GUIOA CAV. (SAPINDACEAE): TAXONOMY, PHYLOGENY, AND HISTORICAL BIOGEOGRAPHY

P.C. VAN WELZEN

Rijksherbarium, Leiden, The Netherlands

1. CONTENTS

(Contents continued)

2. SUMMARY

A monograph of the genus *Guioa* Cav. (Sapindaceae) is presented. 64 species are recognized; one species, *Guioa subfalcata*, is regarded as a dubious species. A general key and several regional keys provide access to the species. One species, *Guioa glauca*, is subdivided into two varieties. The infrageneric classification contains three levels: subgenera, sections, and subsections. The classification is based on a phylogenetic analysis of the genus.

The leaf anatomy was studied besides the macromorphology. This resulted in 67 characters for a cladistic analysis. The outcome of the initial analysis was rejected for several reasons (chapter 11.6). An alteration of the method resulted in an acceptable cladogram: the genus was subdivided, based on several characters, into 5 groups, 4 of which were subordinate to each other. Each subgroup was analysed separately and contained a representative species for a higher group and an outgroup which was obtained from a lower group. The cladograms of the 5 subgroups were pieced together to form the accepted cladogram. The computer programs HENNIG86 and PAUP provided the best method for a cladistic analysis (Wagner algorithm combined with some kind of 'branch and bound'-option).

A historical biogeographic analysis was performed with two aims: a) to find the historical relationships between the different distribution areas and b) to test the generic cladogram by comparing it with cladograms of independent groups of plants and animals. Like with the genus, the areas were subdivided into several groups, which were analysed separately under assumption 0 via a parsimony method instead of a consensus method. The complete generalized areagram was later on pieced together. The partial generalized areagrams did not falsify the accepted cladogram of *Guioa*. In two areas, the Pacific and West Malesia, *Guioa* mainly showed a pattern of dispersal and not of vicariance. The computer program CAFCA (group- and component-compatibility) presented the best method for a historical biogeograpic analysis.

A comparison between the presumed results of the classical, evolutionary school and the phylogenetic school showed that the results of the phylogenetic school had a higher information content in the sense of natural relations and that only they could be used for a historical biogeographic analysis.

The ecological part contains data on the habitat of some *Guioa* species, a compilation of mainly literature data on floral biology of Sapindaceae in general and on fruit biology, data on seed germination and seedling morphology.

In order to unravel the species complex (*Guioa rigidiuscula* group) on New Guinea only an artificial technique could be used to separate the 14 species. These appear to be natural due to correlating characters and coherent, non-disjunct distributions. It is discussed that species complexes are mainly found in especially geologically dynamic areas and that the mode of speciation is then best explained by the model of punctuated equilibria.

3. INTRODUCTION

The genus *Guioa* Cav. (Sapindaceae) constitutes the subject of the present monographic study. The genus has never been revised as a whole. Even Radlkofer, who revised almost the whole family at the end of the last century and at the beginning of the present one, never revised *Guioa*.

The present revision is part of the Flora Malesiana project, the revision of the flora of the Malesian Archipelago. Several species of *Guioa* are also found outside this region; these were also included in the study as the revision should serve as a Ph.D. thesis.

A study of the theory of systematics showed that the phylogenetic or cladistic method provided the best method for the construction of a natural classification as this school acknowledges the importance of monophyletic taxa. Consequently, a cladistic analysis was performed and the infrageneric classification was based on it.

A cladistic analysis presupposes the presence of characters and more important: a sufficient number of characters. Depending on the analytical method chosen, there should at least be two times minus 1 as many character states as species, but when homoplasies are present even more characters are needed. Macromorphology provided not enough characters, therefore a leaf anatomical survey was performed as well. The results of this survey were utilized in the cladistic analysis.

Due to the presence of many homologies, an alteration of the cladistic method was necessary (chapter 11.7). The alteration resulted in an acceptable cladogram. The latter was tested during a historical biogeographic analysis which of course also served to unravel possible historical distributions.

Van der Ham & Van Heuven (1989) made a survey of the pollen morphology of *Guioa*. Due to the small generic variation and the relatively large specific variation, the results could not be used for the cladistic analysis. The groupings of species as based on the pollen morphology and the four supposed evolutionary trends in the pollen therefore cannot be confirmed.

During three months, field work was performed in Sabah, N Borneo. One of the purposes of this trip was to collect ecological data about several *Guioa* species. Unfortunately, flowering and fruiting trees were only found at the end of the trip. Consequently, only ecological data about the habitats could be gathered. All the information about flowering and fruiting biology is a compilation mainly of literature, but also of field notes and observations on herbarium material.

4. HISTORY

In 1798, Cavanilles described the genus *Guioa*. The name is in honour of Mr. J. Guio y Sanchez, a botanical artist, who together with L. Née travelled the world. During this trip he made many drawings of living plants. Née was the collector of the material after which Cavanilles described the first *Guioa* species: *G. lentiscifolia*.

After Cavanilles there were several other authors, who thought that they described a new genus or a new section, but all of them created synonyms only. Labillardière (1825) described the genus *Dimereza* (*D. glauca*), which later on was wrongly renamed *Diplopetalon* by Sprengel (1827). Blume (1849) described the genus *Hemigyrosa* and a section in *Cupania*: *Cupania* section *Pleuropteris*.

Don (1831) transferred some of these genera to *Cupania* and described them as new sections. *Guioa lentiscifolia* was placed in *Cupania* section *Guioa*, and *Dimereza glauca* in *Cupania* section *Dimereza*. Obviously Don had not seen Blume's descriptions, otherwise these would have been added. By then, *Cupania* became a very large genus, almost entirely comprising that what now is known as the tribe Cupanieae of the Sapindaceae. Later on more *Guioa* species were described in *Cupania*, and also in *Arytera*, *Nephelium*, and *Sapindus*.

Radlkofer (1879a, b), so far the only monographer of the whole family, and a good one, reinstated *Guioa* and transferred or described many new species in it. Many of the new species were sent to him by Merrill. Unfortunately, although he reached a very high age, his death was untimely for *Guioa*. *Guioa* remained the only genus which he never has revised completely. Consequently, Radlkofer's treatment of *Guioa* in Engler's Pflanzenfamilien (1933) is only a mere compilation of former descriptions. A key is lacking and the descriptions are not congruous.

After Radlkofer's death a few more new species were described, most of them by Merrill and Perry (1940), who identified the plants collected by Brass during the Archbold expeditions to New Guinea.

Miss Reynolds (1984, 1985) made an excellent revision of *Guioa* for Australia. That revision was the starting point for the present monograph.

The present study is the first complete revision of *Guioa*. As a first result nineteen species have been newly described, together with one new combination (Van Welzen, 1988b).

5. CONCEPTS

The revision of *Guioa* has been based on herbarium specimens only. The criterion on which basis species are distinguished is the presence of at least two characters in which any two species differ from each other, i.e., the morphological gaps between the species. The same criterion has been applied by Van Steenis (1957) and by Geesink (1984) in his generic delimitation of the tribe Millettieae (Papilionaceae). Normally, of course, this criterion is implicitly used to distinguish species in herbarium studies, but strangely enough it is seldom acknowledged. Species distinguished this way will always possess a monothetic set of characters (i.e., a unique combination of character states present in all specimens of a species). As soon as the set of characters becomes polythetic (the unique combination is not present in all specimens), the recognizability of the species will be obscured.

In East Malesia, the Pacific, and Australia the specific delimitation complies with the above mentioned criterion. All species possess a monothetic set of characters. In West Malesia the situation is somewhat different. The widespread species, especially *Guioa diplopetala* and *Guioa pleuropteris*, are very heterogeneous and their character set is polythetic; see for instance the leaflet shapes, the presence of a winged rhachis, and the presence of domatia in figs. 77 and 110. However, every time when two specimens from the same collecting site, belonging to different species, are compared, at least two differences can be observed: there always is a morphological gap between the species, but the gap is different in the various areas. Consequently, these widespread species key out several times in the general key. Presumably, the explanation for this phenomenon is historical. The species could diffuse over the Sunda Shelf during the glacial times of the Pleistocene; nowadays, their distribution is disrupted (rise of the sea-level) and the different island populations develop independently with the present polymorphy as a result.

It is debatable whether the herbarium technique is sufficient to recognize all species, just as it is debatable whether differences in characters are sufficient to discover all species. Species are real entities, existing in nature; they are natural individuals as (after Geesink & Kornet, 1989): 1) they are spatio-temporally restricted (they have a beginning and end in time), 2) they exist in nature as cohesive wholes (interbreeding and descent), independent of our ability to recognize them, and 3) they can only be described by their characters, not defined (somebody can still belong to the species Homo sapiens when he misses a leg). Opposite are natural classes, natural kinds, 1) these are spatio-temporally unrestricted, 2) they do not need cohesion to exist (the individual members are the real things, e.g. atoms), and 3) they are defined by their properties, characters (nuclear fusion changes elements into other elements, into other classes, which have their own characteristics again). The members of a class do not have a history in common (spatio-temporally unrestricted), the members of an individual (e.g. the specimens) do; therefore classes do not show evolution, individuals do (Geesink & Kornet, 1989). For more literature on the concept of species as individuals see for instance Ghiselin (1974) and Zandee & Geesink (1987).

If species are coherent, natural wholes, what are infraspecific taxa? Infraspecific taxa can be individuals too when the coherence between populations varies: an infraspecific taxon can be equal to one or several populations which among themselves show more coherence than with other populations. Only two infraspecific taxa are recognized in the present study: *Guioa glauca* var. *glauca* and *Guioa glauca* var. *vulgaris*. *Guioa glauca* var. *glauca* seems to be very homogeneous and may consist of coherent populations, but *Guioa glauca* var. *vulgaris* is very heterogeneous and contains some more or less distinct forms and is likely to be a collection of several groups of coherent populations, which are not distinguished separately. Consequently, both varieties are presumably classes, defined by their characters.

Genera (and other infrageneric, supraspecific taxa) are (passive) historical products of continuing evolution (Geesink & Kornet, 1989; Wiley, 1981a). They, too, are wholes existing in nature, real individuals. Paraphyletic groups, which are often easy to characterize, constitute a problem. Monophyletic as well as paraphyletic groups of species are descendents of one ancestral species, but a monophyletic group encompasses all descendents and a paraphyletic group only part of them. Only monophyletic groups are individuals (historic groups). Paraphyletic groups are classes as they are no wholes (criterium 2), consequently they can only be defined by characters (criterium 3). Comparable to a paraphyletic group is for instance treating a part of a species as a species, ignoring e.g. women or some race while talking about humans, or considering a cell as the part without the DNA. These classes show no evolution and can likewise never be the product of evolution. Consequently, a natural classification, which displays the course of evolution, can only contain monophyletic groups as building stones. N.B.: The application of the rank of genus to a certain monophyletic group just depends on human conventions, not on its existence in nature. For a short summary of the problems in the delimitation of genera see Kornet (1988). Wiley (1981b, 1987a) shows that paraphyletic groups are inconsistent with a natural classification.

Of the three schools present in systematics the phylogenetic or cladistic school recognizes monophyletic groups as the only valid building stones for a natural classification. The phylogenetic school assumes that evolution has occurred. As species differ from each other evolution had to be accompanied by modification: characters change in the course of evolution. If the sequence of character changes could be reconstructed then the course of evolution could be understood. Newly formed character states are called apomorphies (the former state a plesiomorphy). Apomorphies are the character states with which monophyletic groups are recognized (an ancestral species which formed the new character state passes it on to its descendents). Because of the importance of monophyletic taxa as natural taxa a phylogenetic analysis and a classification based on that analysis are realized in the present revision.

6. MACROMORPHOLOGICAL CHARACTERS

Anatomical characters are discussed in chapter 7. Sometimes macromorphological and anatomical characters overlap (e.g. indumentum, domatia), but this overlap is kept minimal. The leaf anatomical analysis is not united with this chapter, because most researchers are only interested in the one or the other.

Habit

The *Guioa* species are usually shrubs or small trees, but may be trees up to about 30 m high. In some instances collector's labels indicate that the plant is a woody vine (e.g. *Guioa pleuropteris*), but this is possibly an error.

Indumentum

The young branchlets are usually sericeous with simple hairs only, sometimes hirsute; in most species the hairs disappear with age. The leaflets are normally subglabrous when not papillate (*Guioa molliuscula* and some forms of *Guioa diplopetala* for instance excepted). When the leaflets are papillate then a sericeous (prostrate long stiff hairs) or sometimes a hirsute indumentum (patent long stiff hairs) is present (*Guioa acutifolia* and *Guioa novobritannica* are almost glabrous). *Guioa hospita* has a puberulous indumentum (short patent stiff hairs) on the leaflets, *Guioa melanopoda* a somewhat tomentose indumentum (short patent wavy hairs), and the *'Guioa bullata'* form of *Guioa diplopetala* has a slightly villose indumentum (long wavy patent hairs). Differences in indumentum of the leaflets constitute apomorphies in the *Guioa rigidiuscula*- and the Australian/New Caledonian group.

Several species were described as new based on a kind of indumentum. After this revision it became obvious that a hirsute and a sericeous indumentum were interchangeable, sericeous species may sometimes include specimens with hirsute hairs and vice versa. Examples are *Guioa chrysea, Guioa myriadenia, Guioa pleuropteris, Guioa reticulata, Guioa subsericea,* and *Guioa villosa.* The two forms look very different and are almost automatically regarded as separate species, but the difference in indumentum is the only character in which the forms differ. Because of this single difference, and the regular occurrence, several names are regarded as synonyms (see notes under the above mentioned species).

Papillae form a rather constant character, only a few species show non-papillate as well as papillate leaflets (e.g. *Guioa bijuga, Guioa diplopetala,* and *Guioa oligotricha*). When papillate, every cell on the lower surface of the leaflets forms a papilla, consequently the lower surface will look dull and usually greyish or glaucous; when not papillate the leaflets are shiny below. Less shiny leaflets, regarded as without papillae in the key, have a slight development of papillae around the stomata. A dissecting microscope has to be used to prove the presence of papillae properly when one is still inexperienced with this character. The presence of papillae is apomorphic for the Pacific group, and parts of the New Guinean, *Guioa rigidiuscula*-, and West Malesian group.

Scale hairs, often found in Sapindaceae, are absent in *Guioa.*

Glandular hairs are seldom present and very inconspicuous except for the type of glands of *Guioa hirsuta.* These glandular hairs resemble small red hairs and are especially present on the lower surface of the leaflets.

Leaves (fig. 1)

Only the first pair of leaves of a seedling is opposite, all other leaves are alternate. The leaves normally show about 3 jugae. The number of jugae is more or less correlated with the size of the leaflets, leaves with small leaflets show more jugae (e.g. *Guioa pseudoamabilis*) than leaves with large leaflets (e.g. *Guioa grandifoliola*). A number of 1–6 jugae is apomorphic for the New Guinean group, but reversals to 1–3 jugae (*Guioa melanopoda* and *Guioa patentinervis*) and a further development to 1–9 jugae (*Guioa pseudoamabilis* and *Guioa pteropoda*) occur in this group too; 1–6 jugae is also typical for several species and species groups in the *Guioa rigidiuscula* group, where reversals to 1–3 jugae are present too.

The rhachis is usually not winged (fig. 1a), but can be flattened or somewhat broadened below the jugae. Several species show a narrow wing (less than 1 mm broad; fig. 1b), while others have a broad wing (usually c. 3 mm broad; fig. 1c). Only a few species vary between wingless and broadly winged (*Guioa bijuga, Guioa*

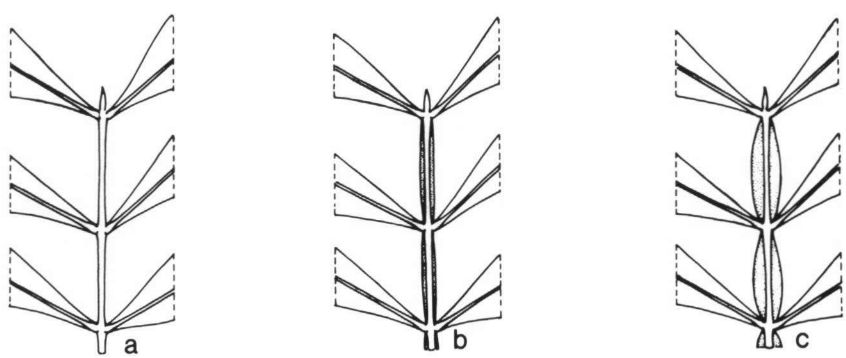


Fig. 1. Rhachis wing: a. not winged; b. slightly winged; c. broadly winged.

comesperma, and *Guioa pleuropteris*). The narrow wings are an apomorphic reversal, a neoteny, as juveniles also possess them (see chapter 8.5). Broad wings are also an apomorphic character state. The narrow wing as well as the broad one are several times the result of parallel developments or reversals (e.g. *Guioa comesperma, Guioa melanopoda,* and *Guioa bijuga–Guioa pleuropteris–Guioa pterorhachis* have broad wings).

The petiole and petiolules show a basal pulvinus.

Leaflets

General — The leaflet attachment varies from opposite to alternate, but is usually subopposite. Most leaflets are subsessile (only pulvus between rhachis and leaflet present as petiolule). The thickness of the leaflets varies between thin and very coriaceous. Punctation is usually present, due to secretory idioblasts.

Shape (figs. 2, 3) — Most species vary between ovate (fig. 2a, leaflets widest below middle) and elliptic (fig. 2b, leaflets widest in middle) or between elliptic and obovate (fig. 2c, leaflets widest above middle). The change from elliptic to ovate is apomorphic for several species and species groups in the *Guioa rigidiuscula* group.

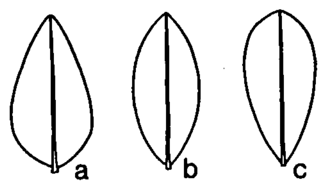


Fig. 2. Leaflet shape, largest width: a. ovate; b. elliptic; c. obovate.

The leaflets are usually slightly asymmetric (fig. 3d), the acroscopic side (leaflet half which points towards the leaf apex) is always broader than the basiscopic side. Often the leaflets are very asymmetric (fig. 3a–c) with two special types: The falcate type (fig. 3a), ovate usually narrow sickle-like leaflets; and a type with an asymmetric base and top (quite often the base broader on the acroscopic side and the top on the basiscopic side; fig. 3c). The degree of asymmetry forms two apomorphic characters for the Pacific group, but parallel developments are present in other groups (e.g. the falcate leaflets of *Guioa plurinervis* in the *Guioa rigidiuscula* group or those of most Philippine species in the West Malesian group). Almost symmetrical leaflets are apomorphic for part of the New Guinean group.

Base — The base of the leaflets mainly varies between cuneate and attenuate.

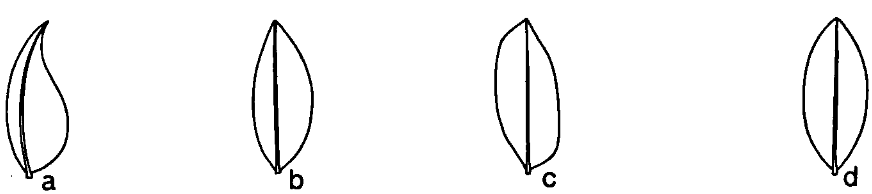


Fig. 3. Leaflet shape, symmetry: a. falcate; b. asymmetric; c. asymmetric; d. slightly asymmetric.

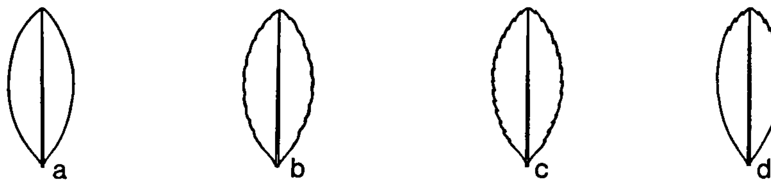


Fig. 4. Leaflet margin: a. entire; b. crenate; c. serrate; d. only apex serrate.

Margin (fig. 4) — Normally the margin is entire (fig. 4a), but quite some species show, as a neoteny, a crenate margin (fig. 4b). Some species have a somewhat serrate margin (fig. 4c), which probably is some form of a crenate margin. In several species only a few subapical teeth (fig. 4d) remain of a serrate margin. The character states crenate and serrate are apomorphic, but with several parallels (e.g. crenate margins are twice an apomorphy in the New Caledonian group, and once, just like the serrate margins, an apomorphy for parts of the New Guinean group).

Apex (fig. 5) — Fig. 5a–g shows the different types of apex which are distinguished in the descriptions. Normally species vary between retuse and acute or between (obtuse-)acute and caudate. In the latter case the transition to the leaf apex may be gradual (fig. 5h; no or almost no sinus present) or it may be rather abrupt (fig. 5i; sinus present).

In most species the apex ends in a small mucro.

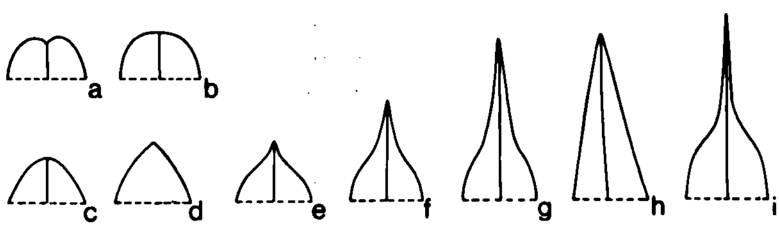


Fig. 5. Leaflet apex: a. retuse; b. rounded; c. obtuse; d. acute; e. acuminate; f. cuspidate; g. caudate; h. caudate, apex without a sinus; i. caudate, apex with a sinus.

Upper and lower surface (fig. 6) — The upper surface is always smooth, the lower may be papillate. If an indumentum is present hairs are more numerous along the (basal part of the) midrib and on the lower surface. The lower surface normally shows a different colour than the upper surface does. In some species the upper surface is often covered with wax.

Domatia are often present on the lower surface in the axil of the midrib and the second basiscopic nerve, only very few species always lack them. Most species either have (n)one or many domatia. Several types exist; usually a species shows only one type. Pockets (figs. 6a, 32, 33) are formed by a thin triangular roof, which

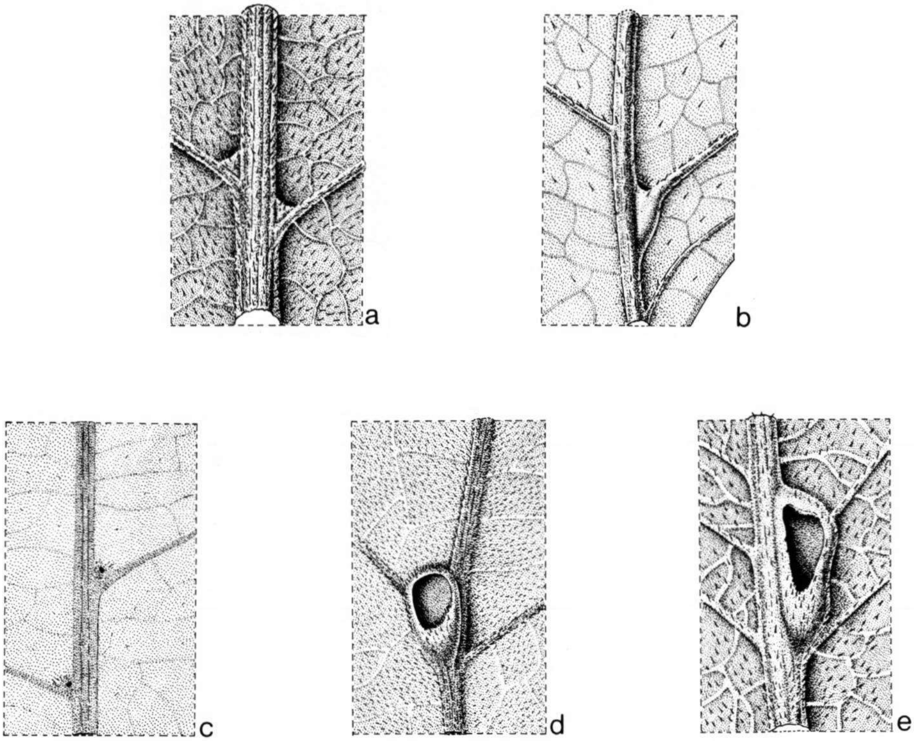


Fig. 6. Domatium types: a. pockets; b. sac with opening in front; c. sac sunken into leaflet, notice flat midrib; d. large sac with round opening on top; e. large sac with slit-like opening on top.

connects the veins in the axil; consequently the front is completely open. Sacs (figs. 6b, 20, 21) have the front also covered except for a little hole. Quite often transitional forms are found, with small incomplete walls in the front part. Species with many sacs will show pockets in the upper nerve axils. The sacs can be quite large (figs. 6d, 22) with the opening not any more in the front but in the top; this is an apomorphy for the Fiji and Tonga species of the Pacific group. Sometimes the opening is not round but a long slit (fig. 6e). In *Guioa pterorhachis* the sacs are sunken in the leaf surface (figs. 6c, 23). The terminology of the domatia is after Wilkinson (1979); in the literature the pockets are quite often called sacs and the sacs are called domes. O'Dowd & Willson (1989) concluded that the domatia are part of a symbiotic relationship between plant and predaceous and fungivorous mites. The domatia act as protection and breeding sites for these mites, which in turn protect the plant from fungi and herbivorous mites and insects.

Venation — The venation is usually slightly sunken or flat on the upper surface, but may be raised, as it always is on the lower surface. The number of main nerves is impossible to count due to intercalary smaller nerves; these cannot be distinguished from the main nerves in the apical region of the leaflets. The major nerves are normally marginally looped, but quite often less distinctly so in the lower third of the leaflets (the incomplete marginal vein is an apomorphy for the *Guioa bijuga–Guioa pleuropteris- Guioa pterorhachis* group of West Malesia; however, parallels occur in for instance the *Guioa rigidiuscula* group). The veins vary between laxly and densely reticulate; the former are usually rather indistinct, the latter very distinct. *Guioa pauciflora* and *Guioa reticulata* are two species in which the densely reticulate, very distinct venation is raised on both sides. Indistinct venation is an apomorphy for part of the Australian/New Caledonian group. A distinct venation is apomorphic for *Guioa myriadenia* and *Guioa reticulata* of the West Malesian group.

Inflorescence

The inflorescences are normally axillary, but can be pseudoterminal (endbud still present; e.g. *Guioa subsericea*) or ramiflorous (apomorphy for a part of the *Guioa rigidiuscula* group; *Guioa diplopetala* shows a parallel development). The thickness of the flowering twigs constitutes an apomorphy for the New Guinean group.

The inflorescence can branch in or near to the axil of the axis with the branchlet and along the main axis. Most species either mainly show the former or the latter. The branches are oblique and usually rather laxly few-flowered.

The inflorescences are thyrses: the flowers occur in cymes, the latter are raceme-like arranged along the axis. The cymes are mainly cincinnate, but can also be dichasial.

Bracts and bracteoles

Bracts to the axis and to the cymules are present. The bracts and bracteoles are always triangular, outside sericeous and inside normally glabrous. The bracteoles can be found at the base of the pedicels, but sometimes one might be present subapically as a sepal. Sometimes small leaves are found on the inflorescence (as for instance *Brousmiche s.n.*, 1882, *Guioa villosa*), which shows the homology of the bracts with leaves.

Flowers

General (fig. 7) — Most flowers are small, at most up to about 6 mm in diameter. Presumably the flowers are unisexual (either stamens well-developed and stigma not, fig. 7a, male; or vice versa, fig. 7c, female), or, if hermaphrodite, then presumably functionally male (fig. 7b). Unfortunately the stamens and pistil of the latter type of flowers are both well-developed, but intermediate between those of male and female flowers: this makes it impossible to tell whether the *Guioa* species are hermaphrodite, dichogamous or dioecious.

Pedicel — The pedicel is divided into two parts, at about a third from the top an abscission zone is present. Usually, the upper part of the pedicel is less pilose than the lower part.

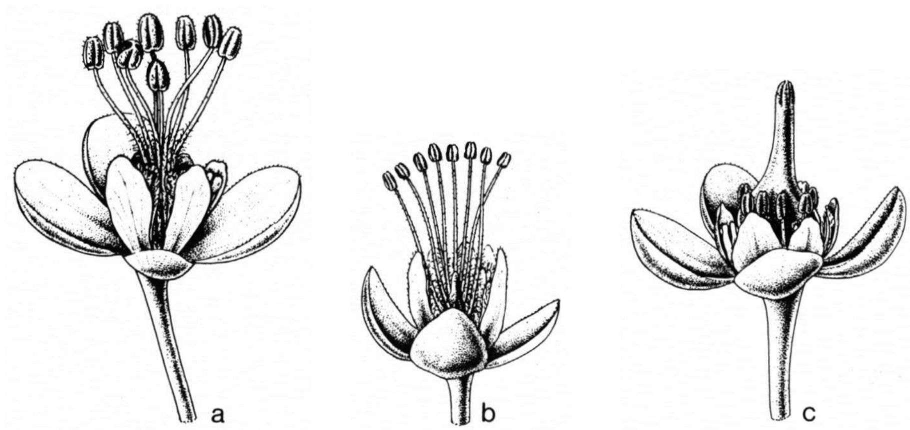


Fig. 7. Flowers (a & c *Guioa glauca* var. *vulgaris*; b *Guioa koelreuteria*), all × 6: a. male flower, stamens long, pistil short (*MacKee 42277*, L); b. hermaphrodite flower, presumably functionally male, stamens and pistil well-developed (*Iwatsuki et al. s.n.*, 7-XII-1975, L); c. female flower, stamens short, pistil well-developed (*MacKee 42781*, L).

Sepals — The 5 sepals, seldom 6, are usually dimorph and petaloid. The outer two are smaller than the inner three. The only exception is *Guioa microsepala* with 5 small (reduced), equal, but still petaloid sepals. *Guioa crenata* and less so *Guioa crenulata*, like *Guioa microsepala* also from New Caledonia, have small sepals too, but these are dimorph like in the other *Guioa* species. The dimorphism of the sepals is an apomorphy of the genus together with *Cupaniopsis anacardioides*, the petaloid appearance of the sepals is an apomorphy of *Guioa*.

If 6 sepals are present, then usually a bracteole is sepal-like (as a small outer sepal), only seldom 4 inner large sepals are present.

Usually only the margin of the sepals has long stiff hairs and usually small reddish glands (type of glands as found in *Guioa hirsuta* on the leaflets). Sometimes the outside, especially of the hirsute species, is pilose too. Only the papillate species of New Caledonia, together with *Guioa microsepala*, also have hairs inside.

The glands on the margin are normally present on both outer and inner sepals, but sometimes only on the outer sepals, and in very few species completely absent.

The sepals are normally persistent in fruit.

Petals (figs. 8–11) — All species show 5 petals, except for *Guioa pteropoda* which has 4 petals. The petals are caducous in fruit. The petal can be divided into a claw and a blade, with between them usually two scales with quite often on top of each a crest. The claw is almost absent when the scales are reduced (fig. 8c). The transition between claw and blade can be gradual (fig. 8b) or abrupt (fig. 8a). The edge of the petals is pilose, sometimes the outside and even less so the inside too. The *Guioa rigidiuscula* group and the West Malesian group have rather typical petals. The former have a claw of normal length, well-developed scales with rather broad

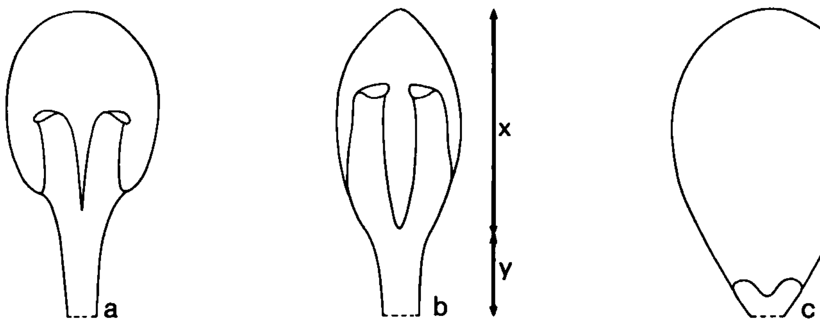


Fig. 8. Petal shapes, with the scales between claw and blade: a. transition between claw and blade abrupt; b. transition between claw (y) and blade (x) gradual; c. claw almost absent.

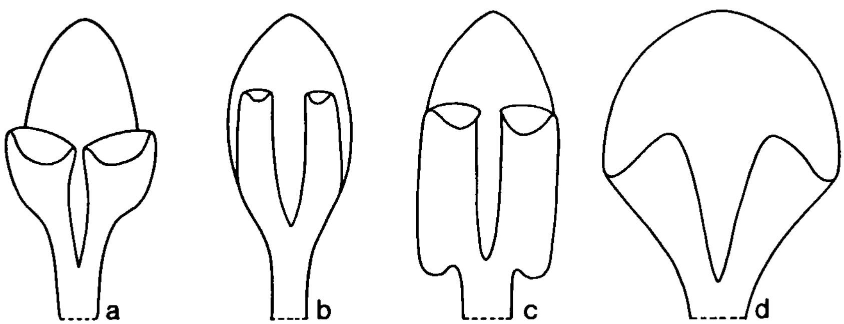


Fig. 9. Petal scales, a–c scales free, d adnate to petal: a. apex of scales very broad; b. apex small, scales without auricles; c. apex small, scales basally auricled; d. scales as folded margins of petal.

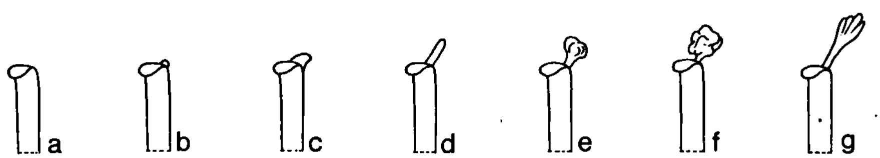


Fig. 10. Petal scale crests: a. scale without crest; b. crest an enation; c. crest as part of bifid scale apex; d. crest linear; e. crest shortly stiped, clavate, rather small; f. crest shortly stiped, clavate, large; g. crest longly stiped, clavate.

membranaceous margins, and a well-developed glabrous crest. The latter have a high stipe, well-developed scales with rather small membranaceous margins, and bifid pilose scale apices.

The fifth petal (inserted between the two adjacent large sepals) is normally reduced in size. This is an apomorphy for most *Guioa* species except for the Pacific group (reversals in *Guioa scalariformis* and *Guioa unguiculata*).

The scales can be adnate folded margins of the petal (fig. 9d) or are more or less free (except for basal part) from the petal margin (fig. 9a–c). The apex of the scales is normally small (fig. 9b, c), but can be very broad when the crest is absent (fig.

9a). The scales of *Guioa acuminata* show basal auricles (fig. 9c). The membranaceous edge along the scales can be small or broad. The margins of the scales are always long pilose. The absence, reductions, and presence of the scales are apomorphic characters in the Australian/New Caledonian and West Malesian groups.

Several species always lack a crest (fig. 10a), sometimes the crest is present as an enation, a cockle (fig. 10b). Several species show a bifid scale apex, where both parts are pilose (fig. 10c); this character is an apomorphy for the West Malesian group, but parallel developments occurred in for instance *Guioa pteropoda* and *Guioa unguiculata*. In most species the crest is clavate with a short (fig. 10e, f) or a long stipe (fig. 10g; e.g. *Guioa coriacea*). When the stipe is short the crest apex may be simple (fig. 10e) or very complex (fig. 10f; found in several New Caledonian species). When the crest is clavate the indumentum is normally absent (except in the Philippine species and *Guioa membranifolia*). A few species show a linear crest (fig. 10d; e.g. *Guioa acuminata*, and forms of *Guioa glauca* and *Guioa villosa*). The different types of crest form several apomorphies in the Australian/New Caledonian and West Malesian groups.

As already discussed above, the scales are homologous with the margins of the petals, but they, or the petal itself, may also be homologous with stamens, as several specimens were found with a scale developed as a filament and a crest as an anther (fig. 11). Presumably, as only one scale developed into a stamen, the petals are homologous with the stamens. The appearance of the disc (in between the petals and the real stamens) is probably a later development, after the petals were formed.

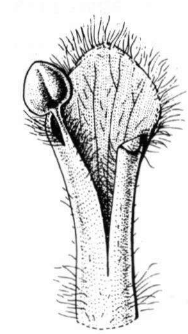


Fig. 11. Inside view of a petal of *Guioa unguiculata* showing homology between a stamen and the scale and the crest (*Vink 16407*, L, × 12.5).

Disc (fig. 12) — The plesiomorphic state is a completely circular, nectar secreting rise of the receptacle (fig. 12a). Apomorphic states are discs with either a broad gap (fig. 12c) or with one or usually two small slits (fig. 12b). The slits are found near the insertion of the two adjacent large inner sepals. If a gap is present, then the disc part between the slits is not developed. Reversals from an interrupted disc to a complete disc occur often (e.g. the *Guioa rigidiuscula* and West Malesian groups).

Nair & Joseph (1960) showed that the disc of *Cardiospermum halicacabum* is of receptacular origin as it receives four vascular bundles from one side of the receptacular stele.

The disc is always glabrous, an apomorphy of *Guioa*.

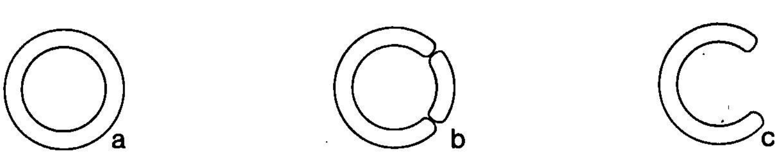


Fig. 12. Disc: a. complete; b. with two small slits; c. interrupted with a large gap.

The disc can still be studied in fruit, but disappeared disc parts may then resemble an incomplete disc. Always observe the position of the two adjacent large inner sepals first, before the degree of completeness of the disc is established.

Stamens — Always 8 stamens are present. The filaments are completely, but mainly basally, pilose except for the filaments of *Guioa pteropoda,* which are only basally pilose. The anthers are more or less caudate, basifixed in the cleft, and open latrorsely, lengthwise in the male and hermaphrodite flowers. The anthers may occasionally bear a few hairs. The stamens are caducous in fruit.

Pistil — The ovary is 3-lobed, 3-locular (once an exceptional 4-locular fruit was found in *Guioa waigeoensis*). The ovary is smooth and normally subglabrous, but can be densely hirsute in some species (e.g. *Guioa pubescens*).

Per locule one axillary ovule is present.

The style and stigma form a pyramid, of which the upper surfaces have stigmatic small papillae. The stigma lobes do not recurve as for instance in *Mischocarpus,* but remain united and erect, also in fruit.

Fruit

General — The shape is always obcordate and lobed, although *Guioa contracta* can have almost non-lobed fruits. The fruits usually possess a stipe; the wall is usually thin; the outside is smooth to rugose when dry, glabrous except for the glabrescent sericeous fruits of *Guioa pubescens*; the inside is very smooth and glabrous.

Stipe length and shape (fig. 13) — Fig. 13a shows a fruit with a well developed, slender stipe (stipe at least 2 mm high, e.g. *Guioa membranifolia*). Fig. 13b shows a fruit with a broadly cuneate, hardly distinguishable stipe (e.g. *Guioa subsericea*) and fig. 13c shows a fruit with a broadly cuneate, almost absent stipe (e.g. *Guioa aryterifolia*). Usually the stipe is either well developed and slender or short and broadly cuneate (stipe length and shape are highly correlated), only few species show well developed, broadly cuneate stipes (e.g. *Guioa microsepala*). These two characters show many reversals and parallel developments, but are quite often distinctive for several groups (e.g. Pacific species, *Guioa aryterifolia–Guioa rigidius*

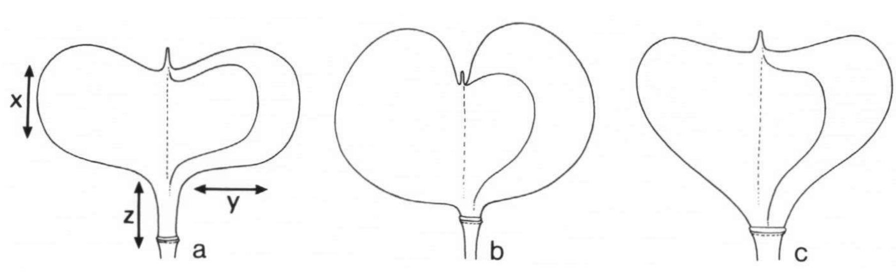


Fig. 13. Fruit shapes: a. stipe high and slender, upper and lower margin of lobes about parallel to each other, straight; b. stipe almost absent, broad, lower and especially upper margin highly convex; c. stipe short, broadly cuneate, margins not parallel, straight. – x: Width of lobes; y: length of lobes; z: height of stipe.

cula–Guioa contracta–Guioa grandifoliola group, and the greater part of the Australian/New Caledonian and West Malesian group. In the latter group combined with the shape of the stipe).

Wall thickness — *Cupaniosis anacardioides,* the outgroup, has very thick-walled fruits. *Guioa* has thin-walled fruits (apomorphy of the genus), with a reversal to thick-walled fruits in *Guioa contracta* and *Guioa grandifoliola.* In *Guioa contracta* this phenomenon seems to be correlated with a diminished dehiscence of the fruit.

Colour — The fruits are usually blackish when dry (red when fresh), but reddish to reddish black in some species. The red colour is an apomorphic character in *Guioa,* but shows parallel developments (*Guioa comesperma, Guioa fusca–Guioa gracilis, Guioa pleuropteris–Guioa pterorhachis*). The outgroups, *Cupaniopsis anacardioides* and *Cupania americana* have brown fruits, consequently the black colour is regarded as an apomorphy for *Guioa.*

Lobes (fig. 13) — The relative length of the fruit lobes is a character which can be used to key out species, but it cannot be used in a cladistic analysis, because the length/width ratios do not show any disjunctions. Fig. 13a shows how the measures can be taken. Most species usually show either lobes which are about as high as long, or they show lobes which are longer than high. Only some species show both shapes.

Upper margin of lobes (fig. 13) — The upper margin of the lobe is usually parallel to the lower margin (fig. 13a), but in some species, especially in *Guioa rigidiuscula,* the upper margin is highly convex and not parallel to the lower margin (fig. 13c).

Arilloid — The fleshy part around the seed of the Sapindaceae has caused a lot of terminological and morphological confusion. In this revision the definitions by Van der Pijl (1957) will be followed. The fleshy part is usually called aril. However, the aril is an outgrowth of the funicle, but Sapindaceae do not possess a funicle, the ovules develop directly on the placenta, therefore the term aril is incorrect. A sarcotesta (as found in for instance *Nephelium*) is the swollen part of the outer integument, consequently it is completely attached to the seed.

An arillode is also a part of the outer integument, but it is only locally developed around the micropyle and the placental connection. Quite a few genera of Sapindaceae possess an arillode which remains present as a small basal rim. The arillode can also grow and envelop the seed completely (as in lychee, *Litchi chinensis,* and mata kucing, *Dimocarpus longan*), but then opposite to a sarcotesta only the basal part is connected to the seed, the rest is free of the seed.

Arilloid is the general term for any outgrowth on or near the seed, in this sense the term aril is generally (mis)used.

In *Guioa* the term arilloid will be used for two reasons. a) The development of the ovule was never studied anatomically. b) Van der Pijl (1957) uses the term endocarp pulpa for the arilloid of *Guioa* without defining this term, while macromorphologically the development of the arilloid does not seem to differ from that of the arillodes of for instance *Litchi* or *Harpullia*. The development of the arilloid is described in chapter 8.3. Typical (apomorphic) for *Guioa* is the presence of an arilloid which completely envelops the seed and which possesses a basal rim with a curling, thread-like appendix, called pseudo-funicle. The pseudo-funicle is attached to the basal inside corner of the locule and the seeds remain dangling on it when the fruit dehisces. This character is also found in *Mischocarpus*, but is apomorphic for *Guioa* relative to the outgroup. The pseudo-funicle may have caused Van der Pijl to use the term endocarp pulpa for the arilloid of *Guioa*, because when mature it is not clear whether or not the arilloid developed as an arillode or as an outgrowth of the endocarp of the fruit. Within *Guioa* the secondary loss of the pseudo-funicle (not the rim) is a later apomorphy (*Guioa aryterifolia–Guioa contracta–Guioa grandifoliola–Guioa rigidiuscula*).

Seed — The seeds are obovoid (to globose), laterally somewhat flattened, blackish or dark brown, smooth, glabrous, shiny. The inner testa has a radicular pocket pointing towards the micropyle. From the pocket hardly visible pleurograms (predesigned fracture lines in the testa) are present up to the subapical region of the seed.

The hilum is oval and separated in a true and a pseudo-hilum (Van der Pijl, 1957). The true hilum is the scar of the placenta (as no *Sapindaceae* show a funicle), the pseudo-hilum includes the true hilum, which is surrounded by the scar tissue of the arilloid.

The measures given for the hilum are those of the pseudo-hilum along its longest axis.

Cotyledons (fig. 14) — The outgroup, the species of New Guinea, and those of the Pacific (New Caledonia excepted) show the plesiomorphous state with the two cotyledons dorsoventrally above each other (fig. 14a), the apices are usually not elongated or only that of the upper cotyledon is shortly so. The West Malesian, Australian, and New Caledonian species show the advanced state; the cotyledons are secondarily laterally besides each other; the apices are usually elongated and the one of the lower cotyledon is usually recurved, sometimes also the apex of the upper cotyledon (fig. 14b); the cotyledons then become S-shaped. The elongated apices are

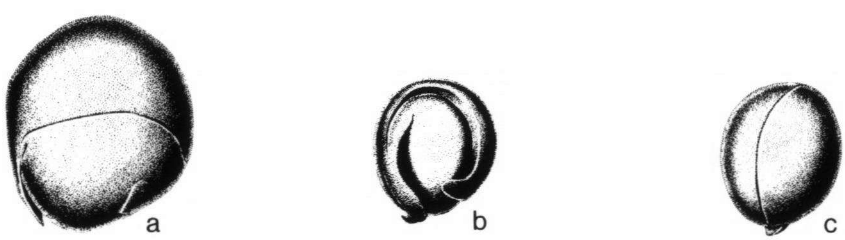


Fig. 14. Embryo types, a & b notorrhizal (radicle parallel to slit between cotyledons), c lomatorrhizal (radicle perpendicular to slit), all × 3: a. cotyledons dorsoventrally above each other, apices almost not elongated (*Guioa lentiscifolia, Parks 16162*, L); b. cotyledons secondarily laterally besides each other, apices elongated (*Guioa pleuropteris, Carrick 797*, K); c. cotyledons laterally besides each other (*Cupania americana, Urban 4521*, L).

always dorsoventrally flattened, just like the radicle. The plumule is very indistinct. The upper cotyledon is usually larger than the lower one.

The notorrhizal cotyledons (radicle parallel to slit between cotyledons) are apomorphic for *Guioa* and *Cupaniopsis anacardioides*. *Cupania americana* has lomatorrhizal cotyledons (radicle perpendicular to slit between cotyledons; fig. 14c).

7. LEAF ANATOMY OF GUIOA

7.1. INTRODUCTION

Radlkofer, who was the first to provide a taxonomic revision of the Sapindaceae, was also one of the pioneers in systematic plant anatomy. His anatomical notes can be found throughout his papers. Summaries are given in his account of *Serjania* (1889) and in an official address on the occasion of the birthday of King Ludwig II (1883). Radlkofer saw three aims for anatomy: 1) Identification of the non-interpretable type specimens in the Linnaeus and Wallace herbarium (mainly sterile ones); 2) To provide additional information besides macromorphological data; 3) Clarification of phylogenetic relationships among plants. This last aim of Radlkofer, as for instance used in his revision of *Serjania,* is also the purpose of the present study. It can perhaps demonstrate whether anatomical characters can provide apomorphies for plant groups or not. In the zoological literature, anatomical data seem to account for most of the apomorphies (see for instance Wiley, 1981a).

Radlkofer's pupil Solereder (1889, 1908) provided a summary of the anatomical data of the whole family (in German). A more up to date English summary can be found in Metcalfe & Chalk's Anatomy of the Dicotyledons (1950), and notes about Sapindaceae, spread over several chapters, in the second edition of 1979.

This chapter contains a general leaf anatomical survey of *Guioa.* Of species with a rather limited distribution only one specimen was examined; of species with a large distribution up to 10 specimens were seen, either evenly distributed over their complete distribution area or representing all different leaflet forms.

In order to understand the position of *Guioa* among other Sapindaceae, specimens of related genera were also investigated leaf anatomically. *Cupaniopsis* was taken into account because *Guioa* is likely to be derived from it; *Diploglottis* (and the sometimes as congeneric regarded *Euphorianthus*) and *Sisyrolepis* were sometimes regarded to have arisen from *Guioa*; and *Rhysotoechia* might be an alternative outgroup for *Cupaniopsis* (Muller & Leenhouts, 1976; Leenhouts, pers. comm.).

