{~mm}$ long, short ones $1.5-4.5 \mathrm{~mm}$ long. Pistil $1.3-4.5 \mathrm{~mm}$ long; style with a few or many hairs; ovary pilose. Follicles one to three per flower rarely more, 20-35 $\times 10-25 \mathrm{~mm}$, often beaked, velutinous and sometimes also with a few glandular hairs. Free parts of the sepals in fruit unequal, $5-10 \times 10-15 \mathrm{~mm}$, coriaceous, sometimes with small glandular hairs. Seedcoat for one fourth fleshy, other parts of testa thin, shining, and black. Radicle ventral. Seedling hypogeal; first leaves often scalelike or abortive.

Distribution: West and Central Africa.
Ecology: From rain forest to savanna and to the sea shore. Alt. 0-650 m.
Selection of the ca 150 specimens examined:
Sierra Leone: sin. loc. (fr.) Afzelius s.n. (BM, type); Njala (fl. May) Deighton 3000 (P); Makump (fr. July) N.W.Thomas 961 (P); Rowala (fr. July) N.W.Thomas 1158 (P).

Liberia: Sangwin (y.fr. March) Baldwin 11310 (K, WAG); between Zorzor and Voinjama (fl. Dec.) Bos 2615 (WAG); Louisiana (fl. Jan.) Bos 2620 (BR, K, P, WAG); 3 mls W of Tapita (fl. July) Jansen 859 (WAG); Bomi Hills (fl. Aug.) Voorhoeve 1216 (WAG).
Ivory Coast: Yapo Bot. Reserve (fr. Feb.) de Koning 232 (WAG); Banco F.R. (fr. June) de Koning 1789 (WAG); (fl. Feb.) de Koning 5380 (WAG); km 119 Tabou-Tai Road (fl. March) J.J.de Wilde et al. 3597 (WAG); Abouadou Forest (fr. July) Leeuwenberg 2703 (WAG); 34 km N Sassandra (fl. April) Leeuwenberg 4024 (WAG); 17 km W Abidjan (fl. July) Oldeman 174 (B, G, WAG, Z); NNE Béréby (fr. Nov.) Oldeman 616 (WAG).
Ghana: Takoradi-Tarkwa Road (fl. July) Enti R774 (BR, WAG); Andabra mouth (fr. Feb.) Hall 2911 (K); Bronikrom (y.fr. May) Hall \& Nabooh GC46619 (K); Aiyinasi (fr. Nov.) Hepper et al. 7472 (K); Bonsa R. (y.fr. Aug.) Vigne 139 (K).
Nigeria: Awi-Akamkpa Road (fl. Feb.) Daramola FHI 55531 (K); Grace Camp (fr. March) Jones \& Onochie FHI 17035 (K); Oyo (fl. Aug.) Keay FHI 25360 (K); Benin near aerodrome (fl. Jan.) Keay FHI 37348 (K); Ibaji Ojoko N.A.F.R. (fl., fr. June) Latilo FHI 47690 (K, P); Sapoba (fr.


Fig. 176. Distribution of Rourea solanderi

Nov.) Meikle 609 (K); Eket distr. (fl.) P.A. Talbot 3349 (Z); 32 mls ENE Ijebu Ode (fr. April) van Meer 730 (WAG).

Cameroun: 2 km S of Kribi (fl. June) Bos 4836 (MO, P, WAG); 2 km N of Longii (fr. June) Bos 4913 (P, WAG); Bertoua (fl. March) Breteler 1217 (WAG); 65 km SSW of Eséka (fl. June) W.de Wilde et al. 2753 (B, MO, WAG, Z); near Konye (fr. April) Nemba \& Thomas 13 (MO, WAG); Ndian R. (fl., fr. July) D.W.Thomas 2362 (MO, P, YA).

Central African Republic: Boukoko (fl. Feb.) Equipe Tisserant 1661 (BM); (fr. June) Equipe Tisserant 1770 (BM).
Equatorial Guinea: Sanje, Benito R. (fl. Sept.) Bates 574 (G, L, P).
Gabon: road Libreville-Kango (fr. Oct.) Breteler \& Lemmens 8391 (WAG); Mboro (fr. Oct.) Fleury 27101 (P); road from Booué along Ivindo R. (fl. Oct.) Floret et al. 1879 (P); SW Ndjolé (fl. April) Hallé 1620 (P, WAG); SW Lambaréné (fr. May) Hallé 2099 (P); Mouila (fl. Jan.) Le Testu 5199 (BR, LISC, P); Ghediba (fl. June) Le Testu 5957 (BM, BR, P); Lastoursville (fl.) Le Testu 7405 (BM, P); Lopé Reserve (fl. Nov.) Louis et al. 65 (LBV, WAG); Lopé Reserve (fr. May) Reitsma 2300 (WAG).

Congo: 41 km from Boko Songko (fr. July) de Neré 1497 (P); S.B.B. Makaba (fl.b. June) Sita 3124 (P).

Zaire: Makaw (fr. Dec.) Jans 986 (BR).
Angola: Cabinda, Bélize (fl.) Gossweiler 7080 (COI, LISU).
Cult.: Seedlings from Ivory Coast, de Koning 3191, 3364, 4621 (WAG).
Note: In Schellenberg's revision this species forms the genus Spiropetalum, with four species, only based on differences in leaf shape and indumentum. The shape of the leaflets is very variable. Some leaf forms are restricted to a part of the area of the species, like the form represented by the former Spiropetalum triplinerve that is confined to Liberia and Ivory Coast.

Rourea thomsonii (Baker) Jongkind comb.nov.
Fig. 177-179

Basionym: Connarus thomsonii Baker, 1868: 458.