7.2. MATERIAL AND METHODS

Herbarium material for anatomical research was obtained from the Rijksherbarium at Leiden (L), unless stated otherwise (herbarium abbreviations as in Index Herbariorum). Mature leaflets were rehydrated by boiling in water. Transverse sections of the basal and of the middle portion of the lamina (including midrib and margin of the latter) of part of the material (specimens marked (1)) were prepared on a sledge microtome and bleached in household bleach. The sections were stained with Astrablue. In addition Sudan IV-stained cuticular macerations were studied; these were obtained after incubation of leaflet fragments overnight in a mixture of equal volumes of 30% hydrogen peroxide and glacial acetic acid (specimens marked (2)). Also unstained leaf clearings (also marked (1)) were made by boiling the leaflets for 20 minutes in an autoclave in a 5% KOH solution; after cooling down and rinsing the leaflets were bleached in household bleach until translucent. All material was mounted in glycerin jelly.

Leaf surfaces were, after sputter-coating with gold (Polaron SEM coating unit E5100), also studied with a JEOL JSM-35 scanning electron microscope.

The following species and specimens were studied:

Arytera arcuata Radlk.: New Caledonia, MacKee 2437 (2).

Atalaya papuana (Radlk.) Leenh.: New Guinea, Brass 8244 (2).

Cupaniopsis anacardioides (A. Rich.) Radlk.: Australia, Hubbard 3715 (1+2). — *Cupaniopsis bilocularis* Adema: New Guinea, LAE 51730 (2). — *Cupaniopsis concolor* (Gillespie) Van der Ham: Fiji, A.C. Smith 8171 (1+2). — *Cupaniopsis platycarpa* Radlk.: New Guinea, NGF 43860 (1+2). — *Cupaniopsis shirleya* (Bail.) Domin: Australia, L.S. Smith 4119 (1+2). — *Cupaniopsis squamosa* Adema: New Caledonia, MacKee 20428 (1+2).

Diploglottis australis (Don) Radlk.: New Guinea, Clemens 41671 (1+2). — *Diploglottis diphyllostegia* (F. Muell.) Bail.: Australia, Hyland 2754 (1+2). — *Diploglottis obovata* Reynolds: Australia, Kanis 2128 (1+2).

Euphorianthus euneurus (Miq.) Leenh.: New Guinea, NGF 43427 (1+2); Celebes, (NIFS) Cel/IV-58 (1+2).

Guioa acuminata Radlk.: Philippines, FPRI 525 (1+2). — *Guioa acutifolia* Radlk.: New Guinea, Brass 7513 (2), 7739 (1); BW 8295 (1); NGF 33500 (2); Australia, Irvine 1504 (1). — *Guioa amabilis* Kaneh. & Hatus.: New Guinea, BW 14124 (2), 14202 (1). — *Guioa aryterifolia* Radlk.: New Guinea, Brass 614 (1+2); NGF 19594 (1). — *Guioa asquamosa* Welzen: Lesser Sunda Islands, Metzner 226 (1+2). — *Guioa bicolor* Merrill: Philippines, BS 25450 (A) (1+2), 33798 (NSW) (1). — *Guioa bijuga* (Hiern) Radlk.: Thailand, BKF 14593 (1+2); Malacca, KEP 80164 (2); KEP FRI 11785 (2), 15932 (1); Sumatra, Boeea 7098 (A) (1); Borneo, BRUN 5038 (1+2); Castro 4515 (2); Elmer 21392 (A) (2); Kostermans 4731 (1); SAN 41343 (2); Philippines, BS 463 (US) (1); Ebalo 483 (A) (1+2). — *Guioa chrysea* A.C. Smith: Fiji, A.C. Smith 1715 (A) (1), 4632 (1+2), 5400 (1). — *Guioa comesperma* Radlk.: New Guinea, Carr 12291 (1); Clemens 8500 (1); Hartley 12221 (2); Moi 125 (2); NGF 14484 (2), 44194 (2); Schodde 2928 (2); UPNG 2080 (2). — *Guioa contracta* Radlk.: New Guinea, Clemens 430 (1); Darbyshire 1216 (2); Hartley 10976 (1+2); NGF 18858 (2). — *Guioa coriacea* (Radlk.) Radlk.: Australia, Cormish 53a (1+2); Johnson & Rodd 1317 (2). — *Guioa crenata* Radlk.: New Caledonia, MacKee 24911 (1+2). — *Guioa crenulata* Radlk.: New Caledonia, MacKee 19989 (1); MacPherson 4534 (2). — *Guioa diplopetala* (Hassk.) Radlk.: Burma, Helfer 993 (2); Thailand, Kerr 14135 (1); Malacca, KEP FRI 3892 (1); SF

7001 (A) (1), 11151 (A) (1); Stone 8645 (1); Sumatra, Meijer 5592 (2); Java, Coert 869 (2); Kostermans 23078 (2); Van Steenis 10683 (2); Waitz s.n., L 908.269-769 (2); Zollinger 1662-2 (1); Borneo, Haviland 2137 (2); Maidin 5480 (2); S 33515 (1); SAN 62371 (2); Wiriadinata 861 (1); Celebes, Riedel s.n. (W) (1); 'Moluccas' (presumably Java), De Vriese & Teijsmann s.n., L 908.268-985 (2), L 908.269-353 (2); Cultivar, Hortus Bogor. s.n., VIII-1917 (2). — *Guioa discolor* Radlk.: Philippines, Elmer 7493 (2), 9321 (M) (1). — *Guioa elliptica* Welzen: Solomon Islands, BSIP 2410 (1), 16776 (2). — *Guioa fusca* Radlk.: New Caledonia, MacKee 40827 (1+2). — *Guioa glauca* (Labill.) Radlk. var. *glauca*: New Caledonia, Bernardi 9795 (1+2); Hartley 14895 (2). — *Guioa glauca* (Labill.) Radlk. var. *vulgaris* Welzen: New Caledonia, Bernardi 9843 (2), 10248 (2); MacKee 4261 (1+2), 32558 (1), 35407 (1), 36668 (1); MacMillan 5065a (2). — *Guioa gracilis* (Panch. & Séb.) Radlk.: New Caledonia, MacKee 26122 (1+2); Whitmee s.n. (BM) (1+2). — *Guioa grandifoliola* Welzen: New Guinea, Conn & Students 195 (1+2). — *Guioa hirsuta* Welzen: Celebes, Van Balgooy 3942 (1+2); Meijer 11420 (2); (NIFS) Cel/IV-93 (2). — *Guioa hospita* Radlk.: New Guinea, Exp. Roy. Geogr. Soc. Aus. s.n. (W) (1+2). — *Guioa koelreuteria* (Blanco) Merrill: Borneo, SAN 86708 (1); Philippines, Aranez 15 (2); Elmer 11264 (2), 12286 (1+2); Jacobs 7771 (2); PNH 10683 (2), 11137 (1), 17632 (1), 17949 (2), 36946 (1); Vidal 719 (1+2). — *Guioa lasioneura* Radlk.: Australia, Hyland 3725 (1+2); Webb & Tracey 10051 (BRI) (1). — *Guioa lentiscifolia* Cav.: Tonga, Parks 16156 (1+2). — *Guioa malukuensis* Welzen: Moluccas, Kostermans 1206 (1+2). — *Guioa megacarpa* Welzen: Solomon Islands, BSIP 338 (2), 1566 (1). — *Guioa melanopoda* Merrill & Perry: New Guinea, Brass 12783 (1+2). — *Guioa membranifolia* Radlk.: Moluccas, Kostermans 805 (1); Tuyama 1892 (2); New Guinea, Anang 655 (2). — *Guioa microsepala* Radlk.: New Caledonia, Hartley 14899 (1); MacKee 5637 (2), 16757 (1), 21811 (1); Schodde 5233 (2). — *Guioa misimaensis* Welzen: New Guinea, Brass 27661 (1+2). — *Guioa molliuscula* Radlk.: New Guinea, NGF 31702 (1+2); Schlechter 19521 (K) (1). — *Guioa montana* C.T. White: Australia, K.J. White 888 (BRI) (1+2). — *Guioa multijuga* Welzen: New Guinea, BW 4061 (1+2). — *Guioa myriadenia* Radlk.: Philippines, BS 26636 (A) (1); Clemens 17182 (NY) (1); Elmer 8704 (1); Loher 13275 (M) (1); Merrill 9650 (2). — *Guioa normanbiensis* Welzen: New Guinea, Brass 25521 (1+2); LAE 52521 (2). — *Guioa novobritannica* Welzen: New Guinea, NGF 26918 (1+2). — *Guioa novoëbudaënsis* Welzen: New Hybrides, Bernardi 13284 (1+2); Morrison s.n., 28-V-1896 (2). — *Guioa oligotricha* Merrill & Perry: New Guinea, Brass 8290 (1+2); BW 6412 (2). — *Guioa ovalis* Radlk.: New Caledonia, Jaffré 880 (1); MacKee 14699 (1); MacMillan 5166 (2). — *Guioa palawanica* Welzen: Philippines, BS 697 (2); SMHI 247 (1). — *Guioa parvifoliola* Merrill: Philippines, BS 33187 (A) (1+2). — *Guioa patentinervis* Radlk.: Moluccas, Kornassi 1171 (2); De Vogel 4210 (1), 4228 (2). — *Guioa pauciflora* Radlk.: New Guinea, Ledermann 9026 (1); NGF 41517 (1+2); Pulle 937 (1). — *Guioa pectinata* Radlk.: New Caledonia, MacKee 23796 (1+2). — *Guioa pleuropteris* (Blume) Radlk.: Thailand, Charoenphol et al. 4944 (1+2); Malacca, Burkill 1324 (1); Davidson 1325 (2); KEP FRI 5037 (2); Maxwell 81-34

[2]; Sumatra, Forbes 2617 [1+2]; Borneo, BRUN 709 [1+2]; Kato et al. 10120 [2]; S 35375 [2]; SAN 21617 [2]; Sikajat 7770 [2]; Philippines, BS 7412 [1], 20611 [1+2], 41273 [1+2]; Elmer 9827 [2], 15516 [2]; PNH 14 [1+2], 9995 [1+2], 12373 [2]; SMHI 105 [1]; Cultivar, Hortus Bogor. III-I-43 [2]. — *Guioa plurinervis* Radlk.: New Guinea, Brass 28291 [1+2]. — *Guioa pseudoamabilis* Welzen: New Guinea, ANU 2649 [1]; Hartley 12560 [2]. — *Guioa pteropoda* Radlk.: New Guinea, Brass 13082 [1], 13702 [2]. — *Guioa pterorhachis* Welzen: Borneo, Enggoh 10173 [2]; SAN 19996 [2], 86666 [1]. — *Guioa pubescens* (Zoll. & Mor.) Radlk.: Malacca, Van Beusekom 2688 [2]; KL 3287 [2]; Maxwell 82-24 [1+2]; Sumatra, Bünnemeijer 7632 [2]; Kostermans & Anta 1108 [2]; Meijer 7146 [1]; Java, Zollinger 1105 [1+2]; Borneo, bb 34880 [1]; Clemens 26823 [2]; Nooteboom & Aban 1577 [1]; S 29279 [2]; SAN 34608 [2], 92978 [2]; Philippines, Elmer 13103 [2]; PNH 12427 [1]; Cultivar, Hortus Bogor. III-I-20 [2]. — *Guioa punctata* Welzen: Fiji, Saint John 18143 [1]; A.C. Smith 4603 [2]. — *Guioa reticulata* Radlk.: Philippines, Santos 5715 [1+2]. — *Guioa rhoifolia* (A. Gray) Radlk.: Fiji, Koroiveibau et al. 14451 [2]; Koroiveibau & Singh 17093 [1]. — *Guioa rigidiuscula* Radlk.: New Guinea, Clemens 1746 [2]; Darbyshire 759 [1]; Heyligers 1380 [2]; LAE 71089 [1+2]; Sayer s.n., MEL 31966 [2]; UPNG 227 [2]. — *Guioa scalariformis* Welzen: New Guinea, NGF 21576 [1+2]. — *Guioa semiglauca* (F. Muell.) Radlk.: Australia, Clemens s.n., XI-1947 [1+2]; K.A. Williams 81237 (BRI) [1]. — *Guioa subfalcata* Radlk.: Samoa, Christophersen 560 (NY) [1+2]. — *Guioa subsericea* Radlk.: New Guinea, ANU 2772 [1+2]; Brass & Versteegh 12505 [2]; BW 1981 [1+2]; Hartley 11835 [2], 12108 [1]; Hoogland 9265 [2], 9575 [2]; Jacobs 8641 [2]; Kairo 22 [2]; NGF 39707 [2]. — *Guioa sufusana* Welzen: Solomon Islands, BSIP 4376 [2], 8604 [1], 10975 [2]. — *Guioa truncata* Radlk.: Philippines, Elmer 11219 [1]; PNH 10053 [2]. — *Guioa unguiculata* Welzen: New Guinea, Hartley 12670 [1]; Hoogland & Pullen 61931 [1]; Vink 16407 [2]. — *Guioa venusta* Radlk.: New Guinea, Britton 54 [1+2]. — *Guioa villosa* Radlk.: New Caledonia, Bernardi 10162 [2]; Jaffré 1403 [1]; MacKee 3173 [2], 3424 [1], 4296 [1], 13290 [1]; Thorne 28050 [2]. — *Guioa waigeoensis* Welzen: New Guinea, Van Royen 5409 [1+2].

Jagera spec.: New Guinea, Ledermann 10365 [2]. Type of *Guioa dasyantha* Radlk. conspecific with *Jagera discolor* Reynolds.

Rhysotoechia flavescens Radlk.: New Guinea, Van Royen 4710 [1+2]. — *Rhysotoechia koordersii* Radlk.: Celebes, Koorders 18844 [1+2]. — *Rhysotoechia* spec.: New Guinea, Carr 14999 [2].

Sapindaceae spec.: Lesser Sunda Islands, Kooy 366 [1+2].

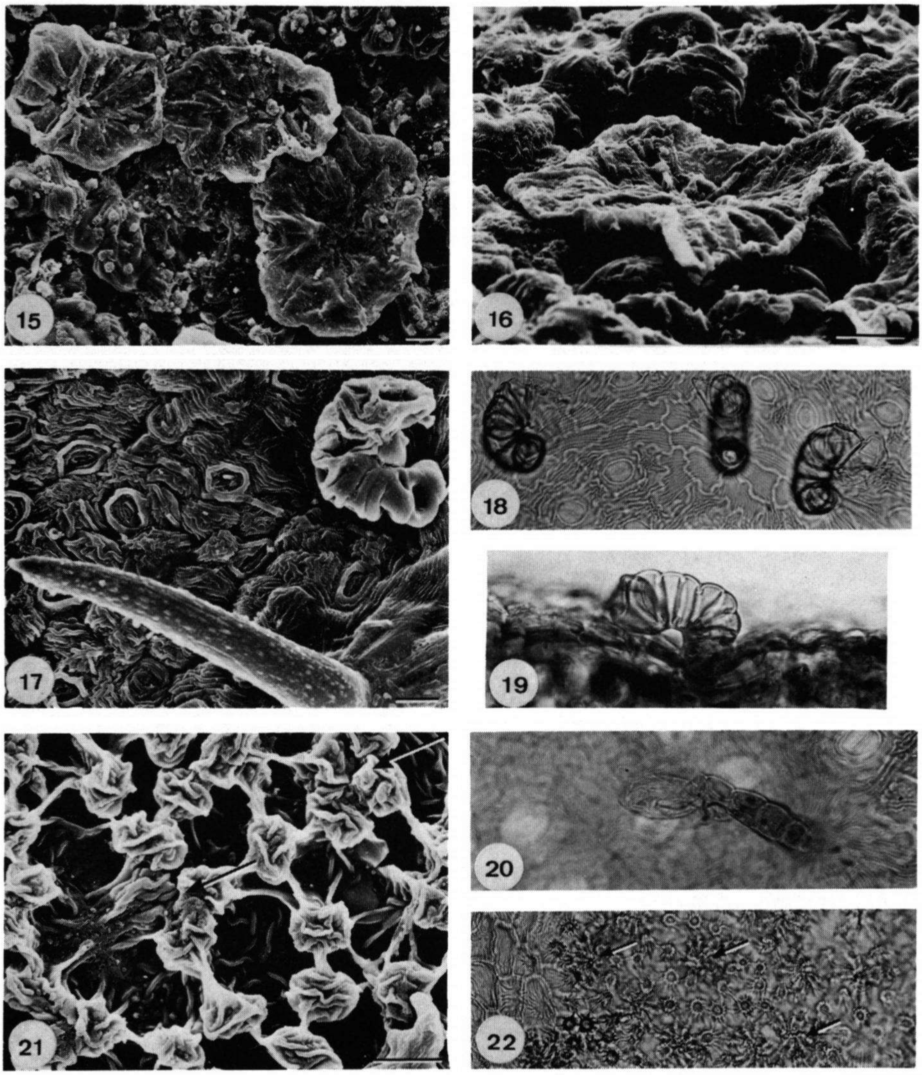
Sarcopteryx spec.: New Guinea, BW 5217 [2], 14174 [2]; Carr 13646 [2]; Hoogland & Schodde 5437 [2]; LAE 73256 [2]; Pullen 6722 [2].

Sarcotoechia apetala Leenh.: New Guinea, Brass 31795 [2].

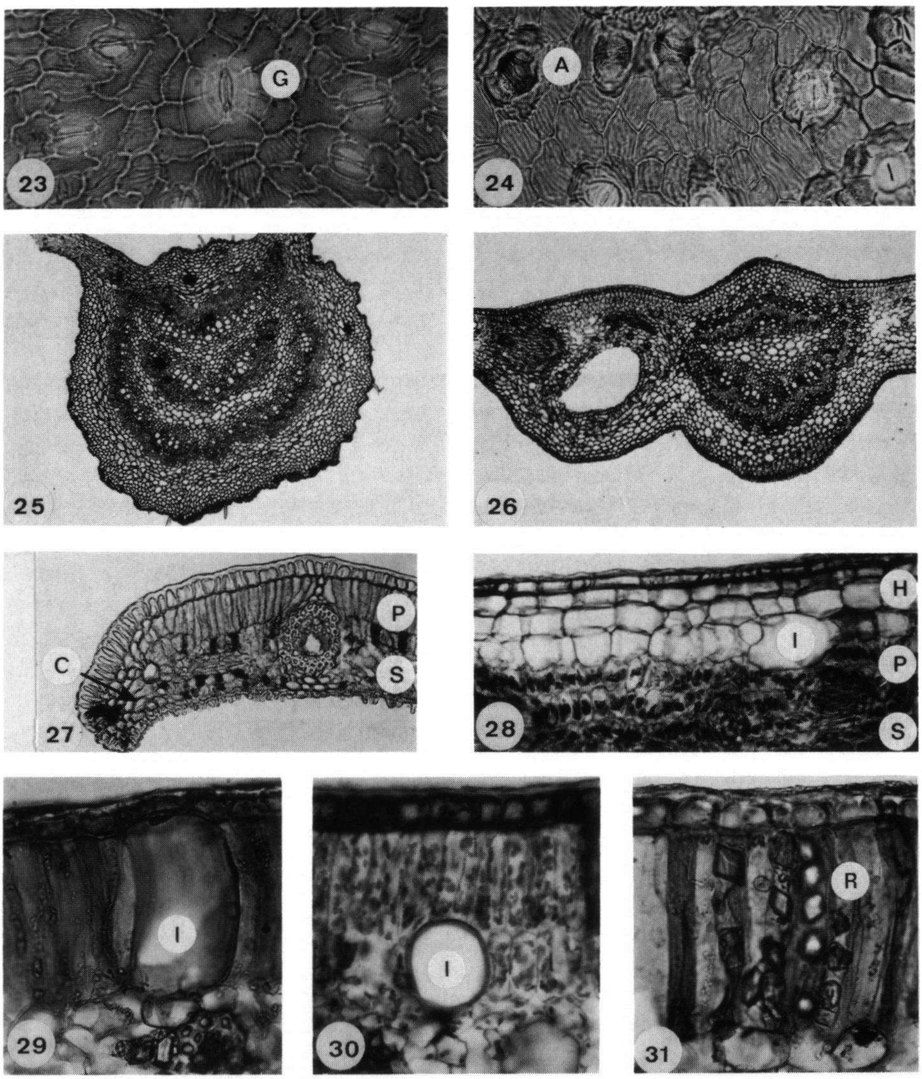
Sisyrolepis muricata (Pierre) Leenh.: Thailand, Larsen et al. 31753 [1+2]; Larsen & Larsen 34055 [1+2].

Toechima erythrocarpum (F. Muell.) Radlk. subsp. *papuanum* Leenh.: New Guinea, Hartley 10850 [2]; Kostermans & Soegeng 271 [2].

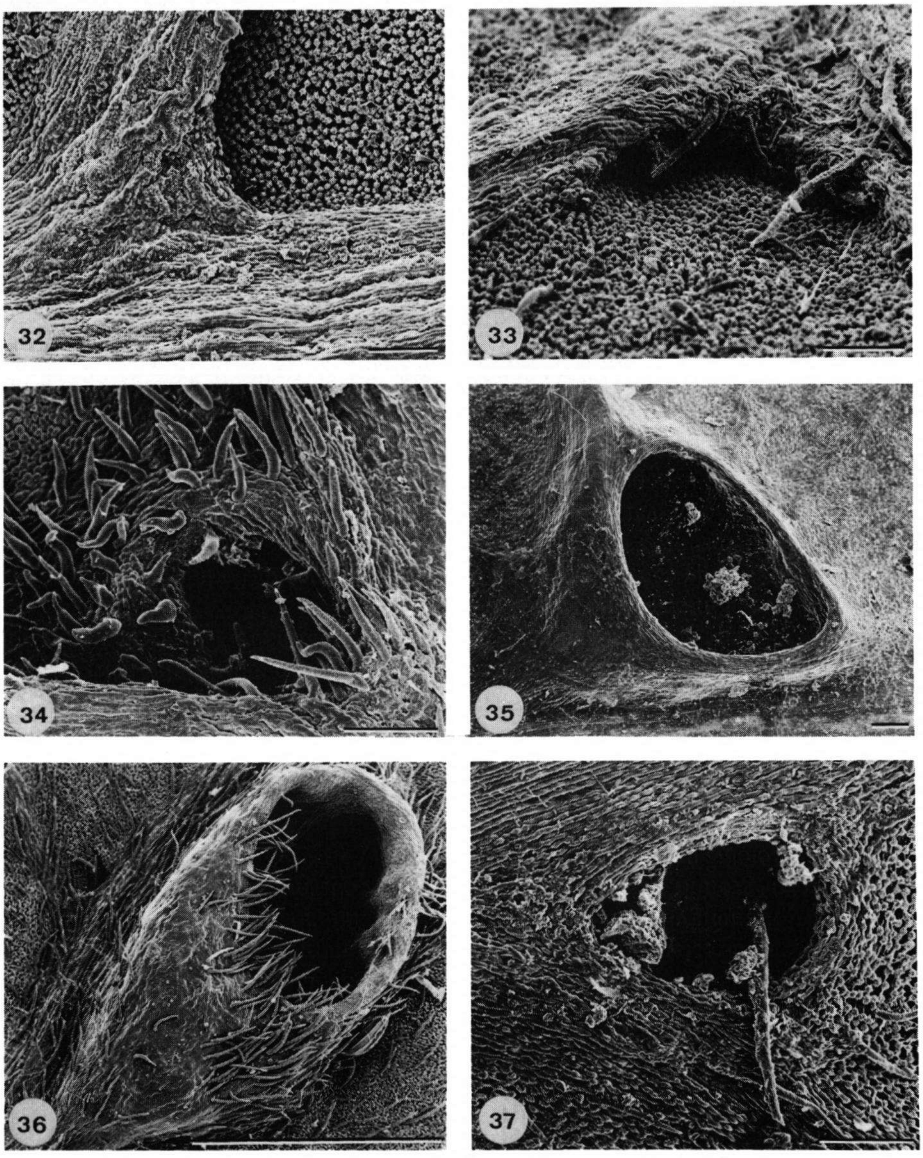
Zollingeria dongnaiensis Pierre: Thailand, Van Beusekom et al.3959 [2].



Figs. 15–22: 15. *Cupaniopsis squamosa.* Scale hair, surface view; scale bar = 10 μm. – 16. *Cupaniopsis squamosa.* Scale hair, side view; scale bar = 10 μm. – 17. *Guioa hirsuta.* Abaxially epidermis with unicellular hair, striate cuticle, cyclocytic stomata and glandular hair (many stalk cells, small glandular top cell); scale bar = 10 μm. – 18. *Guioa hirsuta.* Glandular hair (for type see former), leaflet maceration, × 290. – 19. *Guioa hirsuta.* Glandular hair (for type see former), transverse section of leaflet, × 385. – 20. *Guioa diplopetala.* Glandular hair (few stalk cells, large glandular top cell), leaflet maceration, × 385. – 21. *Guioa pterorhachis.* Papillae of abaxial epidermis with cuticular ridges on top and between them (arrow: stoma covered by papillae); scale bar = 10 μm. – 22. *Guioa acutifolia.* Papillae in leaflet maceration (arrow: stoma covered by papillae), × 245.



Figs. 23–31: 23. *Guioa diplopetala.* Giant cyclocytic stoma (G) among normal ones, × 330. – 24. *Guioa gracilis.* Abnormal stomata with extra large outer stomatal ridges (A) among normal ones, × 320. – 25. *Euphorianthus euneurus.* Midrib with complex vascularisation (extra vascular arc in pith), × 29. – 26. *Guioa asquamosa.* Domatium and midrib with simple closed vascularisation, × 36. – 27. *Euphorianthus euneurus.* Leaflet margin with collenchymatous tissue near edge (C) instead of palisade (P) and spongy tissue (S), × 90. – 28. Sapindaceae indet., *Kooy 366.* Hypodermis (H = hypodermis; I = secretory idioblast; P = palisade; s = spongy tissue), × 100. – 29. *Guioa acuminata.* Secretory idioblast (I) in palisade, × 256. – 30. *Guioa semiglauca.* Secretory idioblasts (I) in upper part of spongy tissue, × 205. – 31. *Guioa acuminata.* Rhomboidal crystals (R) in palisade, × 375.



Figs. 32–37: 32. *Guioa elliptica.* Pocket domatium, surface view; scale bar = 100 µm. – 33. *Guioa elliptica.* Pocket domatium, frontal view; scale bar = 100 µm. – 34. *Guioa elliptica.* Transition from pocket to sac domatium; scale bar = 100 µm. – 35. *Guioa fusca.* Sac domatium with frontal opening; scale bar = 100 µm. – 36. *Guioa lentiscifolia.* Sac domatium with top opening; scale bar = 1000 µm. – 37. *Guioa pterorhachis.* Sunken sac domatium; scale bar = 100 µm.

7.3. LEAF ANATOMICAL GENERIC DESCRIPTION

Below a general leaf anatomical description of the genus *Guioa* is given. Details about the characters of the different species can be obtained from table 1. See figures 15–37.

Table 1. Anatomical characters of species of *Guioa* and of related genera.

Legend: ( ) in table = sometimes present; / = and; – = absent; ± = slightly present; + = present; ? = possibly present; • = character state unknown.

Column:

1: Species names.
2: Distribution of hairs on adaxial surface (e = over entire surface; v = on midrib and/or venation).
3: Distribution of hairs on abaxial surface (see legend of 2).
4: Type of glandular hairs on adaxial surface (l = few stalk cells and large glandular top cell; o = entire glandular hair 1-celled; m = many stalk cells and small glandular top cell; s = few stalk cells and small glandular top cell).
5: Type of glandular hairs on abaxial surface (see legend of 4).
6: Papillae abaxially (s = weakly developed around stomata; ! = different type of papillae).
7: Length of papillae (± $<$ 20 µm; + $>$ 20 µm).
8: Papillae with cuticular ridges on top (n = narrow ridges).
9: Adaxial cuticle with thin areas in the loops of the undulations.
10: Abaxial cuticle with thin areas in the loops of the undulations.
11: Adaxial cuticle striate (v = above veins).
12: Abaxial cuticle striate (v = above veins).
13: Anticlinal walls of adaxial epidermis undulating.
14: Anticlinal walls of abaxial epidermis undulating.
15: Large stomata present besides normal ones in abaxial epidermis.
16: Stomata present in adaxial epidermis.
17: Some stomata with extra large outer cuticular ledges.
18: Number of palisade layers (number of palisade layers + number of transition layers).
19: Veins embedded in mesophyll.
20: Large veins transcurrent to adaxial epidermis, bundle sheath extension not sclerified.
21: Large veins transcurrent to adaxial epidermis, bundle sheath extension sclerified.
22: Large veins transcurrent to abaxial epidermis, bundle sheath extension not sclerified.
23: Large veins completely transcurrent, bundle sheath extensions not sclerified.
24: Large veins completely transcurrent, bundle sheath extensions sclerified to adaxial epidermis
25: Large veins completely transcurrent, bundle sheath extensions sclerified. [only.
26: Large veins completely transcurrent, bundle sheath sclerified around vein, extensions not scleri-
27: Sclerenchyma around domatia (ad = adaxially of domatium only). [fied.
28: Crystals around midrib sclerenchyma sheath (d: mainly druses; r: mainly rhomboidal crystals).
29: Crystals in phloem (see legend of 28).
30: Crystals in pith (see legend of 28).
31: Crystals around domatium (see legend of 28).
32: Crystals around veins (see legend of 28).
33: Crystals present in adaxial subepidermal mesophyll layer (see legend of 28).
34: Crystals present in abaxial subepidermal mesophyll layer (see legend of 28).
35: Frequency of secretory idioblasts (f = few; r = regular; m = many).
36: Secretory idioblasts in palisade tissue.
37: Secretory idioblasts in spongy tissue, directly below palisade tissue.
38: Secretory idioblasts in central part of spongy tissue.
39: Secretory idioblasts in abaxial subepidermal mesophyll layer.

(Table 1 continued: columns 1–18)

Column: 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Guioa																	
acuminata	–	v	–	–	–	–	•	–	–	–	+	±	–	+	–	–	1
acutifolia	–	v	–	–	+	+	+n	–	–	+	+	±	–	+	–	–	1
amabilis	v	e	–	–	+	+	±	–	–	–	–	–	–	+	–	–	1+1
aryterifolia	v	v	l?	l	–	–	•	±	–	–	v	±	–	+	–	–	1
asquamosa	v	v	l	l	–	–	•	±	–	–	+	±	–	+	–	–	1
bicolor	–	v	–	–	+	+	+	–	–	+	–	–	–	+	–	–	1(+1)
bijuga	v	v	o-l?	l	–-+	–-+	±n	+	–	–	+	+	±	+	–	–	1
chrysea	e	e	l	l	+	+	+	–	–	+	±	–	–	+	–	–	1(-2)
comesperma	v	v	l	l	–	–/±	(+)	–/+	–	–	+	±	–	+	–	–	1(+1)
contracta	v	v	l	l	–	–	•	+	–	–	+	+	±	+	–	–	1(+1)
coriacea	–	v	–	–	–	–	•	–	–	+	+	–	–	+	–	–	3(-4)
crenata	e	e	–	–	+	+	+	–	–	–	v	±	–	+	–	–	2
crenulata	v	e	o	l	+	+	+	–	–	±	v	±	–	+	–	–	1(+1)
diplopetala	v	v	l	l	–	–	•	+	–	–	+	+	+	+	–	–	1
discolor	v	e	–	–	+	+	+n	–	–	–	–	–	–	+	–	–	1
elliptica	v	v	l	–	+	+	+	–	–	+	+	±	–	+	+	–	1
fusca	–	v	o	–	–	–	•	–	–	–	+	+	+	+	–	+	1
glauca var. glauca	e	e	o	o	+	+	+	–	–	+	–	–	–	+	–	–	1
glauca var. vulgaris	e	e	–	–	+	+	+	–	–	+	–	–	–	+	–	–	1–2 (+1)
gracilis	–	v	–/o	o	–	–	•	+	–	–	v	+	±	+	–	+	1+1
grandifoliola	–	–	l?	–	–	–	•	–	–	–	+	–	–	+	–	–	1(+1)
hirsuta	e	e	s	s	–	–	•	+	–	+	+	+	+	+	–	–	1
hospita	v	v	l	l	–	–	•	±	–	–	–	±	–	+	–	–	1
koelreuteria	v	v	l	l	–	–/±	±	+	–	–	±	+	–/+	+	–/+	–	1(+1)
lasioneura	v	e	l	–	+	+	+n	–	–	–	–	–	–	+	–	–	1
lentiscifolia	e	e	–	–	+	+	+	–	–	±	–	–	–	+	–	–	1–2
malukuensis	e	e	l	l	+	+	+	–	–	–	+	–	–	+	–	–	1
megacarpa	v	v	l	l	+	+	+	–	–	+	(±)	–	–	+	–	–	1
melanopoda	v	v	–	l	–	–	•	+	–	–	–	±	±	+	–	–	1
membranifolia	v	v	l	l	–	–	•	–/+	–	–	+	+	–	+	–	–	1
microsepala	v	v	l	l	–	–	•	–	–	+	+	–	–	+	–	–	1(+1)
misimaensis	v	e	l	–	+	+	+	–	–	+	+	–	–	+	–	–	1(+1)
molliuscula	e	e	l	l	s	–/±	•	+	–	–	+	+	–	+	–	–	1
montana	v	e	–	–	+	+	+n	–	–	–	–	–	–	+	–	–	1+1
multijuga	v	v	–	–	+	+	+	–	–	–	–	±	–	+	–	–	1
myriadenia	e	e	l	l	+	+	+n	–	–	+	+	–	–	+	–	–	1
normanbiensis	–	v	l	l	–	–	•	±	–	–	–	±	–	+	–	–	1
novobritannica	v	v	l?	–	+	+	+	–	–	+	–	–	–	+	–	–	1(-2)+1
novoëbudaënsis	v	v	l	l	+	+	+	–	–	+	±	–	–	+	–	–	1
oligotricha	v	v	–/l	–/l	–/+	+	+n	–	–	+	+	+	–/+	+	–	–	1
ovalis	–	v	l	l	–	–	•	+	–	–	+	+	–	+	+	–	1–2(+1)
palawanica	e	e	l?	l	+	+	+	–	–	+	+	–	–	+	+	–	1+1
parvifoliola	e	e	l?	–	+	+	+	–	–	+	–	–	–	+	–	–	1
patentinervis	v/e	v	–	–	–	–	•	+	–	–	+	+	+	+	–	–	1(+1)
pauciflora	–	–	–	–	+	+	+	–	–	–	+	–	–	+	–	–	2
pectinata	–	v	l	l	–	–	•	–	–	+	+	±	–	+	–	+	1+1
pleuropteris	e	e	–	–	+	+	+n	–	–	+	–	±	–	+	–	–	1(+1)
plurinervis	v	e	–	–	+	+	+	–	–	+	–	–	–	+	–	–	1+1

(Table 1 continued: columns 1–18)

Column: 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
(Guioa)																	
pseudoamabilis	v	v	l?	–	–	–	•	–	–	v	+	–	–	+	–	–	1(+1)
pteropoda	–	v	l	l	–	–	•	–	–	–	–	+	+	+	–	–	1
pterorhachis	v/e	e	l	l	+	+	+n	–	–	+	–	+	–	+	–	–	1
pubescens	e	e	o/l	l	+	+	+n	–	–	+	–	–	–	+	–	–	1(+1)
punctata	–	v	–	–	+	+	+	–	–	–	±	–	–	+	–	–	1
reticulata	v	e	l	o?	+	+	+	±	–	–	–	±	–	+	+	–	1+1
rhoifolia	v	v	l	l	+	+	+	–	–	–	–	–	–	+	–	–	1+1
rigidiuscula	v	v	l	l	–	–/±	•	+	–	–	+	+	–	+	–	–	1(+1)
scalariformis	v	v	l	l	–	–	•	±	–	–	v	±	±	+	–	–	1
semiglauca	v	e	o?	–	+	+	+n	–	–	±	–	–	–	+	–	–	2
subfalcata	v	v	–	–	–	–	•	–	–	±	+	±	±	–	–	–	1(-2)
subsericea	e	e	l	l	+	+	+	–	–	±	–/+	–	–	+	–	–	1(-2+1)
sufusana	v	v	–	–	+	+	+	–	–	v	–	–	–	+	–	–	1
truncata	v	v	o	l	–	–	•	–	–	–	+	–	–	+	–	–	1
unguiculata	–	v	l	l	–	–	•	±	+	–	v	±	+	+	–	–	1(-2)
venusta	v	v	l	l	–	–	•	–	–	–	–	+	–	+	–	–	1+1
villosa	e	e	–	–	+	+	+	–	–	–	–v+	–	–	+	–	–	1(-2+1)
waigeoensis	e	e	–	–	+	+	+	–	–	+	v	–	–	+	–	–	1
Arytera arcuata	v	v	–	–	–	–	•	–	+	–	v	+	+	+	–	–	•
Atalaya																	
papuana	v	v	l	l	–	–	•	–	+	–	–	±	+	+	–	–	•
Cupaniopsis																	
anacardioides	–	v	l	l	–	–	•	–	–	+	+	–	–	+	+	–	1
bilocularis	v	e	m	m	s	–	•	–	–	–	+	–	–	+	–	–	•
concolor	–	–	o	o	–	–	•	+	±	–	v	+	+	+	–	–	1
platycarpa	v	v	m	m	–	–	•	–	–	–	–	±	±	+	–	–	1
shirleya	–	e	l	l	–	–	•	–	–	+	+	–	±	+	+	–	1
squamosa	–	–	–	–	+!	+	•	–	–	–	–	–	–	+	–	–	1
Diploglottis																	
australis	e	e	m	m	–	–	•	–	–	–	v	–	–	–	+	–	2
diphyllostegia	e	e	m	m	–	–	•	–	–	+	+	–	±	–	+	–	2
obovata	e	e	m	m	–	–	•	–	–	+	±	–	±	–	+	–	2
Euphorianthus																	
euneurus	v	v	m	m	–/+	–/+	±	–	–	+	+	–	±	+	+	–	2
Kooy 366	–	v	m	m	–	–	•	–	–	–	–	–	–	+	+	–	4=hypo
Jagera 'dasyantha'	–	e	–	–	+	+	+	–	–	–	–	–	–	+	–	–	•
Rhysotoechia																	
flavescens	–	–-v	l?	l?	–	–	•	–	–	–	v	–	–	+	–	–	1
koordersii	v	v	l	l	–	–	•	–	–	v	+	–	–	+	–	–	1
spec.	–	–	l	l	–	–	•	–	–	–	–	–	–	+	–	–	•
Sarcopteryx spec.	v	v-e	–/l	–/l	–/+	–	±	–	–	–	–	–	–/+	+	–	–	•
Sarcotoechia																	
apetala	v	v	–	–	–	–	•	–	–	–	–	–	–	+	–	–	•
Sisyrolepis																	
muricata	v	v	–	–	–	–	•	–	–	+	–	–	±	–	+	–	1
Toechima																	
erythrocarpum	–	v	–	–	–	–	•	–	–	–/+	–	±	–	+	–/+	–	•
Zollingeria																	
dongnaiensis	e	e	o	s	–	–	•	–	–	–	–	–	–	+	–	–	•

(Table 1 continued: columns 1 & 19–39)

Column: 1	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Guioa																					
acuminata	–	–	–	–	–	1	–	–	–	r	r	–	r	r	r	r	m	i	i	i	i
acutifolia	1	–	–	–	(1)	–	–	–	–	r	d	–	r	r	–	–	m	i	i	i	–
amabilis	–	–	–	–	–	1	–	–	•	r	–	–	–	r	–	–	r	i	–	–	–
aryterifolia	1	–	–	–	–	–	–	–	–	r	r	d/r	r	r	–	r	–	–	–	–	–
asquamosa	–	–	–	–	1	–	–	–	–	r	d	–	r	r	–	r	f	–	i	–	–
bicolor	–	–	–	–	–	1	–	1	•	r	r	–	–	r	r	r	f/m	i	–	–	i
bijuga	1	–	–	–	–	–	–	1	–	r	d	r	r	r	–	r	m	i	i	i	i
chrysea	–	–	–	–	1	(1)	–	–	+	r	d	–	r	r	–	r	r	i	i	–	–
comesperma	–	–	–	–	1	–	–	–	–	r	d	r	r	r	r	r	m	i	i	i	i
contracta	1	–	–	–	(1)	–	–	–	•	r	d	d	–	r	–	r	r/m	–	i	i	–
coriacea	–	–	–	1	–	–	–	–	•	r	d	–	–	r	–	–	–	–	–	–	–
crenata	–	–	–	–	1	–	–	–	–	r	d	–	r	d	–	–	m	–	i	–	i
crenulata	–	–	1	–	–	–	–	–	•	r	d	–	–	r	–	–	m	i	i	i	i
diplopetala	1	–	–	1	1	–	–	1	–	(r)	r	(r)	(r)	r	–	(r)	–/r	i	i	i	i
discolor	–	–	–	–	–	1	–	–	+	r	d	–	r	r	–	r	–	–	–	–	–
elliptica	–	–	–	–	–	1	–	–	–	–	–	–	–	r	–	r	m	i	i	i	i
fusca	–	–	–	–	1	–	–	–	+	r	d	–	r	d	–	–	f	i	i	–	–
glauca																					
var. glauca	–	–	–	–	1	–	–	–	–	r	d	r	r	r	r	r	r	–	i	–	–
var. vulgaris	–	–	1	–	1	–	–	–	–	r	d	–	r	r	–	–	--m	i	i	–	–
gracilis	–	–	–	–	1	–	(1)	–	+	r	d	–	r	d	–	–	f/r	i	i	i	–
grandifoliola	–	–	–	–	1	–	–	–	•	r	d	–	–	r	–	–	–	–	–	–	–
hirsuta	–	–	–	–	–	1	–	–	•	r	r	–	–	r	–	–	r	–	i	i	–
hospita	1	–	–	–	(1)	–	–	–	•	r	d	–	–	r	–	–	m	i	i	–	–
koelreuteria	–	–	–	–	1	1	–	–	–	r	d	–	(r)	r	(r)	(r)	m	i	i	i	i
lasioneura	–	1	1	–	–	–	–	–	–	r	r	–	r	r	–	r	r	i	i	i	i
lentiscifolia	–	–	–	–	1	–	–	–	+	r	–	–	–	r	–	–	f	–	i	–	–
malukuensis	–	–	–	–	–	1	–	–	–	r	d	–	r	r	–	–	f	i	–	–	–
megacarpa	–	–	–	–	1	–	–	–	–	r	r	–	–	d/r	–	–	f	i	i	i	–
melanopoda	–	–	–	–	–	1	–	–	•	r	–	–	–	r	–	–	m	i	i	i	–
membranifolia	–	–	–	–	1	–	–	–	–	r	r	r	–	r	–	r	m	i	i	–	–
microsepala	1	–	–	–	(1)	–	–	–	+	r	r	r	–	r	–	–	--f	i	i	–	–
misimaensis	–	1?	–	–	–	–	–	–	•	–	d	–	–	r	–	–	m	i	i	i	–
molliuscula	–	–	–	1	–	–	–	–	–	r	d	–	r	r	–	–	f	i	i	–	–
montana	–	–	–	–	–	1	–	–	•	r	d	–	–	r	–	–	m	i	i	–	–
multijuga	–	–	–	–	1	–	–	–	•	r	r	r	–	r	–	r	r	i	i	i	–
myriadenia	–	–	–	–	–	1	–	–	–	(r)	r	–	(r)	r	–	(r)	f	i	i	i	i
normanbiensis	1	–	–	–	–	–	–	–	–	r	d	–	r	r	–	–	–	–	–	–	–
novobritannica	–	–	–	–	–	1	–	–	+	r	r	–	r	r	–	–	m	–	i	i	–
novoëbudaënsis	–	–	–	–	1	–	–	–	–	r	–	r	–	r	–	r	f	i	i	i	–
oligotricha	–	–	–	1	–	–	–	–	–	r	d	–	–	r	–	–	r	i	i	–	–
ovalis	–	–	–	1	1	–	–	–	•	r	d	–	–	r	–	–	–/m	–	i	–	i
palawanica	–	–	–	–	–	1	–	–	–	–	r	–	–	r	–	–	f	–	i	–	–
parvifoliola	–	–	–	–	–	1	–	–	–	r	r	–	r	r	–	–	r	i	i	i	i
patentinervis	–	–	–	1	–	–	–	–	•	r	r	–	–	d	–	r	f	–	i	–	–
pauciflora	–	–	–	–	–	1	–	–	+	r	d	–	–	d/r	–	–	–/m	i	i	–	–
pectinata	1	–	–	–	–	–	–	–	–	r	r	–	d	d	–	–	r	i	i	–	i
pleuropteris	1	–	–	–	1	1	–	1	–	r	r	–	d	d	–	d	--m	–	i	i	i
plurinervis	1	–	–	–	–	–	–	–	–	r	r	–	–	–	–	–	–	–	–	–	–

(Table 1 continued: columns 1 & 19–39)

Column: 1	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
(Guioa)																					
pseudoamabilis	1	–	–	–	–	–	–	–	–	r	–	–	r	r	–	–	m	i	–	i	i
pteropoda –	1	–	–	–	–	–	–	–	–	–	–	–	–	r	–	–	m?	–	–	–	–
pterorhachis	–	–	–	–	–	1	–	–	–	r	r	–	r	r	–	r	r	–	i	–	i
pubescens	–	–	–	1	1	–	–	1	ad	r	d	–	(r)	r	–	–	–	–	–	–	–
punctata	–	–	–	–	1	–	–	–	±	r	r	r	d	r	–	d	m	i	i	i	–
reticulata	–	–	–	–	–	–	1	–	ad	r	r	–	d	r	–	–	–	–	–	–	–
rhoifolia	–	–	–	–	1	–	–	–	–	r	r	–	d	r	–	–	–	–	–	–	–
rigidiuscula	1	–	–	–	–	–	–	–	–	r	r	d	d	r	–	d	–/r	–	i	–	–
scalariformis	1	–	–	–	–	–	–	–	•	r	–	–	–	r	–	r	–	–	–	–	–
semiglauca	–	1	(1)	–	–	–	–	–	•	r	r	d	–	r	–	–	r	i	i	–	–
subfalcata	–	–	–	–	1	–	–	–	±	r	r	r	–	d	–	–	–	–	–	–	–
subsericea	–	–	–	–	–	1	–	–	–	r	r	r	d	d	–	–	–/f	–	i	i	–
sufusana	–	–	–	–	1	–	–	–	–	r	r	–	d	r	–	–	f	–	i	–	–
truncata	–	–	–	–	–	1	–	–	±	r	d	–	–	r	–	r	r	i	i	i	i
unguiculata	1	–	–	–	(1)	–	–	–	•	r	r	r	–	r	r	r	–/m	–	i	i	i
venusta	–	–	–	–	1	–	–	–	–	r	r	–	r	r	–	r	m	i	i	i	–
villosa	(1)	–	1	–	–	–	–	–	±	r	r	–	r	r	–	–	--r	–	i	–	–
waigeoensis	1	–	–	–	–	–	–	–	•	–	d	d	–	d	–	–	f	–	i	–	–
Cupaniopsis																					
anacardioides	1	–	–	–	–	–	–	–	•	–	–	–	–	–	–	–	f	–	–	–	i
concolor	–	–	–	–	1	–	–	–	•	r	–	–	–	r	–	–	m	i	i	i	i
platycarpa	1	–	–	–	–	–	–	–	–	r	r	r	(r)	r	–	–	–	–	–	–	–
shirleya	–	–	–	–	1	–	–	–	•	r	–	r	–	r	–	–	m	i	i	–	i
squamosa	1	–	–	–	–	–	–	–	•	r	r	r	–	r	–	–	f	–	i	–	–
Diploglottis																					
australis	–	–	–	–	1	–	–	–	•	r	r	r	–	r	–	–	–	–	–	–	–
diphyllostegia	–	–	–	–	1	–	–	–	•	r	r	r	–	r	–	–	–	–	–	–	–
obovata	–	–	–	–	1	–	–	–	•	r	r	r	–	r	–	–	–	–	–	–	–
Euphorianthus																					
euneurus	–	–	–	–	1	–	–	–	•	r	r	r	–	r	–	–	f/r	–	i	–	–
Kooy 366	–	–	–	–	–	–	–	1	•	r	d	–	–	r	–	d	r	–	i	–	–
Rhysotoechia																					
flavescens	1	–	–	–	–	–	–	–	•	r	d	r	–	r	d	d	–	–	–	–	–
koordersii	1	–	–	–	–	–	–	–	•	d	d	–	–	r	r	r	–	–	–	–	–
Sisyrolepis																					
muricata	–	–	–	–	–	–	1	–	•	r	r	r	–	r	–	–	–/r	–	i	i	–

Guioa Cav.