Type: Nigeria, Old Calabar, Thomson 26 (holo: K; iso: E).
R. pseudobaccata Gilg, 1891b: 325. Type: Zaire, Lande der Niamniam, Schweinfurth 2969 (para: B $\dagger$; iso: Z); 3855 (B $\dagger$; lecto: K; iso: P).
R. monticola Gilg, 1895b: 68. Type: Tanzania, Uluguru Mts, Stuhlmann 8857 \& 9071 (syn: B $\dagger$ ). Neotype: Tanzania, Uluguru Mts, Morogoro, Schlieben 2794 (holo: BR; iso: B, G, Z).
R. buchholzii Gilg, 1895b: 67. Type: Cameroun, Abo, Buchholz s.n. anno 1874 (holo: $\mathrm{B} \dagger$ ). Neotype: Cameroun, Bipindi, Zenker 2503 (holo: WAG; iso: E, G, L, M, MO, Z).
R. baumannii Gilg, 1896: 211. Type: Togo, Miso Heights, Baumann 31 (holo: B, alc! n.v.).
R.nivea Gilg, 1896: 210. Type: Cameroun, Lolodorf, Staudt 6 (holo: B $\dagger$; lecto: P ; iso: $G$ ).
R. venulosa Hiern, 1896: 187. Type: Angola, Pungo Alto, Welwitsch 4630 (holo: BM; iso: COI, G, K).
R. albido-flavescens Gilg, 1901: 316. Type: Tanzania, Ukinga, Mt Manganyema, Goetze 1212 (holo: B $\dagger$; lecto: BR; iso: E, G, L, P).
R. lescrauwaetii De Wildeman, 1909: 92; 1912: 405. Type: Zaire, Lac Foa, Lescrauwaet 198 (lecto: BR); Eala, Seret 868 \& Eala, M.Laurent 839 \& Eala, Pynaert 1403 (para: BR).
R. lescrauwaetii var. sereti De Wildeman, 1909: 92. Type: Zaire, Nala, Seret 826 (holo: BR).
R. lescrauwaetii var. tenuifolia De Wildeman, 1909: 93. Type: Zaire, Mongo, Huyghe \& Ledoux 32 (lecto: BR); Mogandjo, M.Laurent 1630 (para: BR).
R. oddoni De Wildeman, 1909: 93. Type: Zaire, Sanda, Gillet 3755 (holo: BR).
R. verrucolosa De Wildeman, 1909: 95. Type: Zaire, Lubefu, Lescrauwaet 368 (holo: BR).
R. claessensii De Wildeman, 1911a: 258; 1912: 403. Type: Zaire, Dobo, Claessens 725 (holo: BR).
R. hypovellerea Gilg, nomen in herbarium Zenker.

Cnestis pinnata Palisot de Beauvois 1804: 98 \& fig. 60; Don, 1832: 91. Type: Nigeria, sin. loc., P.de Beauv. s.n. (holo: G) (see Note 1).

Manotes palisotii Planchon, 1850: 439, nom. illeg. Type: the same as for Cnestis pinnata (see above).

Connarus pubescens Baker, 1868: 458. Type: Nigeria, Old Calabar, Mann 2254 (holo: K).

Connarus libericus Stapf, 1906: 94. Type: Liberia, 6 mls of Monrovia, Whyte s.n. (holo: K).

Jaundea pinnata (P.de Beauv.) Schellenberg, 1938: 164; Andrews, 1952: 354; Troupin, 1952: 87, fig. 6; Exell \& Mendonça, 1954: 151; Hemsley, 1956: 21, fig. 7; Hepper, 1958: 741; Irvine, 1961: 573; Mendes, 1966: 627; Adam, 1971: 871,874; Berhaut, 1975: 34; Troupin, 1978: 160; Liberato, 1980a: 14; Hall \& Swaine, 1981: 217; Troupin, 1982: 224; de Koning, 1983: 286; Ern, 1984: 165; Burkill, 1985: 523; Caballé, 1986: 194. Basionym: Cnestis pinnata P.de Beauv. (see above).

Jaundea pubescens (Baker) Schellenberg, 1919: 462; 1938: 162; Troupin, 1952: 84; Exell \& Mendonça, 1954: 151; Hepper, 1958: 741; Burkill, 1985: 523; Caballé 1986: 194. Basionym: Connarus pubescens (see above).
Jaundea pubescens var. oddonii (De Wild.) Troupin, 1952: 86. Basionym: $R$. oddonii De Wild. (see above).

Jaundea pseudobaccata (Gilg) Schellenberg, 1919: 462. Basionym: R. pseudobaccata Gilg (see above).
Jaundea zenkeri Gilg, 1894: 388; 1895b: 66. Type: Cameroun, Yaounde, Zenker 613 (holo: $\dagger \dagger$; lecto: K).

Jaundea monticola (Gilg) Schellenberg, 1919: 461; 1938: 166; Andrews, 1952: 354; Troupin, 1952: 88. Basionym: R. monticola Gilg (see above).

Jaundea baumannii (Gilg) Schellenberg, 1919: 460; 1938: 164; Hepper, 1958: 741; Ern, 1984: 165. Basionym: R. baumannii Gilg (see above).

Jaundea lescrauwaetii (De Wild.) Schellenberg, 1919: 461; 1938: 163. Basionym: R. lescrauwaetii De Wild. (see above).
Jaundea oddonii (De Wild.) Schellenberg, 1919: 461; 1938: 162; Exell \& Mendonça, 1954: 152. Basionym: R. oddonii De Wild. (see above).

Jaundea congolana Schellenberg, 1919: 460. Type: Zaire, Kimuenza, Gillet 2176 (syn: B $\dagger$; lecto: BR).

Santalodes monticola (Gilg) O.Kuntze 1903: 155. Basionym: R.monticola Gilg (see above).

Paxia dewevrei De Wildeman \& Durand, 1899b: 83. Type: Zaire, Dewevre 237 (holo: BR).

Byrsocarpus pseudobaccatus (Gilg) Schellenberg, 1910: 45; 1912: 245. Basionym: R. pseudobaccata Gilg (see above).

Byrsocarpus monticolus (Gilg) Schellenberg, 1910: 44; 1912: 244. Basionym: R. monticola Gilg (see above).