In surface view: *Non-glandular hairs* 1-celled, absent to abundantly present on both surfaces (on 'glabrous' leaflets often a few near the midrib), usually hairs of two lengths present; base narrow; wall thick, usually sclerified, especially in long hairs. *Glandular hairs* usually present, especially abaxially; sometimes consisting of a single glandular, ellipsoid, large cell, but usually with c. 3 small, flat, uniseriate stalk cells below the large, glandular top cell; *Guioa hirsuta* with a different type: 7 or 8 stalk cells underneath a small top cell. *Papillae* abaxially absent to weakly developed (then especially around the stomata) to well-developed and dense (every epidermal cell papillate); on top of the papillae narrow or wide ridges and between the apicular thickenings interconnecting, radiating ridges. *Cuticle* smooth to striate; if anticlinal wall sinuate then cuticle often thin in the loops of the undulations. *Unspecialized epidermal cells* polygonal, anticlinal walls straight to undulate (latter especially when abaxially epidermis papillate); cells around hairs, glandular hairs and stomata in a radiating pattern. *Epidermal cells above veins* usually rectangular, in rows, parallel to veins, thereby showing venation pattern of mainly the midrib and major nerves; minor veins on both sides, especially adaxially, usually slightly or not visible in epidermal cell pattern. *Stomata* predominantly cyclocytic (to anomo- or anisocytic); usually only abundantly present abaxially, in a few species some also adaxially (*Guioa elliptica, Guioa ovalis, Guioa palawanica, Guioa reticulata,* sometimes *Guioa koelreuteria*), small, less than 20 µm long; giant stomata infrequently present, especially near the midrib; guard cells slightly sunken; outer stomatal rim present, latter extra large (almost blocking stomatal pore) in several stomata near the midrib in *Guioa fusca, Guioa gracilis,* and *Guioa pectinata. Cork warts* seldomly present, presumably of traumatic origin.

In transverse section: *Lamina* dorsiventral. *Unspecialized epidermal cells* square to flat rectangular, but erect over midrib and along margin of leaflet; in abaxial surface of some species outer periclinal walls developed into papillae, otherwise walls flat, except near midrib and margin, where they are domed. *Hypodermis* locally developed over the midrib as a uniseriate continuation of the ground tissue of round, somewhat collenchymatous cells. *Mesophyll:* palisade tissue composed of 1 or 2 layers (in *Guioa coriacea* 3 or 4) of long, erect cells, often with a transition layer of shorter, less compact cells towards the spongy tissue; the latter rather compact, especially subepidermally, with square to flat rectangular cells. *Midrib* usually raised on both sides, especially abaxially; ground tissue of round, somewhat collenchymatous cells, more developed on abaxial side; sclerenchyma sheath present around vascular system; the latter collateral, simple closed, with a rather flat, small adaxial arc and a domed, larger abaxial arc; pith consisting of large, round, parenchyma cells, often filled with starch grains, with between the cells numerous small, triangular, intercellular spaces. *Major veins* usually slightly raised, especially abaxially; bundles either embedded in mesophyll or transcurrent to either the adaxial or the abaxial epidermis or usually completely transcurrent by bundle sheath extensions; the latter usually sclerified to adaxial epidermis and with ground tissue-like parenchyma to abaxial epidermis, sometimes only ground tissue-like parenchyma or only sclerenchyma, especially when the veins are only partly transcurrent; sclerenchyma sheath present around bundle. *Leaf margin* with marginal vein and normal mesophyll. *Domatia* usually present in one or several vein axils (for different types and occurrence see chapter 6); epidermis a continuation of the abaxial epidermis, but papillae diminishing in heigth in domed part; subepidermal cells often containing crystals or sometimes weakly sclerified, then mainly so on adaxial side, but sometimes domatium completely surrounded by sclerenchyma (especially in New Guinea, Pacific and Philippine species). *Rhomboidal crystals* and *druses* always present, varying from few to abundant; subepidermally in parenchyma, especially abaxially, either mainly druses or mainly rhomboidal crystals; in ground tissue of midrib usually large rhomboidal crystals; in phloem usually small druses; in pith either mainly large druses or mainly large rhomboidal crystals; around veins usually rhomboidal crystals outside the sclerenchyma sheath; around domatia often abundant, mainly rhomboidal crystals. *Secretory idioblasts* rarely absent, few to abundant, small to very large, usually round, but often rectangular in palisade; occurring in mesophyll, then especially in upper part of spongy tissue, but also in palisade and abaxial subepidermis; sometimes also in ground tissue of midrib, but then cells much smaller; wall slightly sclerified; contents unknown.

7.4. INFRASPECIFIC VARIATION

The genus *Guioa* is leaf anatomically very homogeneous: a dorsiventral mesophyll with a few layers of palisade and a compact spongy tissue, secretory idioblasts usually present, a simple closed collateral vascular system, unicellular hairs usually present, cyclocytic stomata, and usually a few glandular hairs. Consequently, infraspecific and even interspecific variation is low.

Usually variation can only be found in the abundance of certain characters. The characters, which show variation, are listed below.

N.B.: Infraspecific variation was only studied for a few, mainly West Malesian species. Therefore the species mentioned are only examples. It should not be concluded that the species which are not mentioned do not possess variation.

Within a species the crystals, glandular hairs, hairs and secretory idioblasts can vary in frequency and often in distribution. For instance secretory idioblasts in *Guioa glauca, Guioa ovalis, Guioa pleuropteris,* etc. vary between absent and abundant. In this context absence only means absent in the sections studied; secretory idioblasts (or crystals, glandular hairs and hairs) may still be present in other parts of the leaflet or in other leaflets of the same specimen.

The crystal type may also vary, from mainly rhomboidal in one specimen to mainly druses in another, as for instance in *Guioa megacarpa* or *Guioa pauciflora*.

The glandular hairs can vary between the type which only consists of a single secretory cell and the type which also has a stalk (e.g. adaxially in *Guioa bijuga* and *Guioa pubescens*).

Domatia can be present or absent, the variation in this character is treated more elaborately in chapter 6, Macromorphological characters.

Papillae usually form a constant character; they are either present, or absent to only weakly developed around stomata. Only *Guioa bijuga, Guioa diplopetala,* and *Guioa oligotricha* vary between papillae absent to every epidermal cell papillate.

Striation of the abaxial cuticle, undulation of the epidermal anticlinal walls and thin areas of the cuticle in the loops of these undulations are characters which sometimes vary, usually from absent to present. The thin areas are usually absent when the leaflets are papillate. *Guioa comesperma* and *Guioa membranifolia* show variation in the thin cuticle areas (absent/present). *Guioa subsericea* and *Guioa villosa* have smooth to striate abaxial cuticles, while *Guioa koelreuteria* and *Guioa oligo-*

tricha have specimens with epidermal cells with straight (papillate) or undulated anticlinal walls.

Guioa koelreuteria is the only species which shows variation in the presence of adaxial stomata (present/absent). Most species do not possess adaxial stomata, only a few have them, but of these (*Guioa elliptica, Guioa ovalis, Guioa palawanica* and *Guioa reticulata*) only one specimen was investigated.

The number of palisade layers shows little variation. There may be an additional layer or the transitional layer from palisade to spongy tissue may be present or absent.

The veins can vary between embedded in the mesophyll to completely transcurrent (e.g. *Guioa diplopetala, Guioa pleuropteris*).

7.5. CHARACTERISTICS AND INFRAGENERIC GROUPINGS

This chapter contains a discussion of the anatomical characters observed in the genus *Guioa*, related to infrageneric groupings. All character states mentioned occur in *Guioa*, unless stated otherwise.

Papillae — Most species with papillae show papillae with broad cuticular ridges. Only a few geographical groups (an Australian and a West Malesian group) show narrow ridges. *Guioa oligotricha* (New Guinea) also has narrow ridges.

Hairs — The hairs are adaxially absent in several species of the *Guioa rigidiuscula*-complex (*Guioa grandifoliola, Guioa normanbiensis*, and *Guioa unguiculata*) and in most of the non-papillate species of New Caledonia (*Guioa fusca, Guioa gracilis, Guioa pectinata*, and *Guioa ovalis*). Most abaxial cells with hairs is apomorphic for *Guioa subsericea* and the representatives of the Australian/New Caledonian group in the cladogram of the New Guinean group.

Glandular hairs — All species (also species of other genera besides *Guioa*) showed glandular hairs of which the top cell was unicellular. Apparently, multicellular heads may also be found, as Farooqui (1982) reported for *Sapindus laurifolia*, Nair & Joseph (1960) for *Cardiospermum halicacabum*, and Rénard (1913) for *Koelreuteria paniculata* (all three species are placed in other tribes than the Cupanieae). The specimen *Kooy 366* (an unidentified species of Sapindaceae) may also have them. All *Guioa* species showed the same type of glandular hairs, except *Guioa hirsuta*, which has a different type (more stalk cells, a smaller glandular top cell). The presence of four-celled glandular hairs is apomorphic for *Guioa melanopoda* and *Guioa patentinervis* of the New Guinea group.

Thin areas in the loops of the adaxial cuticle is apomorphic for *Guioa melanopoda* and *Guioa patentinervis* of the New Guinean group, but many parallels and reversals exist.

Undulating abaxial epidermal anticlinal walls are typical for *Guioa melanopoda, Guioa patentinervis*, and *Guioa unguiculata* of the New Guinean group; a parallel exists for *Guioa pteropoda*.

Stomata — Three species show several stomata with an almost closed stomatal aperture, because of large outer stomatal rims, at first sight an aberrant character.

These three species (*Guioa fusca, Guioa gracilis,* and *Guioa pectinata*) of New Caledonia are however closely related.

Domatia — The domatia are usually not supported by sclerenchyma. Species with very large, high sacs, like *Guioa lentiscifolia, Guioa microsepala, Guioa novobritannica, Guioa pauciflora,* and *Guioa truncata,* have sclerenchyma around the domatium. The function of sclerenchyma in these instances is presumably support. However, some species with smaller domatia also possess sclerenchyma, some of which are related: *Guioa pubescens, Guioa reticulata* (both only adaxially sclerenchyma), and *Guioa discolor,* all mainly from the Philippines; *Guioa fusca* and *Guioa gracilis,* both closely related; and some more unrelated Pacific species: *Guioa punctata, Guioa villosa,* and *Guioa subfalcata* (the latter presumably not a *Guioa*). The presence of sclerenchyma around the domatium constitutes two apomorphies within the Pacific group: *Guioa chrysea–Guioa lentiscifolia–Guioa punctata* (partly sclerified) and *Guioa chrysea–Guioa lentiscifolia* (completely sclerified). The epidermis within the domatia showed a continuation of the normal epidermis, no special, gland-like structures were observed. This is conform the observations of O'Dowd & Willson (1989).

Mesophyll — Only *Guioa coriacea* shows an exceptional feature: instead of 1 or 2 layers of palisade cells, this species possesses 3 or 4 layers.

Transcurrent veins — a) The veins are not transcurrent (embedded in the mesophyll) in many New Guinea plants, especially in species of the *Guioa rigidiuscula*-complex. b) *Guioa lasioneura* and *Guioa semiglauca* (both Australian species) have veins which are only transcurrent to the adaxial epidermis. The ground tissue can be 'collenchymatous' or sclerenchymatous. c) The latter type of vein is also found among some New Caledonian species: *Guioa crenulata, Guioa glauca,* and *Guioa villosa,* three of the four papillate species of this island. d) Completely transcurrent veins with non-sclerified ground tissue are mainly found among Pacific and New Guinean species, but also among a few West Malesian ones. e) Completely transcurrent veins with adaxially sclerenchyma to the epidermis or with sclerenchyma only in the sheath part are found among West Malesian species.

Crystals — a) Crystals in the phloem are absent in some Pacific and New Guinean species. b) Crystals in the pith of the midrib are found in East Malesia (*Guioa bijuga* and *Guioa diplopetala* pro parte excepted).

Secretory idioblasts — Several (11) species lack the secretory idioblasts, while others only sometimes lack them (10). Of these *Guioa aryterifolia, Guioa grandifoliola, Guioa normanbiensis, Guioa plurinervis, Guioa rigidiuscula, Guioa scalariformis,* and *Guioa unguiculata* are related (*Guioa rigidiuscula*-complex).

7.6. GENERIC DELIMITATION

Guioa has no unique anatomical characters; all characters can be found in other Sapindaceae. In spite of the lack of unique characters, *Guioa* can be distinguished from most other genera, due to a different combination of anatomical characters.

Guioa has been compared with specimens of some genera which are regarded to be closely related: *Cupaniopsis, Diploglottis, Euphorianthus, Rhysotoechia,* and *Sisyrolepis.* The differences between the genera are summarized in table 2.

Table 2. Differences between *Guioa* and related genera.

See general legend of table 1 for explanation of •, /, –, ±, and +.

Column:
1 : Genus names.
2 : Scale hairs present.
3 : Type of glandular hairs on adaxial surface (c = multicellular glandular part; l = few stalk cells and large glandular top cell; o = entire glandular hair 1-celled; m = many stalk cells and small glandular top cell; s = few stalk cells and small glandular top cell).
4 : Papillae abaxially present (s = weakly developed around stomata; ! = different type).
5 : Anticlinal walls adaxial epidermis straight.
6 : Stomatal size (l = large, > 20 µm long; sm = small, ≤ 20 µm long).
7 : Midrib vascularisation (c = complex closed, with additional vascular bundles in pith; s = simple closed).
8 : Hypodermis present.
9 : Secretory idioblasts present.

Column: 1	2	3	4	5	6	7	8	9
Arytera	+	–	–	+	sm	•	•	•
Atalaya	–	l	–	±	sm	•	•	•
Cupaniopsis	–/+	o/l/m	–/s/+!	–/+	sm	s	–	–/+
Diploglottis	–	m	–	–	sm	c	–	–
Euphorianthus	–	m	–/+	–	sm	c	–	+
Guioa	–	–/o/l/s	–/s/+	–/+	sm	s	–	–/+
Jagera	–	–	+	–	sm	•	•	•
Kooy 366	–	c	–	–	sm	s	+	+
Rhysotoechia	–	l	–	–	l/(sm)	s	–	–
Sarcopteryx	–	–/l	–/+	–	sm	•	•	•
Sarcotoechia	–	–	–	–	sm	•	•	•
Sisyrolepis	–	–	–	–	sm	s	–	–/+
Toechima	–	–	–	±	sm	•	•	•
Zollingeria	–	o/s	–	–	l	•	•	•

Diploglottis australis, Diploglottis diphyllostegia, Diploglottis obovata, and *Euphorianthus euneurus* were studied leaf anatomically. The genera *Diploglottis* and *Euphorianthus* are thought to be closely related (compare Leenhouts, 1978 and 1988). Both genera differ from *Guioa* (and all other Sapindaceae studied) by their more complex midrib vascularisation, with in the pith extra vascular bundles (usually an arc, often with additional bundles). They also possess glandular hairs with many (c. 10) stalk cells and a small glandular top cell; this type is present in other Sapindaceae too, but is absent in *Guioa.*

Euphorianthus differs from *Diploglottis* as it possesses secretory idioblasts and often a papillate abaxial epidermis, characters which are absent in *Diploglottis*. These differences support the latest view by Leenhouts, namely to keep both genera separated.

Rhysotoechia flavescens and *Rhysotoechia koordersii* both lack the secretory idioblasts which are found in *Guioa*; the absence of this character is not exclusive for *Rhysotoechia* as several species of *Guioa* also lack these cells. The anticlinal walls are very straight; the stomata of most *Rhysotoechia* species are more than 20 µm long (*Rhysotoechia flavescens* excepted), those of *Guioa* are less than 20 µm long. Solereder (1899) and Metcalfe & Chalk (1950) recorded the palisade cells to be only slightly higher than broad. This was not found for *Rhysotoechia australis* and, less so, for *Rhysotoechia flavescens*. Solereder also mentions secretory idioblasts for *Rhysotoechia*; these were not observed in the specimens studied.

Sisyrolepis muricata possesses an epidermis with mucilage cells, a phenomenon absent in *Guioa*. *Sisyrolepis* also has scale hairs, just like *Arytera arcuata* and *Cupaniopsis squamosa*. This type of hairs has never been found in *Guioa*. These characters of *Sisyrolepis*, together with the possession of secretory idioblasts and crystals, were also reported by Solereder (1908).

Of *Cupaniopsis* 5 species (of each one specimen) have been studied. Only two species can be separated from *Guioa*, all others are not completely distinguishable. All specimens studied of *Cupaniopsis* more or less lack the type of papillae often found in *Guioa*; sometimes they are weakly developed around the stomata.

Cupaniopsis anacardioides, *Cupaniopsis concolor*, and *Cupaniopsis shirleyana* cannot be separated from *Guioa*, although the midrib of *Cupaniopsis anacardioides* is slightly different as the upper vascular arc is as big and arched as the lower vascular arc. *Cupaniopsis anacardioides* also possesses stomata adaxially, just like *Cupaniopsis shirleyana*; a phenomenon rare in *Guioa*.

Cupaniopsis platycarpa has a different type of glandular hairs, which resemble those of *Guioa hirsuta*, but the glandular hairs of *Cupaniopsis platycarpa* show more stalk cells (10 or more instead of 7 or 8, just like those of *Cupaniopsis bilocularis*, *Diploglottis* and *Euphorianthus*).

Cupaniopsis squamosa shows the most striking differences: the adaxial epidermis often shows periclinal division walls; the cuticle above the anticlinal walls is thickened, so that an intricate pattern of rims is formed; the abaxial epidermis is somewhat papillate, and here the cuticle has the same thickenings, but only on a finer scale; moreover, scale hairs are present on both sides.

Solereder (1899) and Metcalfe & Chalk (1950) mention delicate vertical walls in the epidermal cells of *Cupaniopsis* species. These were not found in the specimens studied. *Cupaniopsis inoplea* seems to possess sclerenchymatous fibres or sclerosed cells (Solereder, 1899). Several species lack secretory idioblasts (Solereder, 1899), like *Cupaniopsis platycarpa* in the present study.

Besides the above mentioned specimens several other species were examined in surface view only (leaf macerations):

Arytera arcuata shows scale hairs (only section *Azarytera*; Solereder, 1899), just like *Cupaniopsis squamosa* and *Sisyrolepis muricata*. Solereder (1899) and Metcalfe & Chalk (1950) mention the following characters, which are different from those of *Guioa*: delicate vertical walls in the epidermal cells, sometimes a hypodermis, a lack of glandular hairs (except section *Azarytera*). Some *Arytera* species may also lack the secretory idioblasts, just like several *Guioa* species.

Atalaya papuana cannot be distinguished from *Guioa*.

Cupaniopsis bilocularis possesses, like *Cupaniopsis platycarpa, Diploglottis,* and *Euphorianthus,* a different type of glandular hairs.

Kooy 366 (Sapindaceae spec.) has a complete, 4-layered hypodermis, and possesses numerous druses. Macromorphologically this specimen resembles *Guioa diplopetala*; palynologically and anatomically it is also quite unlike *Guioa* (Van der Ham & Van Heuven, pers. comm.). The glandular hairs appear to have a multicellular glandular part (unicellular in *Guioa*).

Ledermann 10365 (type of *Guioa dasyantha* Radlk.), conspecific with *Jagera discolor* Reynolds, cannot be distinguished from *Guioa*. It shows the same type of papillae as *Guioa*.

Sarcopteryx spec. is indistinguishable from *Guioa*. Some specimens also show the above mentioned papillae, but most have a smooth epidermis.

Sarcotoechia apetala has, just like *Rhysotoechia,* very straight anticlinal walls.

Toechima erythrocarpum subsp. *papuanum* is not separable from *Guioa. Toechima* lacks glandular hairs (unlike most *Guioa* species) and the palisade cells are hardly longer than broad (Solereder, 1899; Metcalfe & Chalk, 1950).

Zollingeria dongnaiensis has two types of glandular hairs, the normal *Guioa* type with a few stalk cells and a rather large glandular top cell, and the *Guioa hirsuta* type with more (5 or 6) stalk cells and a smaller glandular top cell. *Guioa* always shows only one type of glandular hair. The stomata are, like those of most *Rhysotoechia* species, more than 20 μm long.

8. ECOLOGICAL ASPECTS

8.1. HABITAT OF SOME GUIOA SPECIES

Most *Guioa* specimens live between sea-level and 1000 m altitude. Only the specimens of a few New Guinean species are exclusively found in the mountains, e.g. *Guioa amabilis, Guioa pauciflora, Guioa pseudoamabilis.*

Probably most individuals can adapt themselves to extreme environments. Examples: A species like *Guioa koelreuteria* is found on ultrabasic soil. Most New Caledonian specimens are capable of living on ultrabasic soil, but are also found on other soil types. Other extreme environments are salty areas, like along the beach, and the nutrient-poor peat swamp forests. Normally, the habit of the plants found in extreme environments differs from those of the less extreme areas. The specimens show a tendency to have papillate leaflets in peat swamp forests and to lose the papillae in salty environments. In the latter two areas the plants possess smaller leaflets than on other soils.

During a field trip in Sabah, N Borneo, the habitat of three *Guioa* species was studied in five transects. The first three transects were established in Sepilok Laut (Sepilok Forest Reserve, Sandakan): one in the mangrove, along the path; the second in the transition zone between mangrove and secondary forest; in both areas *Guioa bijuga* was found. The third was along the path in the transition zone between secondary and primary forest, where *Guioa pterorhachis* occurred. The fourth transect was established in secondary forest along a path in the study area of the Agricultural Research Station Ulu Dusun (near Sandakan); here too, *Guioa pterorhachis* was studied. The fifth transect was in Kiau (east of Mt. Kinabalu National Park) along a river in secondary forest/belukar; here *Guioa pleuropteris* was found.

In all five areas the *Guioa* species were only found at the secondary edges of forests, along paths and rivers. The field notes on labels of dried material of other species indicate that this is a typical environment for *Guioa* specimens. However, there must be sufficient light, but the weeds may not be high and dense. No treelets will be found in dense, high grass margins of roads. When the correct conditions are met with, seeds of *Guioa* germinate rapidly, probably even after a period of dormancy, as for instance in a piece of bamboo forest in Poring (west part of Mt. Kinabalu National Park), which was cleared of undergrowth and showed hundreds of recently germinated seedlings of *Guioa bijuga*. Intriguing was that no mature trees were found (Van Balgooy, pers. comm., had a similar experience in Borneo).

Some of the (identified) species which grow along the transects are listed below. The sequence of the transects is the same as described above. The fact that the *Guioa* species are found at the margin of primary forest is demonstrated by the presence of for instance the Dipterocarpaceae, which are typical primary forest species, and by the presence of secondary forest plants, like species in the families Euphorbiaceae, Melastomataceae, Rubiaceae, and Zingiberaceae. The absence of high, dense weeds is demonstrated by the presence of the ground orchid, the ground ferns, and by the grasses. The latter are grasses which grow in woods; most of them are low, creeping or ascending plants, which do not form high, dense tussocks (e.g. *Dinochloa* excepted).

Family	Genus/Species	Transect				
Annonaceae	*Artobotrys roseus* Boerl.		2		4	
Annonaceae	*Polyalthia insignis* (Hook. f.) Airy Shaw			3		
Annonaceae	cf. *Trivalvaria*				4	
Apocynaceae		1				
Araceae			2	3		5
Aristolochiaceae	*Aristolochia tagala* Cham.			3		
Aspidiaceae	*Tectaria barberi* (Hook.) Copel.				4	
Begoniaceae	*Begonia*			3		
Compositae						5
Connaraceae	*Rourea minor* Alston				4	
Dichapetalaceae	*Dichapetalum gelonoides* (Bedd) Engl.		2			
Dilleniaceae	*Dillenia beccariana* Mart.	1				
Dilleniaceae	*Dillenia exelsa* (Jack) Gilg		2			
Dipterocarpaceae	*Parashorea*				4	
Dipterocarpaceae	*Parashorea tomentella* Meijer		2			
Dipterocarpaceae	*Shorea foxworthyii* Sym.			3		
Dipterocarpaceae	*Shorea macroptera* Dyer		2			
Dipterocarpaceae	*Shorea smithiana* Sym.			3		
Dipterocarpaceae	*Vatica albiramis* Van Slooten	1				
Ebenaceae	*Diospyros buxifolia* (Blume) Hiern			3		

Family	Genus / Species	Transect				
Euphorbiaceae	*Antidesma neurocarpa* Miq.		2			
Euphorbiaceae	*Aporusa grandistipula* Merr.				4	
Euphorbiaceae	*Baccaurea trigonocarpus* Merr.				4	
Euphorbiaceae	*Baccauria parviflora* Muell. Arg.				4	
Euphorbiaceae	*Croton argyratus* Blume				4	
Euphorbiaceae	*Fahrenheitsia pendula* Airy Shaw			3		
Euphorbiaceae	*Glochidion rubrum* Blume	1				
Euphorbiaceae	*Macaranga*				4	
Euphorbiaceae	*Macaranga triloba* Muell. Arg.				4	
Euphorbiaceae	*Mallotus lackyii* Elmer			3		
Euphorbiaceae	*Mallotus wrayi* King ex Hook. f.				4	
Fagaceae	*Lithocarpus*		2			
Flacourtiaceae				3		
Gesneriaceae	*Cyrtandra*				4	
Gramineae	*Centotheca lappacea* (L.) Desv.		2	3		
Gramineae	*Cyrtococcum accressens* (Trin.) Stapf		2			
Gramineae	*Cyrtococcum oxyphyllum* (Steud.) Stapf			3		
Gramineae	*Dinochloa*				4	5
Gramineae	*Oplismenus compositus* (L.) Beauv.			3		
Gramineae	*Scrotochloa urceolata* (Roxb.) R. Br.				4	
Gymnogrammaceae	*Taenitis blechnoides* (Willd.) Sw.				4	
Labiatae						5
Lauraceae	*Actinodaphne glomerata* (Blume) Nees		2			
Lauraceae	*Eusideroxylon zwagerii* Teijsm. & Binn.			3		
Lauraceae	*Litsea* cf. *megacarpa* Gamble			3		
Lecythidaceae	*Barringtonia curranii* Merr.				4	
Leguminosae	*Albizia pedicellata* Baker ex Benth.	1				
Leguminosae	*Bauhinia semibifida* Roxb.		2			
Leguminosae	*Derris*		2			
Leguminosae	*Derris elliptica* Benth.			3		
Leguminosae	*Fordia splendidissima* (Miq.) Buysen				4	
Loganiaceae	*Strychnos ignatii* Berg.				4	
Maranthaceae	*Donax*		2			
Melastomataceae	*Dissochaeta rostrata* Korth.		2			
Melastomataceae	*Melastoma*	1	2			
Melastomataceae	*Memecylon*	1				
Melastomataceae	*Pternandra*		2			
Menispermaceae	*Diplochisia kunstleri* (King) Diels			3		
Moraceae	*Ficus*				4	5
Moraceae	*Ficus uncinata* Becc.		2	3		
Moraceae	*Poikilospermum cordifolium* Merr.			3		
Myrsinaceae	*Ardisia colorata* Roxb.	1				
Myrtaceae	*Eugenia*	1	2		4	
Ochnaceae	*Gomphia serrata* (Gaertn.) Kanis			3		
Oleaceae	*Chionanthus cuspidatus* Blume	1				
Oleandraceae	*Nephrolepis*					5
Orchidaceae	*Liparis*			3		

Family	Genus / Species	Transect				
Palmae	*Calamus*				4	
Pandanaceae	*Pandanus*	1				
Pittospermaceae	*Pittospermum resiniferum* Hensl.	1				
Rosaceae	*Rubus rosifolius* J.E. Sm.					5
Rubiaceae		1			4	
Rubiaceae	*Maschalocorymbus*				4	
Rubiaceae	*Psychoteria valentonii* Hockr.			3		
Rutaceae	*Evodia*			3		
Rutaceae	*Lunasea amara* Blanco		2			
Sapindaceae	*Guioa bijuga* (Hiern) Radlk.	1	2			
Sapindaceae	*Guioa pleuropteris* (Blume) Radlk.					5
Sapindaceae	*Guioa pterorhachis* Welzen			3	4	
Saurauiaceae	*Saurauia acuminata* Merr.			3		
Schizaeaceae	*Lygodium circinnatum* (Burm. f.) Sw.			3		
Schizaeaceae	*Lygodium longifolium* (Willd.) Sw.	1	2			
	Selaginella				4	
Smilacaceae	*Smilax leucophylla* Blume		2			
Solanaceae	*Solanum torvum* Sw.					5
Sterculiaceae	*Sterculia rubiginosa* Vent.			3	4	
Thelypteridaceae	*Christella arida* (Don) Holttum					5
Thelypteridaceae	*Macrothelypteris torreniana* Ching					5
Verbenaceae	*Teysmanniodendron pteropodum* Bakh.		2			
Verbenaceae	*Vitex*	1				
Vitidaceae	*Leea*		2	3		
Vitidaceae	*Leea indica* (Burm. f.) Merr.			3		
Vitidaceae	*Tetrastigma pedunculare* (Wall.) Planch.			3		
Zingiberaceae	*Alpinia*	1	2	3		
Zingiberaceae	*Globba*			3		

8.2. FLORAL BIOLOGY OF SAPINDACEAE IN RELATION TO GUIOA

Sapindaceae have been recorded to be either monoecious or dioecious (except *Dodonaea,* which can have bisexual flowers). A special form of monoecy, prevalent among most Sapindaceae, is (duo)dichogamy. The plants show, in the case of duodichogamy, a sequence of three phases. During the first phase male flowers develop. These have well developed stamens with dehiscent anthers containing functional pollen and a reduced pistil. When they have dropped, female flowers appear on the same inflorescence. The female flowers have a well developed pistil and short stamens with indehiscent anthers. The phases may overlap for a few days. The third phase appears after the female flowers started fruit-set. These flowers are seemingly hermaphrodite, both pistil and stamens are well developed, but usually they are effectively male (in *Acer,* instead of the 'hermaphrodite' phase, a second female phase can appear when the first female phase has been suppressed for some reason; De Jong, 1976). Dichogamous plants either miss the first or usually the last phase. The overall result of (duo)dichogamy is that monoecious plants are in effect dioecious. Some examples of flowering types: *Litchi chinensis* (Mustard, Liu & Nelson, 1954) is duodichogamous and shows two sequences consecutively, but the second sequence often lacks the initial male phase. The male and 'hermaphrodite' flowers of *Litchi* can be divided into two types, one with short filaments and the other with long ones. *Paullinia cupana* var. *sorbilis* also is duodichogamous with two consecutive sequences of the three flower phases, but of the second sequence the first male phase is lacking (Gondim, 1984). *Cupania guatemalensis* (Bawa, 1977) and *Sapindus emarginatus* (Subba Reddi et al., 1983; *Sapindus emarginatus* is a forma of *Sapindus trifoliatis*) are duodichogamous species. *Xerospermum intermedium* (a synonym of *Xerospermum noronhianum*, see Leenhouts, Blumea 28, 1983: 389–401) is truly dioecious (Appanah, 1982). *Pometia pinnata* and *Allophylus cobbe* are both polygamous (probably also dichogamous); *Nephelium lappaceum* too, but the latter species may also produce male trees (Ha et al., 1988). Later on several of these species will be discussed in more detail.

The floral biology of *Guioa* has never been studied and is not readily deduced from herbarium specimens as the latter always show one phase of flowers. Usually two types of flowers can be observed: male flowers with a small pistil, long filaments and open anthers (fig. 7a); and female flowers with large pistil, short filaments and indehiscent anthers (fig. 7c). Sometimes a third type can be found: 'hermaphrodite' flowers with a rather large pistil and long filaments (fig. 7b). The anthers of the latter are usually dehisced, so they are presumably male; however, drying of the plants may also have caused the anthers to dehisce. The 'hermaphrodite' flowers are intermediate, in filament and pistil length, between the male and the female flowers. This makes it very difficult to establish which type of flowers is present on a sheet. Graphs show continuous length ranges. Duodichogamy seems to be the case in *Guioa*. Quite often specimens are found with, usually on separate branches, fruits and either buds or male/hermaphrodite flowers, as if part of the tree already switched to the next phase. Some examples in different species are:

Guioa diplopetala	Haviland 1003
	Korthals s.n., s.d., L 925.250-625
Guioa chrysea	Damanu 57
	MacDaniels 1040
Guioa coriacea	Moore 30
Guioa elliptica	Brass 2884
	BSIP (Whitmore) 2410
Guioa gracilis	MacKee 25661
Guioa lentiscifolia	Crosby 29
	Lister s.n., XII-1889
	Yuncker 16106
Guioa megacarpa	BSIP (Whitmore) 1566
Guioa pleuropteris	Bremer 1842
	KEP (Zainal) 18356
	SAN (Singh) 24025
	SAN (Shea & Minjulu) 76159
Guioa semiglauca	Ford s.n., s.d., NSW 168602
	Wilcox s.n., XI-1875
	Woolls s.n., s.d., MEL 1537253
Guioa sufusana	BSIP (Gafui et al.) 16993

The situation might, of course, be more complex, e.g. some species can be dioecious instead of dichogamous, a situation also found in *Acer* (De Jong, 1976). Sometimes exceptions are encountered, which may indicate the flowering of a next phase: the last flowers of a female inflorescence can be male/hermaphrodite (*Guioa koelreuteria:* BS (Ramos) 88 (see habit drawing), PNH (Sulit) 11758); or inflorescences with hermaphrodite or male flowers may bear fruit-setting female flowers in the lower half (*Guioa fusca:* MacKee 25661; *Guioa koelreuteria:* BS (Ramos) 13048, Iwatsuki et al. s.n., 7-XII-1975).

In case of (duo)dichogamy or dioecy fertilization has to be ensured by cross-pollination. However, Appanah (1982) found that *Xerospermum* has a low percentage of (delayed) self-pollination, due to the eventual breakdown of the anther wall of the stamens of the female flowers, whereby the longest anthers, which touch the stigma, leave some pollen behind. Ha et al. (1988) could not confirm the partial self-compatibility of *Xerospermum* with direct observations, but of the female flowers, the two longest stamens were the only ones to show pollen germination (10%). (*Nephelium lappaceum* could not be selfed; Lin, 1984; Ha et al., 1988). Apart from the partial self-compatibility, Appanah found two ways in which *Xerospermum* may promote cross-pollination.

a) Daily, the male and female flowers produce pulses of nectar in an alternating rhythm. The female flowers show about three, not very distinct, production peaks, while the male flowers have two intermittent peaks. Insects showed two activity peaks while they visited the male flowers; these corresponded with the nectar peaks. In between these two peaks they visited the female flowers; this activity peak corresponded to the middle nectar peak of the female flowers. Bawa (1977) found the same insect activity for *Cupania guatemalensis*. Uji (1987) recorded a slightly, but not significantly higher male than female activity in the morning and afternoon for *Nephelium lappaceum*, during noon both sexes were visited in equal numbers.
b) The composition of the nectar is the same per sex, but complementary in amounts of nutrients. Male flowers produce a low amount of amino acids (compensated for by the pollen), a high level of hexoses and little sucrose. Female flowers show a high level of amino acids and sucrose, but little hexoses.

Sapindus emarginatus (Subba Reddi et al., 1983) possibly has another mechanism. The male flowers show a nectar peak in the morning, just like the female flowers. The latter have a second peak in the afternoon. In *Xerospermum* the male flowers produce more nectar than the females, in *Sapindus* it is the opposite, the female flowers produce about three times as much nectar as the male flowers do. Male flowers compensate the lower amount of nectar with their pollen. Insect activity, although dependent on the species, roughly shows a morning and an afternoon peak, independent of the flower sex. *Paullinia cupana* (Gondim, 1984) shows the same insect activity, although the afternoon peak is very low. Apparently the different types and amounts of food have to attract the pollinators to both sexes. An alternation between sexes was not observed. Subba Reddi et al. also studied the chemical composition of the nectar, but they did not look for differences between the sexes.

Appanah, just like Subba Reddi et al., sees the nectar as the main reward for the insects, while Bawa points to the pollen as the insect's main nutritional source. Bawa's opinion is brought about by the absence of nectar, when he probed the flowers with a micropipette. Consequently he sees the non-functional anthers in female flowers as mimics. This opinion is corroborated by the facts that there are far more male than female flowers (a fact valid for all Sapindaceae discussed in this chapter), the female flowers have a short duration, and female flowers are far less often visited than male flowers. However, Bawa also suggests two other reasons for the high amount of male flowers: a) the high energy cost of fruit production; b) heavy loss of pollen to insects. Presumably, Bawa's method of measuring nectar was too crude, as *Cupania guatemalensis* possesses a well developed disc. This makes it more logical to assume that the nectar, and for male flowers together with the pollen, forms the main food source.

Both *Cupania guatemalensis* and *Xerospermum intermedium* are most efficiently pollinated by bees of the genus *Trigona*. Hawkeswood (1983) found the same for *Cupaniopsis anacardioides*. *Nephelium lappaceum* is mainly pollinated by *Apis* and by *Trigona* (Uji, 1987; Van Welzen et al., 1988). Free & Williams (1976) recorded bees to be the best pollinators of *Blighia sapida*. *Sapindus emarginatus* and *Paullinia cupana* are also mainly pollinated by bees, but in both studies (part of) the plots were cultivated fields, where the insect composition might be very different from natural habitats; in both species *Trigona* bees were present among the pollinators. Labels on herbarium specimens suggest that *Guioa* flowers are mainly visited by bees too.

Trigona, apparently an important pollinator for Sapindaceae, is recorded to be an opportunistic feeder (Baker, 1973). An opportunistic feeder, a social bee spending much time while feeding on many flowers of one plant with little inter-tree movement, does not seem to be a reliable cross-pollinator. However, bees can learn which flowers have to be visited at which time (Gould & Marler, 1987). They learn in the following sequence of decreasing importance: odour, colour, shape/pattern; besides they learn the time at wich a flower is to be visited (up to a maximum of 9 'appointments' in 8 hours) and the relative geographical position of the plant. A change in one of these factors erases everything they have learned. Martinez del Rio & Eguiarte (1987) hint at the ability of *Trigona* to learn; while Appanah et al. (1986) even show this ability. The almost complete absence of foreign pollen on the *Trigona* bees who visited *Xerospermum* (Appanah, 1982) also indicates the ability to learn.

The mechanisms which promote cross-pollination, the ability of bees to learn and a limited possibility of self-compatibility may account for the successful fruit set of the Sapindaceae. Inherent to cross-pollination, especially when social insects (opportunistic feeders) are important pollinators, is that the trees with the different sexes are situated near each other. An increased distance between trees will decrease inter-tree movements and consequently pollen dispersal will be limited (Subba Reddi et al., 1983).

From an evolutionary point of view, (duo)dichogamy presumably is symplesiomorphous (primitive) for the Sapindaceae, as genera with few apomorphous characters possess this feature (e.g. *Cupania, Cupaniopsis*). Dioecy seems to be a derived (advanced) character; genera with several apomorphous characters show it (e.g. *Nephelium, Xerospermum*). Besides a tendency towards dioecy, there also is a tendency towards anemophily, instead of entomophily, as is demonstrated by the more derived, but closely related family of the Aceraceae (Hesse, 1979). N.B.: The phylogenetic relations are inferred from Muller & Leenhouts, 1976.

Outcrossing, as is obligate with duodichogamy or with dioecy, resulting in heterozygosity, allows for a greater adaptability of the species and is advantageous against pests and diseases. Heterogeneity, macromorphologically and genetically, has been shown for *Xerospermum* (Gan et al., 1977).

8.3. FRUIT DEVELOPMENT AND FRUITING BIOLOGY OF GUIOA

Young fruits develop very quickly, but maturation may take a long time or mature fruits are soon dropped or eaten, as many herbarium specimens show green fruits and only few red, mature ones. During fruit development the petals and stamens will soon drop. The sepals usually remain attached. The seeds develop at a late stage; usually they start growing when the fruit has almost reached its full size. However, herbarium specimens with ripe, opened fruits without any seeds (only non- or partly developed ovules) are often encountered, presumably fertilization has failed for some reason. Usually, during normal development, only 2 out of 3 fruit lobes develop, the third remains abortive; fruits with either one or all three lobes developed are also regularly found.

The arilloid starts its development as a thickened part near the hilar region. Then a lobe develops underneath the ovule towards the side opposite to where the ovule is attached to the fruit axis. The lobe continues growing until it reaches the top of the growing ovule. During further seed development the arilloid will ultimately envelop the seed almost completely. Around the top of the seed the arilloid will be open and the margin will be lobed. The first lobe which developed will form a rim along the basal part of the arilloid. The end of the rim opposite to the seed attachment will form an elongation, called pseudo-funicle (Van Welzen, 1988a). This pseudo-funicle will attach itself to the basal corner of the fruit lobe, where it gets clenched by the stipe of the fruit.

During dehiscence the downward hanging fruits open their lobes, until these lobes are almost in one plane; then the seeds will fall out and remain dangling on the pseudo-funicle. They are attractive to birds, not only because of the dangling movement, but also because of the colour combination: red fruits, orange arilloid, and dark brown, almost black, shiny seeds (see Van der Pijl, 1982, for a further discussion of this syndrome). Labels on herbarium specimens record seeds of *Guioa unguiculata* to be eaten by birds (*Jackson 109*) and *Guioa glauca* var. *vulgaris* by parakeets (*MacKee 38209*). Although the arilloid is small and thin man also eats it (for this reason many vernacular names exist). Insects also like the arilloid, as many seeds on herbarium specimens lack the arilloid because of glutton. But insects and, less so, man are poor means of seed dispersal.

Young fruits of Sapindaceae are generally green, hard, and full of tannin. When mature, the colour has changed (usually to red) and the fruit wall has softened (Ha et al., 1988). Another, perhaps general, phenomenon is, that sapindaceous trees often show a good harvest during one season, followed by a poor one during the next season. This is recorded for *Cupania guatemalensis* (Bawa, 1977), *Xerospermum intermedium* (Appanah, 1982), and *Nephelium lappaceum* (Van Welzen & Verheij, 1989).

Pannell (Pannell & White, 1988) has shown that in *Aglaia* (Meliaceae) the indehiscent, usually larger fruits were eaten by mammals and the dehiscent, usually smaller fruits by birds. Most Cupanieae show small dehiscent red fruits with brightly coloured arilloids, which are probably all bird dispersed. Most Nephelieae (thought to be derived from the Cupanieae) have larger indehiscent fruits with white or translucent arilloids, which are mammal dispersed.

8.4. SEEDLINGS AND GERMINATION

Seeds of *Guioa pleuropteris* obtained from the botanical garden in Bogor (Indonesia: Hortus Bogoriense III-J-45, -103a, and -103b) were cultivated in the botanical garden of Leiden University (the Netherlands). Ha et al. (1984) found that the seeds germinate better if pericarp and arilloid/sarcotesta are removed, mimicking in this way the passage of fruit through the digestive system of an animal. For *Guioa* this proved to be unnecessary.

In the seed the cotyledons of *Guioa pleuropteris* are dorsoventrally situated above each other, the apices of both are elongated and dorsoventrally flattened. The apex of the upper cotyledon is straight, that of the lower one is folded backwards and upwards. The two cotyledons somewhat resemble a handshake (fig. 14b). The radicle is also dorsoventrally flattened and can be found in a pocket of the testa. The apex of the radicle and the petioles of the cotyledons point towards the micropyle. From the pockets upwards, along the outline of the radicle and the petioles, the (usually hardly visible) pleurograms can be found, one on either side of the seed.

During germination the radicle and the petioles swell and become terete. The testa pocket breaks open and the seed opens along the pleurograms. The opening might be purely mechanical by the swelling of the radicle and petioles, but can also occur because of wear of the testa. Next the radicle, hypocotyl and petioles elongate. The testa remains loosely draped around the cotyledons. The latter turn green. De Vogel (1980) classified this type of seedling as the *Horsfieldia* type and subtype. This type was also observed by the author for *Guioa bijuga, Guioa coriacea,* and *Guioa pterorhachis.*

Seedlings of *Guioa* often differ markedly from the mature plants. The first pair of leaves are opposite, instead of alternate. The rhachis of the leaves is slightly winged. The leaflets still lack domatia and papillae, while the margin is serrate (to crenate). Some of these characters rapidly disappear: the leaflets become papillate and will show domatia (if the species concerned has them). Seedlings of *Guioa pterorhachis* show basal leaflets without domatia and papillae, while leaflets of the upper part already possess them (usually still less domatia than mature specimens show). The winged rhachis and the serrate leaflets still remain for a long time, these characters disappear when the plant has reached maturity (winged, serrate, flowering specimens are occasionally encountered). Observed juvenile plants with winged rhachises and serrate leaflets:

Guioa acutifolia:	Webb & Tracey 6366, 6754, 6807, 6864, 7833, 8514, 8903, 9107, 13254, 13255, 13256.
Guioa bijuga:	Welzen 717, 764, 918, 932, 933.

Guioa coriacea:	Johnson & Rodd 1317.
Guioa diplopetala:	Hoogerwerf 238; Koorders 11006, 24803; Posthumus 2212; S 21957; Teijsmann HB 12443; Waitz s.n.
Guioa hirsuta:	Meijer 9930.
Guioa koelreuteria:	PNH 36946.
Guioa ovalis:	Jaffré 880; MacKee 22428.
Guioa pleuropteris:	Amdjah 209; Welzen 947.
Guioa pterorhachis:	Welzen 715, 719, 847, 876, 917.
Guioa semiglauca:	C.T. White s.n., X-1919.

9. DELIMITATION WITHIN THE GUIOA RIGIDIUSCULA-COMPLEX

The material of New Guinea was revised after that of Australia. Several species could easily be distinguished, but a large part of the material appeared to be a heterogeneous mass in which almost no species delimitations could be made. These plants all showed the same type of petal (fig. 121b): an elliptic blade; a distinct claw; free scales and spathulate crests (the only exception was *Guioa unguiculata,* which had been added because of the fruit type). Radlkofer (1933) had distinguished 8 species in this complex, but he only had a very limited amount of specimens available during his study. A limited amount of specimens often facilitates revision, because 'gaps' between 'species' are not blurred by species variation. At first, during the present study which encompassed much more material, only three species could be distinguished: *Guioa comesperma, Guioa plurinervis* and *Guioa rigidiuscula.* The latter, after which the complex has been named, contained all the specimens which could not be attributed to the former two and became a heterogeneous dustbin species. Moreover, the more material that arrived for examination the more variable and the less satisfactory *Guioa rigidiuscula* became.

Some forms within the complex were rather apparent, e.g. one form (now distinguished as *Guioa grandifoliola*) showed very large leaflets; others had fruits with a short, slender stipe and long, strongly diverging lobes (*Guioa aryterifolia*). Most of the observed differences appeared to be describable in quantitative characters, rather than in qualitative ones. A principal component analysis was used to obtain delimitation within the *Guioa rigidiuscula*-complex, but failed to result in distinct clusters of specimens. One of the reasons for this failure is lack of material. In total about 100 specimens were used in the analysis, an already rather small sample for the 14 species which were distinguished in the end. Moreover, about a quarter of the specimens could not be used because they were either sterile, in bud, or had young fruits. The remaining specimens had to be divided into two groups (for two analyses), because flowering specimens showed no fruits and vice versa. Another reason for the failure is the complication that immature fruits of *Guioa* tend to open during drying of the plant. They then resemble mature fruits and when used in the analysis their dimensions blur possible gaps in measurements. This was the more annoying as the fruits, together with the leaflets, had to provide most of the delimitative characters, as the petals were uniform for the species complex.

When the quantitative analysis failed, only a qualitative one remained. This analysis was undertaken after the remainder of the genus had been revised. Then characters were known, which showed interspecific variation and (almost) no intraspecific variation. These were characters like: presence or absence of papillae, domatia, indumentum; shape of the leaflets; completeness of the disc, etc. These characters were used to divide the *Guioa rigidiuscula*-complex artificially. The first character divided the complex into two groups, the second one resulted in four piles, etc. Fortunately no parallel groups appeared. On the contrary, very homogeneous piles were formed, piles which started to show corroborating characters, independent of the ones used to form the piles. For instance, *Guioa contracta* appeared to have, besides a lack of papillae, indumentum and domatia, rather large, elliptic leaflets and a peculiar type of fruit (very thick walls, and almost indehiscent); *Guioa aryterifolia* always had fruits with a very short, slender stipe, and long, very diverging lobes. Moreover, the piles/species usually had a very limited distribution, while the more widespread species showed no disjunctions.