Byrsocarpus buchholzii (Gilg) Schellenberg, 1912a: 245. Basionym: R. buchholzii Gilg (see above).

Byrsocarpus baumannii (Gilg) Schellenberg, 1910: 44; 1912: 244. Basionym: R. baumannii Gilg (see above).

Byrsocarpus niveus (Gilg) Schellenberg, 1910: 44. Basionym: R. nivea Gilg (see above).

Byrsocarpus alb(id)o-flavescens (Gilg) Greenway ex Burtt Davy 1940: 41. Basionym: R. albido-flavescens Gilg (see above).

Byrsocarpus oddoni (De Wild.) Schellenberg 1912: 401. Basionym: R. oddoni De Wild. (see above).

Spiropetalum heterophyllum auct. non (Baker) Gilg, Liberato, 1980a: 10.
Evergreen large liana, shrub, or small tree. Branches often brown lenticellate, terete; branchlets puberulous or glabrous. Wood without interxylary phloem. Petiole $2.5-11 \mathrm{~cm}$ long; rachis 2-26 cm long; petiolules 3-6 mm long; leaflets $5-13$, ovate or oblong to oblong-obovate, chartaceous to thinly coriaceous, pubescent to glabrous, 4-11 pairs of main lateral nerves, all nerves usually prominent beneath, the tertiary nervation frequently forming a pattern of almost par-


Fig. 177. Rourea thomsonii: 1-2. leaflets, $2 / 3 \times$; 3-4. flowering branchlets, $2 / 3 \times$; 5 . flower, $4 \times$; 6. connivent petals, $4 \times$; 7. stamens and pistils of a long-styled flower, $10 \times ; 8$. pistils, $10 \times$; $9-10$. fruits, $2 / 3 \times ; 11-13$. open follicle, $2 / 3 \times, 11$. ventral view, 12. dorsal view, 13. lateral view; 14. seed, $2 / 3 \times ; 15$. seed from below, showing the hilum surrounded by the sarcotesta, $2 / 3 \times$; 16. cross section of seed, $2 / 3 \times ; 17$. cotyledon inside with ventral radicle, $2 / 3 \times$. (1-2. Leeuwenberg 11312; 3. Hart 214; 4-8. de Koning 6497; 9. J.de Wilde 8382; 10. Leeuwenberg 9471; 11-17. Breteler \& de Wilde 803).


Fig. 178. Distribution of Rourea thomsonii
allel lines; apex acuminate, mucronate; terminal leaflet 7.7-21 $\times 2-11 \mathrm{~cm}$; lateral leaflets 5-20 $\times 1.5-9 \mathrm{~cm}$, nearly symmetric. Inflorescence up to 18 cm long, often one or more together at the end of a leafy branch and resembling a terminal inflorescence, glabrous or pubescent. Pedicel above the joint $1-8 \mathrm{~mm}$ long. Sepals $1.5-3.5 \times 1-2 \mathrm{~mm}$, almost glabrous inside. Petals $6-11 \times 1-2.5 \mathrm{~mm}$, coherent near base, inrolled in bud, with acute apex. Long stamens $1.5-6 \mathrm{~mm}$ long, short ones $1-5 \mathrm{~mm}$ long. Pistil $1-5 \mathrm{~mm}$ long; style with some hairs; ovary pilose. Follicles one per flower sometimes more, $20-45 \times 10-25 \mathrm{~mm}$, symmetrical with rounded apex or oblique with acute apex, glabrous, dehiscing by a ventral suture. Sepals in fruit 2-3 $\times 2-4 \mathrm{~mm}$, often wider than long. Testa almost entirely fleshy, the thin, black part situated in a ventral groove. Radicle ventral. Seedling hypogeal; first two leaves opposite but often scale like or abortive; first fully developed leaves unifoliolate.

Distribution: From Guinea Bissau to Kenya and Mozambique in the East and to Angola in the South.

Ecology: Wet tropical forest including periodically inundated riverine forest and semi-deciduous forest, from sea level up to 3500 m alt.; in East Africa only and abundant in evergreen mountain forest ( $1200-3500 \mathrm{~m}$ alt.).

Selection of the more than 450 examined specimens:
Senegal: Basse-Casamance (fl. Dec.) v.d. Berghen 1565 (BR).
Guinea Bissau: Ilha dos Galinhas (fr. June) Espirito Santo 717 (COI, LISJC); Fulacunda (fr. May) Espirito Santo 2039 (COI, LISC).

Guinea: near Kouria (fl. Nov.) Caille 14810 in herb. Chevalier (BR, P, WAG); Dalaba (fl. Nov.) Chevalier 34579 (P); Konkore (fr. Sept.) Pobéguin K31 (P).

Sierra Leone: ml 96 from Makeni on Falaba to Kabala Road (fl. Nov.) Morton SL2864 (K, WAG); Kangumu (fl.) Smythe 118 (K, P).

Liberia: Nimba-Gangra (fl.b. Oct.) Adam 26217 (P); Genna, Tanyehun, Baldwin jr. 10752 (K); Duport (fr. Oct.) Barker 1437 (K); Ganta (fr. April) Harley 372 (K).

Ivory Coast: Toumodi (fr. March) Aké Assi 8521 (G); Tate village, Chevalier $19800 b$ (P); Daloa (fl. Sept.-Oct.) Chevalier 34156 (P); Banco F.R. (fr. Nov.) de Koning 2857 (WAG); (fr. Dec.) de Koning 4972 (WAG).

Ghana: Akropong, Akwapim, Adams 4730 (K); ml 33 Takoradi-Tarkwa Road (fl. July) Enti R774 (K); Kumasi (fl. Jan.) Irvine 39 (K); Secondi (fr. March) Irvine 2402 (E); Adamsu (fl. Dec.) Vigne 3497 (BR, K).