The table below shows the characters used to distinguish all 14 species. N.B.: The table does not show phylogenetic relationships, only phenetic similarities and differences:

- Leaflets papillate below:
  - Leaflets sericeous, no domatia or 1 or 2 pockets:
    - Leaflets elliptic, symmetric: .... *Guioa misimaensis*
    - Leaflets ovate, falcate: .... *Guioa plurinervis*
  - Leaflets glabrous, 1 large sac: .... *Guioa novobritannica*
- Leaflets smooth, without papillae:
  - Petal type like fig. 126b: .... *Guioa unguiculata*
  - Petal type like fig. 121b:
    - Disc complete:
      - Leaflets hirsute: .... *Guioa molliuscula*
      - Leaflets glabrous:
        - Fruit stipe 2.5 mm, petals 2.5–3.8 mm: ...... *Guioa scalariformis*
        - Fruit stipe 1.5 mm, petals 1.8–1.9 mm: .... *Guioa aryterifolia*
    - Disc incomplete:
      - Veins puberulous: .... *Guioa hospita*
      - Veins glabrous or sparsely sericeous:
        - Domatia 2 to many: .... *Guioa comesperma*
        - Domatia absent or 1:
          - Leaflets ovate:
            - Stipe of fruit 3–3.5 mm, slender: ..... *Guioa normanbiensis*
            - Stipe of fruit 1–1.5 mm, broad: .... *Guioa grandifoliola*
          - Leaflets elliptic:
            - Domatia absent: .... *Guioa contracta*
            - Domatia 1 sac:
              - Upper margin fruit straight: .... *Guioa membranifolia*
              - Upper margin fruit highly convex: ..... *Guioa rigidiuscula*

The delimitation within the *Guioa rigidiuscula*-complex has been difficult. One might wonder why the groups in the *Guioa rigidiuscula*-complex have been given specific rank. Three reasons explain this choice: 1) The species concept is the same as for other *Guioa* species in East Malesia, the Pacific and Australia (see also chapter 5). 2) The gaps between the species were constant, while the distributions were usually restricted and never disjunct. 3) The third reason is a practical one: stability of names, because the species which already were distinguished by Radlkofer were confirmed by the present analysis. Quite often a species complex cannot be resolved or artificial solutions are reached and one or no species at all are distinguished: Within *Drimys* (Winteraceae), Vink (1970) only distinguished entities without any taxonomic status, just because the specific delimitation could not be resolved in a satisfactory way. Grey-Wilson (1980) had a slightly different solution for *Impatiens* (Balsaminaceae); he distinguished one very heterogeneous species for New Guinea with 15 infraspecific, informal groups.

This chapter shows that an artificial technique may lead to delimitation in a species complex. The term artificial has been used for two reasons. a) The technique is opposite to the one used to delimit the other species, now differences instead of similarities were used to distinguish species. b) At first, the species were characterized by only one character, quite opposite to the criterium which was proposed in chapter 5 (two characters should at least be present). Only later on additive characters were found.

10. PUNCTUATED EQUILIBRIA: COMPLEX SPECIES EXPLAINED?

In New Guinea the species complexes in *Guioa, Drimys* and *Impatiens* are not exceptional, more genera/species show them: *Sarcopteryx* and *Cupaniopsis* (Sapindaceae; resp. Jaspars & Leenhouts and Adema, pers. comm.), *Epiblastus* and *Bulbophyllum* (Orchidaceae; resp. Eriks and Vermeulen, pers. comm.), *Diospyros ferrea* (Ebenaceae; Pannell & White, 1988), *Vavaea amicorum* (Meliaceae; Pennington, 1969).

Another region with a high number of species complexes is Borneo. Some examples: The distinction between *Guioa bijuga* and *Guioa pubescens* becomes rather blurred on the Crocker Range. *Bulbophyllum mutabile* (Orchidaceae) becomes very heterogeneous in these mountains, even starts to show new characters in several populations (Vermeulen, pers. comm.). In Borneo *Xanthophyllum* (Polygalaceae), Dipterocarpaceae and *Nephelium* show numerous species and several species complexes.

The occurrence of species complexes within different plant families in several areas indicates that a historical cause may exist. The remainder of this chapter will discuss a putative explanation.

Presently two more or less competing theories about evolution exist: Phyletic gradualism versus Punctuated equilibria.

Phyletic gradualism sees the events of speciation as gradual, constant processes of anagenetic change, culminating now and then in cladogenesis. The mode of change is more or less constant, stasis does not exist.

Punctuated equilibria on the other hand sees speciation as quick outbursts of change, during a relatively short (geological) period of time. The speciation moments are then followed by longer periods of stasis, during which the anagenetic change of the species is practically absent. The mode of change fluctuates. The theory of Punctuated equilibria was presented by Eldredge & Gould (1972). They asserted that the evidence of the fossil record should be taken literally. Fossils show the same form during a long geological period and are then 'suddenly' replaced by other forms. Phyletic gradualism insists that the normal gradual, constant change is still present, but only obscured by missing links in the fossil record.

The theory of Punctuated equilibria was supported by the case of *Phacops rana*, a trilobite of the Middle Devonian. At the beginning of the Middle Devonian (380 m.a.) *Phacops milleri*, a species with 18 rows of eye lenses, was found widely spread in the shallow Mid-American sea. After the sea had retracted for the greater part and increased again, *Phacops milleri* was substituted by *Phacops rana*, a species with 17 columns of eye lenses. A population of *Phacops milleri* was found, existing prior to the restriction of the sea, which showed transversions from 18 to 17 columns. The explaining model for this event is: a peripheral population of *Phacops milleri*, like the transitional population, speciated into *Phacops rana*. During the regression of the sea *Phacops milleri* became extinct and after the sea expanded again the surviving *Phacops rana* could replace its ancestor. N.B.: In this situation phyletic gradualism can also be valid as an explanation, as during the fall and rise of the sea fossils were scarce and a gradual change may have been present (Eldredge, 1985).

A possible mechanism is shown by the butterfly *Melitaea aurinea*. Between 1884 and 1897 a constant number of butterflies was present in England. They showed a small amount of variability. Till 1920 the number of butterflies decreased. Between 1920 and 1924 the number increased enormously and many different wing patterns and abnormal forms were found, also many deformities. The increase happened during a period of low or different selection pressure (biotic and abiotic factors together). After 1924 the number more or less stabilized to the pre-1897 level and the population showed again a low amount of variability, but now centered around a different form (Ford, 1971).

This example is not a case of speciation, just like the industrial melanism of the pepper moth is not. The reaction of *Melitaea* is normal within its genetic variation. Subsequent to a change in selection pressure radiation follows and after a while forms will stabilize around (a) different phenotype(s), which was (were) already defined by the genotype (Scharloo, 1987). However, it cannot be excluded that speciation can happen within the same genotype.

The stasis in form of a species can be explained by a constant selective pressure (Scharloo, 1987), which conserves and stabilizes a form. The replicational and developmental processes of DNA form another conservative factor (Geesink & Kornet, 1989): chickens still possess the genetical information for enamel (teeth; Kollar & Fisher, 1980). The more or less sudden outburst of forms after a change in selection pressure is to be expected, not only because the genotype allows it, but also on the basis of the laws of statistical thermodynamics (Brooks & Wiley, 1988): remove order (constant selective pressure) and chaos (polymorphism) will result.

The following discussion will focus on geologically unstable areas. In geologically unstable areas, i.e. areas with altering selection pressures, form-radiation (polymorphism) is to be expected: geological events can disrupt species distributions and will change selection pressure, as a result, due to lack of gene flow, genetic drift, etc., polymorphism and perhaps speciation will be the result. The polymorphism will usually be recognized as a complex of a very heterogeneous species (see former chapter: *Drimys, Impatiens*) or of sibling species (*Guioa rigidiuscula*-complex). The changes in geologically unstable areas are fast, consequently polymorphism becomes apparent shortly after a change. This mode of speciation or change in species is best explained by the model of Punctuated equilibria as Phyletic gradualism only allows for gradual change and not for a sudden change.

New Guinea is a geologically very unstable area. Apart from plate tectonics and orogenesis, the alteration between glacial and interglacial periods has had a pronounced effect (Johns, 1986). Short term disturbances (e.g. gales, earthquakes, slides, etc.) are also important in New Guinea. Johns records them for this last century. Johns (1986), in his figure 15, a kind of summary, shows that these disasters often occur and vast areas are influenced by them, often for a rather long time. The overall picture is one of a dynamically changing landscape. Consequently, species complexes of plants are regularly found in New Guinea (see also Pannell & White, 1988; they also discuss the likely influence of seed dispersal by different animal groups, e.g. birds or mammals, on speciation). Species complexes among plants will be more numerous than among animals as the latter can escape unsuitable conditions (see also Eldredge, 1985). The same applies to Borneo, which too is a geologically active area (orogenesis: Mt. Kinabalu; plate tectonics: Crocker Range; glacial and interglacial periods: river systems; poor soil). And again, species complexes are found.

Examples of former species complexes are described by Bryce (1986) for several large lakes (for instance the ciclid fishes in Lake Victoria).

Stanley (1973) provides an alternative/additional theory (besides the one of sufficient amounts of oxygen having been built up) for the sudden increase in life forms and species between the Precambrian and the Cambrian. In the Precambrian only a few species of mainly prokaryotic autotrophic blue algae existed. Stanley reasoned that the formation of eukaryotic herbivorous and carnivorous protists, which eat the algae and each other, triggered the species radiation in the Cambrian. So, a change in the selective pressures (introduction of higher trophic levels and/or high enough amounts of oxygen) resulted in (geologically) quick speciation.

There is another check of the validity of the application of the theory of Punctuated equilibria to species complexes. Within the theory of Phyletic gradualism species complexes can be expected at the moment of speciation after a gradual accumulation of anagenetic change. The anagenetic change is constant and not influenced by changes in selective pressure. Therefore, geologically stable areas should not show significantly less species complexes than instable areas, provided Phyletic gradualism applies. On the basis of Punctuated equilibria the opposite may be expected. This statistical notion still has to be corroborated by more examples than the ones already mentioned. At the moment it appears that unstable areas show more species complexes than stable areas do. This supports the view that complex species are best explained by Punctuated equilibria.

The genetical mechanism(s) behind the geologically quick speciation events will not be touched upon here. Except for two remarks. 1) The genome is usually very flexible and large parts of it are not used. This probably accounts for the polymorphism. 2) Hybridization and polyploidy can account for fast speciation moments, especially in plants. However, the species status of polyploids and hybrids often remains disputed. Two examples: a) *Galeopsis tetrahit* (Lamiaceae), a tetraploid back-cross between the diploid *Galeopsis pubescens* and the triploid hybrid of the diploids *Galeopsis pubescens* and *Galeopsis speciosa* (Müntzing, 1930; Priddle Houts & Hillebrand, 1976) and b) *Potentilla anglica* (Rosaceae), a hecta- or octoploid hybrid of the tetraploids *Potentilla reptans* and *Potentilla erecta* (Schwendener, 1970).

A question remains: Is the concept of Punctuated equilibria really opposed to Phyletic gradualism or not. The answer is: not really. 1) The theory of Phyletic gradualism was developed from an ecological/genetical standpoint, while the concept of Punctuated equilibria was developed from a paleontological viewpoint. A gradual process on an ecological time scale can be a sudden process on a paleontological time scale. 2) Both theories can be fitted into the Neo-Darwinian theory. Phyletic gradualism and Punctuated equilibria are in fact the extremes on the same, continuous scale. The 'synthetic theory' for instance stands in between as it allows for stasis and rather quick speciation events. Many have tried to falsify one of the two theories, but falsification, if possible at all, will only result in a narrowing of the scale width. Instead of falsification, it is better to judge each lineage separately and to see which part(s) of the lineage is (are) better described by a form of Phyletic gradualism and which by a form of Punctuated equilibria. Even this view is too simplistic, as it pertains to species only; there may even be differences between populations: *Guioa pleuropteris* is very uniform on Sumatra, but very polymorphic on N Borneo and Palawan.

11. PHYLOGENETIC ANALYSIS OF GUIOA

11.1. IS GUIOA MONOPHYLETIC?

A natural classification of *Guioa* is the goal of the present thesis. In order to achieve this aim a phylogenetic analysis and the presence of monophyletic groups are imperative, as was already expounded in chapter 5. The assumption that *Guioa* is monophyletic is based on three arguments, which are shown below in order of increasing importance:

1. The genus is very homogeneous in its characteristics, especially in fruit (see next argument), leaf anatomy (chapter 7) and pollen morphology (Van der Ham & Van Heuven, 1989), and somewhat less so in vegetative and floral characters: The leaves are always paripinnate. The sepals are discussed under 2. The normally 5 petals usually have crested scales. The stamens are always 8 in number and the ovary is always 3-locular with a non-lobed style-stigma on top.

2. The genus has a (mainly) monothetic, unique set of characters: the fruit is lobed, obcordate, thin-walled, with a glabrous, very smooth inside; the seed is completely surrounded by an arilloid with basically a rim from which a pseudo-funicle reaches to the bottom corner of the lobe; the notorrhizal cotyledons are situated dorsoventrally above each other. The sepals are dimorphic and petaloid.

   The following of these characters are polythetic: sepals dimorphic (all equal in *Guioa microsepala*); fruit thin-walled (thick-walled in *Guioa contracta* and *Guioa grandifoliola*); pseudo-funicle present (absent in *Guioa aryterifolia, Guioa contracta, Guioa grandifoliola,* and *Guioa rigidiuscula*); cotyledons dorsoventrally above each other (secondarily laterally besides each other in Australian, New Caledonian, and West Malesian species).

   The exceptions mentioned above are secondary developments after the ancestral species of *Guioa* originated (see later sections). The characters in the first paragraph of this page can therefore be regarded as synapomorphies of *Guioa*.

These two arguments make it highly likely that the species of *Guioa* all originated from the same ancestral species, but it is not certain that all descendants are included, *Guioa* might still be paraphyletic. Usually the possession of a unique character is sufficient to assume monophyly (Wiley, 1981a, chapter 5), but all mentioned characters of *Guioa* can also be found in other genera of Sapindaceae. Only the combination of characters is unique. An outgroup comparison has to reveal whether *Guioa* is monophyletic or not.

3. Muller & Leenhouts (1976) have made a general survey of the possible phylogenetic relationships among the genera of Sapindaceae. *Guioa* (page 424, group 3) is thought to have arisen from a *Cupaniopsis* ancestor. The genus *Diploglottis* (page 425, group 6) is the only genus which could have been derived from *Guioa*. Later Leenhouts (pers. comm.) regarded *Diploglottis* (petals fewer than 5, petal scales free, disc interrupted) to be derived from *Rhysotoechia* (scales folded petal margins) or *Cupaniopsis* (petal scales free). *Cupaniopsis* might also be derived from *Rhysotoechia,* but is generally regarded to be derived from the South American genus *Cupania*.

   There is only one *Guioa* species with 4 petals (an apomorphy of *Diploglottis*), namely *Guioa pteropoda*. This species also has an interrupted disc, but the arilloid appendage (rim and pseudo-funicle) is still present, the fruit is glabrous inside, and the petal scales have a crest; moreover, the fruit shows some autapomorphies: sharp, almost winged edges, and an incomplete dissepiment. The fruits of *Diploglottis* are not lobed, the edges are round, the fruit is hairy inside, the dissepiments are complete, and the arilloid lacks an appendage, while the petal scales lack a crest. The differences between *Diploglottis* and *Cupaniopsis* are less than between *Diploglottis* and *Guioa*. Therefore, the most parsimonious assumption is that *Diploglottis* has arisen from *Cupaniopsis* or an ancestral species of *Cupaniopsis* (two steps: a decrease in the number of petals and an interruption of the disc). A derivation of *Diploglottis* from *Rhysotoechia* instead of from *Cupaniopsis* needs one more step (petal scales free instead of folded margins). N.B.: With derivation from a genus is meant that a taxonomic group has arisen from an ancestral species within that genus (the genus will then be paraphyletic) or that it shares an ancestral species with that particular genus (the genus will then be monophyletic).

Leenhouts (pers. comm.) also considered *Sisyrolepis* and *Phyllotrichum* as possibly derived from *Guioa,* but this was mainly because these two probably closely related genera do not fit with any genus. However, *Sisyrolepis* and *Phyllotrichum* lack the arilloid appendage, have no petals, and have highly zygomorphic flowers. A derivation from *Diploglottis* is therefore more likely (more parsimonious), as *Diploglottis* already has less petals and also lacks the arilloid appendage.

Based on the above three arguments, of which especially the last is very important, *Guioa* is regarded to be monophyletic.

11.2. COMPUTER ALGORITHMS

The three computer programs used are PAUP version 2.4 (Phylogenetic Analysis Using Parsimony; Swofford, 1985), HENNIG86 version 1.5 (Farris, 1988), and CAFCA version 1.9.6 (Collection of APL Functions for Cladistic Analysis; Zandee, 1987, 1988).

PAUP and HENNIG86 use the same method: Wagner algorithm, combined with a 'branch and bound'-option. The selection criterion by which a tree is selected as the best one is always parsimony: the tree with the lowest number of state changes (steps). First an initial tree is made via the Wagner algorithm (for a demonstration of this basic operation, see Brooks, 1984), in which taxa are arranged according to their possible apomorphic characters. Dependant on the sequence in which the taxa are added to the initial tree the resulting tree may not be the most parsimonious one or there may be more, equally parsimonious trees. To find equally or more parsimonious trees some kind of branch swapping or branch and bound algorithm is used (commands: 'alltrees', 'bandb', and 'swap=global' in PAUP; 'ie', 'mhennig', and 'bb' in HENNIG86). Estimations of the most parsimonious character state changes of the HTU's (Hypothetical Taxonomic Units) are explained in Maddison et al. (1984), Wiley (1987b).

Both programs need the a priori designation of an outgroup. The character states of the outgroup are always regarded as plesiomorphic. Even if characters are used as unordered (the evolutionary direction of the character states is not a priori determined), then one character state of every character will always be the starting point of the transformation series, namely the character state of the outgroup. If a character only has two states the transformation series is automatically determined. Unordered characters are obtained by the command 'unordered all' (PAUP) or 'ccode –.' (HENNIG86).

Quite often several equally parsimonious trees are found. As parsimony was the only tree selection criterion, character weights (Farris, 1988; Carpenter, 1988) can be applied during iterative weighing, whereby the character weights are adjusted after each analysis until either the weights do not alter or one tree is selected. HENNIG86 provides an option to have the weights calculated automatically (repetitive use of the command 'xsteps w', followed again by a branch and bound command). The weight factors are dependant of the consistency and retention index of the characters. The retention index probably is a measure for a character's importance as apomorphy, but this index is not explained in the HENNIG86 manual. The character consistency index (theoretical minimum number of steps per character divided by the number of steps used) shows the fit of a character to a cladogram: if the index is 1, then the fit is unique, only apomorphies are present; if less than 1, then homoplasies are present (Farris, 1988).

PAUP has as major drawback that it cannot handle polytomies; these are always shown as dichotomies, but then in all combinations. So a trichotomy will result in three trees, a four-fork in 15 trees, etc. PAUP may find many trees, but these are usually only representatives of a few trees, as will be shown in the next sections, where the many trees found by PAUP equal the few found by HENNIG86. The next, already announced, version 3.0 of PAUP will cope with this deficit. HENNIG86 has as its major drawbacks that the manual and the output are extremely user unfriendly. Occasionally HENNIG86 may produce fully resolved trees with an empty branch.

CAFCA uses quite a different method: group-compatibility (hierarchically, mutually including, sets of taxa). The groups of taxa are first recognized by their unique characters (partial monothetic sets of characters) or by their unique combination of characters (strict monothetic sets of characters), for instance within the taxon comprising the species A, B, and C: the groups ABC, AB, BC, A, B, C all have unique characters. Then group-compatibility is established: groups of taxa are compatible when they completely exclude or include each other, overlap means incompatibility, e.g. the groups ABC, AB, A, B, and C are all compatible, but the group BC is not compatible with the group AB, BC is again compatible with the others (ABC, A, B, and C). Next, hierarchical cliques are formed; in the example two cliques will be found:

ABC includes group AB and C, AB includes A and B; or
ABC includes group A and BC, BC includes B and C.

These cliques become cladograms after the character distributions over the HTU's and OTU's are evaluated. CAFCA offers several parsimony criteria with which a cladogram can be selected. Two were used in the phylogenetic analysis, the criterium of minimal steps, e.g. the parsimony as applied by PAUP and HENNIG86, and the Redundancy Index (RI) as defined by Geesink & Zandee (msc.; see also Geesink & Kornet, 1989). The RI is the result of the application of information theory to evolutionary parsimony (see also Brooks & Wiley, 1988). The cladogram with the highest RI has the highest information content and the lowest amount of chaos that can be drawn from a particular datamatrix.

CAFCA has two advantages over PAUP and HENNIG86: a) Characters can be used in a completely unordered way, even when an outgroup is indicated (the character states of the outgroup are not considered to be primitive during the clique search). b) Consequently, an outgroup is not a priori necessary. However, when an outgroup is defined, it will be used in the character evaluation to polarize the transformation series. So, in contrast to PAUP and HENNIG86, in CAFCA an outgroup may still have its autapomorphies after cladogram optimization, which is a more sound approach, as the notion of an overall primitive outgroup is nonsensical (Zandee, pers. comm.). A result of the clique method can be that the outgroup is not recognized as such; it happens when the outgroup and ingroup do not include or exclude each other completely. PAUP and HENNIG86 will always regard the designated outgroup as outgroup.

Unfortunately the compatibility method has one very major drawback: when many homoplasies exist, CAFCA will find many incomplete or non-cliques and as a result incorrect cladograms can and will be formed: a) In case of reversals paraphyletic groups will be found (the taxa with the reversal will not be included). b) In case of parallels polyphyletic groups can be found. When these paraphyletic or polyphyletic groups are included in the selected clique, then a false cladogram will be the result. With a small amount of homoplasy the primary analysis will find one or several polytomies. The polytomies can be solved during the secondary analysis in which only the taxa of the polytomy are included, so that characters which are not unique because of homoplasies, may now be unique because of the limited amount of taxa and the polytomy may be solved in dichotomies. In practice, CAFCA usually finds trees which are less parsimonious than the ones found by PAUP or HENNIG86.

Farris (1979) mentions more disadvantages of the clique methods, although quite a lot of his objections only concern character compatibility and not group- or component-compatibility.

For a cladistic analysis PAUP and HENNIG86 proved to be the best programs. However, the reverse is true for a biogeographical analyses and then CAFCA performs better (see chapter 12, especially section 12.4).

During the analysis the programs were first used to find the most parsimonious cladograms. When several parsimonious trees existed these were evaluated as users trees in CAFCA and the one with the highest Redundancy Index was selected as the best cladogram. (N.B.: The often less parsimonious trees found by CAFCA always had a lower RI than the more parsimonious ones of PAUP and HENNIG86.)

11.3. CHARACTERS AND DATA MATRICES

The character states of the different characters were always entered in the matrices as multistate (one column per character with every character state a different number), and not binary (every character state in a different column with a coding for presence). Multistate coding has to be used, because PAUP and HENNIG86 do not possess the possibility, in contrast to CAFCA, to designate which binary columns (the character states) form one character. A solution would be to use additive binary coding, but then the transformation series have to be directed a priori. The directions of the latter were normally unknown, therefore multistate coding was used and the characters were treated as unordered, i.e. the sequence of character states does not show the transformation series.

Quite often polytypism (some species possess more than one character state) is regarded as a separate character state; e.g. the crest of the West Malesian species for instance shows the following character states: crest bifid, crest bifid and sometimes clavate, crest clavate. Usually these characters were used as ordered in the present analysis; the direction of the transformation series is then shown by the increase of the character state number.

Characters which are absent (e.g. the crest of *Guioa crenulata*) are coded as unknown, because this may either be primitive absence (in that case a plesiomorphy) or be due to reduction (an apomorphy). It cannot be decided a priori which of these two applies to the species analysed; therefore the advice by Pimentel & Riggins (1987), to code plesiomorphic absence as unknown and apomorphic absence as known, is redundant.

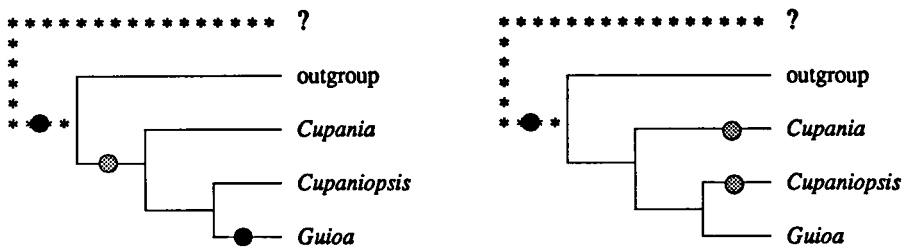
Quantitative characters were normally not used, because gaps in measures were not present. Sometimes quantitative characters are more or less used qualitatively, as for instance fruit stipe present (at least 2 mm high) or absent (stipe less than 2 mm high). If quantitative characters were used, then the boundaries of the character states did apply to the majority of the species (e.g. species with few jugae normally vary between 1 and 3 jugae, while many-jugate species vary between 1 and 6 or 1 and 9 jugae). Exceptional numbers per species were disregarded then.

11.4. OUTGROUP

The outgroup, as necessary for PAUP and HENNIG86, can pose problems. The outgroup should be the sister group of the group under study, but it is quite often unclear which group this will be. The situation in this study was rather fortunate, due to previous phylogenetically orientated research with genera as OTU's (Muller & Leenhouts, 1976). The analysis of Muller & Leenhouts showed that (part of) *Cupaniopsis* is the outgroup of *Guioa*, and (part of) *Cupania* of *Cupaniopsis* and *Guioa*. Instead of using general character sets of these genera, a character set of a single species of each genus is used during the phylogenetic analysis of *Guioa*. There are several reasons for doing so. Presumably the two genera are paraphyletic as several genera are possibly derived from them (a general generic character set will therefore never be general as long as these derived genera are not included). Moreover, if the outgroup is paraphyletic, then a general character set (that is, of the whole genus) can contain character states which do not apply to the lineage from which *Guioa* perhaps developed and they will only indicate false apomorphies for *Guioa*. Also, if a general character set is made, quite a few characters will appear to be polytypic (several character states are present); when these character states are also present in the ingroup, then the outgroup is useless to designate which state is primitive and which derived.

The species *Cupania americana* and *Cupaniopsis anacardioides* were selected because they both showed many assumedly primitive characters. Taxa with more apomorphies can give rise to more (false) synapomorphies for *Guioa*. For example the *Cupaniopsis bilocularis* group has a 2-locular ovary, *Guioa* and the other *Cupaniopsis* species have 3-locular ovaries. When *Cupaniopsis bilocularis* with its 2-locular ovary would have been selected as only outgroup, *Guioa* would have had an additional apomorphy: 3-locularity. *Cupania americana* has been added to prevent these false apomorphies; this species is also 3-locular. In case of *Cupaniopsis bilocularis* as outgroup the most parsimonious solution would be to assume that 3-locularity is plesiomorphic and that 2-locularity is an autapomorphy of *Cupaniopsis bilocularis*.

Although two outgroups are used, it is still not possible to interpret the root characters of *Guioa* (sepals petaloid, disc glabrous, fruit wall thin, fruit black, arilloid with pseudo-funicle). To be able to do this two more outgroups are necessary. As an example the character distribution of the pseudo-funicle is taken. This structure is absent in *Cupania* and *Cupaniopsis*, but present in *Guioa* and in an assumed outgroup of *Cupania+Cupaniopsis+Guioa*:



● = absence of pseudo-funicle; ◍ = presence.

It is as parsimonious (both two steps) to assume that either (left) the character disappeared and reappeared or that (right) the disappearance occurred twice, which is not unlikely with reductions. In the first instance the possession of a pseudo-funicle is an apomorphy for *Guioa*, but in the second instance a plesiomorphy. Only an outgroup of the outgroup (called ? above) makes the character distribution decisive (if it possesses a pseudo-funicle then the character will be a plesiomorphy for *Guioa*; if it lacks one, then it will be an apomorphy for *Guioa*). For this reason the program HENNIG86 shows the root as a polytomy.

11.5. USE OF ONTOGENY IN PHYLOGENY

The ontogeny of several characters, as observed by comparing juvenile and mature plants (chapter 8.4), can be used to establish the direction of several transformation series:

	plesiomorphous	apomorphous
Rhachis	slightly winged	not winged or broadly winged
Leaflet margin	serrate/crenate	entire
Domatia	absent	present
Papillae	absent	present

Ontogenetic data were always regarded as reliable for the establishment of the direction of transformation series. The ontogenetic data and the outgroup could both be used for this purpose (Wiley, 1981a). The first stage to be recognizable was always the most primitive character state, the last the most derived, although terminal deletions in the ontogenetic series can be present and other, earlier developing stages will be, secondarily, more derived. Recently, Brooks & Wiley (1985) and Kluge (1985) showed that the ontogeny could be replaced by the outgroup rule alone, because the outgroup rule could resolve the same and even more cases than ontogeny could. Ontogeny is included in the outgroup rule. Nelson (1985) replied in making a strong case for ontogeny, stating that it could solve all cases which the outgroup rule could too, but sometimes even better by providing more parsimonious trees. However, Nelson's reply is full of little tricks (e.g. including the outgroup in the analysis, counting root characters as steps, using ancestors with an incomplete ontogeny to create more parsimonious trees, etc.), which undermine his case completely.

Another criticism on the ontogenetic method in phylogeny came from Roos et al. (msc.) and Hennipman (1987). They showed that the data matrices, as far as these were more or less explicitly used in the examples cited above, contained far too little ontogenetic information. They included data about the results of the ontogeny (presence of ontogenetic stages in all or some of the developmental phases) and about the different transformation sequences themselves (stage changes). A character with three character states and three developmental stages could be translated into a matrix with c. 24 character states instead of three. A result of their analysis was the theoretical possibility of proximal addition to an ontogenetic series, e.g., earlier stages are added to the ontogenetic series. Consequently, it cannot be assumed a priori that the first visible stage is the most primitive stage; it can also be the most derived.

The ontogenetic data of *Guioa* only contain two (at most three) character states and two developmental stages. When the method of Hennipman (1987) and Roos et al. (msc.) was applied, a matrix with a lot of iterative parts was the result; after these were eliminated the rest of the information was rather redundant:

Species A:	Stage I:		Domatia absent →	Stage II:	Domatia absent
Species B:			Domatia absent →		Domatia present

Character	A	B	Character state	Developmental stage
1	1	1	Domatia absent	I + II
	0	1	Domatia present	
2	1	1	Domatia absent	I
3	1	0	Domatia absent	II
	0	1	Domatia present	
4	1	0	Domatia absent → domatia absent	I → II
	0	1	Domatia absent → domatia present	

Character 1–3 show the character states in the different stages and character 4 the process of change. Character 3 and 4 contain the same information. Character 1 overlaps with character 2 and 4. Character 2 is completely uninformative. The matrix can be reduced to character 1 and 4, although the information of the latter is included in character 1 (e.g. character 1 is an additive binary coding of characer 4).

For the phylogenetic analysis of *Guioa* it was decided to let the outgroup rule prevail over ontogenetic information. Sometimes, ontogenetic data were used to show the sequence in a transformation series: Rhachis wing in the West Malesian and Australian/New Caledonian group and the leaflet margin in the latter group. The coding was always simple (just additive binary coding as in character 1 and not as elaborate as in Hennipman (1987) and Roos et al. (msc.). Due to the outgroups the presence of a small wing and a crenate margin was always regarded as an apomorphy, as a neoteny, in spite of the fact that these character states were present as the first stages in the ontogeny, because *Cupania americana* as well as *Cupaniopsis anacardioides* lack a wing and have an entire leaflet margin.

11.6. INITIAL ANALYSIS

For a general analysis of the whole genus 67 characters were used, each consisting of two or more character states. Table 3 shows the multistate matrix. The characters were treated as unordered.

Table 3. Characters as used in the initial cladistic analysis of *Guioa*.

1: Disc
- a = complete
- b = small slit(s)
- c = gap

2: Fruit wall
- a = thin wall
- b = thick wall

3: Fruit lobe
- a = as long as high (≤ 2 mm difference)
- b = longer than high (> 2 mm difference)

4: Fruit stipe
- a = absent (≤ 2 mm high)
- b = present (> 2mm high)

5: Fruit stipe shape
- a = broadly cuneate
- b = slender
- c = broadly cuneate to slender

6: Fruit upper margin
- a = not convex
- b = convex

7: Pseudofunicle
- a = absent
- b = present

8: Pseudofunicle
- a = well-developed
- b = present as a rim

9: Fruit colour
- a = mainly black when dry
- b = mainly red when dry
- c = brown

10: Cotyledons
- a = dorsoventrally above each other
- b = laterally besides each other

11: Flowering branch thickness
- a = ≤ 5 mm thick
- b = ≤ 10 mm thick
- c = ≤ 15 mm thick
- d = ≤ 20 mm thick
- e = ≤ 25 mm thick

12: Axis pilosity
- a = pilose when young
- b = always pilose

13: Jugae number
- a = 1–3 jugae
- b = 1–6 jugae
- c = 1–9 jugae

14: Wing
- a = not present
- b = small (≤ 1 mm broad)
- c = broad (> 1 mm broad)
- d = absent to broad

15: Leaflet shape
- a = ovate
- b = elliptic
- c = obovate

(Table 3 continued)

16: Leaflet falcate
  a = not falcate
  b = falcate
17: Leaflet length
  a = ≤ 5 cm long
  b = ≤ 20 cm long
  c = ≤ 25 cm long
  d = ≤ 30 cm long
18: Leaflet width
  a = ≤ 3 cm broad
  b = ≤ 9 cm broad
  c = ≤ 12 cm broad
19: Leaflet symmetry
  a = ± symmetric
  b = slightly asymmetric
  c = asymmetric
20: Leaflet thickness
  a = thin
  b = coriaceous
  c = very coriaceous
  d = coriaceous to very coriaceous
21: Leaflet margin
  a = serrate
  b = entire
  c = crenate
22: Leaflet margin
  a = flat
  b = recurved
  c = flat to recurved
23: Leaflet apex
  a = emarginate to acuminate
  b = acute to caudate
24: Leaflet very apex
  a = not mucronulate
  b = mucronulate
25: Leaflet upper surface
  a = without wax
  b = sometimes wax present
26: Domatium type
  a = absent
  b = pocket
  c = sac
27: Domatium size
  a = small
  b = large
  c = small to large
28: Domatium opening
  a = front
  b = top
  c = front to top
29: Marginal vein
  a = completely present
  b = present in upper part of leaflet
30: Venation density
  a = densely reticulate
  b = laxly reticulate
31: Venation distinctiveness
  a = distinct
  b = indistinct
32: Inflorescence
  a = axillary (and pseudoterminal)
  b = axillary and ramiflorous
  c = axillary, ramiflorous, and pseudoterminal
33: Cymules
  a = cincinnate
  b = dichasial
34: Pedicel
  a = upper part less pilose than lower part
  b = as pilose
35: Sepals
  a = sepaloid
  b = petaloid
36: Sepals outside
  a = glabrous
  b = pilose
37: Sepals inside
  a = glabrous
  b = pilose
38: Sepal margin
  a = without glands
  b = only small sepals with glands
  c = all sepals with glands
39: Shape petal blade
  a = ovate
  b = globose
  c = obovate
40: Claw length
  a = short
  b = normal
  c = long
41: Claw-blade transition
  a = gradual
  b = sharp
42: Scales
  a = absent
  b = enation
  c = present
  d = reduced

(Table 3 continued)

43: Scale margin
- a = folded petal margins
- b = free

44: Scale top
- a = not broadened
- b = broadened

45: Crest
- a = absent to slightly developed
- b = bifid
- c = linear
- d = clavate, short stipe
- e = absent to clavate on short stipe
- f = clavate, long stipe

46: Crest pilosity
- a = glabrous
- b = pilose

Leaf anatomy:

47: Hairs adaxially
- a = absent
- b = on veins
- c = everywhere
- d = on veins only to everywhere

48: Hairs abaxially
- a = absent
- b = on veins
- c = everywhere

49: Glands adaxially
- a = absent
- b = one cell
- c = *Guioa* type
- d = *Cupaniopsis* type

50: Glands abaxially
- a = absent
- b = one cell
- c = *Guioa* type
- d = *Cupaniopsis* type

51: Papillae abaxially
- a = absent
- b = developed around stomata
- c = every cell
- d = absent or present around every cell
- e = absent to present around every cell

52: Papillae ridges
- a = narrow
- b = wide

53: Thin cuticular areas adaxially
- a = absent
- b = (slightly) present
- c = absent and present

54: Thin cuticular areas abaxially
- a = absent
- b = (slightly) present

55: Cuticle adaxially
- a = not striate
- b = (slightly) striate

56: Cuticle abaxially
- a = not striate
- b = (slightly) striate
- c = not striate and striate

57: Adaxial anticlinal epidermal walls
- a = straight
- b = (slightly) undulate

58: Abaxial anticlinal epidermal walls
- a = straight
- b = (slightly) undulate
- c = straight and undulate

59: Stomata
- a = normal
- b = some with extra rim

60: Veins
- a = embedded in mesophyll
- b = (partly) transcurrent

61: Veins
- a = transcurrent to adaxial epidermis, not sclerified
- b = different

62: Veins
- a = transcurrent to adaxial epidermis, sclerified
- b = different

63: Veins
- a = completely transcurrent or to abaxial epidermis, sclerified
- b = different

64: Veins
- a = completely transcurrent, sclerenchyma around veins
- b = different

65: Sclerenchyma around domatia
- a = absent
- b = slightly sclerified
- c = adaxially sclerified
- d = completely sclerified

66: Idioblasts
- a = absent
- b = present

67: Fifth petal
- a = not reduced
- b = reduced

(Table 3 continued)

Species \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Cupaniopsis																																		
anacardioides	1	2	1	1	1	1	1	?	3	1	1	2	2	2	3	1	2	2	2	2	3	1	1	1	1	1	?	?	1	2	1	1	2	2
Guioa																																		
acuminata	3	1	1	2	2	1	2	1	1	?	1	1	1	2	1	2	2	2	3	2	3	1	2	2	1	3	1	1	1	1	2	1	1	1
acutifolia	1	1	2	1	1	1	2	1	1	2	3	1	1	2	2	1	3	2	1	1	3	1	2	2	2	3	1	1	1	2	2	1	1	1
amabilis	1	1	1	1	1	1	2	1	1	?	1	2	2	1	2	1	1	1	3	3	1	2	1	1	2	1	?	?	1	1	2	1	1	1
aryterifolia	1	1	2	1	1	1	2	2	1	1	2	1	2	2	2	1	2	2	1	2	3	1	2	2	1	3	1	1	2	2	2	2	1	2
asquamosa	1	1	1	1	1	1	2	1	1	?	1	1	2	2	1	1	2	1	3	2	3	1	2	1	2	3	1	2	1	2	1	1	1	1
bicolor	3	1	2	2	2	1	2	1	1	2	2	1	2	2	2	1	2	2	3	3	3	3	2	2	1	3	1	1	2	2	1	1	1	1
bijuga	3	1	1	2	2	1	2	1	1	2	2	1	2	4	2	1	2	2	1	2	3	1	2	1	1	3	1	1	1	2	2	1	1	2
chrysea	3	1	1	2	2	1	2	1	1	1	1	2	2	2	1	1	2	2	3	2	3	1	2	1	1	3	2	2	1	1	1	1	2	2
comesperma	3	1	1	2	2	1	2	1	2	1	2	1	2	4	2	1	2	2	3	2	3	1	2	2	1	3	1	1	2	2	1	1	1	1
contracta	3	2	1	1	1	1	2	2	1	1	3	1	1	2	2	1	2	2	1	2	3	1	2	1	1	1	?	?	2	2	2	2	1	2
coriacea	1	1	2	2	2	1	2	1	1	2	2	1	2	2	2	1	2	2	3	3	3	2	1	1	1	3	2	2	1	2	2	1	1	1
crenata	1	1	1	1	2	1	2	1	1	2	1	1	3	1	2	1	1	1	2	3	1	2	1	1	1	3	1	1	1	1	2	1	1	2
crenulata	3	?	?	?	?	?	2	?	?	?	1	1	2	1	2	1	1	1	1	3	1	2	1	1	1	1	?	?	1	1	2	1	1	2
diplopetala	1	1	1	2	2	1	2	1	1	2	5	1	3	2	2	1	3	2	3	2	3	1	2	1	1	3	1	1	1	2	2	3	1	2
discolor	3	?	?	?	?	?	2	?	1	?	2	1	2	2	1	2	2	2	3	3	3	3	2	2	1	3	1	1	1	2	2	1	1	1
elliptica	2	1	1	2	2	1	2	1	1	1	1	2	1	2	2	1	2	1	3	2	3	2	1	2	1	3	1	1	1	2	2	1	1	1
fusca	3	1	1	2	2	1	2	1	2	?	1	1	2	1	2	1	2	1	1	2	3	1	1	1	1	3	1	2	1	2	1	1	1	1
glauca	3	1	1	2	3	1	2	1	1	2	3	2	1	2	3	1	2	2	1	3	3	2	1	1	2	1	3	3	1	2	2	1	1	2
gracilis	2	1	1	2	2	1	2	1	2	2	1	1	2	2	1	1	2	2	1	2	3	1	1	1	1	3	1	1	1	2	2	1	2	1
grandifoliola	3	2	1	1	1	2	2	2	1	1	4	1	1	2	1	1	4	3	1	2	3	1	2	2	2	1	?	?	2	2	2	2	1	1
hirsuta	1	1	1	2	2	1	2	1	1	2	2	2	3	2	2	1	2	1	2	2	3	1	2	1	1	2	1	1	1	2	2	1	1	1
hospita	3	1	2	2	2	1	2	1	1	?	1	1	1	2	1	1	3	2	2	2	3	1	2	2	1	2	1	1	2	2	1	1	?	2
koelreuteria	3	1	1	2	2	1	2	1	1	2	2	1	2	2	1	1	2	2	3	2	3	1	2	2	1	3	1	1	1	2	1	1	1	1
lasioneura	3	1	1	1	1	1	2	1	1	2	1	2	1	2	2	1	2	2	1	2	3	1	2	2	1	2	1	1	2	1	1	1	1	1
lentiscifolia	1	1	2	2	2	1	2	1	1	1	1	1	2	1	2	1	2	1	3	2	3	1	1	1	1	3	2	2	1	2	2	1	2	1
malukuensis	1	?	?	?	?	?	2	?	?	?	1	2	2	1	2	1	2	1	1	2	3	1	1	1	1	3	1	1	1	1	1	1	1	1
megacarpa	1	1	2	2	2	1	2	1	1	1	1	1	2	2	1	2	2	1	3	2	3	2	2	1	1	3	1	1	1	1	1	1	1	1
melanopoda	1	1	2	1	1	1	2	1	1	1	2	1	2	3	2	1	2	2	2	2	3	1	2	2	1	1	1	1	2	1	1	1	?	2
membranifolia	3	1	2	2	2	1	2	1	1	1	2	1	1	2	2	1	2	2	2	2	3	1	2	2	1	3	1	1	2	2	2	2	1	1

microsepala	1	1	1	2	1	1	2	1	1	2	1	1	1	2	2	1	2	2	1	3	3	2	1	1	2	3	2	2	1	2	2	1	1	2
misimaensis	3	?	?	?	?	?	2	?	?	?	1	1	1	2	2	1	2	2	1	2	3	1	1	2	1	1	?	?	1	2	2	1	1	1
molliuscula	1	?	?	?	?	?	2	?	?	?	1	2	1	2	1	1	2	2	1	2	3	1	2	2	1	3	1	1	2	2	2	1	?	?
montana	2	1	1	1	1	1	2	1	1	?	1	1	1	2	2	1	2	1	1	3	3	2	2	2	1	1	?	?	1	2	1	1	1	2
multijuga	1	?	?	?	?	?	2	?	?	?	1	1	3	1	2	1	2	1	3	2	3	1	2	2	1	3	1	2	1	2	2	1	1	1
myriadenia	3	1	1	2	2	1	2	1	1	2	2	2	2	2	1	2	2	2	3	2	3	2	2	2	1	2	1	1	1	1	1	1	1	2
normanbiensis	3	1	2	2	2	1	2	1	1	?	3	1	2	2	1	1	2	2	1	2	3	1	2	2	1	3	1	1	2	2	2	2	1	1
novobritannica	3	?	?	?	?	?	2	?	?	?	1	1	1	2	2	1	1	1	3	2	3	1	1	2	1	3	2	2	2	1	1	1	1	1
novoëbudaënsis	1	1	1	2	2	1	2	1	1	1	1	1	2	2	1	2	2	1	3	2	3	1	2	1	1	3	1	1	1	1	1	1	1	1
oligotricha	1	1	1	1	2	1	2	1	1	1	3	1	1	2	2	1	2	2	1	2	2	1	2	1	1	2	1	1	2	2	1	1	1	1
ovalis	2	1	2	2	2	1	2	1	1	2	2	1	2	2	2	1	3	2	1	3	3	2	1	1	2	3	1	1	1	2	2	1	1	1
palawanica	3	1	1	2	2	1	2	1	1	2	1	1	1	2	2	1	2	1	1	3	3	2	1	1	1	3	1	1	1	2	1	1	1	2
parvifoliola	3	1	1	1	2	1	2	1	1	2	1	1	1	2	3	1	1	1	2	3	3	2	1	1	1	3	1	1	1	1	1	1	?	2
patentinervis	1	1	1	2	2	1	2	1	1	1	2	1	2	2	2	1	2	2	2	2	3	1	2	1	1	3	1	1	1	2	1	1	1	1
pauciflora	1	1	2	2	1	1	2	1	1	?	1	2	1	1	3	1	2	1	1	3	3	2	1	1	2	3	3	3	1	1	1	1	1	?
pectinata	3	1	1	2	2	1	2	1	1	?	1	1	1	2	2	1	2	1	1	3	3	2	1	1	2	3	1	2	1	2	2	1	1	2
pleuropteris	3	1	1	2	2	1	2	1	2	2	2	2	2	4	3	1	2	2	3	2	3	1	2	2	1	2	1	1	2	2	1	1	1	2
plurinervis	3	1	1	2	1	1	2	1	1	1	1	1	2	2	1	2	2	1	3	2	3	1	2	2	1	2	1	1	1	2	2	1	1	1
pseudoamabilis	1	1	2	2	2	1	2	1	1	1	1	2	3	1	2	1	1	1	3	2	1	3	1	2	1	3	2	3	1	1	2	1	1	1
pteropoda	3	1	2	1	1	1	2	1	1	?	1	1	3	1	2	1	2	1	3	2	1	2	2	2	2	3	1	2	1	2	2	1	1	1
pterorhachis	3	1	1	2	2	1	2	1	1	2	1	1	3	3	2	1	2	2	2	2	3	1	2	1	1	3	1	2	2	2	2	1	1	2
pubescens	3	1	1	2	2	1	2	1	1	2	2	1	2	2	1	2	2	2	3	2	3	1	2	2	2	3	1	1	1	2	2	1	1	2
punctata	1	1	1	2	2	1	2	1	1	1	1	1	2	2	1	2	2	1	3	2	3	1	2	1	1	3	2	2	1	2	2	1	2	2
reticulata	3	1	2	2	2	1	2	2	1	2	1	1	2	2	1	2	2	1	3	3	3	3	2	2	1	3	2	1	1	1	1	1	1	1
rhoifolia	1	1	2	2	2	1	2	1	1	1	1	2	3	2	1	2	2	1	3	2	3	1	2	2	1	3	2	2	1	1	1	1	1	1
rigidiuscula	3	1	2	1	1	2	2	1	1	1	2	1	2	2	2	1	2	2	3	2	3	1	2	2	1	3	1	1	2	2	2	1	1	1
scalariformis	1	1	2	2	2	1	2	1	1	1	2	1	1	2	1	1	3	3	2	2	3	1	2	2	1	1	?	?	2	2	1	1	1	1
semiglauca	1	1	2	1	1	1	2	1	1	2	2	2	1	2	3	1	2	2	1	2	3	2	1	2	1	1	?	?	1	2	2	1	2	1
subfalcata	1	?	?	?	?	?	2	?	?	?	1	1	1	2	1	2	2	1	3	2	3	1	2	2	1	3	1	2	1	1	1	1	?	2
subsericea	1	1	2	1	1	1	2	1	1	1	2	2	1	2	1	1	2	2	3	3	3	1	2	2	1	3	1	3	2	2	1	1	1	1
sufusana	1	1	2	2	2	1	2	1	1	1	1	2	2	2	1	1	2	2	2	2	3	1	2	1	1	3	1	1	2	2	1	1	1	1
truncata	3	1	?	?	?	?	2	?	1	?	1	1	1	1	2	1	2	1	3	2	3	1	1	2	1	3	2	2	1	2	1	1	1	1
unguiculata	1	1	2	2	2	1	2	1	1	?	2	1	1	2	2	1	2	2	2	2	3	1	2	2	1	1	?	?	2	2	2	1	1	1
venusta	1	1	1	2	2	1	2	1	1	?	1	1	3	1	2	1	2	1	3	1	2	1	1	2	1	2	1	1	1	2	1	1	1	1
villosa	3	1	1	2	2	1	2	1	1	2	1	2	2	2	3	1	2	1	2	4	3	2	1	1	1	2	1	1	1	1	2	1	1	2
waigeoensis	1	1	1	2	2	1	2	1	1	?	1	2	2	1	2	1	1	1	1	2	2	2	1	2	1	3	1	1	1	1	2	1	?	1

(Table 3 continued)

Species \ Character	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67
Cupaniopsis																																	
anacardioides	1	2	1	3	3	1	1	3	2	1	1	?	1	2	3	3	1	?	1	1	2	2	1	1	1	1	2	2	2	2	?	2	1
Guioa																																	
acuminata	2	1	1	3	3	3	1	3	2	1	3	2	1	2	1	1	1	?	1	1	1	2	2	1	1	2	2	2	1	2	1	2	2
acutifolia	2	1	1	3	3	1	1	4	2	1	1	1	1	2	1	1	3	1	1	1	2	2	2	1	1	1	2	2	1	2	1	2	2
amabilis	2	1	1	3	?	?	?	?	2	?	?	?	2	3	1	1	3	2	1	1	1	1	1	1	1	2	2	2	1	2	?	2	?
aryterifolia	2	1	1	3	3	2	2	3	2	1	6	1	2	2	3	3	1	?	2	1	1	2	2	1	1	1	2	2	2	2	1	1	2
asquamosa	2	1	1	1	3	1	1	2	2	1	1	2	2	2	3	3	1	?	2	1	1	2	2	1	1	2	2	2	1	2	1	2	2
bicolor	2	1	1	3	?	?	?	?	?	?	?	?	1	2	1	1	3	2	1	1	2	1	1	1	1	2	2	2	1	1	?	2	?
bijuga	2	1	1	3	3	3	1	3	2	1	2	2	2	2	3	3	5	1	2	1	1	2	2	2	1	1	2	2	2	1	1	2	2
chrysea	2	1	1	1	3	1	1	3	2	1	1	1	3	3	3	3	3	2	1	1	2	2	1	1	1	2	2	2	1	2	4	2	1
comesperma	2	1	1	3	3	2	2	3	2	1	6	1	2	2	3	3	2	2	3	1	1	2	2	1	1	2	2	2	1	2	1	2	2
contracta	2	1	1	3	3	2	1	3	2	1	6	1	2	2	3	3	1	?	2	1	1	2	2	2	1	1	2	2	1	2	?	2	2
coriacea	2	1	1	3	2	2	1	3	1	1	6	1	1	2	1	1	1	?	1	1	2	2	1	1	1	2	2	2	1	2	?	1	2
crenata	2	2	2	3	3	1	1	4	2	1	1	1	3	3	1	1	3	2	1	1	1	2	2	1	1	2	2	2	1	2	1	2	2
crenulata	2	2	2	3	3	1	1	4	2	1	1	1	2	3	2	3	3	2	1	1	2	2	2	1	1	2	2	1	2	2	?	2	2
diplopetala	2	1	1	3	3	3	1	3	2	2	1	2	2	2	3	3	1	?	2	1	1	2	2	2	1	1	2	2	1	1	1	2	2
discolor	2	1	1	3	3	3	1	3	2	1	2	2	2	3	1	1	3	1	1	1	1	1	1	1	1	2	2	2	1	2	4	1	2
elliptica	2	1	1	2	3	1	1	3	2	1	4	1	2	2	3	1	3	2	1	1	2	2	2	1	1	2	2	2	1	2	1	2	1
fusca	2	1	1	1	3	1	1	3	2	1	4	1	1	2	2	1	1	?	1	1	1	2	2	2	2	2	2	2	1	2	4	2	2
glauca	2	2	2	3	3	1	1	3	2	1	6	1	3	3	2	2	3	2	1	1	2	1	1	1	1	2	2	1	1	2	1	2	2
gracilis	2	1	1	1	3	1	1	3	2	1	4	1	1	2	2	2	1	?	2	1	1	2	2	2	2	2	2	2	1	2	4	2	2
grandifoliola	2	1	1	2	?	?	?	?	?	?	?	?	1	1	3	1	1	?	1	1	1	2	1	1	1	2	2	2	1	2	?	1	?
hirsuta	2	1	1	3	3	2	1	3	2	2	1	2	3	3	4	4	1	?	2	1	2	2	2	2	1	2	2	2	1	2	?	2	2
hospita	2	?	?	?	?	?	?	?	?	?	?	?	2	2	3	3	1	?	2	1	1	1	2	1	1	1	2	2	1	2	?	2	?
koelreuteria	2	1	1	3	3	3	1	3	2	1	2	2	2	2	3	3	2	2	2	1	1	2	2	3	1	2	2	2	1	2	1	2	2
lasioneura	2	2	1	3	3	2	1	3	2	1	4	1	2	3	3	1	3	1	1	1	1	1	1	1	1	2	1	1	2	2	1	2	2
lentiscifolia	2	1	1	1	3	1	1	1	?	1	1	?	3	3	1	1	3	2	1	1	2	1	1	1	1	2	2	2	1	2	4	2	1
malukuensis	2	1	1	3	3	1	2	3	1	1	1	?	3	3	3	3	3	2	1	1	1	2	1	1	1	2	2	2	1	2	1	2	2
megacarpa	2	1	1	2	3	1	1	3	2	1	4	1	2	2	3	3	3	2	1	1	2	2	1	1	1	2	2	2	1	2	1	2	1
melanopoda	2	1	1	1	1	1	1	3	2	1	1	?	2	2	1	3	1	?	2	1	1	1	2	2	1	2	2	2	1	2	?	2	?
membranifolia	2	1	1	3	3	2	2	3	2	1	6	1	2	2	3	3	1	?	3	1	1	2	2	1	1	2	2	2	1	2	1	2	2

microsepala	2	2	2	3	3	1	1	3	2	2	2	1	2	2	3	3	1	?	1	1	2	2	1	1	1	1	2	2	1	2	4	2	2
misimaensis	2	1	1	2	?	?	?	?	?	?	?	?	2	3	3	1	3	2	1	1	2	2	1	1	1	2	2	2	1	2	?	2	2
molliuscula	2	?	?	?	?	?	?	?	?	?	?	?	3	3	3	3	2	?	2	1	1	2	2	1	1	2	2	2	1	2	1	2	?
montana	2	2	1	3	3	1	1	4	2	1	4	1	2	3	1	1	3	1	1	1	1	1	1	1	1	2	2	2	1	2	?	2	2
multijuga	2	1	1	2	3	1	1	4	2	1	1	?	2	2	1	1	3	2	1	1	1	1	2	1	1	2	2	2	1	2	?	2	1
myriadenia	2	2	1	3	2	3	2	3	2	1	4	2	3	3	3	3	3	1	1	1	2	2	1	1	1	2	2	2	1	2	1	2	2
normanbiensis	2	1	1	2	3	2	2	3	2	1	6	1	1	2	3	3	1	?	2	1	1	1	2	1	1	1	2	2	2	2	1	1	2
novobritannica	2	1	1	3	3	2	2	3	2	1	6	1	2	2	3	1	3	2	1	1	2	1	1	1	1	2	2	2	1	2	4	2	1
novoëbudaënsis	2	1	1	2	3	1	1	4	2	1	1	?	2	2	3	3	3	2	1	1	2	2	1	1	1	2	2	2	1	2	1	2	1
oligotricha	2	2	1	3	3	1	1	4	2	1	1	?	2	2	3	3	4	1	1	1	2	2	2	3	1	2	2	2	1	2	1	2	2
ovalis	2	1	1	1	3	1	1	3	2	1	4	1	1	2	3	3	1	?	2	1	1	2	2	1	1	2	2	2	1	2	?	2	2
palawanica	2	2	1	?	?	?	?	?	?	?	?	?	3	3	3	3	3	2	1	1	2	2	1	1	1	2	2	2	1	2	1	2	?
parvifoliola	2	2	1	?	?	?	?	?	?	?	?	?	3	3	3	1	3	2	1	1	2	1	1	1	1	2	2	2	1	2	1	2	?
patentinervis	2	1	1	2	3	1	1	4	2	1	1	?	4	2	1	1	1	?	2	1	1	2	2	2	1	2	2	2	1	2	?	2	2
pauciflora	2	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	3	2	1	1	1	2	1	1	1	2	2	2	1	2	4	2	?
pectinata	2	1	1	3	3	1	1	3	2	1	4	1	1	2	3	3	1	?	1	1	2	2	2	1	2	1	2	2	2	2	1	2	2
pleuropteris	2	2	1	3	3	3	1	3	2	1	2	2	3	3	1	1	3	1	1	1	2	1	2	1	1	1	2	2	1	1	1	2	2
plurinervis	2	1	1	3	3	2	2	3	2	1	6	1	2	3	1	1	3	2	1	1	2	1	1	1	1	1	2	2	2	2	1	1	2
pseudoamabilis	2	1	1	3	3	2	1	3	2	1	6	1	2	2	3	1	1	?	1	1	2	2	1	1	1	1	2	2	2	2	1	2	2
pteropoda	2	1	1	2	3	1	1	3	2	1	2	2	1	2	3	3	1	?	1	1	1	1	2	2	1	1	2	2	2	2	1	2	2
pterorhachis	2	1	1	3	3	2	1	3	2	1	2	2	4	3	3	3	3	1	1	1	2	1	2	1	1	2	2	2	1	2	1	2	2
pubescens	2	1	1	3	3	3	1	3	2	1	2	2	3	3	3	3	3	1	1	1	2	1	1	1	1	2	2	2	1	1	3	1	2
punctata	2	1	1	3	3	1	1	3	2	1	4	1	1	2	1	1	3	2	1	1	1	2	1	1	1	2	2	2	1	2	2	2	1
reticulata	2	1	1	3	3	3	1	3	2	1	2	2	2	3	3	2	3	2	2	1	1	1	2	1	1	2	2	2	1	2	3	1	2
rhoifolia	2	1	1	3	3	1	1	4	2	1	6	1	2	2	3	3	3	2	1	1	1	1	1	1	1	2	2	2	1	2	1	1	1
rigidiuscula	2	1	1	2	3	2	2	3	2	1	6	1	2	2	3	3	2	?	2	1	1	2	2	1	1	1	2	2	2	2	1	2	2
scalariformis	2	1	1	3	3	2	2	3	2	1	6	1	2	2	3	3	1	?	2	1	1	2	2	2	1	1	2	2	2	2	?	1	1
semiglauca	2	1	1	3	3	1	1	4	2	1	5	1	2	3	2	1	3	1	1	1	2	1	1	1	1	2	1	1	2	2	?	2	2
subfalcata	2	1	1	?	?	3	1	?	?	1	?	?	2	2	1	1	1	?	1	1	2	2	2	2	1	2	2	2	1	2	2	1	?
subsericea	2	1	1	3	3	1	2	3	1	1	1	1	3	3	3	3	3	2	1	1	2	3	1	1	1	2	2	2	1	2	1	2	2
sufusana	2	1	1	2	3	1	1	4	2	1	1	?	2	2	1	1	3	2	1	1	2	1	1	1	1	2	2	2	1	2	1	2	1
truncata	2	1	1	3	2	3	2	3	2	1	2	2	2	2	2	3	1	?	1	1	1	2	1	1	1	2	2	2	1	2	2	2	2
unguiculata	2	1	1	3	3	3	1	3	1	1	1	?	1	2	3	3	1	?	2	2	1	2	2	2	1	1	2	2	1	2	?	2	1
venusta	2	1	1	3	?	?	?	?	?	?	?	?	2	2	3	3	1	?	1	1	1	1	2	1	1	2	2	2	1	2	1	2	2
villosa	2	2	2	3	3	1	1	3	2	1	6	1	3	3	1	1	3	2	1	1	1	3	1	1	1	1	2	1	2	2	2	2	2
waigeoensis	2	?	?	?	?	?	?	?	?	?	?	?	3	3	1	1	3	2	1	1	2	2	1	1	1	1	2	2	2	2	?	2	?

The program PAUP, which only analysed the 40 completely known species, found more than a 100 trees (commands 'mulpars' in combination with 'maxtree =100' and 'swap=global'). HENNIG86, which analysed all 65 species, found 22 fully resolved trees (commands 'Hennig' and 'bb').

Figure 38 shows one of the latter complete trees. The consistency index of this tree is 0.17, which already indicates the enormous amount of homoplasies (more than 4 out of every 5 state changes are homoplasies). In total the tree length was 648 steps.

Figure 38 also shows an indication of the geographical distribution of the species. It is apparent that a lot of species, which inhabit the same area, form groups or are split off sequentially, for instance the Pacific group (P) is split off sequentially at the basis of the cladogram, starting with the Fiji species and ending with the Solomon species. Only *Guioa lentiscifolia* of Tonga is split off later, but together with *Guioa multijuga* of New Guinea; this means that the ancestor of these two species either had a very strange, very disjunct distribution or it dispersed. More of these strange aberrations exist. Three Australian (A) species form a monophyletic group, but another one, *Guioa montana,* which is very difficult to separate from the Australian *Guioa semiglauca,* is split off much later. N.B.: The fifth Australian species, *Guioa coriacea* of Lord Howe Island, also branches off in a different part of the cladogram, but this is to be expected as it is very different from the other Australian species. The New Caledonian species occur as a monophyletic group, but are united with an Australian, a New Guinean, and two West Malesian species of the Philippines. The *Guioa rigidiuscula* group of New Guinea is split into several monophyletic groups. The West Malesian species more or less form one group, only three species are placed outside: *Guioa palawanica* and *Guioa parvifoliola* can be found in the New Caledonian group, and *Guioa truncata* among the New Guinean species. The West Malesian group contains three strange elements: *Guioa oligotricha* and *Guioa plurinervis* of New Guinea, and *Guioa subfalcata* of Samoa. Probably the latter is no *Guioa* and will consequently be left out of the analysis.

In spite of the fact that the tree contained several strange elements, it was apparent that most of the species from a geographical area were present together (for instance the Pacific species), quite often as a monophyletic group (West Malesian, New Caledonian, and Australian species). Consequently, the New Guinean species also remained together. N.B.: The other 21 trees showed more or less the same groupings.

Changes in the data matrix (coding putative homoplasies differently) did not resolve the inconsistencies, and quite often added other, also quite unlikely, groups of species. The inconsistencies were usually mainly due to correlating characters which often showed high numbers of homoplasies, or they were caused by a single character state (for instance large domatia) which was coded as homologous but which presumably contained more states (parallel developments). Coding these as separate states, as was done, creates a rather artificial solution and a circular reasoning (only those improvements are selected which support the geological distribution; consequently, when the geography is later on used as a check of the cladogram, the two will be in complete accordance).

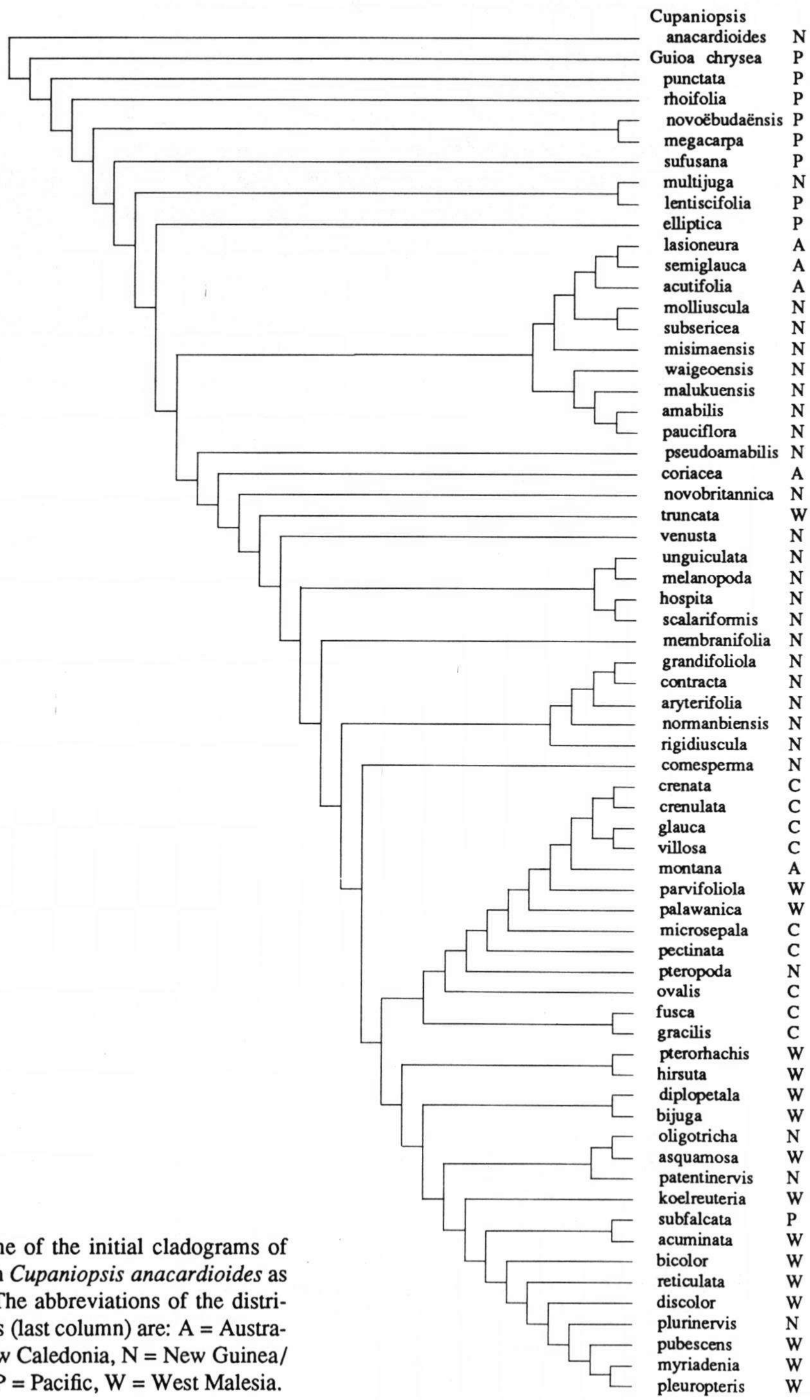


Fig. 38. One of the initial cladograms of *Guioa*, with *Cupaniopsis anacardioides* as outgroup. The abbreviations of the distribution areas (last column) are: A = Australia, C = New Caledonia, N = New Guinea/ Moluccas, P = Pacific, W = West Malesia.

The cladogram shown in figure 38 is rejected, because:

1. It is one of many equally parsimonious trees.
2. The number of homoplasies is very high.
3. Several geographical inconsistencies are present.
4. Improvements of the data matrix resulted in the same type of trees.
5. Iterative weighing, as can be executed with the program HENNIG86, cannot undo all influences of the homoplasies, e.g. geographical inconsistencies remain.

11.7. AMPLIFICATION OF THE CLADISTIC METHOD

The cladogram shown in the previous section was rejected for several reasons. The enormous amount of homoplasies is the main cause of the rejection as they quite likely prevent the detection of the 'correct' cladogram. A reduction in the number of homoplasies has to be provoked in order to find a more acceptable cladogram. One way of reducing the number of homoplasies is decreasing the number of taxa involved in the analysis. The group under analysis has to be split into several groups, then the analysis of a group will not be influenced by the character states present in other groups. All groups can be analysed separately. Afterwards they can be pieced together and an overall cladogram has been constructed. An example in this section will demonstrate how the method operates.

Figure 39e shows an example of a cladogram with 13 species in the ingroup (A–M) and one as outgroup (OG). Thirteen characters provide a complete solution of the cladogram (fig. 39a contains the character distribution). The characters include two reversals (characters 7 and 8) and one parallel development (character 10). PAUP (option: 'bandb') and HENNIG86 (option: 'ie*') found the example tree as the most parsimonious tree (16 steps, consistency index 0.813). After the primary analysis CAFCA (options: 'partial monothetic sets' 'minimal steps') found two partly resolved trees, of which the second one, with the highest redundancy index, was selected for the secondary analysis. The secondary analysis found 8 trees, among which the example tree as the most parsimonious one and the one with the highest redundancy index.

The division of a group meets with two demands: it has to be based on characters and the subgroups have to contain a reasonable number of species, not too few nor too many (during the analysis of *Guioa* it appeared that groups containing between 10 and 15 species could still be analysed easily). The characters must completely include or exclude each other, they may not overlap: if one character divides a group, the second character may only divide one of the subgroups, but the remainder may not have any taxa with the second character.

The choice of the characters is more or less a priori and subjective. Two particulars may help in guiding the choice of the characters: the initial cladogram and the character consistency index as obtained from the initial cladogram (choose characters with a high index).

In the example the characters 6 and 11 were chosen (marked with a vertical line in fig. 39e). Character 6 divides the group into OG + A–D and E–M. Character 11 divides the second subgroup (E–M) into E–I and J–M. OG and A–D all lack character 11. In total three groups are formed: OG + A–D, E–I, and J–M.

The three groups are still phenetic groups, not yet phylogenetic groups, as it is still unknown whether the absence or presence of characters 6 and 11 is plesiomorphous or apomorphous. The initial cladogram and the outgroup (OG) help to polarize the character states. Then the subordination of the groups becomes apparent: OG + A–I of course form the basal group as this group contains the outgroup. The most parsimonious solution is to consider E–I as the middle group (they differ in one character from the basal group) and J–M as the upper group (they differ in two characters from the basal group and in one character from the middle group).

To know the subordination of the groups is important. The upper group is monophyletic, but the other two are quite likely to be paraphyletic. Only monophyletic groups can be considered in a phylogenetic analysis. In order to overcome this problem a representative species of a higher group (the basal ancestral species) is added to a lower group as the data of this species are mainly used to optimize the character distribution over the ancestral species of the lower group. In the example the data of the ancestral species Y (fig. 39e) should be added to the matrix of the middle group and the data of X should be added to those of the basal group. The data of X and Y are of course unknown as long as the upper and middle group have not been analysed, therefore the basal terminal taxon is added as a representative species: J as representative species of the upper group to the middle group and E as representative of the middle group to the basal group. J and E probably still possess the characters of Y and X for the greater part.

Also, the outgroups have to be added to all groups. For the basal group this is OG. For the middle group this is D and for the upper group I. The initial cladogram may help in selecting the outgroups and the representative species.

After the groups have been divided and the outgroups and representative species have been added, all groups can be analysed separately.

The analysis of the basal part (species OG, A–E; matrix fig. 39b) resulted in fig. 39f (steps 7, consistency index 1). The analysis of the middle part (species D–J; matrix fig. 39c) resulted in fig. 39g (steps 8, consistency index 0.875). CAFCA needed a secondary analysis, as due to the reversal (character 8) a polytomy remained after the primary analysis. The analysis of the upper part (species I–M; matrix fig. 39d) showed figure 39h as a result (steps 5, consistency index 1).

After the analysis the subcladograms have to be united, during which process the root characters of the subcladograms and the characters of the representing species have to be evaluated. Of the basal part the ingroup (A–E) contains two apomorphies, one of which (character 2) was meant as an apomorphy of the outgroup OG. As already explained in the previous section the root characters can only be interpreted correctly when more outgroups are added. This is different for the outgroups of the middle and upper part, where the former cladograms (respectively the basal and middle part) show the correct interpretation of the characters. Consequently character 3 in the middle part should be considered as an apomorphy for A–D and not for the ingroup E–J, and character 8 in the upper part as an apomorphy for F–I and not for J–M.

Ch.	1	2	3	4	5	6	7	8	9	10	11	12	13
OG	1	2	1	1	1	1	1	1	1	1	1	1	1
A	2	1	2	2	2	1	1	1	1	2*	1	1	1
B	2	1	2	2	2	1	1	1	1	2*	1	1	1
C	2	1	2	2	1	1	1	1	1	1	1	1	1
D	2	1	2	1	1	1	1	1	1	1	1	1	1
E	2	1	1	1	1	2	1	1	1	1	1	1	1
F	2	1	1	1	1	2	2	1*	2	2	1	1	1
G	2	1	1	1	1	2	2	2	2	2	1	1	1
H	2	1	1	1	1	2	2	2	2	1	1	1	1
I	2	1	1	1	1	2	2	2	1	1	1	1	1
J	2	1	1	1	1	2	2	1	1	1	2	1	1
K	2	1	1	1	1	2	2	1	1	1	2	2	1
L	2	1	1	1	1	2	1*	1	1	1	2	2	2
M	2	1	1	1	1	2	1*	1	1	1	2	2	2

a. Matrix for complete cladogram.

	7	8	11	12	13
I	2	2	1	1	1
J	2	1	2	1	1
K	2	1	2	2	1
L	1*	1	2	2	2
M	1*	1	2	2	2

d. Matrix upper part.

	1	2	3	4	5	6	10
OG	1	2	1	1	1	1	1
A	2	1	2	2	2	1	2*
B	2	1	2	2	2	1	2*
C	2	1	2	2	1	1	1
D	2	1	2	1	1	1	1
E	2	1	1	1	1	2	1
J	1	2	2	1	1	1	2

b. Matrix for basal part.

	3	6	7	8	9	10	11
D	2	1	1	1	1	1	1
E	1	2	1	1	1	1	1
F	1	2	2	1*	2	2	1
G	1	2	2	2	2	2	1
H	1	2	2	2	2	1	1
I	1	2	2	2	1	1	1

c. Matrix middle part.

* = parallel or reversal.

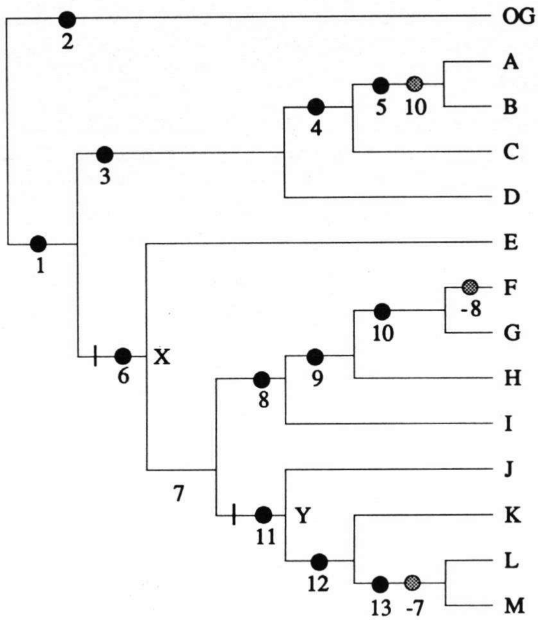
Fig. 39. Construction of a complete cladogram from partial ones. a–d: matrices for respectively the complete cladogram, the basal, middle, and upper part; e–h: the respective cladograms.

E and J were taken as representative species in the basal and middle part and D and I as outgroups in the middle and upper part. If these species would have had autapomorphies, then these character states would have become apomorphies for respectively the non-included species (the upper groups) and the ingroups. These characters also have to be placed correctly during the evaluation of the cladograms.

The advantages and disadvantages of this method are threefold. Advantageous is:

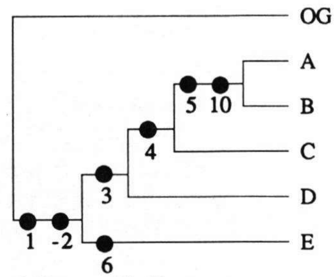
a) The reduction in the number of homoplasies per partial cladogram. Characters 10 and 7 do not constitute homoplasies in the basal and upper cladogram (fig. 39f &

(Fig. 39 continued)

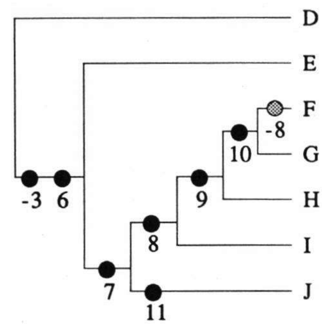


● = apomorphy, ◍ = reversal/parallel,
X and Y = ancestors, | = group limit.

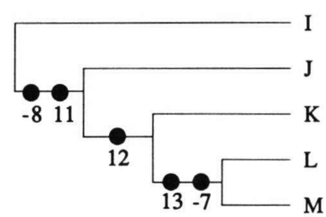
e. Complete cladogram.



f. Base, with E as representative for other species.



g. Middle, D as outgroup, J for other species.



h. Top, I as outgroup.

h). Usually the less homoplasies the less alternative, as parsimonious cladograms are found by the computer algorithms and the choice of a cladogram becomes less complicated. In other words: homoplasies in other groups will not influence the analysis anymore.

b) Per partial cladogram fewer species are involved, likewise fewer characters are needed to find a dichotomous cladogram.

c) The set of characters necessary to constitute a cladogram may differ per partial cladogram (see example, fig. 39).

The disadvantages are:

a) The overall cladogram, formed from the partial ones, may be globally less parsimonious. Usually it will then be disregarded. However, the analysis of *Guioa* is in fact also only a partial analysis, more parsimonious trees may be found when more Sapindaceae genera are included in the analysis. Parsimony in the present study means that all partial cladograms are the most parsimonious to be found (showing the lowest amount of state changes and therefore showing the highest amount of homology of characters).

b) The division of a genus into several parts has to be based on characters. In the example characters 6 and 11 were selected. One will never be sure whether or not the groups of species based on these characters will encompass all descendants (the character may show no reversals). Geography may help in this respect, for example: if one species of West Malesia is left out of a group which includes all other West Malesian species, it will be likely that this is due to character reversal. Parallel developments may also be detected this way, for example if West Malesian species form a group with Pacific species.

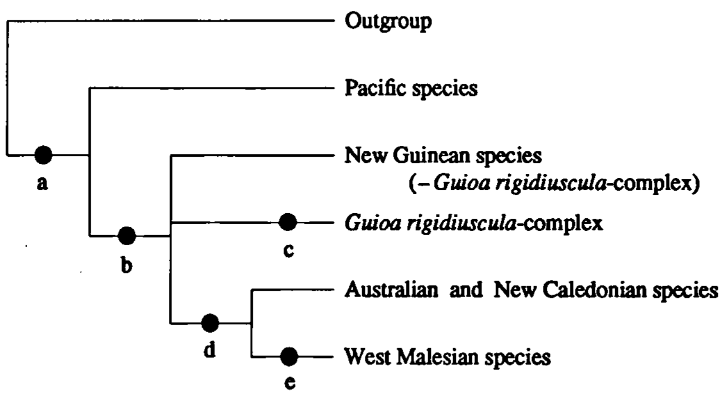
c) Another difficulty will be the selection of the outgroups and the root species which are representative for the species left out. As with the outgroup of the genus as a whole, if no species are obvious several have to be tried.

The method was used during the analysis of *Guioa*. After an initial analysis of the complete genus had been made and rejected, characters were selected on which a division of the genus could be based; this division was to a great extent in accordance with the initial cladogram. When the characters were selected and the genus had been divided into several groups, each group was analysed separately.

Usually the choice of outgroups and representative species was the most difficult choice. The best way to proceed with the analysis of the subsequent partial groups is to start with the top one and with the bottom one. The bottom one will show an outgroup for an upper cladogram and the top cladogram will show a representative species for the analysis of a lower cladogram. Normally, several switches between the different groups are necessary until the representing species in a lower cladogram actually becomes the root species in an upper cladogram, e.g. species J in the example has to become the representative of the upper cladogram in the middle cladogram (fig. 39g) and the root species in the upper cladogram (fig. 39h). The realization of congruence among the cladograms took most of the time.

During the analysis of each group a cladogram was first produced based on the complete set of characters. From these, characters were selected which uniquely fitted the cladogram (character consistency index of 1). With these characters a second analysis of the partial group was performed. If polytomies remained, characters were sought which could solve these polytomies. Quite often these characters showed parallels or reversals.

The following characters were found with which *Guioa* could be divided into several groups: The cotyledons of the embryo show two character states: either the cotyledons are dorsoventrally above each other and the apices usually not elongated or they are more or less laterally besides each other with the apices usually elongated and recurved (resp. fig. 14a and b). This character separated the genus into two, the Pacific and New Guinean (+ Moluccan) species showed the first type; the Australian, New Caledonian, and West Malesian species showed the second type. The West Malesian species show another kind of crest (always pilose) than the Australian and New Caledonian species do (always glabrous); this character was used to separate these two groups. The Pacific species together with two New Guinean species (*Guioa scalariformis* and *Guioa unguiculata*) always had a non-reduced fifth petal; the other New Guinea species had the fifth petal reduced. Later on, during the analysis of the Pacific and New Guinean group it appeared that the non-reduced fifth petal of the two New Guinean species was a reversal, as both are part of the *Guioa rigidiuscula*-complex and this complex appeared to be monophyletic with as apomorphy the petal-type (well-developed scales and crests, and claw of normal length). In total five groups were recognized (besides the outgroup): The Pacific group, the New Guinean group, the *Guioa rigidiuscula* group, the Australian/New Caledonian group, and the West Malesian group. The phylogenetic relations among these groups could be inferred with the aid of the outgroup; the result is shown in figure 40. The polytomy was later on solved by adding representatives of the *Guioa rigidiuscula* and Australian group to the analysis of the New Guinean species. The New Guinean group appeared to be paraphyletic as both other groups are derived from it.



● = apomorphy; a = sepals petaloid, fruit black and wall thin, pseudo-funicle present; b = fifth petal reduced; c = petal type; d = cotyledons laterally besides each other; e = crest pilose.

Fig. 40. Separation of *Guioa* into five subsets of species.

In the next sections the subsequent groups of species will be analysed phylogenetically. The characters as used in the separate analyses were mainly taken from the main matrix, but were always adjusted: 1) Sometimes character states were absent in the group under analysis and were ignored. 2) Sometimes more character states could be distinguished (the computer programs can mainly handle characters with less than 10 states, therefore the main matrix had to contain less well separated character states in some instances).

Introduction

Guioa subfalcata has been omitted from the analysis of the Pacific group. Knowledge of this species is very incomplete (only buds present) and some of the characters it shows are very different from those of the other Pacific species (no papillae, different type of petal scales). This makes it doubtful whether this species is part of *Guioa* or not. As outgroup *Cupania americana* has been chosen, together with *Cupaniopsis anacardioides,* and two of the New Guinean species, *Guioa oligotricha* and *Guioa pteropoda.* The latter two are root species in the cladogram of the other monophyletic part of *Guioa.*

Characters

The following characters were used to analyse the Pacific group:

Character	Character state
1. Leaflets	1 = (Sub)symmetric 2 = Asymmetric
2. Leaflets	1 = Not falcate 2 = Falcate
3. Papillae	1 = Absent 2 = Absent to present 3 = Present
4. Domatium size	1 = Small 2 = Large
5. Domatium opening	1 = Front 2 = Top
6. Sclerenchyma around domatia	1 = Absent 2 = Slightly present 3 = Completely surrounding
7. Sepals	1 = Sepaloid 2 = Petaloid
8. Sepals	1 = Equal in size 2 = Dimorphic
9. Fifth petal	1 = Not reduced 2 = Reduced
10. Disc	1 = Pilose 2 = Glabrous
11. Fruit wall	1 = Thick 2 = Thin
12. Fruit stipe	1 = Absent 2 = Present
13. Fruit colour	1 = Brown 2 = Black
14. Pseudofunicle	1 = Absent 2 = Present
15. Cotyledons	1 = Lomatorrhizal 2 = Notorrhizal

The following character matrix is used:

Taxon\Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Cupania americana	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1
Cupaniopsis anacardioides	1	1	1	?	?	?	1	2	1	1	1	1	1	1	2
Guioa oligotricha	1	1	2	1	1	1	2	2	2	2	2	1	2	2	2
Guioa pteropoda	2	1	1	1	2	1	2	2	2	2	2	1	2	2	2
Guioa chrysea	2	1	3	2	2	3	2	2	1	2	2	2	2	2	2
Guioa elliptica	2	1	3	1	1	1	2	2	1	2	2	2	2	2	2
Guioa lentiscifolia	2	1	3	2	2	3	2	2	1	2	2	2	2	2	2
Guioa megacarpa	2	2	3	1	1	1	2	2	1	2	2	2	2	2	2
Guioa novoëbudaënsis	2	2	3	1	1	1	2	2	1	2	2	2	2	2	2
Guioa punctata	2	2	3	2	2	2	2	2	1	2	2	2	2	2	2
Guioa rhoifolia	2	2	3	2	2	1	2	2	1	2	2	2	2	2	2
Guioa sufusana	1	1	3	1	1	1	2	2	1	2	2	2	2	2	2

The ? is used for characters which are unknown (*Cupaniopsis anacardioides* has no domatia and anatomical data of *Cupania americana* are lacking).

The species *Guioa megacarpa* and *Guioa novoëbudaënsis* have the same data. These two can only be separated by differences in the dimensions of several characters. The latter characters are omitted from the data matrix as the other species of the Pacific group overlap the gaps in measures. Consequently, two analyses were performed, one with both species included and the second with only *Guioa megacarpa* included and *Guioa novoëbudaënsis* added afterwards as a polytomy.

Analysis

In all three programs the characters were unordered and as outgroup *Cupania americana* has been selected.

The second analysis, with *Guioa novoëbudaënsis* left out, provided the same results as the first analysis except for CAFCA, which found a less parsimonious cladogram than PAUP and HENNIG86 did. Only the results of the first analysis will be discussed.

PAUP and HENNIG86 found the same trees.

In CAFCA the option 'partial monothetic sets' was used to create clades and the criterium 'minimal steps' to choose among trees. After a primary analysis a secondary had to be performed, because two polytomies were still present. A cladogram like the one shown below was selected as the best cladogram, however, with one difference, *Guioa rhoifolia* and *Guioa punctata* were sister species and together they formed the sister group of *Guioa chrysea* and *Guioa lentiscifolia.*

PAUP was used with the default options except that the command 'bandb' was invoked to find the most parsimonious trees. PAUP found 11 trees. Of these only one tree (see below) was completely resolved except for the polytomy with *Guioa megacarpa* and *Guioa novoëbudaënsis.*

HENNIG86 was used with the option 'ie*' to find the most parsimonious trees. During both runs (with and without *Guioa novoëbudaënsis*) four cladograms were found, of which one was fully resolved, also the polytomy with *Guioa megacarpa* and *Guioa novoëbudaënsis.*

The four trees found by HENNIG86 were evaluated in CAFCA as user trees with the redundancy index as the selection criterion instead of minimal steps. The selected tree (fig. 41) was the tree with the highest information content (redundancy index = 0.753; r.i. of the other three: 0.743, 0.745, 0.750). The r.i. of 0.750 was found for the completely resolved tree; this tree was also rejected because it always possessed a group without any apomorphies. The total amount of character changes is 20, the consistency index = 0.85.

There is one reversal (character 2, leaflets falcate) and three parallel developments (character 1, leaflets asymmetric; character 3, papillae; and character 5, position of domatium opening). Character 6 (sclerification of the domatium) shows two steps. The changes in these five characters are depicted in the cladogram. The numbers in the data matrix already show the directions of the other transformation series.

The monophyly of the Pacific group is based on two characters: 1) the possession of papillae, and 2) a fruit with a slender stipe. These characters show several parallel

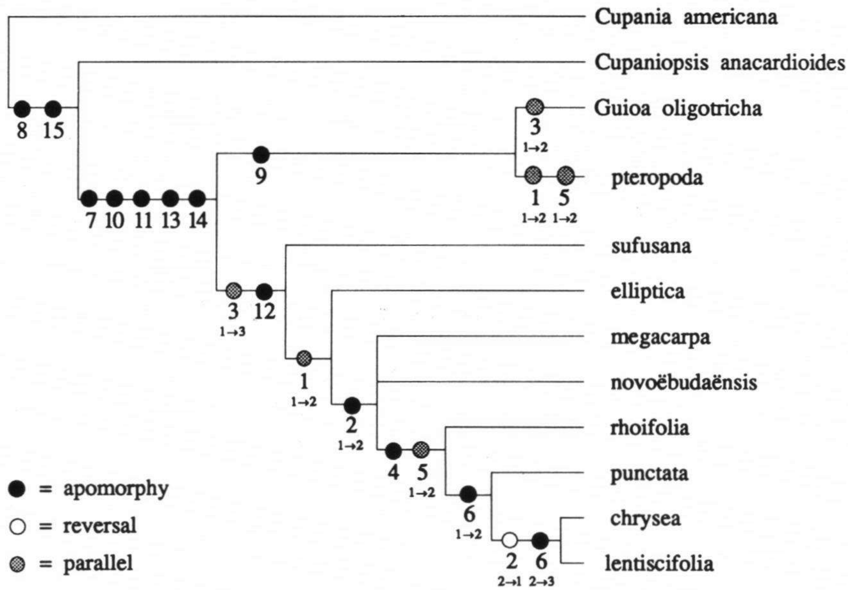


Fig. 41. Phylogenetic analysis of the Pacific species of *Guioa*.

developments and reversals (e.g. from a slender stipe to a broadly cuneate stipe and vice versa; see cladograms of other groups), but as the outgroup lacks papillae and a slender stipe, these characters are apomorphic for the Pacific group.

Geographically it is interesting to note that the species split off in a sequential way, starting near New Guinea (where *Cupaniopsis anacardioides* is found) with the Solomon Islands (*Guioa elliptica* and *Guioa sufusana*), followed by the Santa Cruz group of the Solomon Islands (southern part) and the New Hebrides (*Guioa megacarpa* and *Guioa novoëbudaënsis*), Fiji (*Guioa chrysea, Guioa punctata*, and *Guioa rhoifolia*); and last Tonga (*Guioa lentiscifolia*). The sequence indicates that the polytomy can be solved by regarding *Guioa megacarpa* as sister species of the species of the New Hebrides, Fiji, and Tonga. Note that the sequence is precisely opposite to that of the first cladogram (fig. 38) of the initial analysis of the complete genus; there *Guioa chrysea* splits off first and *Guioa elliptica* as last.

Within *Guioa* the Pacific group contains the most primitive characters, the fifth petal (the petal inserted between the two adjacent large sepals) is unreduced or only slightly reduced, the cotyledons are dorsoventrally above each other and the petal crests (if present) are glabrous. All other *Guioa* species have a reduced fifth petal (the apomorphy of this group) except for a few New Guinea species, where a reversal to the non-reduced state was found.

Apomorphies for *Guioa* are presence of petaloid sepals, a glabrous disc, a thin fruit wall, black fruits, and a pseudo-funicle. In relation to *Cupania americana*, *Cupaniopsis anacardioides* and *Guioa* possess as apomorphies dimorphic sepals and notorrhizal cotelydons. Especially the character of the pseudo-funicle is important, because it is not found in any other genera which are considered to have even more primitive characters than *Cupania* and *Cupaniopsis* have (which genera constitute outgroups of these two genera). Consequently, the pseudo-funicle is an apomorphy of *Guioa*, any other genera added as outgroups cannot change this fact (see also section 11.4).

11.9. THE NEW GUINEAN GROUP (GUIOA RIGIDISCULA-COMPLEX EXCEPTED)

Introduction

This group contains a number of species which are rather incompletely known. These species (*Guioa amabilis*, *Guioa malukuensis*, *Guioa multijuga*, *Guioa pauciflora*, *Guioa venusta*, and *Guioa waigeoensis*) had to be excluded from the analysis. *Cupaniopsis anacardioides* was used as outgroup (*Cupania americana* can be disregarded because the apomorphies of *Cupaniopsis* and *Guioa* are already known from the former analysis). *Guioa lasioneura* and *Guioa semiglauca* are used as root species for the non-included species of *Guioa*.

Characters

The following characters were used to analyse the New Guinean species outside the *Guioa rigidiuscula* group:

Character	Character state
1. Number of jugae	1 = 1–6 2 = 1–3 3 = 1–9
2. Wing	1 = Absent 2 = Narrow 3 = Broad
3. Leaflet breadth	1 = < 9 cm broad 2 = < 3 cm broad
4. Leaflet symmetry	1 = Slightly asymmetric 2 = Symmetric 3 = Asymmetric
5. Leaflet margin	1 = Entire 2 = (Partly) serrate 3 = Crenate
6. Hairs on lower surf.	1 = Only on veins 2 = Everywhere
7. Glands on lower surf.	1 = Absent 2 = One-celled 3 = Four-celled
8. Papillae	1 = Absent 2 = Sometimes present 3 = Present
9. Adaxial cuticle	1 = Thin areas absent 2 = Thin areas present
10. Abaxial anticlinal epidermal walls	1 = Straight 2 = Sometimes undulating 3 = Undulating
11. Branch thickness	1 = < 5 mm thick 2 = < 10 mm thick 3 = < 15 mm thick
12. Sepals	1 = Sepaloid 2 = Petaloid
13. Petal claw length	1 = Short 2 = Normal length 3 = Long
14. Fifth petal	1 = Not reduced 2 = Reduced
15. Fruit wall	1 = Thick 2 = Thin
16. Fruit colour	1 = Brown 2 = Black
17. Pseudofunicle	1 = Absent 2 = Present
18. Cotyledons	1 = Dorsoventrally 2 = Secondarily laterally

The following character matrix was used:

Taxon\Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Cupaniopsis anacardioides	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Guioa lasioneura	2	1	1	2	1	2	1	3	1	1	1	2	2	2	2	2	2	2
Guioa melanopoda	1	3	1	1	1	1	3	1	2	3	2	2	1	?	2	2	2	1
Guioa oligotricha	2	1	1	2	2	1	1	2	1	2	3	2	1	2	2	2	2	1
Guioa patentinervis	1	1	1	1	1	1	3	1	2	3	2	2	1	2	2	2	2	1
Guioa pseudoamabilis	3	2	2	3	3	1	1	1	1	1	1	2	2	2	2	2	2	1
Guioa pteropoda	3	2	2	3	3	1	1	1	1	3	1	2	1	2	2	2	2	1
Guioa semiglauca	2	1	1	2	1	2	2	3	1	1	2	2	1	2	2	2	2	2
Guioa subsericea	2	1	1	3	1	2	1	3	1	1	2	2	1	2	2	2	2	1
Guioa unguiculata	2	1	1	1	1	1	1	1	2	3	2	2	3	1	2	2	2	1

Analysis

The characters were unordered.

HENNIG86 and PAUP found the same tree (fig. 42), the tree which has been accepted as cladogram. CAFCA did not find any cliques with *Cupaniopsis anacar-*

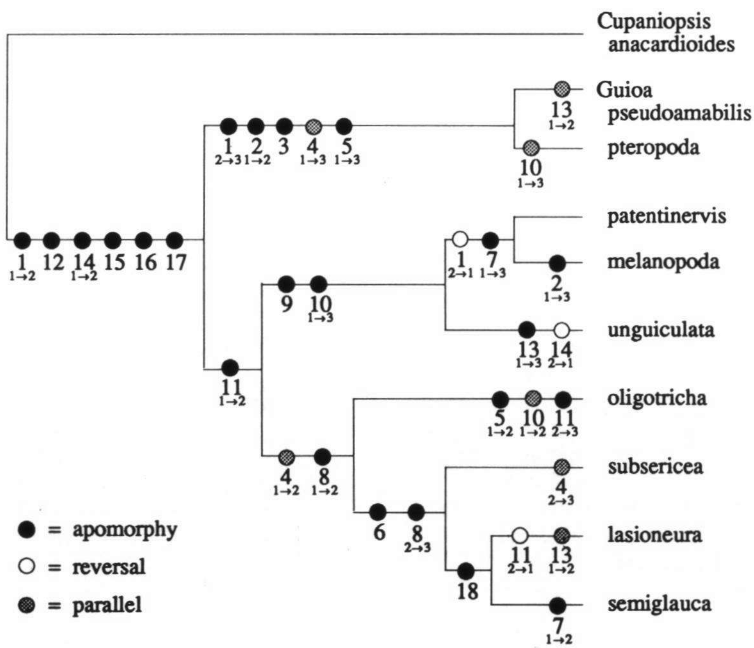


Fig. 42. Phylogenetic analysis of the New Guinea species outside the *Guioa rigidiuscula*-complex.

dioides as the outgroup, but only as part of the ingroup. The results of CAFCA are therefore ignored.

The accepted tree has a length of 33 steps and a consistency index of 0.818. Six homoplasies were found (a reversal in character 1, 11, and 14; and a parallel in character 4, 10, and 13); these, together with the state changes of characters with more than two character states are depicted in the cladogram. Of the other characters the character matrix already shows the direction of the state changes.

The Australian, New Caledonian, and West Malesian species, as represented by *Guioa lasioneura* and *Guioa semiglauca,* arise as a monophyletic group, with *Guioa subsericea* as sister species. The apomorphy of this group is the possession of cotyledons which are situated secondarily laterally besides each other.

Guioa unguiculata, the representative of the *Guioa rigidiuscula* group, is sister species of *Guioa patentinervis* and *Guioa melanopoda.* This group is characterized by anatomical features. *Guioa unguiculata* has as apomorphies the possession of an unreduced fifth petal and a long petal claw.

The excluded species *Guioa amabilis* and *Guioa pauciflora* possibly fit in with *Guioa pseudoamabilis* and *Guioa pteropoda,* because they all possess a slightly winged rhachis and a (partly) crenate leaflet margin. *Guioa venusta* and *Guioa waigeoensis* may fit in with *Guioa patentinervis* and *Guioa melanopoda* because of the slightly serrate leaflet margin. *Guioa malukuensis* fits in with *Guioa subsericea*; both have folded petal margins as scales. *Guioa multijuga* perhaps fits in with *Guioa unguiculata,* both have more or less the same type of petal.

The apomorphy for this monophyletic group, all New Guinean, Australian, New Caledonian and West Malesian species, is the possession of a reduced fifth petal (the petal inserted between the two adjacent large sepals). *Guioa scalariformis* and *Guioa unguiculata* show a reversal of this character.