Togo: E Badou (fr. April) Hakki et al. 583 (B); Atakpamé (fl. Nov.) Mildbraed 7423 (K).
Benin: between Abomey and Boguila (fr. Feb.) Chevalier 23178 (BR, K).
Nigeria: Calabar (fl. Feb.) Daramolo FHI 55523 (K, P); Warrake (fr. June) Dundas FHI 21483 (K); Omo F.R. (fr. June) Gentry \& Pilz 32797 (MO, WAG); Lagos, near Vand (fl. Dec.) Hagerup 75 (P); Benin (fl. Jan.) Keay FHI 37349 (K, P); near Osomba village (fl., fr. March) Latilo \& Oguntayo FHI 70531 (K, WAG); 11 mls S of Ipetu, Onochie FHI 5225 (K); Old Calabar (fl., fr.) Thomson 26 (K, E, type).

Cameroun: 15 km W of Matsari (fr. May) Biholong 515 (P); 17 km from Kribi (fr. Aug.) Bos 5037 (MO, P, WAG); 10 km S of Meiganga (fl. Nov.) W.de Wilde et al. 3998 (P, WAG); Eschou (fl. April) Letouzey 3883 (P); Slopes NE of l'hosere Banyo (fr. June) Letouzey 8572 (P); 65 km NNE of Moloundou (fr. March) Letouzey \& Villiers 10513 (BR, P); Dengdeng (fl. April) Mildbraed 8853 (K); Ngwenfon (fl. Dec.) Satabié 210 (K, P, YA); Ndian R. (fr. July) D.W.Thomas 2359 (MO, YA).

Central African Republic: Krebedje (fl.) Chevalier 10643 (P); Waka area (fl. Oct.) Le Testu 1249 (BM, BR, P); Yalinga (fr.) Le Testu 3833 (P); la Haut-Kotto (fl. Nov.) Le Testu 4392 (BM, BR, P, WAG); Boukoko (fl.) Equipe Tisserant 437 (BR, P, WAG).

Sudan: 10 mls S of Yei (fl. Dec.) Myers 7994 (K); near Issore (fr. Aug.) Myers 11783 (K).
Equatorial Guinea: sin. loc. (fl. March) Tessmann 953 (K).
Gabon: Bélinga (fl. Sept.) Breteler \& de Wilde 712 (LBV, WAG); between Mouila and Yéno (y.fr. Sept.) Breteler \& Lemmens 8096 (LBV, WAG); on Dyem Lake (fr. Aug.) Fleury 26438 (P); old road of the Nke (fr. Oct.) Floret et al. 1830 (P); Tchibanga (fl. May) Le Testu 1730 (BR, K, P); Lastoursville (fl. June) Le Testu 7375 (P).

Congo: Boungolo (fl.b. June) Sita 1292 (P); Chaillu, 30 km from Irogo (y.fr. Feb.) Sita 4014 (P).

Zaire: Mulubule (fl. July) Bequaert 36 (BR); Mobeka (fl.) De Giorgi 1454 (BR); Madabu (fl.b. Dec.) Gérard 2571 (BR); Epulu (fl. Feb.) Hart 428 (BR); Kamina (fl. June) Herman 2162 (BR, K); road to Nsemendwa 15 km from Makaw (fl.b. Jan.) Jans 997 (BR, WAG); Manenga (y.fr. March) Nkunga P6310 (BR, WAG); Mbandaka (=Coquilhatville) (fr.) Pynaert 804 (BR); Lupaya (fr. Aug.) A.Léonard 5718 (BR, WAG); Kisangani (fr. Feb.) Szafranski 1105 (BR, WAG); km 110 Kavumu-Walikale Road (fl. Feb.) Troupin 6353 (BR, WAG).

Angola: Cuanza Norte, Monto Bello (fl.) Gossweiler 689 (BM, K, P); Cabinda, Pango Mungo (fl.) Gossweiler 6114 (BM, COI); Cabinda, Bélize (fl.) Gossweiler 7090 (BM, LISU); Uige, Colonato (fr. Oct.) Raimundo et al. 515 (LISC, WAG); Pungo Alto (fl., fr. Nov.) Welwitsch 4630 (BM, COI, G, K, type $R$. venulosa).

Rwanda: Bushekeli (y.fr. Sept.) Runyinya 594 (BR); Lac Kivu, Wahu I., Van der Ben 245 (BR).
Burundi: Bugarama (fl. June) Lewalle 969 (BR, G); Muyange (fr. Sept.) Reekmans 1030 (BR); near Karuzi (fr. Jan.) Van der Ben 1841 (BR).

Uganda: Kajansi Forest (fl.b. Oct.) Chandler 2476 (B, BR, EA); Bwamba Pass (fl. Aug.) Eggeling 3362 (K); Bujenji county (y.fr. Feb.) Katende 1518 (EA); Khaya Dawei (fr. Sept.) Myers 9460 (K); Kanungu, Kigezi (fl. June) Purseglove 802 (BR, K).

Kenya: Ngangao, Drummond \& Hemsley 4337 (K); Mbololo Hill (fl. Oct.) Joana 8998 (EA); Kirima Mt (y.fr. Oct.) Polhill \& Verdcourt 293 (EA, K); Upland Limuru (fr. Oct.) Verdcourt 359 (EA, K).

Tanzania: Milo (fl. Oct.) Archibold 2476 (K); Kasoje (fl. June) Kakeya 37 (EA); Shagaya F.R. (fr. Oct.) Mgaza 627 (EA); Kirua Vunjo-Kilema Road (fr. March) Semkiwa 80 (EA); Kyimbila (fl.) Stolz 2204 (C, G, M, WAG, Z); Murgwanza (fl. Jan.) Tanner 5805 (B, K, WAG)

Zambia: 16 km SW of Kalene Hill Mission (fl. June) Drummond 8284 (K, SRGH); Abercorn (fl. May) Richards 15140 (K, SRGH); Nyika Plateau (fl., fr. Oct.) Robson 485 (K, SRGH); (fl. Nov.) Robson $615 b$ (K, SRGH).


Fig. 179. Rourea thomsonii: map showing area of the distribution of dominant leaflet shape.

Malawi: Luselo Reserve (fr. Dec.) Banda 743 (K, SRGH); Misuku Hills (fr. Dec.) Pawek 4227 (K).

Cult.: Seedlings, de Koning 3540 (WAG), 3778 (WAG).
Note 1: The oldest known name for this taxon is Cnestis pinnata P.de Beauv. but the combination Rourea pinnata exists already for another species: R. pinnata (Merr.) Veldkamp, 1968: 543.
Note 2: In Schellenberg's revision this species forms the genus Jaundea, with six species, only based on differences in leaf shape and leaf indumentum. As such the delimitation of $R$. thomsonii in the present revision is the same as that of the former genus Jaundea.
The shape of the leaflets and especially their nervation is very variable, and provides numerous intermediary combinations that deny recognition of the former Jaundea species in any rank. Some leaf forms are restricted to a part of the area of the species. The distribution of the most extreme leaf forms is given in fig. 179. The margin of this concentrical distribution pattern is dominated by a leaf shape represented by the former species Jaundea pinnata (leaflet A) in the north and south, and in the east by Jaundea monticola (leaflet C). The median band is dominated by a form represented by the former Jaundea pubescens sensu Troupin (leaflet B). The centre of the pattern is without a clearly dominating leaf form.

Note 3: Fruits are frequently attacked by insects and then become globose and pitted.

Notes on extra African species.

## Asia

Rourea acropetala Pierre, 1898: pl. 379d; Vidal, 1962:32 p.p. (type only).
Type: Laos, Attopeu region, Harmand in Herbarium Pierre 3292 (holo: P; iso: L )
R. oligophlebia Merrill, 1937: 178; Leenhouts, 1958: 513; Vidal, 1962: 31. Type: Sumatra, Bila, Rahmat 2342 (holo: A or NY n.v.; iso: L)

Distribution: Vietnam, Laos, Indonesia (Sumatra).

Specimens examined:
Laos: Attopeu region (fl.) Harmand in Herbarium Pierre 3292 (L, P, type).
Vietnam: Prov. Tuyên Quang (fl. April) Chevalier 37426 (P); near Tourane (fr. June) Clemens 3365 (P); Hung Son (fl.) Eberhardt 3930 (P); Huê (fl., y.fr. March) Squires 225 (P); (fl. March) Squires 244 (P).

Sumatra: between Sunggapa and Pargambiran (fr. May) Bartlett 8161 (G, L); Gunong Susah (fl. May) Rahmat 2342 (L, type of R. oligophlebia); Padang Lawas (fr. July) Rahmat 4912 (L).

Note: Leenhouts (1958: 515) knew R. acropetala only from the flowering type specimen. He reduced it into the synonymy of $R$. minor. In 1962 Vidal treated it as a distinct species once more and made the first description of what, in his opinion, were the fruits of this species. The characters Vidal used to delimitate R. acropetala are leaf characters of the type specimen in combination with fruit characters from the other specimen, Vidal 720. In my opinion these two collections represent different species, the flowering type specimen is conspecific with the collections that were subsequently designated as $R$. oligophlebia, while the fruiting collection, Vidal 720, belongs without any doubt to $R$. minor.

In this revision Roureopsis is united with Rourea which makes the following new combinations necessary:

Rourea asplenifolia (Schellenb.) Jongkind comb.nov.
Basionym: Roureopsis asplenifolia Schellenberg, 1938: 111; Leenhouts, 1958: 506.

Rourea confundens (Leenh.) Jongkind comb.nov.
Basionym: Roureopsis confundens Leenhouts, 1978: 507.
Rourea dictyophylla Jongkind nom.nov.
Agelaea pinnata King, 1897: 18.
Roureopsis pinnata (King) Leenhouts, 1958: 510.
Note: The combination Rourea pinnata exists already for another species: $R$. pinnata (Merr.) Veldkamp, 1968: 543.

Rourea emarginata (Jack) Jongkind comb.nov.
Basionym: Cnestis emarginata Jack, 1822: 42.
Roureopsis emarginata (Jack) Merrill, 1952: 220; Leenhouts, 1958: 508; Vidal, 1962: 24.

Because not all Asiatic species are treated in Flora Malesiana or have been recombined here, some additional literature on the remaining Asiatic species of Rourea is given.

## Rourea acutipetala Miquel

Roureopsis acutipetala (Miq.) Leenhouts, 1958: 509; Vidal, 1962: 26.
Rourea balansea Baillon, 1875: 309.
Rourea fulgens Planchon; Leenhouts, 1958: 519.
Rourea harmandiana Pierre, 1898: pl. 379e; Vidal, 1962: 44.
Rourea mimosoides (Vahl) Planchon; Leenhouts, 1958: 517; Vidal, 1962: 41.
Rourea pinnata (Merr.) Veldkamp, 1967: 543; Leenhouts, 1972: 934.
Rourea prainiana Talbot; Leenhouts, 1958: 520.
Rourea radlkoferiana Schumann; Leenhouts, 1958: 519.
Rourea rugosa Planchon; Leenhouts, 1958: 514.
Rourea stenopetala (Griff.) Hook. f.
Roureopsis stenopetala (Griff.) Schellenb.; Vidal, 1962: 23; Leenhouts, 1972: 933.

## America

The monotypic American genus Bernardinia has also been referred into the synonymy of Rourea. It used to be kept apart because of the absence of an accrescent calyx. In Rourea the accrescence of the calyx varies from very pronounced (R. accrescens, R. erythrocalyx, and R. myriantha) to negligible (R. gardneriana and $R$. coccinea). Moreover, careful observation of material with young fruit shows that the fruiting calyx in Bernardinia fluminensis is accrescent, but this is overlooked as in mature fruits the calyx is often reflexed.