11.10. THE GUIOA RIGIDIUSCULA-COMPLEX

Introduction

Chapter 9 already showed that this group of species is rather similar in appearance. Typical is the type of petal with a claw of normal length and well-developed scales and crests. *Guioa unguiculata,* the outgroup, is the only exception (long claw, short scales and usually no crests; most other New Guinean species have a short claw and short scales with usually no crest).

Several species, *Guioa hospita, Guioa grandifoliola, Guioa misimaensis, Guioa molliuscula,* and *Guioa novobritannica,* were incompletely known, but could fortunately be incorporated in the analysis.

Characters

The following characters were used to analyse the *Guioa rigidiuscula* group of New Guinea and the Moluccas.

Character	Character state
1. Number of jugae	1 = 1–3
	2 = 1–6
2. Leaflet shape	1 = Elliptic
	2 = Ovate
3. Indumentum of leaflets	
	1 = Glabrous
	2 = Patent
	3 = Sericeous
4. Papillae	1 = Absent
	2 = Sometimes present
	3 = Present
5. Inflorescence	1 = Axillary
	2 = Axillary and ramiflorous
6. Claw of petal	1 = Long
	2 = Normal length
7. Crest of petal scale	
	1 = Absent (or bifid)
	2 = Well developed
8. Disc	1 = Complete
	2 = Interrupted
9. Wall of fruit	1 = Thin
	2 = Thick
10. Stipe of fruit	1 = Present
	2 = Absent
11. Pseudo-funicle	1 = Well developed
	2 = Reduced to rim

The following character matrix is used:

Taxon \ Character	1	2	3	4	5	6	7	8	9	10	11
Guioa unguiculata	1	1	1	1	1	1	1	1	1	1	1
Guioa aryterifolia	2	1	1	1	2	2	2	1	1	2	2
Guioa comesperma	2	1	1	2	1	2	2	2	1	1	1
Guioa contracta	1	1	1	1	2	2	2	2	2	2	2
Guioa grandifoliola	1	2	1	1	2	?	?	2	2	2	2
Guioa hospita	1	2	2	1	1	?	?	2	1	1	1
Guioa membranifolia	1	1	1	1	2	2	2	2	1	1	1
Guioa misimaensis	1	1	3	3	1	2	2	2	?	?	?
Guioa molliuscula	1	2	2	1	1	2	2	1	?	?	?
Guioa normanbiensis	2	2	1	1	2	2	2	2	1	1	1
Guioa novobritannica	1	1	1	3	1	2	2	2	?	?	?
Guioa plurinervis	2	2	3	3	1	2	2	2	1	1	1
Guioa rigidiuscula	2	1	1	1	2	2	2	2	1	2	2
Guioa scalariformis	1	2	1	1	1	2	2	1	1	1	1

Analysis

Guioa unguiculata was used as outgroup. The characters were unordered except for character 4, the presence of papillae; the condition papillae sometimes present is regarded as intermediate between absent and always present.

HENNIG86 found three trees and PAUP five (which are included in the three of HENNIG86, because of one polytomy). CAFCA found 24 trees after secondary analysis, of which four were the most parsimonious. Of the latter, two had the highest redundancy index (0.651); these were not accepted because in each one group was present without any apomorphy. Therefore a cladogram was accepted with one polytomy (redundancy index 0.649): *Guioa aryterifolia, Guioa rigidiuscula,* and the putative ancestor of *Guioa contracta* and *Guioa grandifoliola*. The accepted cladogram (fig. 43), one of the trees found by HENNIG86 and PAUP, had the highest

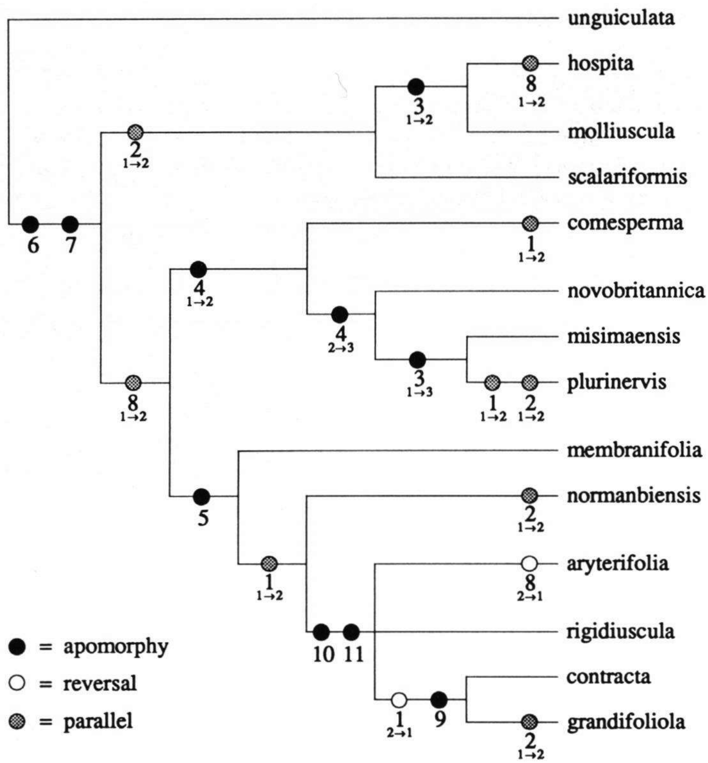


Fig. 43. Phylogenetic analysis of the *Guioa rigidiuscula*-group of New Guinea.

redundancy index after evaluation of the HENNIG86 trees via CAFCA (length 21, consistency index 0.619).

This monophyletic group has as apomorphic characters a well-developed crest (character 7) and a claw of normal length (character 6).

In the cladogram two reversals are present (character 1 and 8) and 5 parallels (twice in character 1 and three times in character 2). The reversals, parallels, and state changes of characters with more than two character states are depicted in the cladogram. The transition series of the two-state characters are already shown in the character matrix.

The *Guioa rigidiuscula*-complex more or less shows three groups: *Guioa hospita, Guioa molliuscula,* and *Guioa scalariformis* form one group (ovate leaflets and perhaps a highly stiped fruit as apomorphies as the latter is unknown for *Guioa molliuscula*). This group is the sistergroup of the other two: the papillate species (*Guioa comesperma, Guioa misiamaensis, Guioa novobritannica,* and *Guioa plurinervis*) and the ramiflorous group (remaining species).

11.11. THE AUSTRALIAN AND NEW CALEDONIAN GROUP

Introduction

All taxa from Australia and New Caledonia have been analysed, including the incompletely known ones like *Guioa crenulata* and *Guioa pectinata*. *Guioa subsericea* was used as outgroup and *Guioa asquamosa, Guioa hirsuta,* and *Guioa diplopetala* as representatives of the West Malesian species.

Characters

The following characters were used to analyse the Australian and New Caledonian species:

Character	Character state
1. Rhachis	1 = Slightly winged 2 = Not to slightly winged 3 = Not winged
2. Leaflet margin	1 = Crenate 2 = Crenate to entire 3 = Entire
3. Leaflet indumentum below	1 = Pilose 2 = Sparsely pilose 3 = Glabrous
4. Stomatal outer rim	1 = Normal 2 = Extra large
5. Venation	1 = Distinct 2 = (Rather) Indistinct
6. Sepals inside	1 = Glabrous 2 = Sericeous
7. Scales	1 = Normal length 2 = Reduced in length
8. Crest shape	1 = Absent 2 = Absent to shortly clavate
(8. Crest shape)	3 = Stipe short, apex small 4 = Stipe short, apex large 5 = Stipe long, apex large 6 = Absent to bifid
9. Crest pilosity	1 = Glabrous 2 = Pilose
10. Disc	1 = Entire 2 = Small slit 3 = Gap
11. Fruit colour	1 = Black 2 = Red
12. Fruit stipe	1 = Absent/Indistinct 2 = Present
13. Cotyledons	1 = Dorsoventally 2 = Secondarily laterally

The following character matrix has been used:

Taxon\Character	1	2	3	4	5	6	7	8	9	10	11	12	13
Guioa subsericea	3	3	1	1	1	1	1	2	1	1	1	1	1
Guioa acutifolia	3	3	2	1	2	1	2	2	1	1	1	1	2
Guioa asquamosa	3	3	2	1	2	1	2	1	2	1	1	2	2
Guioa coriacea	3	3	2	1	2	1	1	5	1	1	1	2	2
Guioa crenata	1	1	1	1	2	2	2	2	1	1	1	2	2
Guioa crenulata	1	1	1	1	2	2	2	2	1	3	?	?	?
Guioa diplopetala	3	3	2	1	2	1	2	6	2	1	1	2	2
Guioa fusca	1	3	3	2	1	1	1	3	1	3	2	2	2
Guioa glauca	3	3	1	1	2	2	1	4	1	3	1	2	2
Guioa gracilis	2	2	3	2	2	1	1	3	1	2	2	2	2

Taxon\Character	1	2	3	4	5	6	7	8	9	10	11	12	13
Guioa hirsuta	3	3	1	1	2	1	2	6	2	1	1	2	2
Guioa lasioneura	3	3	1	1	1	1	1	3	1	3	1	1	2
Guioa microsepala	3	3	3	1	2	2	1	2	1	1	1	2	2
Guioa montana	3	3	1	1	1	1	2	3	1	2	1	1	2
Guioa ovalis	3	3	3	1	2	1	1	4	1	2	1	2	2
Guioa pectinata	3	3	3	2	2	1	1	4	1	3	1	2	2
Guioa semiglauca	2	3	1	1	2	1	2	2	1	1	1	1	2
Guioa villosa	2	2	1	1	2	2	1	4	1	3	1	2	2

The question mark is used for unknown characters (the fruits of *Guioa crenulata* are unknown).

Analysis

The characters were unordered except for the first two: Rhachis wing and leaflet margin. Of these it was assumed that the occasional presence of a sligthly winged rhachis and a crenate leaflet margin was intermediary between wing and crenation always present and wing and crenation absent. Ontogeny supports this opinion (see chapter 8.5). For an analysis in CAFCA the figures in the two first columns should be changed, 1 into 3 and 3 into 1. The latter is necessary because CAFCA treats ordered characters differently than HENNIG86 and PAUP do. CAFCA wants the basal group to start with character state 1, while this is unimportant for HENNIG86 and PAUP; these programs only use ordered for the manner in which the number of steps have to be calculated.

HENNIG86 found 12 trees and PAUP 18; the latter were included in the ones found by HENNIG86. CAFCA found two trees after a primary analysis, of these one was the most parsimonious. A secondary analysis failed on the DOS-type of computer due to lack of memory; however, the new Macintosh version found two equally parsimonious trees with a length of 42 steps (consistency index 0.5). The trees found by the other two programs contained 38 steps and had a consistency index of 0.553. These 12 trees were evaluated via CAFCA as users trees and the accepted cladogram (fig. 44) showed the highest redundancy index: 0.585.

Apomorphies for the Australian, New Caledonian, and West Malesian species are 1) the scales of reduced length, and 2) the cotyledons which are secondarily laterally besides each other. The latter character is unique within *Guioa*.

Of the Australian species *Guioa acutifolia* forms the sister species of the New Caledonian species (together with *Guioa coriacea* of Lord Howe Island) and of the West Malesian species. The apomorphy for the West Malesian group is the pilose petal crest. The apomorphy for the New Caledonian group together with *Guioa coriacea* is the scales of normal length instead of reduced length. The New Caledonian species have as apomorphies leaflets glabrous below and sepals sericeous inside. The New Caledonian species split into two groups of which *Guioa microsepala* is the sister species. The one group (*Guioa fusca, Guioa gracilis, Guioa ovalis,* and *Guioa pectinata*) is characterized by the absence again of hairs inside the sepals; the other

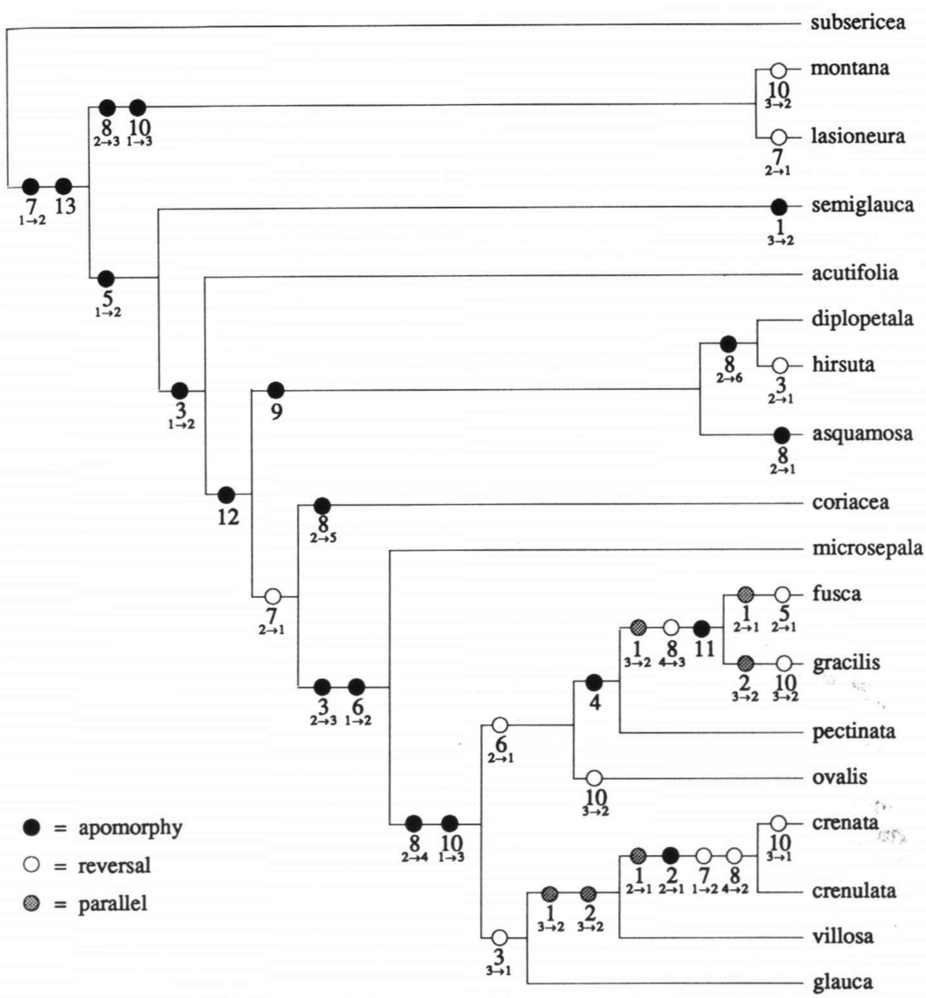


Fig. 44. Phylogenetic analysis of the Australian and New Caledonian species of *Guioa*.

group (*Guioa crenata, Guioa crenulata, Guioa glauca,* and *Guioa villosa*) is characterized by the presence of indumentum on the lower surface of the leaflets; they also possess papillae (a character not used).

Figure 44 shows quite a lot of homoplasies: 13 reversals (twice in character 3 and 8, once in character 5 and 6, three times in character 7, and four times in character 10) and 3 parallels (twice in character 1 and once in character 2). The homoplasies, together with the state changes of characters with more than two character states are shown in the cladogram. Of the other characters the data matrix already shows the direction of the transformation series.

Introduction

In this analysis the Philippine species *Guioa bicolor, Guioa parvifoliola, Guioa palawanica,* and *Guioa truncata* have been omitted. The character sets of these species were incomplete, because either the flowers were unknown or the fruits.

As outgroup *Guioa acutifolia* has been chosen for two reasons. It is the only Australian/New Caledonian species whose distribution reaches West Malesia (up to the Moluccas). And in the phylogenetic analysis of the Australian/New Caledonian group the West Malesian group was selected as the sister group of *Guioa acutifolia.*

Characters

The following characters were used to analyse the West Malesian group:

Character	Character state		
1. Rhachis	1 = Wing absent	7. Scale	1 = Short
	2 = Wing absent to broad		2 = Enation
	3 = Wing broad		3 = Normally developed
2. Leaflet	1 = Not falcate	8. Crest shape	1 = Absent
	2 = Falcate		2 = Broad (and bifid)
3. Papillae	1 = Smooth		3 = Bifid
	2 = Smooth to slightly papillate		4 = Bifid (and clavate)
			5 = Clavate
	3 = Papillate		6 = Linear
	4 = Smooth to papillate	9. Crest pilosity	1 = Glabrous
4. Marginal vein	1 = Complete		2 = Pilose
	2 = Incomplete	10. Disc	1 = Complete
5. Venation	1 = Laxly reticulate		2 = Incomplete
	2 = Densely reticulate	11. Fruit stipe length	1 = Absent
6. Petal claw	1 = Short		2 = Present
	2 = Normal length	12. Fruit stipe shape	1 = Broadly cuneate
	3 = Long		2 = Slender

The following character matrix has been used:

Taxon\Character	1	2	3	4	5	6	7	8	9	10	11	12
Guioa acutifolia	1	1	3	1	1	1	1	1	1	1	1	1
Guioa acuminata	1	2	1	1	1	3	3	6	2	2	2	2
Guioa asquamosa	1	1	1	1	1	1	2	1	?	1	2	1
Guioa bijuga	2	1	4	1	1	3	3	3	2	2	2	2
Guioa diplopetala	1	1	1	1	1	3	3	2	2	1	2	2
Guioa discolor	1	2	3	1	1	3	3	4	2	2	2	2
Guioa hirsuta	1	1	1	1	1	2	3	2	2	1	2	2
Guioa koelreuteria	1	2	2	1	1	3	3	4	2	2	2	2
Guioa myriadenia	1	2	3	1	2	3	3	5	2	2	2	2
Guioa pleuropteris	2	1	3	2	1	3	3	3	2	2	2	2
Guioa pterorhachis	3	1	3	2	1	2	3	3	2	2	2	2
Guioa pubescens	1	2	3	1	1	3	3	3	2	2	2	2
Guioa reticulata	1	2	3	1	2	3	3	4	2	2	2	2

The ? is used for unknown characters (the pilosity of the crest of *Guioa asquamosa* is unknown, because the crest is absent).

All characters are treated as unordered except for character 1 (rhachis wing) and 8 (crest), as this, possibly, offers a more realistic approximation of the biological reality: a) *Guioa pleuropteris* and *Guioa pterorhachis* are closely related, because they were almost inseparable during the revision; therefore character 1 (rhachis wing) is treatened as ordered. b) Several species are polytypic for character 1 and 8. The polytypism is regarded as a separate character state (e.g. wing absent to broad, crest bifid and clavate). Consequently state changes from 'bifid' to 'clavate' (2 steps) and a reversal to 'bifid and clavate' (in total 3 steps) are regarded as unlikely in regard to a change first from 'bifid' to 'bifid and clavate', and next a state change to 'clavate' only (2 steps in total). Character 8 was coded in a branched additive binary way in the ultimate data matrix (substitute column 8 by the 6 columns below), with the 'linear crest' of *Guioa acuminata* regarded as developed directly from the 'bifid and clavate' state, just as the 'clavate crest' of *Guioa myriadenia*:

Character 8:

Taxon \ Character state	1	2	3	4	5	6
Guioa acutifolia	1	0	0	0	0	0
Guioa acuminata	1	1	1	1	0	1
Guioa asquamosa	1	0	0	0	0	0
Guioa bijuga	1	1	1	0	0	0
Guioa diplopetala	1	1	0	0	0	0
Guioa discolor	1	1	1	1	0	0
Guioa hirsuta	1	1	0	0	0	0
Guioa koelreuteria	1	1	1	1	0	0
Guioa myriadenia	1	1	1	1	1	0
Guioa pleuropteris	1	1	1	0	0	0
Guioa pterorhachis	1	1	1	0	0	0
Guioa pubescens	1	1	1	0	0	0
Guioa reticulata	1	1	1	1	0	0

N.B.: The character states correspond with the character state numbers of character 8 in the list of characters.

This way of coding results in 6 different characters for PAUP and HENNIG86 and consequently in 6 character changes, while for CAFCA these 6 columns are regarded as one character with 5 character changes.

Analysis

All three computer programs showed trees with 24 steps to be the most parsimonious. HENNIG86 found six trees, PAUP 45 (these are in fact the same six trees as found by HENNIG86), and CAFCA two slightly different trees. The differences mainly existed in the Philippine species (*Guioa acuminata, Guioa discolor, Guioa koelreuteria, Guioa myriadenia,* and *Guioa reticulata*), whether these formed a three-forked polytomy as shown below or a four-forked one (*Guioa acuminata* and *Guioa koelreuteria* no sister species) and in *Guioa diplopetala* and *Guioa hirsuta,* whether these were sister species, a polytomy, or *Guioa hirsuta* split off earlier as shown below. In fact the number of steps as found by PAUP and HENNIG86 has to be reduced with 1, due to the additive binary coding, which makes the results of these two programs slightly more parsimonious than those found by CAFCA.

The tree below was finally selected, because it had the highest redundancy index (0.605; the others either had 0.599 or 0.602) and because *Guioa koelreuteria* and *Guioa acuminata* form a monophyletic group (these two species strongly resemble each other).

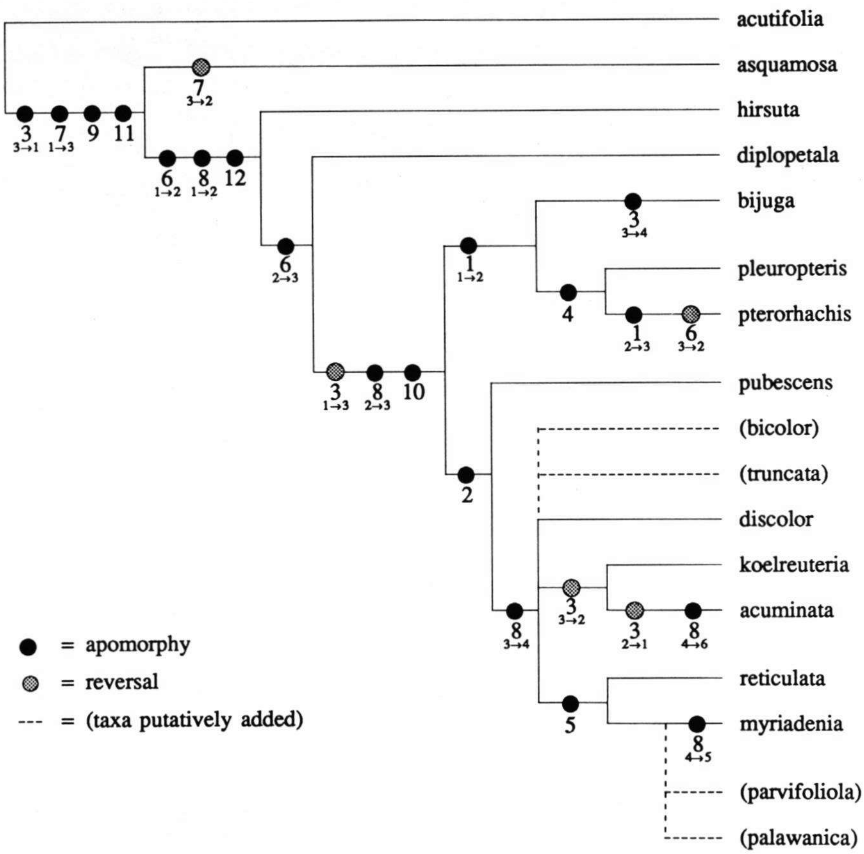
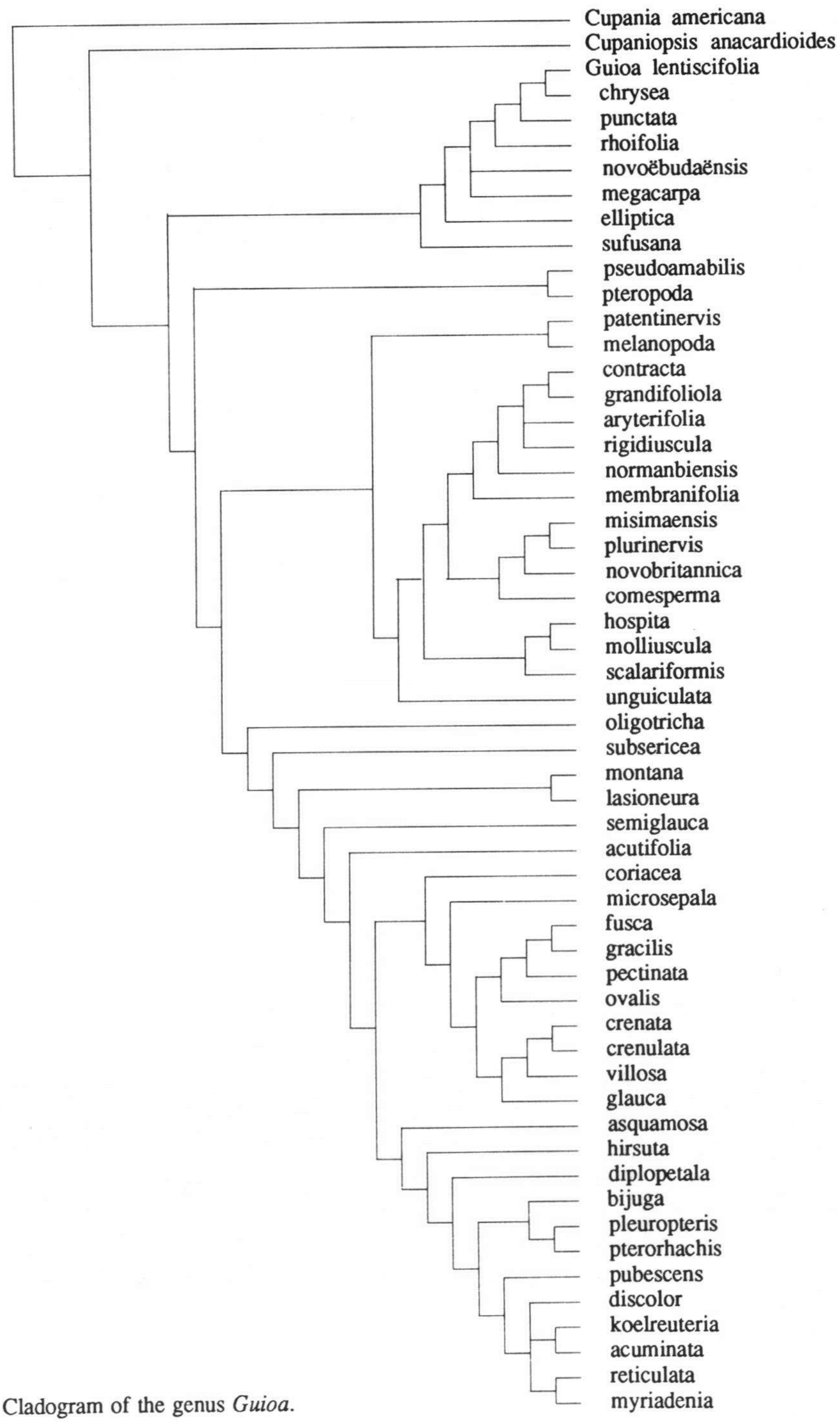


Fig. 45. Phylogenetic analysis of the West Malesian species of *Guioa*.

The cladogram (fig. 45; length 24, consistency index 0.875) contains four reversals, two in character 3 (papillae), one in character 6 (length of the petal claw), and one in character 7 (petal scale). Figure 45 shows the state changes of these three characters together with the changes in characters with more than 2 states. The direction of the transformation series of the remaining species is shown in the data matrix.



46a. Cladogram of the genus *Guioa*.

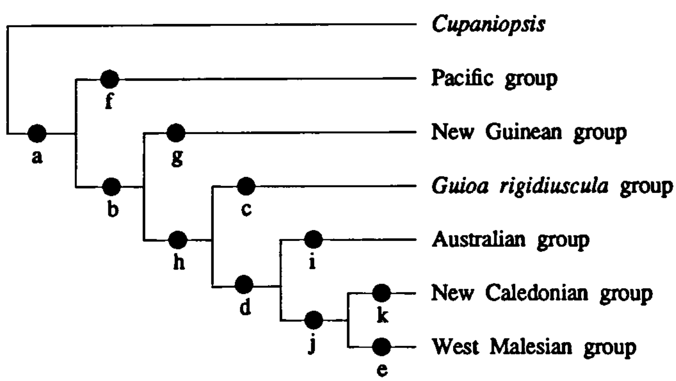
Characters 3 (leaflets smooth), 7 (petal scale normal), 9 (crest pilose), and 11 (fruit stipe present) form apomorphies for the West Malesian species.

The Philippine species form a monophyletic group within the West Malesian group; they are characterized by the presence of crests which can be bifid as well as clavate. Within the Philippine group the relationships are still poorly resolved, due to lack of characters because most of them look quite alike. *Guioa bicolor* and *Guioa truncata* are putatively added to the root polytomy of the Philippine species, because *Guioa bicolor* closely resembles *Guioa discolor* (fortunately the names are also almost the same, so confusion is added); and because *Guioa truncata* possesses many autapomorphies, which makes it difficult to find the sister species. *Guioa parvifoliola* and *Guioa palawanica* (imperfectly known) are added to *Guioa myriadenia*, because they strongly resemble this species.

Another monophyletic group is formed by the species with an (occasionally) winged rhachis: *Guioa bijuga*, *Guioa pleuropteris*, and *Guioa pterorhachis*. This result was somewhat unexpected because *Guioa bijuga* is rather unlike the other two (almost symmetric leaflets, usually without papillae and hairs), although it was originally described as an infraspecific taxon of *Guioa pleuropteris*.

11.13. A COMPLETE CLADOGRAM OF GUIOA

The five separate cladograms of *Guioa* added to each other form the cladogram in figure 46a. The species which were excluded in the analysis of the New Guinean species (*Guioa rigidiuscula* group excepted) and the putatively added species in the analysis of the West Malesian group are omitted.



46b: Cladogram constructed via CAFCA with root characters of all groups in matrix. ● = apomorphy; a = sepals petaloid, fruit black and wall thin, pseudo-funicle present; b = fifth petal reduced; c = petal type; d = cotyledons laterally besides each other; e = crest pilose (a–e as in fig. 40); f = leaflets ovate, only small sepals with glands; g = fruit stipe absent; h = branch thickness ≤ 10 mm, axis pilose when young, jugae 1–3; i = papillae present, fruit stipe absent and broadly cuneate; j = jugae 1–6, leaflets not mucronulate, fruit lobes as long as high; k = leaflets very coriaceous, margin recurved, apex emarginate to acuminate.

Fig. 46. Selected cladogram of *Guioa* and check of this cladogram.

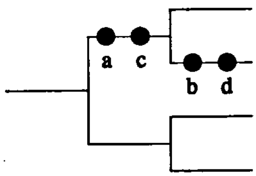
Three of the five subcladograms show monophyletic groups (Pacific species, the *Guioa rigidiuscula*-complex, and the West Malesian species); the other two, the remaining New Guinean species and the Australian and New Caledonian species, are paraphyletic groups to which representatives of the 'higher' groups have been added (N.B.: These paraphyletic groups include monophyletic parts, e.g. the New Caledonian species). The New Guinean group accommodated representatives of the *Guioa rigidiuscula*-complex and of the Australian/New Caledonian group; the Australian/New Caledonian group had representatives of the West Malesian group.

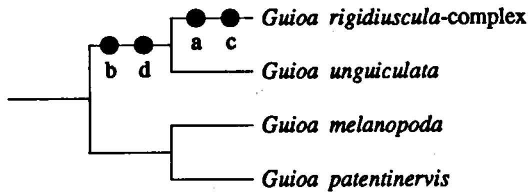
The characters have not been added to the complete cladogram; they can be found in the five subcladograms. The root characters of the subcladograms are evaluated below (those of *Guioa* itself are partly putative as already explained in section 11.4). The apomorphies were obtained by optimization of the complete character matrix over the user-tree of figure 46a via the program HENNIG86.

Apomorphies of *Guioa* and the subcladograms:

Guioa	Sepals petaloid Disc glabrous Cymules cincinnate Fruit wall thin Fruit black when dry Pseudo-funicle present
Pacific	Leaflets ovate Papillae present Only small sepals with glands Fruit stipe present
New Guinea (and all other groups)	Jugae 1–3 Leaflets elliptic Leaflets mucronulate Fifth petal reduced
Guioa rigidiuscula-complex	Petal claw of normal length Crest clavate on long stipe Fruit stipe present
Australia + New Caledonia + West Malesia	Marginal vein visible in upper 2/3rd of leaflets Cotyledons laterally besides each other Glandular hairs abaxially absent
New Caledonia + West Malesia	Jugae 1–6 Leaflet not mucronulate Papillae absent Petal scales present Fruit lobes as long as high Fruit stipe present Fruit stipe slender
New Caledonia	Leaflets very coriaceous Leaflet margin recurved Leaflet apex emarginate to acuminate Crest clavate on long stipe Adaxial anticlinal epidermal walls straight
West Malesia	Leaflets asymmetric Crest pilose Glandular hairs abaxially of *Guioa* type Adaxial cuticle with thin areas in loops of undulations

The outgroup of the *Guioa rigidiuscula*-complex has been *Guioa unguiculata*, this species was also the representative of this group in the New Guinea cladogram. The apomorphies of the *Guioa rigidiuscula*-complex can be evaluated in two ways:





a = Petal claw of normal length
b = Petal claw long
c = Crest well-developed
d = Crest absent (or bifid)

The long petal claw and absent crest can be regarded as autapomorphies of *Guioa unguiculata*, with the normal claw and well-developed crest as apomorphies for *Guioa unguiculata* and the rest of the *Guioa rigidiuscula*-complex (left); or the long petal claw and absent crest are apomorphies of *Guioa unguiculata* and the *Guioa rigidiuscula*-complex together, with the normal claw and well-developed crest as apomorphies for the *Guioa rigidiuscula*-complex only.

In order to confirm the original subdivision of the genus and in order to make the choice of the characters more objective the root characters of all groups, as obtained via HENNIG86 in the above mentioned user-tree evaluation, were placed in a matrix (table 4) and analysed via CAFCA (only those characters were used which were not

Table 4: Root characters of the *Guioa* groups. Only those characters were used which were not constant for all groups. The character number refers to that of table 3.

Group\Character	2	3	4	5	7	9	10	11	12	13	15	19	20	22	23	24	25	26	29	31
Cupaniopsis	2	1	1	1	1	1	1	1	2	2	3	2	2	1	1	1	1	1	1	1
Pacific group	1	1/2	2	2	2	1	1	1	2	2	1	2	2	1	2	1	1	3	1	1
New Guinean group	1	2	2	2	2	1	1	1	1/2	1/2/3	2	2	2	1	2	2	1	3	1	1
Guioa rigidiuscula gr.	1	2	2	2	2	1	1	2	1	1	2	2	2	1	2	2	1	3	2	1
Australian group	1	2	2	1	2	1	2	2	1/2	1	2	1	2	1	2	2	1	3	1/2	1
New Caledonian group	1	1	2	2	2	1	2	2	1	2	2	1	3	2	1	1	1/2	3	1	2
West Malesian group	1	1	2	2	2	1	2	2	1	2	2	3	2	1	2	1	1/2	3	1	2

Group\Character	33	34	35	36	38	40	42	45	46	47	48	50	51	52	53	55	57	60	63	67
Cupaniopsis	2	2	1	2	3	1	3	1	?	1	2	3	1	?	1	2	1	1	2	1
Pacific group	1	1	2	1	2	1	3	1	1	2	2	1/3	3	2	1	2	1	2	1	1
New Guinean group	1	1	2	1	3	1	3	1	1	2	2	3	1	2	1	2	1/2	1/2	1/2	2
Guioa rigidiuscula group	1	1	2	1	3	3	3	6	1	2	2	3	1	2	2	1	2	1/2	1	2
Australian group	1	1	2	1	3	1	4	1	1	2	3	1	3	1	1	2	1	2	1	2
New Caledonian group	1	1	2	1	3	1	3	6	1	1/2	2	1	1	1/2	1	2	1	2	1	2
West Malesian group	1	1	2	1	3	1	3	1	2	2	2	3	1	1	2	1/2	2	2	1	2

constant for all taxa). CAFCA had to be used, because the other programs do not allow for polytypic character states. The result is shown in figure 46b and is in accordance with the selected cladogram (fig. 46a). The characters used to subdivide the genus constitute apomorphies in the same places as in figure 40.

A comparison between figure 38 (the initial total cladogram) and figure 46a (the ultimate total cladogram) shows that although most groups of species are still present the relations within them have changed drastically. The consistency indices of the subcladograms were always above 0.5, much higher than that of the initial tree. The fit of the characters is therefore much better; moreover, the aberrations in the distributions have vanished (all Australian species branch off together, the New Caledonian and Philippine species form monophyletic groups, etc.). The altered method of subdividing the genus has resulted in an more acceptable cladogram.

It can also be concluded that of the computer programs HENNIG86 performed best (PAUP still has the deficit that polytomies are resolved even though apomorphies are absent, but this will be temporarily, till the next version). With a cladistic character analysis CAFCA showed the poorest results of all three programs, due to the impossibility to recognize monothetic sets based on the absence of characters; but see also the next chapter, the cladistic biogeographical analysis, where the reverse applies.

11.14. LEAF ANATOMY AND PHYLOGENY

Anatomical characters are important for the phylogenetic reconstruction of most animal groups (see chapter 7). In this chapter it is evaluated whether or not the same applies to *Guioa*.

In total twenty characters were available for the cladistic analysis. The consistency index of these characters varied between 0.06 and 1 (the c.i. of the user tree: 0.16), the number of steps per character varied between 1 and 21 (mean: c. 11 steps). Although these results indicate that most anatomical characters are rather useless for a cladistic analysis the contrary is often true, because most of the character state changes are autapomorphies.

Character 1 (21 steps), hairs adaxially, constitutes apomorphies for *Guioa lentiscifolia* and *Guioa chrysea,* and for the papillate and non-papillate groups of New Caledonia.

Character 2 (11 steps), hairs abaxially, is apomorphic for *Guioa lentiscifolia* and *Guioa chrysea,* for *Guioa misimaensis* and *Guioa plurinervis,* for the papillate species of New Caledonia, and for most West Malesian species.

Character 3 (17 steps), type of glands on adaxial surface, is mainly autapomorphic. It forms an apomorphy for *Guioa melanopoda* and *Guioa patentinervis.*

Character 4 (21 steps), type of glands on abaxial surface, is apomorphic for the Australian species, and for *Guioa novobritannica, Guioa misimaensis,* and *Guioa plurinervis.*

Character 5 (13 steps), the presence of papillae, is apomorphic for the Pacific group, for *Guioa novobritannica, Guioa misimaensis,* and *Guioa plurinervis* of the

Guioa rigidiuscula group, for the Australian species, for the papillate species of New Caledonia, and for the more western species of the West Malesian group.

Character 6 (5 steps), type of cuticle ridges on the papillae, is apomorphous for Australia/New Caledonia and for West Malesia, with a reversal in the latter for some Philippine species and a reversal for the papillate species of New Caledonia.

Character 7 (12 steps), thin areas in loops of undulations of the adaxial cuticle, is apomorphous for the *Guioa rigidiuscula* group together with *Guioa melanopoda* and *Guioa patentinervis*; within this group the reversal is an apomorphy for *Guioa novobritannica, Guioa misimaensis*, and *Guioa plurinervis*. It is also an apomorphy for the basal species of the West Malesian group and the reversal an apomorphy for the more western species of this group.

Character 8 (1 step), thin areas in loops of undulations of the abaxial cuticle, is an autapomorphy for *Guioa unguiculata*.

Character 9 (15 steps), cuticle adaxially striate, is apomorphic for the *Guioa rigidiuscula* group together with *Guioa melanopoda* and *Guioa patentinervis*. It also forms an apomorphy for *Guioa lasioneura* and *Guioa montana*. This character is rather difficult to interpret for West Malesia and New Caledonia.

Character 10 (18 steps), cuticle abaxially striate, is mainly autapomorphic, but also apomorphic for *Guioa montana, Guioa lasioneura*, and *Guioa semiglauca*.

Character 11 (13 steps), adaxial epidermal cell walls undulate, is apomorphic for the *Guioa rigidiuscula* group together with *Guioa melanopoda* and *Guioa molliuscula*; within this group the reversal is apomorphic for *Guioa novobritannica, Guioa misimaensis*, and *Guioa plurinervis*. This character also constitutes an apomorphy for the West Malesian group, for the non-papillate species of New Caledonia (*Guioa microsepala* excepted), and for *Guioa crenata* and *Guioa crenulata*.

Character 12 (11 steps), abaxial epidermal cell walls undulate, is mainly autapomorphous except for *Guioa fusca* and *Guioa gracilis*.

Character 13 (1 step), some stomata with an extra rim, is apomorphous for *Guioa fusca, Guioa gracilis*, and *Guioa pectinata*.

Character 14 (14 steps), veins not transcurrent, is apomorphous for the Pacific species, and for most of the other species groups, with apomorphic reversals for two groups in the *Guioa rigidiuscula*-complex.

Character 15 (2 steps), veins transcurrent to adaxial epidermis, not sclerified, is only autapomorphous for *Guioa lasioneura* and *Guioa semiglauca*, both of Australia.

Character 16 (4 steps), veins transcurrent to adaxial epidermis, sclerified, is apomorphous for the papillate species of New Caledonia.

Character 17 (12 steps), veins completely or only abaxially transcurrent, completely sclerified, is apomorphic for *Guioa pseudoamabilis* and *Guioa pteropoda*.

Character 18 (3 steps), veins completely transcurrent, only sclerified around vein, is apomorphous for the West Malesian group minus *Guioa asquamosa* and *Guioa hirsuta*, with a further apomorphy (reversal) for the Philippine species.

Character 19 (9 steps), sclerification of domatia, is apomorphous for *Guioa lentiscifolia* and *Guioa chrysea* (plus *Guioa punctata*), and for *Guioa fusca* and *Guioa gracilis*.

Character 20 (10 steps), secretory idioblasts, shows only autapomorphies.

The above list shows that anatomical characters form apomorphies for most groups. However, this result could only be obtained after the cladistic analysis was completed as, due to the many homoplasies, the accepted tree could never have been selected on the anatomical characters alone.

11.15. POLLEN MORPHOLOGY AND PHYLOGENY

Van der Ham & Van Heuven (1989) published a pollen morphological account of *Guioa*. The pollen of *Guioa* appeared to be very homogeneous; leaf anatomy showed a comparable result (chapter 7).

Van der Ham & Van Heuven (1989) divided the genus into four groups. The boundaries of the groups were rather vague. Group 1 and 4 show the extreme forms and group 2 and 3 the intermediary forms. The indistinct boundaries are also shown by some widespread West Malesian species, which can be placed in three or two different groups (e.g. *Guioa diplopetala* and *Guioa pleuropteris*), just like the two varieties of *Guioa glauca*. There is little correlation between the groups based on the pollen morphology and the groups distinguished after the cladistic analysis. Pollen group 4 shows the highest correlation with any of the cladistic groups, e.g. with the West Malesian group (*Guioa asquamosa* and *Guioa truncata* are not included; added are *Guioa glauca* var. *vulgaris* and *Guioa villosa* of the Australian/New Caledonian group, *Guioa comesperma* of the *Guioa rigidiuscula* group, and *Guioa pteropoda* of the New Guinean group).

Van der Ham & Van Heuven (1989) considered pollen group 1 to have most primitive characters and group 4 to possess most derived characters. When the group number is used as a summarising character of all pollen data and when these group numbers are optimized via a user-tree, then pollen type 2 appears to be the most primitive type. A part of the Pacific group (Fiji and Tonga species) shows a character change towards group 1 (with a reversal to 2 for *Guioa chrysea*). The *Guioa rigidiuscula* group and part of the New Guinean group show a character change to type 3, although there is a reversal to 2 again for the group containing *Guioa normanbiensis*, *Guioa aryterifolia*, and *Guioa rigiduscula* (*Guioa contracta* reverses to 3 again). The New Caledonian species together with the ancestral species of the West Malesian group show a parallel (with the Pacific group) development, the ancestral species switched from type 2 to 1, although several terminal species show type 3. The West Malesian group changed from type 1 to 4. In conclusion: type 4 is indeed found in one of the groups with most advanced character states, but type 1 is found in the more 'advanced' part of the Pacific group and in the 'advanced' New Caledonian species. Type 3 is indeed found in an intermediate position between 2 and 4 (+ 1). The main development can be summarized as:

Pollen type 2 ⟶ 1
└⟶ 3 ⟶ 1 ⟶ 4

N.B.: The consistency index was 0.28, a very low value. This may mean that the pollen development can be due to chance alone!

The division into pollen groups and the degree of primitiveness was based on the postulation of four possible directions of transformation series:

a. wide ectoapertures → narrow ectoapertures
b. grain parasyncolporate → grain colporate
c. grain parasyncolporate → grain syncolporate
d. ornamentation rugulate → ornamentation psilate-imperforate

The assumed direction of the transformatic series c and d was based on those of a and b. Especially the transformation direction in the secon' and the fourth character is contrary to a more generally held view. The transformation series could not be confirmed by the cladistic analysis as those character states which were summarized in the species of group 1 appeared not to be the most primitive stages.

12. HISTORICAL BIOGEOGRAPHY

12.1. INTRODUCTION

The cladistic analysis of *Guioa* showed that most groups of species are confined to only a restricted part of its area. The different groups are mainly named after the area in which they are found: Pacific group, New Guinean group, Australian/New Caledonian group, and West Malesian group. The *Guioa rigidiuscula* group is also restricted to New Guinea. This grouping of the *Guioa* species per geographical area is already a rough indication of the degree of credibility of the cladogram.

A further analysis of the history of the biogeographic patterns will probably increase the credibility of the cladogram. Such an analysis will be presented in this chapter.

12.2. METHODS IN HISTORICAL BIOGEOGRAPHY

In the past, distribution patterns of plants were always explained as the result of dispersal (e.g. Van Steenis, 1962). Ancestors of genera originated in one spot (centre of origin) and started to disperse, often followed by speciation (progression rule: near centre of origin the most primitive forms, near edge the most derived forms). The rise of plate tectonics and phylogenetic research changed this view and now it became quite often unnecessary to postulate land bridges to explain distributions. Historical biogeography (e.g. Nelson & Platnick, 1981) tries to explain distributions as the result of splitting of widespread ancestral distributions (vicariance).

Starting-point is the cladogram of a group. The terminal taxa are substituted in this cladogram by their distributions. Already, the cladogram can now show the historical relations between the different areas, but normally redundant information is still present. The ancestors are regarded as having possessed the sum of the distributions of their descendants (although some methods make special allowances for widespread taxa and missing areas). The cladograms of areas are termed areagrams. Areagrams of different groups, showing a distribution over the same areas, are combined into a generalized areagram. The main idea is that generalized areagrams point at common causes of speciation (geological, ecological, or climatological), whereby the daughter species vicariate (occupy a different part of the ancestral range). Inconsistencies of single groups with generalized areagrams have to be explained in terms of dispersal, primitive absence, and extinction. The latter are always ad hoc as they differ from taxon to taxon. Therefore, in this monograph, vicariance events are first considered as explanations for common distribution patterns, because they relate to common historical causes, and dispersal, etc. as secondary explanations when the patterns do not fit a general view.

Vicariance events are also preferred as an explanation of distribution patterns, because, via geographical data, the phylogenies of different groups can be compared with the group under study. They constitute an independent test of the cladograms. Normally, dependent on the characters used, several cladograms are possible. The historical biogeography tests whether the correct tree and correct characters were selected as it is hardly likely that the group under study has not reacted to speciation events in the same way as other groups, although some inconsistencies may be present as dispersal, extinction, etc. can never be excluded.

The distribution patterns of some taxa may always conflict (be homoplasious) due to the method of dispersal, especially taxa – for instance coconut – which are notorious for their ability to disperse over long distances. For these taxa it is unlikely that vicariance events can explain the distribution. Consequently, the cladogram cannot be tested. In less obvious cases this can only be demonstrated after a biogeographic analysis!

A distinction has to be made between dispersal and diffusion. Dispersal is defined as the active crossing of a barrier. Diffusion is the normally slow extension of a distribution before a barrier existed (De Jong, 1987). Likewise, speciation events in the case of dispersal form homoplasies in the areagrams; speciation events in the case of diffusion are vicariance events. Examples of the latter are the distribution extensions of plants and animals after a glacial period, or the substitution of the trilobite *Phacops milleri* by *Phacops rana* (see chapter 10). Diffusion must be a general phenomenon, because otherwise the ancestor of all plants (provided the plants are not polyphyletic) must have covered the earth completely (which is perhaps not far from the truth as the blue algal mats, present in the Precambrian, consisted of a few species only; Stanley, 1973).

Extinction or primitive absence (or an error in sampling) is shown in the areagrams as a reversal (Zandee & Roos, 1987; Wiley, 1988a, b). Especially a reversal to absence in the root part or the terminal part of the areagram might indicate primitive absence (a taxon has never been present in a certain area).