Rourea fluminensis (Gardn.) Jongkind comb.nov.
Basionym: Connarus fluminensis Gardner, 1842: 529.
Bernardinia fluminensis (Gardn.) Planchon, 1850: 413; Baillon, 1870: 18; Forero, 1983: 26.

On different occasions in this revision of the Connaraceae observations have been made on the different species concept used for the revisions of the Malesian and the African species at one hand, and the American species on the other. In order to facilitate comparison of the African, American, and Asiatic species of Rourea, I have arranged the American species into entities of what is felt to have comparable taxonomic level as the Asiatic and African species, resulting in the clusters given below. The taxa in those clusters are given in order of ancientry. These clusters are treated as species, with the first name in the cluster as their collective name. In arranging these clusters the stomata patterns, together with the characters of flowers and fruits, were of decisive importance. I did not see R. laurifolia and R. pseudospadicea, which are only known from their type specimens, and $R$. omissa, which is only known from two specimens. These three species are left out of this classification.

Rourea accrescens Forero
Rourea blanchetiana (Progel) Kuhlm.
Rourea camptoneura Radlk., R. schippii Standley
Rourea frutescens Aublet, R. glabra H.B.K. (excluding material from S Brasil), R. surinamensis Miq., R. adenophora Blake, 1923, R. pittieri Blake, R. sprucei Schellenb. (excl. var. rondoniensis Forero), R. antioquensis Cuatrec., R. araguaensis Forero.

Rourea gardneriana Planchon, R. cuspidata Benth. ex Baker, R. doniana Baker, R. ligulata Baker, R. puberula Baker, R. amazonica (Baker) Radlk., R. duckei Huber, R. gracilis Schellenb., R. neglecta Schellenb., R. kappleri Lanj., R. paraensis Forero, R. sprucei Schellenberg var. rondoniensis Forero, R. glabra auct. non H.B.K. sensu Forero: material from S Brasil.

## Rourea induta Planchon, R. psammophila Forero

Rourea krukovii Steyerm.
Rourea martiana Baker, R. discolor Baker, R. chrysomalla Glaz. ex Schellenb., R. cnestidifolia Schellenb., R. glazioui Schellenb., R. tenuis Schellenb., R. bahiensis Forero

## Rourea prancei Forero

Rourea pubescens (DC.) Radlk.
Rourea revoluta Planchon, R. grosourdyana Baill.
Rourea suerrensis Smith, R. latifoliolata Standley \& Williams

# Vismianthus Mildbr. 

by F.J. Breteler \& J. Brouwer

History of the genus
Vismianthus was first described by Mildbraed in 1935 and based on V. punctatus Mildbraed. The generic name and the epithet refer to the conspicuous glandular dots and streaks in the flowers and the leaves of this species respectively. Vismianthus is, like Burttia, a shrub-treelet with unifoliolate leaves and monocarpellate flowers. Mildbraed (l.c.) remarked upon the similarity between these two genera, but found the presence of the glands and streaks in the flowers sufficient reason to create a new genus. Vismianthus, like Burttia, has always been treated as a monotypic genus, but in this paper the Asiatic genus Schellenbergia is put into its synonymy and the only species of this Asiatic genus is henceforth combined in Vismianthus.

Description of the genus
Vismianthus Mildbraed, 1935: 706; Schellenberg, 1938: 98; Brenan \& Greenway, 1949: 169; Hemsley, 1956: 7.

Type species: V. punctatus Mildbr.
Schellenbergia Parkinson, 1936: 295; Schellenberg, 1938: 179. Type species: S. sterculiaefolia (Prain) Parkins., ( = Vismianthus sterculiifolius (Prain) Breteler \& Brouwer).

Shrub or small tree. Leaves unifoliolate, long-petioled, with glandular dots and streaks. Hairs generally two-armed. Inflorescence racemose, few to many flowered. Pedicel jointed. Flowers heterodistylous, with dark glandular dots and streaks. Sepals 5, (sub)equal, imbricate in bud, very shortly connate, persisting in fruit. Petals 5, free. Stamens 10, all fertile, shortly connate at base. Carpel solitary; ovary sessile, ovules hemitropous, attached near or above middle of ventral suture; stigma (sub)capitate, papillose. Fruit a (sub)glabrous, 1-seeded follicle, glandular dotted, dehiscing along ventral suture, inner and outer pericarp separating. Seed with chalazal sarcotesta, partly free; endosperm rudimentary or absent; cotyledons plano-convex.

Distribution: 2 species, one in south-eastern Tanzania, one in south-western Burma.

Note: According to R.G. van den Berg (pers.comm.) the pollen grains of the two species of Vismianthus (and the one of Burttia) are very much alike in shape, dimensions, type of apertures, etc. Slight differences in ornamentation, espe-
cially the coarseness of the reticulum, wall thickness and shape of apertures do occur however. These do not seem to be of use for taxonomic subdivisions. Furthermore, pollen grains sampled from short or long anthers and from flowers with short or long styles do not differ.

Key to the species
Leaves with 4-6 pairs of main lateral nerves and retuse, sometimes almost cordate at base; petals heavily dark glandularly streaked and dotted; follicle very shortly stalked; sarcotesta fringed. Southern Tanzania . . . V. punctatus

Leaves with 6-8 pairs of main lateral nerves and rounded, seldom retuse, at base; petals without or with a few dark glandular dots and streaks; follicle clearly stalked; sarcotesta with one long appendage only. Western Burma
V. sterculiifolius

Vismianthus punctatus Mildbr.
Fig. 180-181
V. punctatus Mildbraed, 1935: 706; Schellenberg, 1938: 98; Brenan and Greenway, 1949: 169; Hemsley, 1956: 7.

Type: Tanzania, Lindi District, Mlinguru, about 20 km south of Lindi, Schlieben 5757 (holo: B; iso: BM, BR, HBG, K, M, P, Z).

Shrub, up to 4.5 m , branching subradially. Branches grey or brownish with grey patches. Branchlets cylindrical, slightly grooved, tomentose when young with (un)equally two-armed hairs, glabrescent. Leaves usually crowded at end of shoots. Petiole $2-3.5 \mathrm{~cm}$ long, slender, terete to slightly grooved, densely villose when young, glabrescent, with many dark elongated glands, articulate at base of leaflet. Leaf blade herbaceous to papyraceous, ovate to almost cordate, $1.7 \times 1.2$ to $9 \times 5 \mathrm{~cm}$; apex acuminate to cuspidate, acumen $0.3-1.5 \mathrm{~cm}$, base retuse to almost cordate; densely tomentose when young, becoming glabrous, persisting longest along main and secondary veins beneath; dotted and streaked with many small ( 0.3 mm ) dark resinous glands; main lateral nerves $4-6$ pairs. Inflorescence simple or compound (2)3-6 flowered; bracts and bracteoles elliptic to lanceolate or linear, keeled, $1.5-2 \times 0.4-1 \mathrm{~mm}$, densely ferruginously pubescent, caducous; peduncle $1-4.5 \mathrm{~cm}$, densely pilose, glabrescent, with many dark glands. Flowers 5 mm long; pedicel 1-2.5 mm long, articulate, sparsely ferruginously hairy, sparsely dotted with dark resinous glands. Sepals elliptic-oblong, 2-3 $\times 1-1.8 \mathrm{~mm}$, (somewhat) concave, apex obtuse, sparsely sericeous outside, each with approximately 8-20 dark-red resinous glands, concentrated along the axis and towards the base. Petals subequal, elliptic to oblong-obovate, 3-3.5 $\times$ 1.2-1.8 mm, apex obtuse, base truncate, glabrous, whitish yellow or white with many dark elongated glands, orientated lengthwise. Stamens 10 , five episepalous ones $1.6-3 \mathrm{~mm}$ long in long-styled flowers and 4.5 mm in short-styled ones, the five epipetalous stamens $1-1.7 \mathrm{~mm}$ and $2.5-2.8 \mathrm{~mm}$ long respectively;


Fig. 180 . ismianthus punctatus: 1. flowering branch, $2 / 3 \times ; 2$. detail of inflorescence, $2 \times$;3.flower , $4 \times$; 4. petals, $4 \times$; 5. fruit, $2 \times$; 6 . open fruit, $2 \times ; 7$. seed part of seed with hilum and sarcotesta, $4 \times$.(1-4. Eggeling (immature) with sarcotesta, $2 \times ; 8$. basal part of seed with hilum and sarcotesta, $4 \times$. 6402; 5-8. Semsei 647).


Fig. 181. Distribution of Vismianthus punctatus
filaments filiform, glabrous, very shortly connate at base; anthers ovoid, 0.4-0.6 mm long in long-styled and 1 mm long in short-styled flowers. Pistil $3-3.8 \mathrm{~mm}$ long in long-styled flowers, 2 mm in short-styled ones; style filiform, sparsely sericeous-villose, with a few dark glands or not; stigma (sub)capitate, more or less bilobed, papillose; ovary $0.5-1 \mathrm{~mm}$ long, ovoid-lenticular, densely ferruginously sericeous or villose with unequally two-armed hairs, and a few dark glands or not; ovules attached at or above middle of ventral suture, hemitropous. Fruit purplish brown $15-20 \mathrm{~mm}$ long, 6 mm wide, very shortly stalked, with rostrum of up to 3 mm , virtually glabrous when full-grown, prominently veined with many small glands. Seed (immature) ovoid, dark brownish, with fimbriate sarcotesta covering one end; endosperm very thin; cotyledons thin, wide, folded.

## Distribution: S E Tanzania.

Ecology: Undershrub in forest or savanna shrub, between 250 and 800 m altitude.

Specimens examined:

Tanzania: Kilwa District (?)(fl. Nov.) Crosse-Upcott 181 (K); Mchinjori (fl. Nov.) Eggeling 6402 (BR, EA, K); Kitangari (fr. March) Gillman 1315 (EA); Namula (fr. Aug.) Ludanga 1334 (BR, C, EA, K); Mlinguru (fl. Dec.) Schlieben 5757 (B, BM, BR, G, HBG, K, M, P, Z, type); Mchinjiri (fr. Feb.) Semsei 647 (B, BR, K).

Notes: As observed by Hemsley (1956: 9), mature fruits are needed to see whether the suspensor mechanism of $V$. sterculiifolius is also present in this species.

The ovules in $V$. punctatus are not basal and anatropous, as stated by Mildbraed (1935: 707) and Schellenberg (1938: 98), but ventrally attached and hemitropous.

# Vismianthus sterculiifolius (Prain) Breteler \& Brouwer comb.nov. 

Basionym: Ellipanthus sterculiaefolius Prain, 1890: 209, plate VIII.
Type: Burma, Diamond Island, Prain s.n. (holo: K; iso: BM).
Schellenbergia sterculiaefolia (Prain) Parkinson, 1936: 295, plate 23; Schellenberg, 1938: 179, as S. sterculiifolia.