Dispersal is shown as a parallel. Wiley (1988a) even demonstrates the difference between parallelism and convergence. In the case of convergence (different ancestral areas: same area change in two non-neighbouring lines) the parallel distribution is caused by dispersal. In the case of parallelism (same ancestral area: same area switch in two neighbouring lines) the parallelism may be caused by dispersal or by widespread taxa which did not react to a speciation event. The ancestral species of a dispersed taxon and its sister taxon will consequently also show a convergence for the same areas as to which the descendant dispersed. However, this convergence is false and should be absent as the area to which the descendant dispersed must be disregarded for the distribution of the ancestor.

Primitive absence with widespread taxa can also occur as parallel distributions in the areagrams. This will be shown in the last section of this chapter (section 12.7).

Several methods already exist via which a historical biogeographic analysis can be accomplished. In this study a choice between four methods has been made.

Nelson & Platnick (1981) and Humphries & Parenti (1986) use component analysis to create areagrams. A component is the unique distribution of a terminal species or of an ancestor (species with the same distribution have the same component). The components of the ancestors always include those of the descendants. Generalized areagrams were constructed on the basis of consensus: Areagrams of different groups were compared and parts (areas) for which some of the areagrams had no solution, collapsed into a polytomy. Absent taxa and especially widespread taxa caused these generalized areagrams to be poorly resolved. To accommodate widespread taxa assumptions 1 and 2 were used. Under both assumptions the distribution of a widespread taxon is seen as a distribution over different areas. Under assumption 1 these areas are considered to be sister areas; they then form a polytomy with the distribution area of the sister species of the widespread taxon and all different dichotomous tree solutions for this polytomy are added to the datamatrix (in fact the widespread species is considered to be monophyletic or paraphyletic). Under assumption 2 the position of one of the areas of the widespread taxon in the cladogram is considered as being completely wrong; this area is then added to all possible places in the tree. As it is impossible to tell beforehand which area is wrongly placed, they are treated alternatively as being wrongly situated in the cladogram (the widespread species is in fact considered to be monophyletic, paraphyletic, or even polyphyletic). Under assumption 2 the datamatrix expands very fast (see Zandee & Roos, 1987; Wiley, 1988a). The generalized areagram is the intersection of the sets of areagrams of all taxa considered; the selected generalized areagram is not necessarily the most parsimonious one. For more comments on this method see Wiley (1988b).

Wiley (1981a) had a different approach, the 'ancestral map method'. When creating a generalized areagram, instead of leaving out 'conflicting' evidence, he accommodated it all as much as possible. He too used Rosen's example. This method is far easier to understand than the component method under assumption 2. However, especially when a few groups are used to create a generalized areagram, homoplasies (extinctions, dispersal, etc.) will be fit in as vicariance events.

Recently, two new methods were discussed: Zandee & Roos (1987) introduced component-compatibility and Wiley (1988a, b) Brooks parsimony analysis. In both papers the construction of a datamatrix is made more explicit: the areas are entered as taxa and the terminal taxa and all their ancestors as characters, whereby the ancestors always inhabit the sum of the areas of their descendants. In this way the structure of the cladogram is added to the datamatrix (additive binary coding). Wiley (1988a, b) uses for his datamatrix the parasitological technique of Brooks (1981), hence the name Brooks parsimony analysis. The Boolean product which the program CAFCA

(Zandee, 1988) uses to create an area datamatrix, by multiplying a terminal taxa distribution matrix with the tree structure matrix, is user friendly, because after a cladistic analysis the user only has to enter the distribution data of the terminal taxa. The resulting matrix is the same as Wiley (1988a, b) uses. For a generalized areagram the matrices of the different groups are placed after each other in order to analyse all covariation among all components, and not only within restricted sets of components (every taxon analysed separately) as in Nelson & Platnick's method. Wiley (1988a) notes that absent areas should be entered as unknown character states in the matrix, as for instance in his fig. 7b, where South America is absent. However, the unknown character state is placed according to fig. 7a; this activity assumes that fig. 7a is a correct areagram. Moreover this way of coding forces the computer programs to accept fig. 7a as the correct areagram. In the present study species – also ancestral species – are always recorded as being either absent or present in an area and no question marks are entered for missing areas.

The procedures as used in the component-compatibility method and in the Brooks parsimony method are the same as for the cladistic analysis; they are explained in chapter 11.2. The disadvantages of the compatibility method have decreased in the geographical analysis, because now the correct cliques will always be formed, due to the fact that the structure of the cladogram has been included. The absence of the need for an outgroup is profitable in the historical biogeography as it is sometimes impossible to appoint an area as outgroup (see chapter 12.5, the vicariance events in Australia and New Caledonia). One disadvantage remains, polytomies will remain when no unique characters are available to solve them.

The parsimony method has more or less changed into the compatibility method, because the cliques have been added in the form of the grouping information present in the cladogram. Although both methods still operate very differently their results can be mainly attributed to the compatibility method as a result of the way in which the datamatrix has been constructed. As already discussed above, a disadvantage of the parsimony method is the necessity of an outgroup, while an advantage is the better resolution of polytomies that may result.

The historical biogeographic analysis of New Guinea (see chapter 12.4 for a discussion) will show another advantage of the component-compatibility method over the Brooks parsimony method. This benefit favours the component-compatibility method as the most powerful analytical tool in biogeographic analyses.

Zandee & Roos (1987) introduced assumption 0 (also used by Wiley, 1987a, b): The distributions of species have to be interpreted as realities; widespread species are indeed widespread (probably due to diffusion). Even if the distribution of a widespread species has to be regarded as a distribution over two or more separate areas, under assumption 0 these areas will automatically be considered as sister areas. Under assumption 1 the areas will form a polytomy with the distribution of the sister species of the widespread species, and under assumption 2 the areas are normally assumed to be polyphyletic (see fig. 47). Assumptions 1 and 2 automatically include ad hoc explanations such as dispersal and extinction for the widespread species when the paraphyletic or polyphyletic solutions are prefered. For these reasons assumption 0 is used in the different biogeographic analyses below.

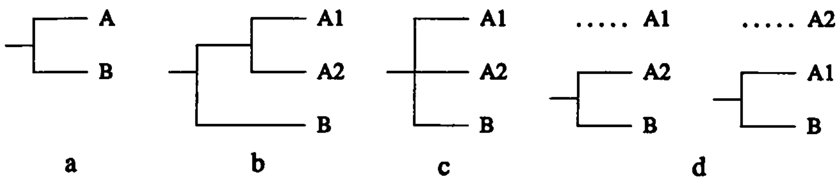


Fig. 47. — a: Widespread species A with distribution A and species B with distribution B are sister species. — b: Under assumption 0 area A can be divided into two sister areas A1 and A2. — c: Under assumption 1 the areas A1 and A2 form a polytomy with area B (the polytomy results in 3 dichotomous trees). — d: Under assumption 2 either area A1 or A2 has been incorrectly interpreted (the area group A1, A2, and B can be polyphyletic) and both should alternatingly be placed on all available branches of the cladogram.

If a historical biogeograpic analysis is accomplished under assumptions 1 or 2, then this analysis cannot any longer serve as a test of the original cladogram, as both assumptions allow for many other trees, with different topologies.

The methods of Zandee & Roos (1987) and of Wiley (1988a, b) are straightforward, because the methods accept assumption 0 (and can consequently serve as an independent test of the original cladogram), and because both methods have been implemented in computer programs (the compatibility method in CAFCA and the Brooks parsimony method in PAUP and HENNIG86). Therefore, both have been favoured in the analysis of the geographical data of *Guioa*. N.B.: CAFCA, when prefered, also allows for assumptions 1 and 2.

Dispersal can sometimes be interpreted as vicariance when several groups show the same dispersal pattern. A common dispersal pattern is to be expected when earth plates meet, or when areas newly arise. An example of the former is the influence of Southeast Asia in West Malesia (see Audley-Charles, 1987); an example of the latter is the distribution of *Guioa* over the Pacific island arcs.

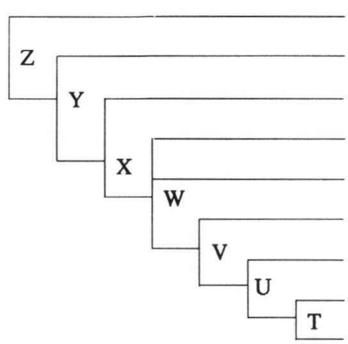
Vicariance does not necessarily always have to be brought about by geological events, climatological events may also have caused them. Van Balgooy (1987), when he used a phenetic method to analyse distributional data, found the parts of Malesia with a dry monsoon (Philippines, Celebes, Java, and the Lesser Sunda Islands) to constitute a distinct floristic area. Hovenkamp (1986) found the climatological border between for instance Borneo and the Philippines or between the Philippines and New Guinea as vicariance events in his areagrams.

12.3. BIOGEOGRAPHIC ANALYSIS OF THE PACIFIC

Eight species of *Guioa* occur in the Pacific. Each is endemic in a small area. The northern part of the Solomon Islands contains two sympatric species and Fiji three.

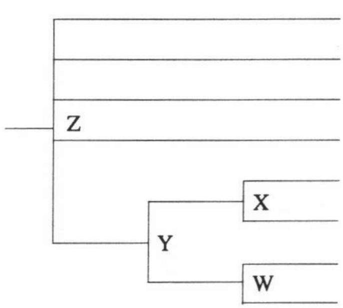
The data of the Pacific *Guioa* species are compared with those of *Aceropyga* (Cicadas; Duffels, 1977). However, the latter data are very incomplete, not only because the cladogram is poorly resolved, but also because several more, new species were observed (21 species instead of 8; Duffels, 1986). The analysis was made under assumption 0, figure 48a and b contain the data for *Guioa* and for *Aceropyga*, figure

(Fig. 48)



	Species \ Area	1	2	3	4	5	6
1	Cupaniopsis anacardioides	1	0	0	0	0	0
2	Guioa sufusana	0	1	0	0	0	0
3	Guioa elliptica	0	1	0	0	0	0
4	Guioa megacarpa	0	0	1	0	0	0
5	Guioa novoëbudaënsis	0	0	0	1	0	0
6	Guioa rhoifolia	0	0	0	0	1	0
7	Guioa punctata	0	0	0	0	1	0
8	Guioa chrysea	0	0	0	0	1	0
9	Guioa lentiscifolia	0	0	0	0	0	1
10	Guioa ancestor T	0	0	0	0	1	1
11	Guioa ancestor U	0	0	0	0	1	1
12	Guioa ancestor V	0	0	0	0	1	1
13	Guioa ancestor W	0	0	1	1	1	1
14	Guioa ancestor X	0	1	1	1	1	1
15	Guioa ancestor Y	0	1	1	1	1	1
16	Guioa ancestor Z	1	1	1	1	1	1

a. Cladogram and distribution of the Pacific species of *Guioa* and their outgroup *Cupaniopsis anacardioides*. Area 1 = New Guinea, 2 = N Solomon Islands, 3 = Santa Cruz Group, 4 = New Hebrides, 5 = Fiji, 6 = Tonga.



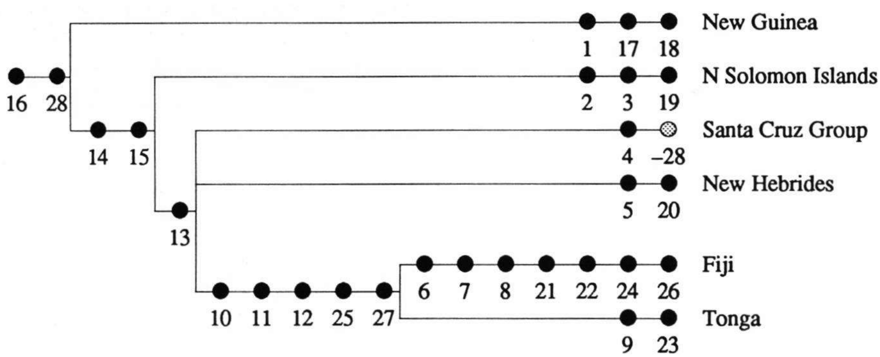
17	Aceropyga novaeirelandicae	1	0	0	0	0	0
18	Aceropyga obliqua	1	0	0	0	0	0
19	Aceropyga aluana	0	1	0	0	0	0
20	Aceropyga poecilochlora	0	0	0	1	0	0
21	Aceropyga corynetus	0	0	0	0	1	0
22	Aceropyga stuarti	0	0	0	0	1	0
23	Aceropyga albostriata	0	0	0	0	0	1
24	Aceropyga distans	0	0	0	0	1	0
25	Aceropyga ancestor W	0	0	0	0	1	1
26	Aceropyga ancestor X	0	0	0	0	1	0
27	Aceropyga ancestor Y	0	0	0	0	1	1
28	Aceropyga ancestor Z	1	1	0	1	1	1

b. Cladogram and distribution of the cicada genus *Aceropyga* (after Duffels, 1977). Areas as in a.

(Fig. 48 continued)

Area \ Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
New Guinea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1
Solomon Islands	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1
Santa Cruz	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
New Hebrides	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1
Fiji	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	1	1
Tonga	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1

c. Data matrix for generalized areagram; species numbers refer to line numbers in a and b.



d. Generalized areagram for the species of *Aceropyga* and for the Pacific *Guioa* species. The species numbers refer to the line numbers in a and b. — ● = apomorphy, ◍ = reversal.

Fig. 48. Historical biogeographic analysis of the Pacific *Guioa* species and of *Aceropyga* (Cicadas).

48c shows the matrix. New Guinea served as outgroup for PAUP and HENNIG86. Options used: CAFCA: 'minimal steps'; PAUP: 'alltrees'; and HENNIG86: 'ie*'.

The generalized areagram (fig. 48d) contains 27 steps, consistency index = 1, redundancy index = 0.462. The latter is rather low because of the polytomy, which is caused by the polytomy in the cladogram of *Guioa* (*Aceropyga* is absent in one of the three areas of the polytomy, the New Hebrides, and hence cannot solve it).

The generalized areagram shows a 'reversal' for ancestor Z of *Aceropyga* (no. 28): the extinction or primitive absence in the New Hebrides.

The pattern displayed by the generalized areagram can be due to vicariance events, but it is more likely that the pattern has been caused by dispersal accompanied by speciation. The dispersal took place from New Guinea to the east, into the Pacific, along the respective island arcs: N Solomon Islands, Santa Cruz Group (S Solomon Islands), New Hebrides, Fiji, and Tonga.

Another analysis made by Duffels (1986) shows a contrasting pattern. The Pacific Cryptotympanini (cicadas) occur in the N Solomon Islands and on Fiji, Samoa, and the Society Islands. The oldest group, the genus *Raiateana,* is found on the latter three island groups. The other less primitive genera (*Heteropsaltria, Nggeliana,* and *Tibicen*) are found on the N Solomon Islands. This analysis was not used for the construction of the generalized areagram, because only two areas were involved, and because this pattern may be due to vicariance instead of dispersal, or, if caused by dispersal, the pattern is opposite to that of *Guioa* and of *Aceropyga.*

The areas as used in the generalized areagram are still too crude for the cicadas. Contrary to *Guioa,* these insects are usually endemic on only one island. If for instance the N Solomon Islands are subdivided into the major islands, then the species of the Pacific Cryptotympanini (*Heteropsaltria, Nggeliana,* and *Tibicen*) on this island group also show a west to east series of vicariance events (or dispersal).

The pattern of the above generalized areagram is supported by the analysis made by Leenhouts (1959) of the *Canarium maluense* group (Burseraceae). *Canarium maluense* is found on New Guinea, the more advanced *Canarium salomonense* on part of New Guinea, but mainly on the N Solomon Islands, and the most advanced *Canarium harveyi* is found ranging from the N Solomon Islands to far east into the Pacific.

Most of the island arcs arose when the Australian plate collided with the Pacific plate and they are relatively young (volcanic activity in Tonga started in the Eocene, but after a temporary submergence, Tonga was uplifted again in the Late Miocene or Pliocene). Only Fiji is exceptional; these islands also resulted from the Australian-Pacific collision, but are thought to be uplifted sea floor from close to the Australian continent. They rifted due to sea floor spreading to their temporary position. Besides evidence from ophiolites, some distributions of plants and animals support this view, as they are only found in Australia and on the Fiji islands (see Raven & Axelrod, 1972).

Based on this information two types of distribution pattern can be expected. A dispersal pattern from New Guinea eastwards into the Pacific, with locally vicariance events (e.g. the cicadas on the Solomons), and a dispersal pattern with Fiji as centre (with also locally vicariance events). *Guioa* and *Aceropyga* show the former type, the Cryptotympanini the latter.

12.4. HISTORICAL BIOGEOGRAPHY OF NEW GUINEA

Duffels (1986) recognized 5 areas of endemism in New Guinea: a) the central mountains, together with b) the south, part of the Inner Melanesian Arc, c) the northern part (part of the Outer Melanesian Arc), d) the Vogelkop with Waigeo, Salawati, and Misool, e) the Papuan Peninsula (an area of overlap between both arcs). N.B.: The southern part was not recognized by Duffels, but was added in this study as it was the remaining area.

The division of New Guinea into 5 areas was considered to be too crude as *Guioa* showed some very local endemism. Several regions were subdivided: the north into an eastern and western part, E and W New Britain, and New Ireland and Manus; the Peninsula into the Peninsula s.s. and the W and E Papuan Islands (the W Islands close to the coast, like Normanby Island, the E Islands further into the Pacific: islands like Misima I. and Woodlark I.). Figure 49 shows the division of New Guinea; added are the N and S Moluccas and the N Solomon Islands.

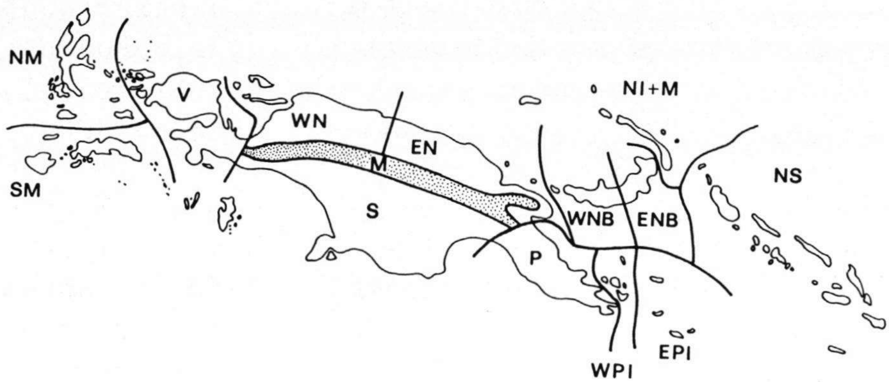
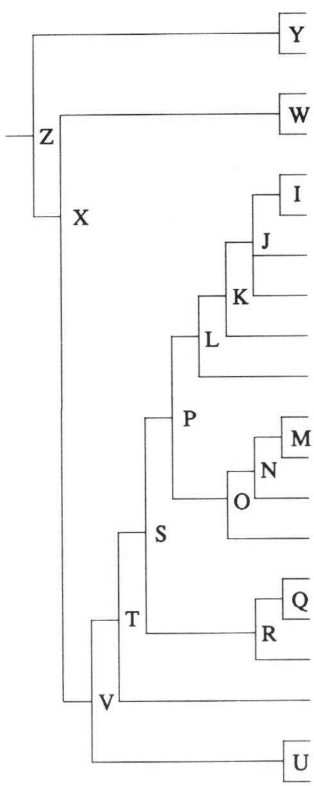


Fig. 49. Division of New Guinea in geographical areas as used in the historical biogeographic analysis. EN = E North; ENB = E New Britain; EPI = E Papuan Islands; M = Mountains; NI+M = New Ireland + Manus; NM = N Moluccas; NS = N Solomon Islands; P = Peninsula; S = South; SM = S Moluccas; V = Vogelkop; WN = W North; WNB = W New Britain; WPI = W Papuan Islands.

The phylogeny of the New Guinea species of *Guioa* together with their distribution over the 14 recognized areas is shown in figure 50a. The phylogeny and distribution of the cicada genus *Diceropyga* is shown in figure 50b (after Duffels, 1977, 1986) and of the cicada genus *Cosmopsaltria* (after Duffels, 1983a, 1986) in figure 50c. The species of *Diceropyga* which occur on Bougainville I. and on the N Solomon Islands are entered as one species with one distribution as these highly endemic species (one per island) show one monophyletic polytomy; consequently the ancestor must have occupied the total of the islands, i.e. the N Solomon Islands. Figure 50d shows the datamatrix.

During the first analysis only *Guioa* and *Diceropyga* were compared with each other (matrix as in fig. 50d but only with the first 64 columns). The four generalized areagrams produced by PAUP (options: root=midpoint addweq=rootless bandb) were completely different and far more parsimonious than the cladogram found by CAFCA (option: minimal steps; steps = 101, consistency index = 0.634, redundancy index = 0.439; fig. 50g–i). Based on the highest redundancy index (via cladogram evaluation in CAFCA) one PAUP areagram was selected (fig. 50e, f; steps = 87, consistency index = 0.736, redundancy index = 0.473). Due to the options used during the PAUP run the root in figure 50e and f is artificial and can be situated elsewhere in the areagram.

(Fig. 50)

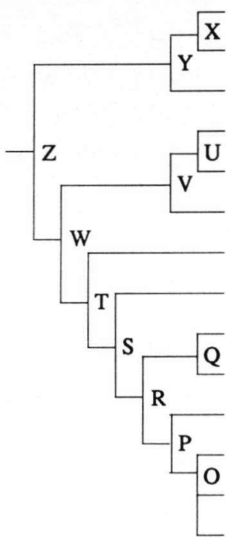


	Species \ Area	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Guioa pseudoamabilis	0	0	0	1	0	0	0	0	0	0	0	0	0	0
2	Guioa pteropoda	0	0	0	0	1	0	0	0	0	0	0	0	0	0
3	Guioa patentinervis	0	1	0	0	0	0	0	0	0	0	0	0	0	0
4	Guioa melanopoda	0	0	0	0	1	0	0	0	0	0	0	0	0	0
5	Guioa contracta	0	0	0	0	0	1	0	1	0	0	0	0	0	0
6	Guioa grandifoliola	0	0	0	0	0	0	0	1	0	0	0	0	0	0
7	Guioa aryterifolia	0	0	0	0	0	0	0	1	0	0	0	0	0	0
8	Guioa rigidiuscula	0	0	0	0	0	1	0	1	1	0	0	0	0	0
9	Guioa normanbiensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0
10	Guioa membranifolia	1	0	1	0	1	0	0	0	0	0	0	0	0	0
11	Guioa misimaensis	0	0	0	0	0	0	0	0	0	1	0	0	0	0
12	Guioa plurinervis	0	0	0	0	0	0	0	0	0	1	0	0	0	0
13	Guioa novobritannica	0	0	0	0	0	0	0	0	0	0	1	0	0	0
14	Guioa comesperma	0	0	0	0	0	1	0	1	1	1	1	1	1	0
15	Guioa hospita	0	0	0	0	0	0	0	1	0	0	0	0	0	0
16	Guioa molliuscula	0	0	0	0	0	0	0	1	0	0	0	0	0	0
17	Guioa scalariformis	0	0	0	0	0	1	0	0	0	0	0	0	0	0
18	Guioa unguiculata	0	0	0	0	0	1	0	1	0	0	0	0	0	0
19	Guioa oligotricha	0	0	0	0	0	0	1	0	0	0	0	0	0	0
20	Guioa subsericea	0	0	1	1	0	0	0	0	0	0	0	0	0	0
21	Guioa ancestor I	0	0	0	0	0	1	0	1	0	0	0	0	0	0
22	Guioa ancestor J	0	0	0	0	0	1	0	1	1	0	0	0	0	0
23	Guioa ancestor K	0	0	0	0	0	1	0	1	1	0	0	0	0	0
24	Guioa ancestor L	1	0	1	0	1	1	0	1	1	0	0	0	0	0
25	Guioa ancestor M	0	0	0	0	0	0	0	0	0	1	0	0	0	0
26	Guioa ancestor N	0	0	0	0	0	0	0	0	0	1	1	0	0	0
27	Guioa ancestor O	0	0	0	0	0	1	0	1	1	1	1	1	1	0
28	Guioa ancestor P	1	0	1	0	1	1	0	1	1	1	1	1	1	0
29	Guioa ancestor Q	0	0	0	0	0	0	0	1	0	0	0	0	0	0
30	Guioa ancestor R	0	0	0	0	0	1	0	1	0	0	0	0	0	0
31	Guioa ancestor S	1	0	1	0	1	1	0	1	1	1	1	1	1	0
32	Guioa ancestor T	1	0	1	0	1	1	0	1	1	1	1	1	1	0
33	Guioa ancestor U	0	0	1	1	0	0	1	0	0	0	0	0	0	0

(Fig. 50 continued)

34	Guioa ancestor V	1 0 1 1 1 1 1 1 1 1 1 1 1 0
35	Guioa ancestor W	0 1 0 0 1 0 0 0 0 0 0 0 0 0
36	Guioa ancestor X	1 1 1 1 1 1 1 1 1 1 1 1 1 0
37	Guioa ancestor Y	0 0 0 1 1 0 0 0 0 0 0 0 0 0
38	Guioa ancestor Z	1 1 1 1 1 1 1 1 1 1 1 1 1 0

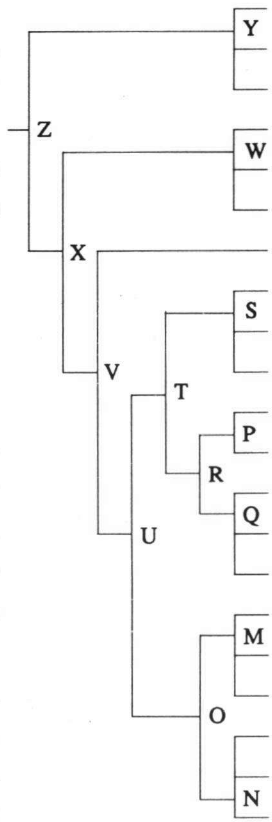
a. Phylogenetic relationships and distribution of New Guinean species of *Guioa*.



39	Diceropyga noonadani	0 0 0 0 0 0 0 0 0 0 0 0 1 0
40	Diceropyga novaebritannicae	0 0 0 0 0 0 0 0 0 0 0 1 0 0
41	Diceropyga obliterans	0 0 0 0 0 0 0 0 0 0 1 0 0 0
42	Diceropyga ochrothorax	1 0 0 0 0 0 0 0 0 0 0 0 0 0
43	Diceropyga junctivitta	1 0 0 0 0 0 0 0 0 0 0 0 0 0
44	Diceropyga obtecta	0 1 0 0 0 0 0 0 0 0 0 0 0 0
45	Diceropyga N Solomon Islands	0 0 0 0 0 0 0 0 0 0 0 0 0 1
46	Diceropyga gravesteini	0 0 0 0 0 1 0 1 0 0 1 1 1 0
47	Diceropyga bihamata	0 0 0 0 1 1 0 0 0 0 0 0 0 0
48	Diceropyga subjuga	0 0 0 0 0 0 0 1 0 0 0 0 0 0
49	Diceropyga woodlarkensis	0 0 0 0 0 0 0 0 0 1 0 0 0 0
50	Diceropyga auriculata	0 0 0 0 0 0 0 0 1 0 0 0 0 0
51	Diceropyga bicornis	0 0 0 0 0 0 0 1 0 0 0 0 0 0
52	Diceropyga subapicalis	0 0 0 0 0 0 1 1 0 0 0 0 0 0
53	Diceropyga ancestor O	0 0 0 0 0 0 1 1 1 0 0 0 0 0
54	Diceropyga ancestor P	0 0 0 0 0 0 1 1 1 1 0 0 0 0
55	Diceropyga ancestor Q	0 0 0 0 1 1 0 1 0 0 0 0 0 0
56	Diceropyga ancestor R	0 0 0 0 1 1 1 1 1 1 0 0 0 0
57	Diceropyga ancestor S	0 0 0 0 1 1 1 1 1 1 1 1 1 0
58	Diceropyga ancestor T	0 0 0 0 1 1 1 1 1 1 1 1 1 1
59	Diceropyga ancestor U	1 0 0 0 0 0 0 0 0 0 0 0 0 0
60	Diceropyga ancestor V	1 1 0 0 0 0 0 0 0 0 0 0 0 0
61	Diceropyga ancestor W	1 1 0 0 1 1 1 1 1 1 1 1 1 1
62	Diceropyga ancestor X	0 0 0 0 0 0 0 0 0 0 0 1 1 0
63	Diceropyga ancestor Y	0 0 0 0 0 0 0 0 0 0 1 1 1 0
64	Diceropyga ancestor Z	1 1 0 0 1 1 1 1 1 1 1 1 1 1

b. Cladogram and distribution of the Cicada genus *Diceropyga* in New Guinea.

(Fig. 50 continued)



65	Cosmopsaltria spec. A	1 0 0 0 0 0 0 0 0 0 0 0 0 0
66	Cosmopsaltria lata	0 1 0 0 0 0 0 0 0 0 0 0 0 0
67	Cosmopsaltria doryca	1 0 1 0 1 0 0 0 0 0 0 0 0 0
68	Cosmopsaltria gestroei	0 0 0 0 1 0 0 1 0 0 0 0 0 0
69	Cosmopsaltria huonensis	0 0 0 1 0 0 0 0 0 0 0 0 0 0
70	Cosmopsaltria gracilis	0 0 0 1 0 0 0 0 0 0 0 0 0 0
71	Cosmopsaltria gigantea	0 0 0 1 0 0 0 0 0 0 0 0 0 0
72	Cosmopsaltria signata	0 0 0 1 0 0 0 0 0 0 0 0 0 0
73	Cosmopsaltria aurata	0 0 0 1 0 0 0 0 0 0 0 0 0 0
74	Cosmopsaltria mimica	0 0 0 1 0 0 0 0 0 0 0 1 1 0
75	Cosmopsaltria emarginata	0 0 0 0 1 0 0 0 0 0 0 0 0 0
76	Cosmopsaltria bloetei	0 0 0 1 0 0 0 0 0 0 0 0 0 0
77	Cosmopsaltria personata	0 0 0 1 0 0 0 0 0 0 0 0 0 0
78	Cosmopsaltria satyrus	0 0 0 1 0 0 0 0 0 0 0 0 0 0
79	Cosmopsaltria meeki	0 0 0 1 0 0 0 0 0 0 0 0 0 0
80	Cosmopsaltria delfae	0 0 1 0 1 0 0 0 0 0 0 0 0 0
81	Cosmopsaltria loriae	0 0 0 0 0 0 0 1 0 0 0 0 0 0
82	Cosmopsaltria capitata	0 0 1 0 1 0 1 0 0 0 0 0 0 0
83	Cosmopsaltria toxopeusi	0 0 0 1 0 0 0 0 0 0 0 0 0 0
84	Cosmopsaltria retrorsa	0 0 0 1 0 0 0 0 0 0 0 0 0 0
85	Cosmopsaltria papuensis	0 0 1 1 0 0 0 0 1 0 0 0 0 0
86	Cosmopsaltria ancestor M	0 0 1 0 1 0 1 1 0 0 0 0 0 0
87	Cosmopsaltria ancestor N	0 0 1 1 0 0 0 0 1 0 0 0 0 0
88	Cosmopsaltria ancestor O	0 0 1 1 1 0 1 1 1 0 0 0 0 0
89	Cosmopsaltria ancestor P	0 0 0 1 1 0 0 0 0 0 0 0 0 0
90	Cosmopsaltria ancestor Q	0 0 0 1 0 0 0 0 0 0 0 0 0 0
91	Cosmopsaltria ancestor R	0 0 0 1 1 0 0 0 0 0 0 0 0 0
92	Cosmopsaltria ancestor S	0 0 0 1 0 0 0 0 0 0 0 1 1 0
93	Cosmopsaltria ancestor T	0 0 0 1 1 0 0 0 0 0 0 1 1 0
94	Cosmopsaltria ancestor U	0 0 1 1 1 0 1 1 1 0 0 1 1 0
95	Cosmopsaltria ancestor V	0 0 1 1 1 0 1 1 1 0 0 1 1 0
96	Cosmopsaltria ancestor W	0 0 0 1 1 0 0 1 0 0 0 0 0 0
97	Cosmopsaltria ancestor X	0 0 1 1 1 0 1 1 1 0 0 1 1 0
98	Cosmopsaltria ancestor Y	1 1 1 0 1 0 0 0 0 0 0 0 0 0
99	Cosmopsaltria ancestor Z	1 1 1 1 1 0 1 1 1 0 0 1 1 0

c. Cladogram and distribution of the Cicada genus *Cosmopsaltria* in New Guinea.

(Fig. 50 continued)

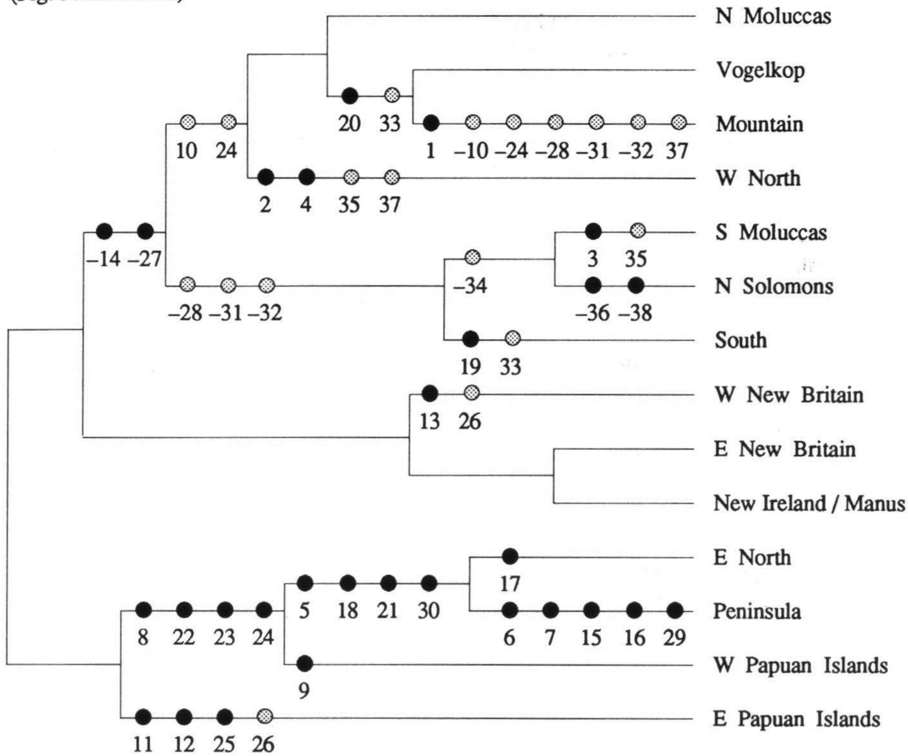
Area \ Species	11111111112222222222333333333344444444445 12345678901234567890123456789012345678901234567890
N Moluccas	00000000010000000000000100010011010101000110000000
S Moluccas	00100000000000000000000000000000011010000001000000
Vogelkop	00000000010000000001000100010011110101000000000000
Mountains	10000000000000000001000000000000011011100000000000
W North	01010000010000000000000010001001101111100000001000
E North	00001001000001001100111100110111010101000000011000
South	00000000000000000100000000000000110101000000000000
Peninsula	00001111000001110100111100111111010101000000010100
W Papuan Islands	00000001100001000000011100110011010101000000000001
E Papuan Islands	00000000011010000000000111100110101010000000000010
W New Britain	00000000000011000000000001110011010101001000010000
E New Britain	00000000000010000000000001100110101010100000010000
New Ireland/Manus	00000000000010000000000001100110101011000000010000
N Solomon Islands	00000000000000000000000000000000000000000000100000

Area \ Species	5555555556666666666777777777788888888889999999999 1234567890123456789012345678901234567890123456789
N Moluccas	0000000011100110100000000000000000000000000000011
S Moluccas	0000000011001010000000000000000000000000000000011
Vogelkop	0000000000000001000000000000101001111000000110111
Mountains	0000000000000000011111101111000111011111111111101
W North	0000111100100100110000001000010100010110101111111
E North	0000111100100100000000000000000000000000000000000
South	0111011100100100000000000000000001000101000001101
Peninsula	1111111100100100010000000000000010000101000000111101
W Papuan Islands	0011011100100100000000000000000000101100000110101
E Papuan Islands	0001011100100100000000000000000000000000000000000
W New Britain	0000001100101100000000000000000000000000000000000
E New Britain	0000001100111100000000000100000000000000000111101
New Ireland / Manus	0000001100111100000000000100000000000000000111101
N Solomon Islands	0000000100100100000000000000000000000000000000000

d. Data matrix of *Guioa*, *Diceropyga*, and *Cosmopsaltria* species and ancestral species. The numbers refer to the line numbers (species) in a–c.

This geographical analysis was the only one which resulted in a difference between the outcome of PAUP and of CAFCA. The result of CAFCA is geographically (fig. 50g–i) very attractive, while the much more parsimonious result of PAUP (fig. 50e, f) is geographically very doubtful (e.g. the N Solomon Islands form a component together with the S Moluccas). The difference is caused by the fact that

(Fig. 50 continued)

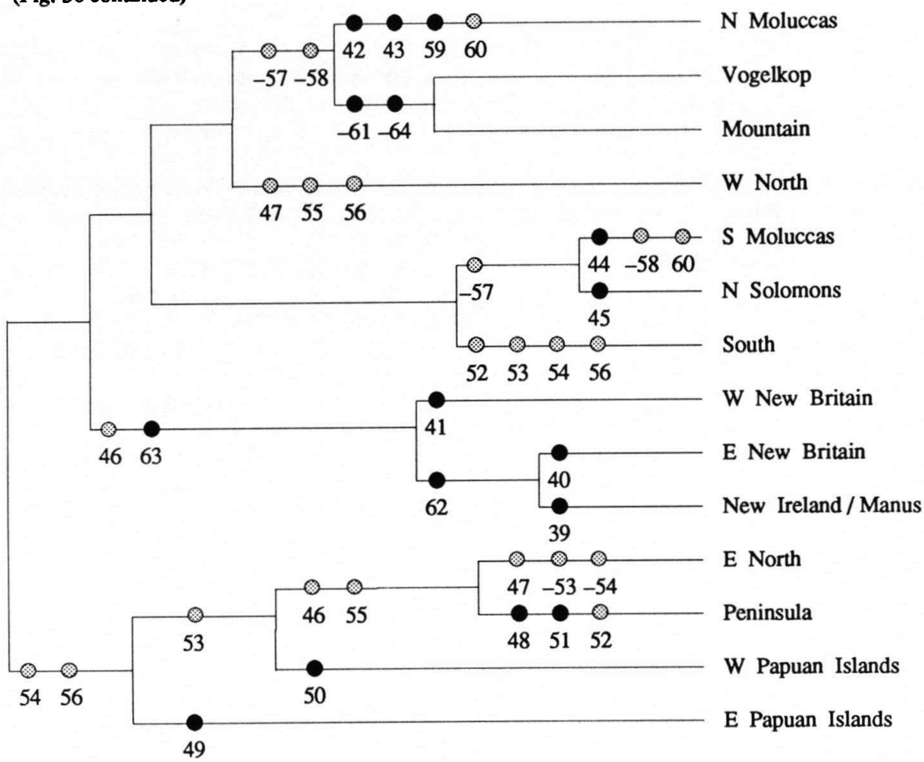


e. Generalized areagram of New Guinea with the *Guioa* species depicted in it (analysis via PAUP of *Guioa* and *Diceropyga* only). The numbers refer to the line numbers (species) in a.

PAUP recognizes components based on the absence of species in certain areas; the four components: 1) N Moluccas, Vogelkop, and Mountains; 2) S Moluccas and N Solomon Islands; 3) S Moluccas, N Solomon Islands, and South, and 4) the component of these 5 areas together with W North are based on the *absence* of ancestors and species. The recognition of components (areas) should be based on the *presence* of species, because absence does not indicate a historical relationship between areas. *Guioa* is absent in Europe and India, but this does not reveal anything about a possible relation between these two areas. Consequently the results of PAUP should be disregarded in this analysis. The recognition of components based on the presence of taxa is another advantage of CAFCA.

This result indicates that the component-compatibility analysis as applied by CAFCA under assumption 0 (Zandee, 1987, 1988; Zandee & Roos, 1987) is the most powerful analytic tool for a historical biogeographic analysis, followed by the Brooks Parsimony Analysis (Wiley, 1988a, b). The chapter Methods in historical biogeography (chapter 12.2) already indicated this outcome.

(Fig. 50 continued)



f. Generalized areagram of New Guinea with the *Diceropyga* species depicted in it (analysis via PAUP of *Guioa* and *Diceropyga* only). The numbers refer to the line numbers (species) in b.

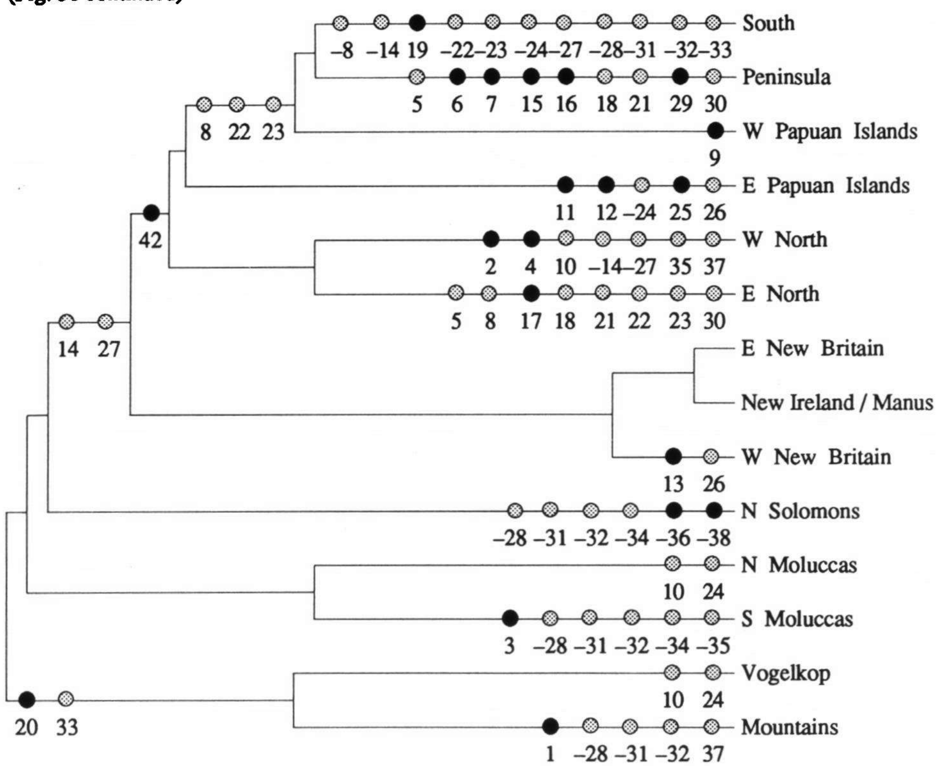
N.B.: Missing areas are normally not a problem with both methods, because the absence of taxa is indicated as reversals during the optimization procedures. Only the recognition of components based on the absence of taxa is not allowed. This is contrary to the normal cladistic analyses where the absence of a character can be a correct apomorphy (e.g. loss of limbs in snakes).

PAUP could form the false components because both *Guioa* and *Diceropyga* are not completely distributed over all distinguished areas.

The above result was enhanced when the genus *Cosmopsaltria* was added and a second analysis was performed. CAFCA found the same tree again (170 steps, consistency index 0.582, redundancy index 0.417), while PAUP found very different trees. These trees were much more parsimonious, but they all contained the same flaw: the recognition of components based on the absence of taxa.

Guioa shows several homoplasies in the generalized areagram. Some of them (e.g. between *Guioa pseudoamabilis*, no. 1, and *Guioa pteropoda*, no. 2; *Guioa*

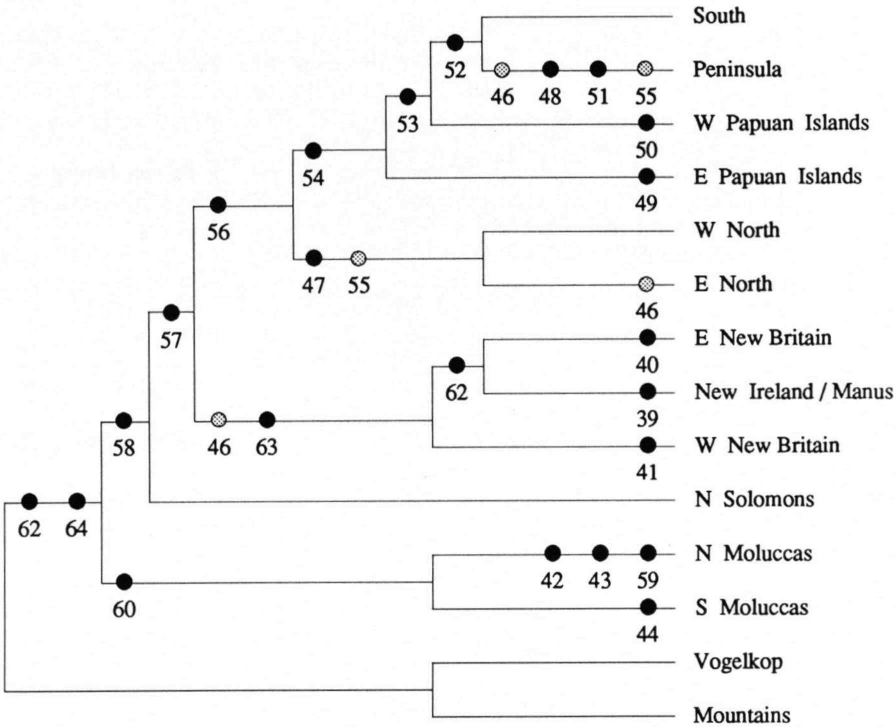
(Fig. 50 continued)



g. Generalized areagram of New Guinea with the *Guioa* species depicted in it (analysis via CAFCA of all three genera). The numbers refer to the line numbers (species) in a.

melanopoda, no. 4, and *Guioa patentinervis,* no. 3; *Guioa oligotricha,* no. 19, and *Guioa subsericea,* no. 20) are quite likely due to the species which were left out in the cladistic analyses, their distributions often fit in between those of the above three couples. Some species, like *Guioa comesperma* (no. 14), *Guioa contracta* (no. 5), and *Guioa rigidiuscula* (no. 8) may have diffused from the E North along the coast and mountains to the south on the Peninsular part of New Guinea, their distributions were interpreted as though they were the result of dispersal. *Guioa contracta* and *Guioa grandifoliola* (no. 6) show vicariance as *Guioa grandifoliola* is found in those parts of the E North where *Guioa contracta* is absent. *Guioa membranifolia* (no. 10) dispersed to the W North, Vogelkop, and N Moluccas. *Guioa misimaensis* (no. 11) and *Guioa plurinervis* (no. 12) show vicariance between resp. Misima I. and Rossel I. The ancestor of the former two and of *Guioa novobritannica* (W New Britain; no. 13) seems to have had a disjunct distribution, but this ancestor, N (no. 26), might also have been widespread and gone extinct in part of its distribution. *Guioa scalariformis* (no. 17) shows vicariance with ancestor Q (no. 29).

(Fig. 50 continued)

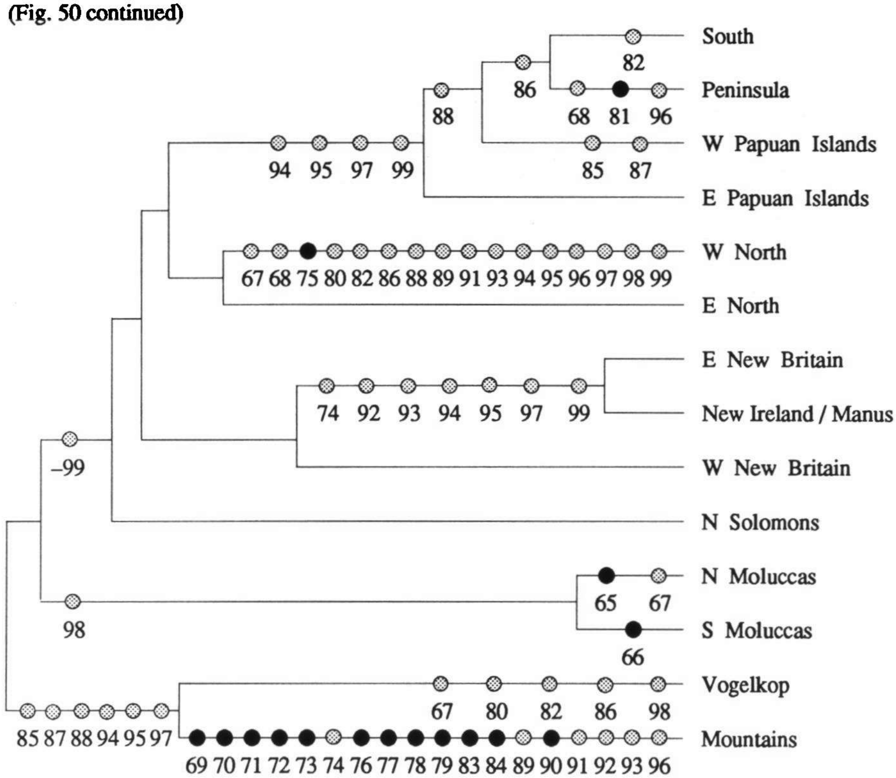


h. Generalized areagram of New Guinea with the *Diceropyga* species depicted in it (analysis via CAFCA of all three genera). The numbers refer to the line numbers (species) in b.