Shrub or tree, up to 4-6 m high, branching subradially. Branches slightly grooved, cylindrical, with many lenticels. Branchlets angular, slightly grooved, becoming terete, densely ferruginously tomentose with unequally two-armed hairs when young, glabrescent. Leaves often crowded at end of shoots. Petiole $2-5.5 \mathrm{~cm}$ long, slender, channeled and shallowly grooved, ferruginously seri-ceous-villose when young, becoming glabrous, with occasional red glandular dot, articulate at base of leaflet. Leaf blade herbaceous-papyraceous, ovate-ellip-tic-oblong, $3.5 \times 2$ to $12 \times 7.5 \mathrm{~cm}$; apex acuminate, acumen $0.5-2 \mathrm{~cm}$; base rounded, sometimes retuse; densely ferruginously tomentose when young, becoming glabrous, persisting longest beneath; dotted with many small dark resinous glands (in young leaves only noticeable near the leaf margin); main lateral nerves, 6-8 pairs, quite apparent. Inflorescence simple or compound raceme, 6-20 flowered; bracts oblong-elliptic, keeled, $3 \times 1.5 \mathrm{~mm}$, to lanceolate and up to $3 \times 0.5 \mathrm{~mm}$, densely ferruginously pilose or sericeous, caducous; peduncle $1.0-4.5 \mathrm{~cm}$, densely ferruginously tomentose, glabrescent; bracteoles lanceolate, up to 0.8 mm long, densely to sparsely tomentose, caducous. Flowers $4.5-6.5 \mathrm{~mm}$ long, fragrant; pedicel up to 3 mm long, articulate, ferruginously sericeous-pubescent, with a few dark glands. Sepals elliptic to elliptic-oblong, $2-3 \times 1.0-1.3 \mathrm{~mm}$, apex obtuse, sericeous-pubescent outside, with ca 8-40 dark resinous glands per sepal, mostly in lower half. Petals white, with up to six dark glands, lanceolate, $3.5-4.5 \times 1.0-1.5 \mathrm{~mm}$, apex obtuse, base truncate, glabrous. Stamens $10(11)$, five episepalous ones $1.5-2 \mathrm{~mm}$ long in long-styled flowers and $5-5.2 \mathrm{~mm}$ in short-styled ones, the five epipetalous stamens $1.3-1.6 \mathrm{~mm}$ and $4-4.2$ mm long respectively; filaments filiform, glabrous, very shortly connate at base; anthers ovoid, $0.4-0.8 \mathrm{~mm}$ long. Pistil $3.5-5 \mathrm{~mm}$ long in long-styled flowers, 3.7 mm in short-styled ones; style filiform, sericeous; stigma (sub)capitate, more or less bilobed, papillose; ovary 0.8 mm long, obliquely ovoid-lenticular, densely ferruginously sericeous with unequally two-armed hairs; ovules attached near middle of ventral suture, at first hemitropous. Fruit dark-brown, $35-40 \mathrm{~mm}$ long, 10 mm wide, clearly stalked (up to 7 mm ), narrowing to slender rostrum of up to 6 mm long, virtually glabrous when ripe, prominently veined, with many small glands, with leathery outer pericarp, inner pericarp detached except along dorsal suture. Seed ovoid, $15 \times 9 \mathrm{~mm}$, with black pseudobaccate seed coat, basal end covered by yellow or reddish undulate sarcotesta with a 10 mm long appendage attached to the base of inner pericarp bringing it in a dangling position after dehiscence; hilum wedge shaped; endosperm rudimentary; cotyledons thick, plano-convex, containing albumen and oil.

Distribution: Burma.
Ecology: sublittoral forest.
Specimens examined:
Burma: Diamond Island (fr. Nov.) Prain s.n. (BM, K, type); Pyinmadon, Thabaung, Bassein District (fl. March) Range Officer (Comm. C.E. Parkinson) 2140 (DD, K).

Notes: Schellenberg (1938) separated this species (as Schellenbergia sterculiifolia) from Vismianthus (and Burttia) at an early phylogenetic stage, apparently because Schellenbergia has an Asiatic as opposed to African distribution. As a result the Asiatic taxon was placed in the tribe Castanoleae near Ellipanthus and the African Vismianthus, together with Burttia, in the Byrsocarpeae. This may be the reason why the strong congeneric characters of Vismianthus and Schellenbergia escaped Schellenberg's attention, probably also because of the supposed absence of resinous glands in Schellenbergia. They are present in this taxon, however, and can be observed in the leaves, flowers, and fruits. This character, together with the others as unifoliolate leaves, unicarpellate flowers with ten stamens, and similar fruit and seed characters makes the unification of the genera Vismianthus and Schellenbergia inevitable.

Parkinson's collection 8729 , cited by him when publishing the new genus Schellenbergia has not been received on loan from DD where C.E. Parkinson's collection is kept. A request for a loan from two Rangoon herbaria (RAF and RANG) was not successful.

# Unidentified material, possibly new species 

by F.J. Breteler

In Gabon, N of Ayem Lake, 10 km SW of Ndjolé, N . Hallé collected under no 1727 a specimen which hitherto could not be identified. It has been collected from a shrub. It bears unifoliolate leaves and young fruits with remnants of sepals, petals, and stamens. Undoubtedly it is Connaraceous. The leaves fit well within the genus Hemandradenia and so do the remnants of calyx and corolla. Also its origin fits the geographical distribution of it. However, there are two characters which refrain me from putting it in this genus. These two are the apparently ten fertile stamens (at least ten long filaments are present) and the shape of the young, glabrescent fruit. This fruit shape, strongly cuneate at both ends, fits better in other genera like Vismianthus and Ellipanthus. Mature fruits and/or complete flowers are needed at least to decide where to place this specimen, that almost surely represents a new species.

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[^0]:    R.H.M.J. Lemmens

    The Connaraceae
    a taxonomic study
    with special emphasis on Africa
    Geography, heterostyly, pollen morphology,
    phylogeny and a revision of the genera
    Cnestis, Connarus and Ellipanthus

[^1]:    C. C. H. Jongkind

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    Indumentum, stomata, fruit, seedlings, phylogeny of the genus
    Rourea, and revision of the genera Agelaea, Manotes, and Rourea.
    Wageningen, 2 juni 1989

[^2]:    * mainly based on Leenhouts (1958b), and including Australia and Melanesia
    ** based on Forero (1983)
    *** including the only species of the former Bernardinia

[^3]:    Liberia: Harbel (fr. July) Stoop v.d. Kasteele 335 (WAG).
    Nigeria: Calabar Prov., Uwet Distr., Buden Dunlop (fr. Aug.) Binuyo FHI 41432 (BR, K); Cala-bar-Mamfe, Oban (fr. Mar.) Onochie FHI 34828 (BR, K, P).

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