The genus *Diceropyga* almost solely shows vicariance events for the 14 distinguished areas except for the Vogelkop and the Mountain area where the genus is absent. Ancestor Q (no. 55) may have shown dispersal, but this does not have to be the case as ancestor Q may have been primitively absent from the Papuan Islands and from the South; then the distribution over the Peninsula and the North could have been present without dispersal. The same applies to *Diceropyga gravesteini* (no. 46) which is spread over the northern islands, E North, and the Peninsula.

Cosmopsaltria is mainly distributed over the Mountains area, all homoplasies can be interpreted as dispersal from this area. The *Cosmopsaltria doryca* group (nos. 65–67) dispersed to the Moluccas, where *Cosmopsaltria lata* (no. 66) and *Cosmopsaltria* spec. A (no. 65) show a perfect vicariance event. *Cosmopsaltria gestroei* (no. 68) dispersed to the Peninsula and the Northern part. *Cosmopsaltria mimica* (no. 74) dispersed over E New Britain and New Ireland. *Cosmopsaltria emarginata* (no. 75) speciated in the W North area after ancestor P (no. 89) dispersed to this area. The *Cosmopsaltria loriae* group (nos. 80–82) dispersed over the whole of

(Fig. 50 continued)



i. Generalized areagram of New Guinea with the *Cosmopsaltria* species depicted in it (analysis via CAFCA of all three genera). The numbers refer to the line numbers (species) in c.

Fig. 50. Reconstruction of a generalized areagram of New Guinea, based on the distribution and phylogenetic data of *Guioa*, *Diceropyga*, and *Cosmopsaltria*. ● = apomorphy; ◎ = homoplasy.

New Guinea; *Cosmopsaltria loriae* (no. 81) and *Cosmopsaltria capitata* (no. 82) show vicariance. *Cosmopsaltria papuensis* (no. 85) dispersed over the Papuan Islands.

The geological history of New Guinea is rather complicated. The next short discussion is based on Duffels (1983b, 1986). New Guinea formed together with New Caledonia and New Zealand the Inner Melanesian Arc, still intact 70 Ma. Probably due to the formation of the Coral Sea the arc was already broken up in the Paleocene; the New Guinea part of the arc rifted northwards and away from the rest. This part of New Guinea is continental. The northern part of New Guinea (north of the Mountain ranges, together with Biak I. and Japen I.) is of oceanic derivation and constituted the Outer Melanesian Arc together with the Bismarck Archipelago; this arc continued in the arc systems of the Solomon Islands, New Hebrides, Fiji, and Tonga. The Outer Melanesian Arc was formed in the late Paleocene or early Eocene. Due to the northward rifting movement of Australia the arc was moved outwards, away from Australia and the Inner Melanesian Arc. In the early Miocene the Outer Melanesian Arc retrograded and collided with the continental part of New Guinea in the Miocene. As a resultant orogenesis started and the central mountain range was formed. The Vogelkop may have undergone clockwise rotation due to the collision of the New Guinean/Australia plate with the Banda arcs (Lesser Sunda Islands and S Moluccas).

Based on this information it is to be expected that the South area is more related to the Mountains and that the North together with the Bismarck Archipelago form a sister group of these two. However, the resultant generalized areagram shows that the South is more related to the North and that the Mountains forms a sister area of these two. This result can be due to the fact that both *Guioa* and *Diceropyga* are lowland taxa and *Cosmopsaltria* is mainly a highland taxon. Ecological demands can have interrupted the correct relations between the three areas. The Vogelkop features together with the Mountains area. The Peninsula, together with the W and E Papuan Islands forms an intermediary area between the North and the South due to diffusion of lowland species around the mountain range.

The Vogelkop together with the islands NW of it still remains an interesting area for future research. This part of New Guinea contains many very local endemics (for instance *Guioa amabilis* and *Guioa waigeoensis*, and the cicada genus *Rhadinopyga*; Duffels, 1986). A historical biogeographic analysis of this area seems worthwile.

The above presented biogeographic analysis of the three genera, *Cosmopsaltria, Diceropyga,* and *Guioa,* resulted in a unique generalized areagram. If the biogeographic analysis is regarded as a test of the cladogram of *Guioa,* then it can be concluded that the areagram supports the cladogram.

12.5. VICARIANCE EVENTS IN AUSTRALIA AND NEW CALEDONIA

Cracraft (1983) published a paper which dealt with vicariance events between five areas in Australia (see fig. 51). Three of the areas are also occupied by *Guioa* species: Cape York Peninsula (*Guioa acutifolia*), Cairns-Atherton region (*Guioa acutifolia,*

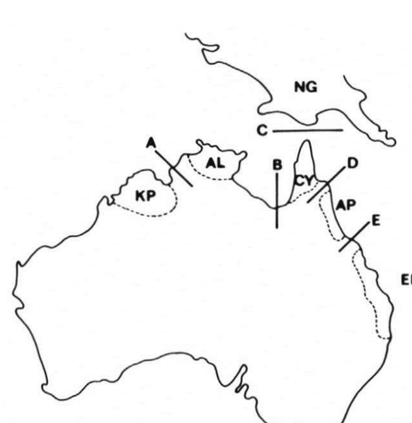


Fig. 51. Division of Australia in geographical areas as used in the historical biogeographic analysis. A–E = vicariance boundaries. AL = Arnhem Land; AP = Atherton Plateau; CY = Cape York Peninsula; EF = E Forests (SE Queensland and NE New South Wales); KP = Kimberley Plateau.

Guioa lasioneura, and *Guioa montana*), and SE Queensland-NE New South Wales (*Guioa acutifolia* and *Guioa semiglauca*). In Australia these three areas have the highest amount of rain. Cracraft elaborated his analysis in 1986. The present study combines both papers. Cracraft used several genera of birds for his analysis; only those bird genera are used which occupy the above mentioned five areas. Of *Malurus* and of *Petrophasa* only (monophyletic) parts of the genera were utilized.

In this analysis a generalized area cladogram of the five areas of endemism in Australia, of New Guinea, of Lord Howe Island, and of three areas in New Caledonia was made. Six genera of birds were used to elucidate the relations between the five areas in Australia. *Guioa* is compared with them. For Lord Howe Island and New Caledonia only the data of *Guioa* were available. New Caledonia could be split into three regions as *Guioa crenulata* and *Guioa pectinata* only occur in the NE of New Caledonia; *Guioa fusca* only in the S and on the islands N of New Caledonia; and *Guioa gracilis* in the NE and the S (plus the northern islands). The other *Guioa* species are widespread over New Caledonia.

The cladograms of the six bird genera together with their distributions are shown in figure 52a–f. The data of *Guioa* are shown in figure 52g. The cladogram of *Guioa* is the same as figure 44, but the representatives of West Malesia are left out as *Guioa acutifolia* must have dispersed to the Moluccas (this area is for the greater part geologically much younger than Australia; Audley-Charles, 1987).

The generalized areagram was constructed under assumption 0. Only CAFCA (minimal steps) and PAUP (root=midpoint addseq=rootless bandb) were used to analyse the data, as no apparent area could serve as an outgroup.

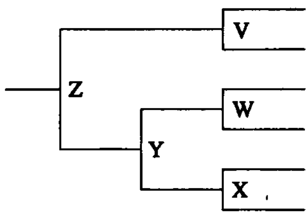
CAFCA found two trees, which were equally parsimonious (81 steps, consistency index 0.877). Of these the selected one (fig. 52i) had the highest redundancy index (0.492, the other 0.476). The non-selected tree was the same as Cracraft (1986) has found, with New Guinea as sister area of Cape York Peninsula. PAUP found 4 trees, the above two and two with New Guinea as sister area of Lord Howe I. and New Caledonia. The latter two trees suffer from the same flaw as was already observed during the New Guinea analysis, the component: New Guinea, Lord Howe I., and New Caledonia is based on the absence of species and is therefore refuted.

The selected tree is almost the same as Cracraft (1986, fig. 9.1) has found, only New Guinea is not considered to be the sister area of Cape York Peninsula but of the three Australian E Coast areas. Perhaps barrier D (fig. 51) is younger than C.

Guioa fits in with the data for the birds. In fact, *Guioa* will fit in with all possible trees for area 1, 4–6, because the data of *Guioa* only allow for a polytomy for these three areas (one species occurs in all four areas and two others, sister species, in the same area).

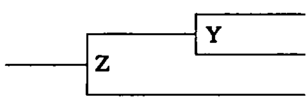
Guioa (nos. 45–71): *Guioa acutifolia* (no. 48) has either not responded to the vicariance events between areas 1, 4, 5, and 6; or it has dispersed/diffused from area 5 and/or 6 to the other areas (this species distributed up to the Moluccas). *Guioa lasioneura* (no. 45) and *Guioa montana* (no. 46) have speciated sympatrically, both inhabit area 5. Most New Caledonian species are widespread and have not responded to vicariance events, only *Guioa crenulata* (no. 56), *Guioa fusca* (no. 51), *Guioa pectinata* (no. 53), and, less so, *Guioa gracilis* (no. 52) have responded.

(Fig. 52)



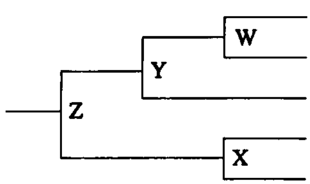
	Species \ Area	1	2	3	4	5	6	7	8	9	10
1	Poephila personata	0	1	1	0	0	0	0	0	0	0
2	Poephila leucotis	0	0	0	1	0	0	0	0	0	0
3	Poephila acuticauda	0	1	0	0	0	0	0	0	0	0
4	Poephila hecki	0	0	1	0	0	0	0	0	0	0
5	Poephila atrophygialis	0	0	0	1	0	0	0	0	0	0
6	Poephila cincta	0	0	0	0	1	1	0	0	0	0
7	Poephila ancestor V	0	1	1	1	0	0	0	0	0	0
8	Poephila ancestor W	0	1	1	0	0	0	0	0	0	0
9	Poephila ancestor X	0	0	0	1	1	1	0	0	0	0
10	Poephila ancestor Y	0	1	1	1	1	1	0	0	0	0
11	Poephila ancestor Z	0	1	1	1	1	1	0	0	0	0

a. Finches (*Poephila*)



12	Malurus rogersi	0	1	0	0	0	0	0	0	0	0
13	Malurus dulcis	0	0	1	0	0	0	0	0	0	0
14	Malurus amabilis	0	0	0	1	0	0	0	0	0	0
15	Malurus ancestor Y	0	1	1	0	0	0	0	0	0	0
16	Malurus ancestor Z	0	1	1	1	0	0	0	0	0	0

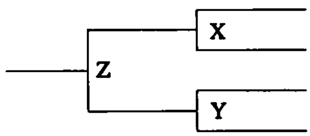
b. Fairy wrens (*Malurus*)



17	Ptiloris magnificus	1	0	0	0	0	0	0	0	0	0
18	Ptiloris intercedens	1	0	0	0	0	0	0	0	0	0
19	Ptiloris alberti	0	0	0	1	0	0	0	0	0	0
20	Ptiloris victoriae	0	0	0	0	1	0	0	0	0	0
21	Ptiloris paradiscus	0	0	0	0	0	1	0	0	0	0
22	Ptiloris ancestor W	1	0	0	0	0	0	0	0	0	0
23	Ptiloris ancestor X	0	0	0	0	1	1	0	0	0	0
24	Ptiloris ancestor Y	1	0	0	1	0	0	0	0	0	0
25	Ptiloris ancestor Z	1	0	0	1	1	1	0	0	0	0

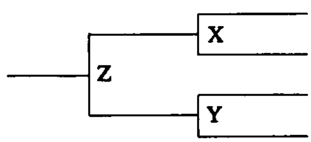
c. Rifle birds (*Ptiloris*)

(Fig. 52 continued)



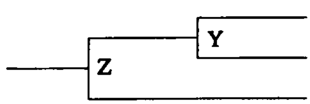
26	Petrophasa blaauwi	0 1 0 0 0 0 0 0 0 0
27	Petrophasa smithii	0 0 1 0 0 0 0 0 0 0
28	Petrophasa peninsulae	0 0 0 1 0 0 0 0 0 0
29	Petrophasa scripta	0 0 0 0 1 1 0 0 0 0
30	Petrophasa ancestor X	0 1 1 0 0 0 0 0 0 0
31	Petrophasa ancestor Y	0 0 0 1 1 1 0 0 0 0
32	Petrophasa ancestor Z	0 1 1 1 1 1 0 0 0 0

d. Pigeons (*Petrophasa*)



33	Tregellasia 'leucops'	1 0 0 0 0 0 0 0 0 0
34	Tregellasia albigularis	0 0 0 1 0 0 0 0 0 0
35	Tregellasia nana	0 0 0 0 1 0 0 0 0 0
36	Tregellasia capito	0 0 0 0 0 1 0 0 0 0
37	Tregellasia ancestor X	1 0 0 1 0 0 0 0 0 0
38	Tregellasia ancestor Y	0 0 0 0 1 1 0 0 0 0
39	Tregellasia ancestor Z	1 0 0 1 1 1 0 0 0 0

e. Robins (*Tregellasia*)



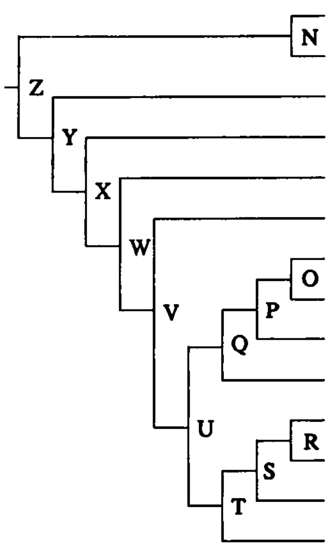
40	Psephotus chrysopterygius	0 0 0 1 0 0 0 0 0 0
41	Psephotus dissimilis	0 0 1 0 0 0 0 0 0 0
42	Psephotus pulcherrimus	0 0 0 0 0 1 0 0 0 0
43	Psephotus ancestor Y	0 0 1 1 0 0 0 0 0 0
44	Psephotus ancestor Z	0 0 1 1 0 1 0 0 0 0

f. Parrots (*Psephotus*)

Malurus (nos. 12–16): This genus was probably primitively absent on Lord Howe I. and on New Caledonia as ancestor Z (no. 16) shows a parallel. It has perfectly responded to the vicariance events between areas 2, 3, and 4.

Petrophasa (nos. 26–32): *Petrophasa scripta* (no. 29) has not responded to the vicariance event that has split areas 5 and 6. This genus is regarded to be primitively absent in New Guinea, Lord Howe I. and New Caledonia (ancestor Z, no. 32, shows a parallel).

(Fig. 52 continued)



45	Guioa lasioneura	0 0 0 0 1 0 0 0 0 0
46	Guioa montana	0 0 0 0 1 0 0 0 0 0
47	Guioa semiglauca	0 0 0 0 0 1 0 0 0 0
48	Guioa acutifolia	1 0 0 1 1 1 0 0 0 0
49	Guioa coriacea	0 0 0 0 0 0 1 0 0 0
50	Guioa microsepala	0 0 0 0 0 0 0 1 1 1
51	Guioa fusca	0 0 0 0 0 0 0 0 0 1
52	Guioa gracilis	0 0 0 0 0 0 0 1 0 1
53	Guioa pectinata	0 0 0 0 0 0 0 1 0 0
54	Guioa ovalis	0 0 0 0 0 0 0 1 1 1
55	Guioa crenata	0 0 0 0 0 0 0 1 1 1
56	Guioa crenulata	0 0 0 0 0 0 0 1 0 0
57	Guioa villosa	0 0 0 0 0 0 0 1 1 1
58	Guioa glauca	0 0 0 0 0 0 0 1 1 1
59	Guioa ancestor N	0 0 0 0 1 0 0 0 0 0
60	Guioa ancestor O	0 0 0 0 0 0 0 1 0 1
61	Guioa ancestor P	0 0 0 0 0 0 0 1 0 1
62	Guioa ancestor Q	0 0 0 0 0 0 0 1 1 1
63	Guioa ancestor R	0 0 0 0 0 0 0 1 1 1
64	Guioa ancestor S	0 0 0 0 0 0 0 1 1 1
65	Guioa ancestor T	0 0 0 0 0 0 0 1 1 1
66	Guioa ancestor U	0 0 0 0 0 0 0 1 1 1
67	Guioa ancestor V	0 0 0 0 0 0 0 1 1 1
68	Guioa ancestor W	0 0 0 0 0 0 1 1 1 1
69	Guioa ancestor X	1 0 0 1 1 1 1 1 1 1
70	Guioa ancestor Y	1 0 0 1 1 1 1 1 1 1
71	Guioa ancestor Z	1 0 0 1 1 1 1 1 1 1

g. *Guioa*.

Poephila (nos. 1–11): *Poephila cincta* (no. 6) has not responded to the vicariance event that has split areas 5 and 6. *Poephila personata* (no. 1) has not responded to the vicariance event that splits areas 2 and 3. This genus was also primitively absent in New Guinea, Lord Howe I., and New Caledonia (the ancestors V, no. 7, Y, no. 10, and Z, no. 11, show parallel events).

Psephotus (nos. 40–44): Ancestor Y (no. 43) shows a parallel development in areas 3 and 4, presumably dispersal occurred from area 4 to area 3, followed by spe-

(Fig. 52 continued)

	Area \ Species	1111111111222222222233333333334 1234567890123456789012345678901234567890
1	New Guinea	0000000000000000110001011000000010001010
2	Kimberley	1010001101110011000000000100010100000000
3	Arnhem Land	1001001101101011000000000010010100000000
4	Cape York	0100101011100101001000011001001101001011
5	Cairns / Atherton	0000010011100000000100101000101100100110
6	E Tropical Forests	0000010011100000000010101000101100010110
7	Lord Howe Island	0000000000000000000000000000000000000000
8	NE New Caledonia	0000000000000000000000000000000000000000
9	Central New Caledonia	0000000000000000000000000000000000000000
10	S New Caledonia	0000000000000000000000000000000000000000

	Area \ Species	4444444445555555555666666666677 1234567890123456789012345678901
1	New Guinea	0000000100000000000000000000111
2	Kimberley	0000000000000000000000000000000
3	Arnhem Land	1011000000000000000000000000000
4	Cape York	0011000100000000000000000000111
5	Cairns / Atherton	0000110100100000001000000000111
6	E Tropical Forests	0101001100000000000000000000111
7	Lord Howe Island	0000000010000000000000000001111
8	NE New Caledonia	0000000001011111101111111111111
9	Central New Caledonia	0000000001000110110001111111111
10	S New Caledonia	0000000001110110110111111111111

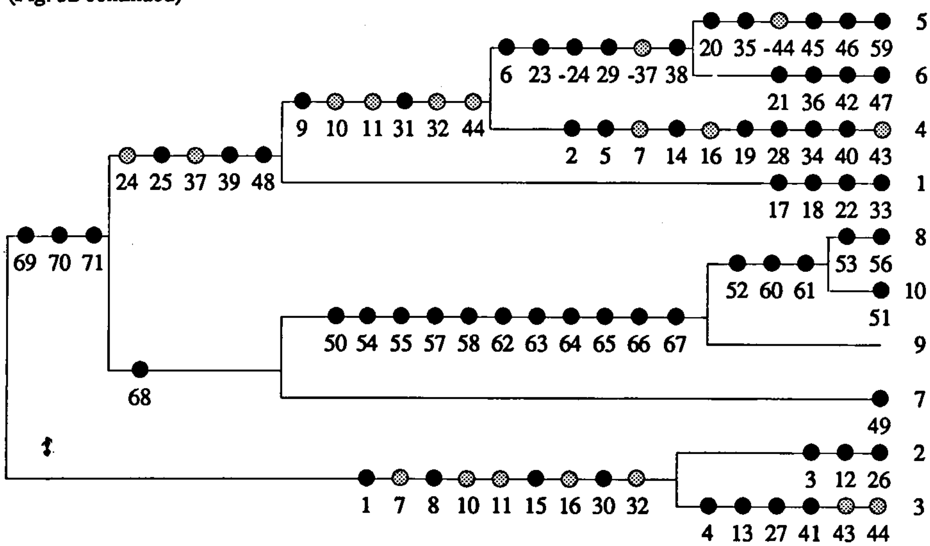
h. Matrix for generalized area-cladogram, colums refer to species, numbers of species according to line numbers in a–g.

ciation into *Psephotus dissimilis* (no. 41). Consequently the parallel of ancestor Y (no. 43) is false; this species may have occurred only in area 3. Moreover, the distribution of ancestor Z (no. 44) is also false. Ancestor Z was presumably widespread over areas 4–6, and it has gone extinct in area 5; the parallel development for area 3 is false and due to the dispersal of one of the descendants.

Ptiloris (nos. 17–25) has perfectly responded to all vicariance events except for ancestor Y (no. 24), which was either primitively absent in areas 5 and 6 or has gone extinct in these two areas.

Tregellasia (nos. 33–39) has also perfectly responded to all vicariance events except for ancestor X, which has either gone extinct in areas 5 and 6 or was primitively absent in these two areas.

(Fig. 52 continued)



i. Generalized area cladogram, numbers or species (apomorphies) refer to line numbers as in a–g; the numbers of the areas (taxa) are explained in the text. ● = apomorphy, ◎ = homoplasy.

Fig. 52. Construction of a generalized area cladogram for five areas in Australia, Lord Howe Island, and three areas in New Caledonia. Area 1 = New Guinea, 2 = Kimberley Plateau, 3 = Arnhem Land (Northern Territory), 4 = Cape York Peninsula, 5 = Cairns-Atherton Region, 6 = SE Queensland and NE New South Wales (E Tropical Forests), 7 = Lord Howe Island, 8 = NE New Caledonia, 9 = Central New Caledonia, 10 = S New Caledonia (and the islands N of New Caledonia).

According to Cracraft (1986) barrier A (fig. 51; lowlands of the Victoria and Daly rivers) forms a climatic barrier, just like barrier B (the region near the head of the Gulf of Carpentaria) which probably dates back to the Eocene. Barrier C (the Torres Strait) is rather young, probably still land until the Pleistocene, although it has been temporarily open several times before the Pleistocene. Barrier D (Torresian Barrier) is a lower, more arid region related to the uplift of the Atherton Plateau; of Cenozoic times. Barrier E (Burdekin Gap and to a lesser extent the Mackay-Rockhampton Gap) is an arid barrier of presumably Pleistocene age.

The apparent connection between the south and north part of New Caledonia is presumably caused by similarities in soil (both areas do not contain serpentine). The relation between Lord Howe Island and New Caledonia is to be expected, because both are situated on the Lord Howe Rise, which is composed of continental rock and was thought to be above sea-level during the Middle Cretaceous (c. 100 Ma). By that time the Lord Howe Rise was still connected to mainland Australia (Raven & Axelrod, 1972) and the *Guioa* ancestor could have been present on as well Australia as the Lord Howe Rise.

Surprisingly, New Caledonia and Lord Howe I. are more related to the Australian E Coast areas than the two Australian N Coast areas are, even though New Caledonia and Lord Howe I. split off far earlier (about 80 Ma ago; Raven & Axelrod, 1972) than the endemic regions in Australia were developed (barrier B c. 50 Ma ago). Presumably, contacts between New Caledonia/Lord Howe I. and Australia remained possible for a long time.

12.6. HISTORICAL BIOGEOGRAPHY OF MALESIA

Audley-Charles (1987) showed that the whole of Malesia, together with W Thailand, Burma, and S Tibet was part of Gondwanaland. The West Malesian part (Malaya, E & W Borneo, Sumatra, W Celebes, and Banda Allochthon) together with E Thailand, Burma, and S Tibet rifted as continental fragments, in the late Jurassic at its latest, but perhaps already in the Perm, in front of Australia and East Malesia towards the Southeast Asian mainland. Important is that Australia and East Malesia were always relatively close to the rifting parts. The rifting parts formed stepping stones for plant and animal dispersal already during the late Mesozoic and early Tertiary. Much later, in the Miocene, when the rifting parts were already in connection with Southeast Asia, Australia and East Malesia (including E Celebes) connected with West Malesia.

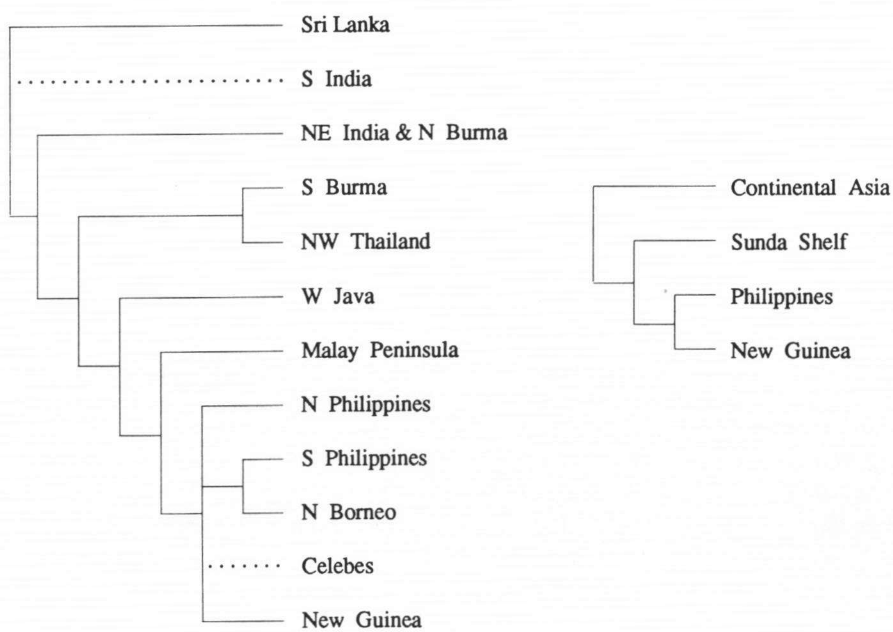


Fig. 53. Generalized areagrams of Malesia and surrounding areas; left-hand part after Schuh & Stonedahl (1986); right-hand part after Hovenkamp (1986).

Based on this, the following historical geographic patterns may be expected: a) Ancestors dispersing from Southeast Asia (Laurasia) into the Malesian area; in an areagram Southeast Asia will be the 'primitive' area and New Guinea the most 'advanced'. b) Ancestors dispersing from Australia/New Guinea into the Malesian area; the areagram will be the opposite of the former, New Guinea will be 'primitive' and Southeast Asia 'advanced'. These areagrams mainly show dispersal schemes, but after the species have been established vicariance may occur. c) Ancestors already present in the West or East Malesian area, showing real vicariance events.

Already several historical biogeographic studies exist for Malesia: Axelius (1987), De Jong (1983, 1987), Holloway (1987), Hovenkamp (1986), Roos (1985), Schuh & Stonedahl (1986).

Axelius (1987) published a cladogram of the plant genus *Lerchea* (Rubiaceae), but as the species are only found on either Sumatra or on Sumatra and Java, no areagram can be made. Obviously, this would have been a c-type of areagram.

A-type of (general) areagrams were shown by De Jong (1983, 1987), Hovenkamp (1986), and Schuh & Stonedahl (1986); see figure 53 for two examples.

Most species of the butterfly genus *Matapa* (De Jong, 1983, 1987) are widespread over Continental Southeast Asia and the Sunda Shelf. De Jong only found one vicariance event (explained as dispersal) between the Sunda Shelf and Celebes/Philippines.

The plant bugs (Schuh & Stonedahl, 1986) and *Pyrrosia* ferns (Hovenkamp, 1986) also show a dispersal from Southeast Asia towards New Guinea. Schuh & Stonedahl more or less found most of the small continental fragments, distinguished by Audley-Charles (1987), as areas of endemism (see fig. 53).

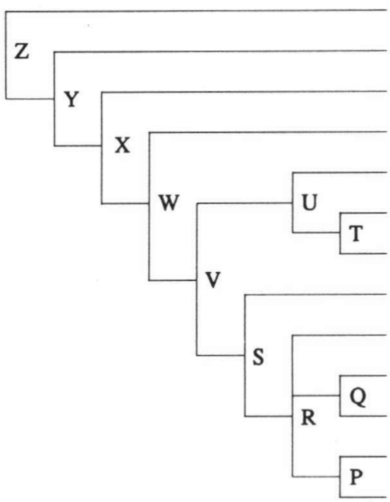
The analysis of *Guioa* showed a b-type of areagram. Very likely *Guioa* dispersed from New Guinea/Australia towards Malesia and Continental Southeast Asia. Figure 54a shows the cladogram of the West Malesian *Guioa* species and their distribution over the different areas; figure 54b shows the datamatrix and figure 54c the resulting areagram.

The datamatrix was constructed under assumption 0. Three computer programs were used: CAFCA (option: minimal steps), PAUP (options: bandb swap=global mulpars), and HENNIG86 (option: ie*). PAUP and HENNIG86 could operate without any problem, because the area New Guinea/Moluccas could be used as outgroup. The areagram found by PAUP and HENNIG86 was the most parsimonious and had the highest redundancy index: steps 29, consistency index 0.793, redundancy index 0.601, homoplasies 6. The tree that CAFCA found was equally parsimonious, but had a lower redundancy index.

The areagram of *Guioa* does not exactly show the opposite image of that of Schuh & Stonedahl (1986) (fig. 53), with Continental Southeast Asia as the most derived area. This is due to *Guioa diplopetala*, a widespread species, which branches off quite early. The distribution of *Guioa pubescens* shows a parallel for Java, while on the map Java appears to be a natural extension of a Sunda Shelf distribution. The parallel is caused by the fact that two species are widespread over Continental Asia, *Guioa diplopetala* and *Guioa pleuropteris*, the latter of which is not present on Java.

If two species would have had a Sunda Shelf distribution of which only one extended up to Continental Asia, while another species would have a continental distribution with an absence for Java, then Java and Continental Asia would have switched places in the areagram and the distribution of the latter species would show a parallel for Continental Asia.

(Fig. 54)



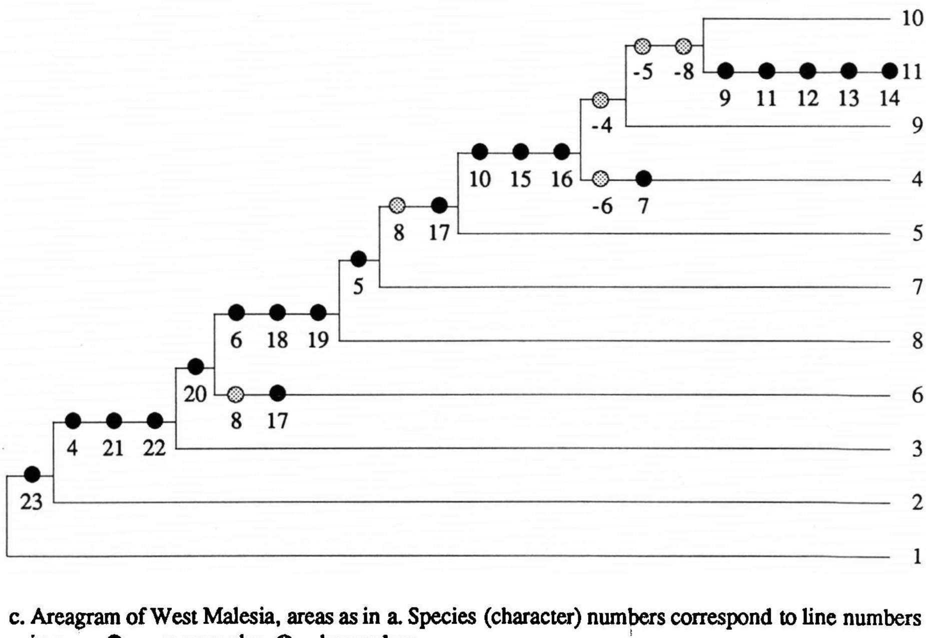
	Species \ Area	1 1 1 2 3 4 5 6 7 8 9 0 1
1	Guioa acutifolia	1 0 0 0 0 0 0 0 0 0 0
2	Guioa asquamosa	0 1 0 0 0 0 0 0 0 0 0
3	Guioa hirsuta	0 0 1 0 0 0 0 0 0 0 0
4	Guioa diplopetala	0 0 1 1 1 1 1 1 0 0 0
5	Guioa bijuga	0 0 0 1 1 0 1 0 1 0 0
6	Guioa pleuropteris	0 0 0 0 1 0 1 1 1 1 1
7	Guioa pterorhachis	0 0 0 1 0 0 0 0 0 0 0
8	Guioa pubescens	0 0 0 1 1 1 0 0 1 0 0
9	Guioa discolor	0 0 0 0 0 0 0 0 0 0 1
10	Guioa koelreuteria	0 0 0 1 0 0 0 0 1 1 1
11	Guioa acuminata	0 0 0 0 0 0 0 0 0 0 1
12	Guioa myriadenia	0 0 0 0 0 0 0 0 0 0 1
13	Guioa reticulata	0 0 0 0 0 0 0 0 0 0 1
14	Guioa ancestor P	0 0 0 0 0 0 0 0 0 0 1
15	Guioa ancestor Q	0 0 0 1 0 0 0 0 1 1 1
16	Guioa ancestor R	0 0 0 1 0 0 0 0 1 1 1
17	Guioa ancestor S	0 0 0 1 1 1 0 0 1 1 1
18	Guioa ancestor T	0 0 0 1 1 0 1 1 1 1 1
19	Guioa ancestor U	0 0 0 1 1 0 1 1 1 1 1
20	Guioa ancestor V	0 0 0 1 1 1 1 1 1 1 1
21	Guioa ancestor W	0 0 1 1 1 1 1 1 1 1 1
22	Guioa ancestor X	0 0 1 1 1 1 1 1 1 1 1
23	Guioa ancestor Y	0 1 1 1 1 1 1 1 1 1 1
24	Guioa ancestor Z	1 1 1 1 1 1 1 1 1 1 1

a. Cladogram of West Malesian *Guioa* species and their distribution over 11 areas (1 = New Guinea, Moluccas; 2 = Lesser Sunda Islands; 3 = Celebes; 4 = NE Borneo; 5 = Remainder of Borneo, Sumatra, and Malay Peninsula; 6 = Java; 7 = S Thailand; 8 = Continental SE Asia; 9 = Palawan; 10 = S Philippines; 11 = N Philippines).

(Fig. 54 continued)

Area \ Species	111111111122222 123456789012345678901234
New Guinea / Moluccas	100000000000000000000001
Lesser Sunda Islands	010000000000000000000011
Celebes	001100000000000000001111
NE Borneo	000110110100001111111111
Borneo / Sumatra / Malay Peninsula	000111010000000011111111
Java	000100010000000010011111
S Thailand	000111000000000001111111
SE Asia	000101000000000001111111
Palawan	000011010100001111111111
S Philippines	000001000100001111111111
N Philippines	000001001111111111111111

b. Character matrix of the distributions of West Malesian *Guioa* species.



c. Areagram of West Malesia, areas as in a. Species (character) numbers correspond to line numbers in a. — ● = apomorphy, ◍ = homoplasy.

Fig. 54. Construction of an areagram of West Malesian areas based on species of *Guioa*.

Dispersal of *Guioa* over West Malesia seems to be the best explanation of the distribution pattern. This conclusion is supported by the distribution of *Guioa diplopetala* (a circular species, see fig. 77) and by the distribution of *Guioa pleuropteris* in the Philippines (see fig. 110).

The areagram shows one vicariance event: *Guioa pterorhachis* (NE Borneo) vicariates with *Guioa pleuropteris*. There are probably also some vicariance events in the Philippines (e.g. *Guioa myriadenia, Guioa palawanica,* and *Guioa parvifoliola*), but not all Philippine species could be included in the analysis and the cladogram for the included Philippine species is poorly resolved.

A complicating factor in West Malesia is the Sunda Shelf. On this shelf most species show a widespread distribution which quite often extends to the Southeast Asian mainland. This pattern is probably due to dispersal/diffusion during the glacial periods. Examples are *Guioa, Matapa* (De Jong, 1983, 1987), *Pyrrosia* (Hovenkamp, 1986), plant bugs (Schuh & Stonedahl, 1986), moths of the Notodontidae and Limacodidae (Holloway, 1987). Consequently in most biogeographic analyses Peninsular Malaysia, Sumatra, Borneo, and often (W) Java will be regarded as one area of endemism. The older pattern of separate Australian continental fragments is normally obliterated.

In the following paragraphs short comments will be made on certain areas of endemism.

Audley-Charles (1987) shows that Celebes may have existed as two separate continental fragments, a western and an eastern part. The former moved along with the fragments rifting in advance towards Continental Southeast Asia; the latter rifted together with Australia and New Guinea. This makes Celebes very interesting, because the western part should show a predominantly Continental Asian influence and the eastern part an Australian/New Guinean influence (Wallace's Line should be drawn over Celebes). Animal and plant distribution patterns normally do not show this division (Whitmore, 1981), just like the two *Guioa* species on Celebes; both are sympatric. Floristically Van Balgooy (1987) could not find a significant difference in plant composition between both halves.

Borneo is biogeographically very interesting as a high degree of endemism is present together with much polymorphism (see also chapter 10). Consequently, several areas of endemism can be distinguished. Schuh & Stonedahl (1986) divided Borneo in a northern and southern part. This division is more or less confirmed by the distribution of *Guioa pterorhachis* and *Guioa koelreuteria,* although these are mainly found in the very north/northeast of Borneo. *Guioa pubescens* is mainly confined to the northern half of Borneo. *Matapa aria* and *Matapa cresta* (De Jong, 1983, 1987) are on Borneo only found in the northern part. The north/south distinction can be due to climatic changes during the glacial period in the Pleistocene, when the south was drier than the north (Morley & Flenley, 1987). Another division is also apparent: a western and an eastern part. *Guioa diplopetala* shows a different form in W Borneo and in E Borneo. *Matapa druna* (De Jong, 1983, 1987) is, on Borneo, only found in E Borneo. Just as for Celebes, Audley-Charles (1987) assumed that Borneo consisted of a western and an eastern continental fragment; both rifted in advance towards Continental Asia. Another interesting part is SE Borneo;

only here *Matapa sasivarna* (De Jong, 1983, 1987) and the orchid *Pholidota articulata* (De Vogel, 1988) occur on the island. It is interesting to see that several species, widespread over the Sunda Shelf, are absent from SW Borneo (see the above mentioned examples except for *Guioa diplopetala*). The mountains form another area of endemism, especially Mt. Kinabalu (see chapter 10). Biogeographically, Borneo is very complicated and interesting.

The Philippines were divided in three areas: Palawan, S Philippines, and N Philippines. Palawan and the S Philippines form a kind of transition areas, species either begin or end their distribution there. Unfortunately, the two endemic species (resp. *Guioa palawanica* and *Guioa truncata*) could not be included in the analysis. Endemism is high in the N Philippines (mainly Luzon). Presumably, the recognition of the N Philippines as one area of endemism is too crude; several species are only endemic in a small part of the N Philippines, but the N Philippines were not subdivided because the cladogram could not be fully resolved, and because not all species were included in the analysis. The presence of *Guioa* in the Philippines must be due to dispersal as the Philippines – presumably of composite origin (partly rifted Chinese fragments and partly an already present oceanic arc; Audley-Charles, 1981) – were no part of the Australian Gondwana shelf from which the rest of the Malay Archipelago originated (Audley-Charles, 1987). N.B.: Palawan is part of the Sunda Shelf.

De Jong (1983, 1987), Holloway (1987), and Hovenkamp (1986) show connections between the Philippines and Celebes, as several species are distributed over these two areas. The connection Borneo–Celebes is thought to occur via the Philippines (Holloway, 1987; De Jong, 1983). The connection Philippines–Celebes may have been caused by climatological conditions, as the Philippines, Celebes, E Java, and the Lesser Sunda Islands have a dry monsoon during part of the year. Many plant species show this distribution pattern, often not only east of the Sunda Shelf but also around the wet Sunda Shelf (Van Steenis, 1979; Van Balgooy, 1987).

During the glacial periods in the Pleistocene, Palawan and the small islands north of it formed a continuous landmass with N Borneo, while Mindoro and Luzon were connected by land to Mindanao and NE Borneo (Morley & Flenley, 1987); *Guioa pleuropteris* shows these landbridges as two transformation series (see note 1 under the species description).

Schuh & Stonedahl (1986) reported W Java as an area of endemism. Of *Guioa* two species occur on Java: *Guioa diplopetala,* spread over the whole of Java, and *Guioa pubescens,* found in W Java only. The reason why W Java can be considered as an area of endemism probably has the above mentioned climatological cause, it has a wetter climate than E Java.

Guioa asquamosa is found on the islands Flores and Timor (Lesser Sunda Islands). This distribution must be (partly) due to dispersal or diffusion as Flores (Inner Banda Arc) was part of a continental fragment that drifted in advance of Australia/New Guinea (called Banda Allochthon) and Timor (Outer Banda Arc) part of the Australian/New Guinean plate (Audley-Charles, 1987).

The isthmus of Kra, one of the floristic borders of the Malesian area (Van Steenis, 1950), is confirmed by the areagram of *Guioa* (resp. Sunda Shelf and S Thailand: areas 5 and 7) and by the generalized areagram of Schuh & Stonedahl (1986).

Conclusion: although some of the historical distribution patterns contradict each other, all more or less indicate the same areas as areas of endemism.

12.7. THE BIOGEOGRAPHY COMPILED

The former chapters contained a historical biogeographic analysis of different areas. In this section the various areagrams will be assembled into a general areagram. The resulting areagram will be checked against others (Roos, 1985; Schuh & Stonedahl, 1986).

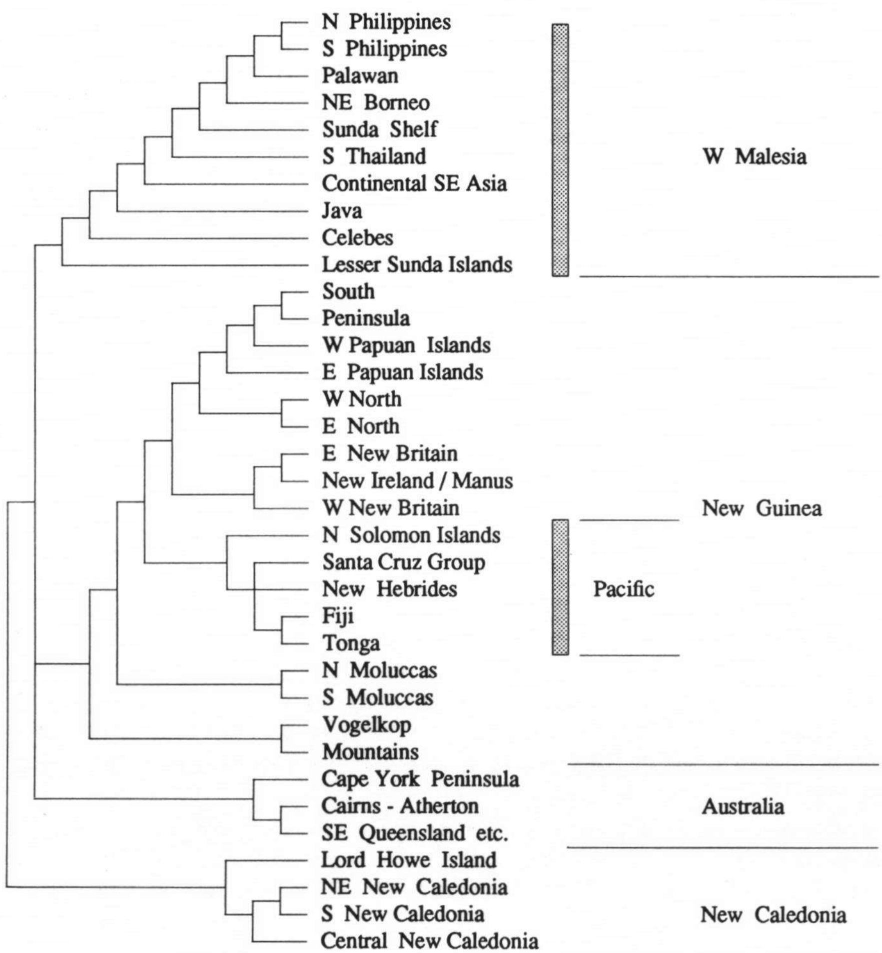


Fig. 55. A compilation of the different generalized areagrams based on the distribution and phylogenetic data of *Guioa*. ▩ = pattern produced by dispersal of *Guioa* species.

Figure 55 shows the resulting areagram. West Malesia and Australia form a trichotomy with New Guinea because New Guinea was the outgroup area for West Malesia and an ingroup area for Australia. New Caledonia together with Lord Howe I. form the outgroup area of the complete distribution. The Pacific areas are added to the N Solomon Islands.

The patterns in two parts of the areagram are the result of dispersal events rather than of vicariance events (marked with a grey bar in fig. 55). Other groups will quite likely show different patterns for West Malesia and for the Pacific. This was already discussed in the chapters 12.3 and 12.6.

The data of Roos (1985) were reinterpreted and analysed under assumption 0 with CAFCA (option: minimal steps). Figure 56a shows the resulting generalized areagram for the fern genera *Drynaria* and *Aglaomorpha*. In comparison with *Guioa* especially the data for West Malesia, New Guinea, and Australia are important as *Guioa* is mainly absent in the Southeast Asian mainland and in Africa. Australia serves as the sistergroup of West Malesia and New Guinea; the same applies more or less to *Guioa*. The position of New Guinea (Hovenkamp, 1986, had a comparable result) is very different in comparison with the position of this island in the *Guioa* analysis, a result quite likely to have been caused by climatic differences. The areagram for the two fern genera is probably the outcome of several dispersal events as the sequence of the areas is often peculiar.

The generalized areagram of Schuh & Stonedahl (1986) (fig. 56b) is for the greater part in accordance with the *Guioa* areagram, but then 180° reversed. The differences are small: In the *Guioa* areagram the Solomon Islands are the sister area, together with the other Pacific areas, of New Guinea and not the sister area of the Bismarck Archipelago (New Britain and New Ireland) as in the Schuh & Stonedahl

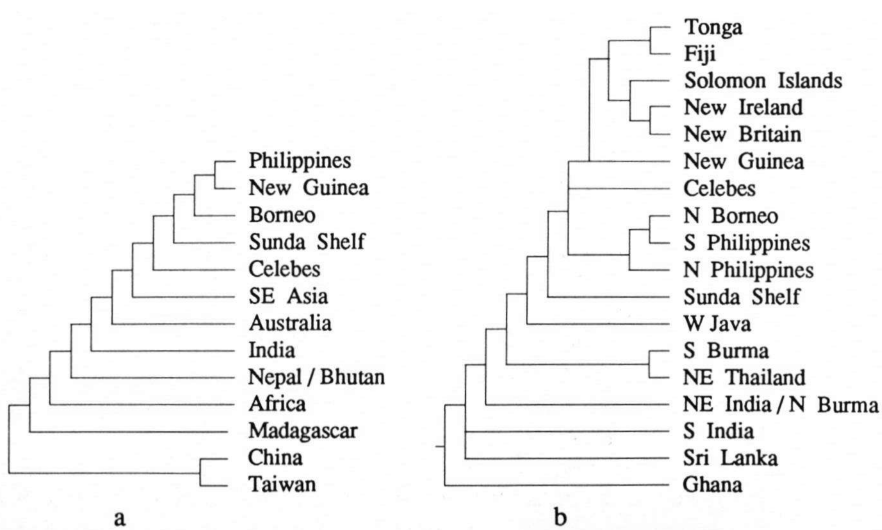


Fig. 56. a. Generalized areagram for the fern genera *Drynaria* and *Aglaomorpha* (data after Roos, 1985). b. Generalized areagram for plant bugs and cicadas (Schuh & Stonedahl, 1986).

areagram (which was partly based on the cicada data of Duffels, 1986). N Borneo features in the *Guioa* areagram as sister area of the Philippines and not as sister area of the S Philippines. The Schuh & Stonedahl areagram quite likely also displays dispersal events, but then from Southeast Asia towards Australia, the opposite of *Guioa.*

In conclusion the areagram for *Guioa* compares not only with the one produced by Schuh & Stonedahl (1986), but also per analysed area with the areagrams for several different groups of animals and plants. The historical biogeographic analysis corroborates the cladogram of *Guioa* (chapter 11.13).

The history of the genus *Guioa* can be shortly summarized (without putting any date tabs to different occurrences): The ancestral species of *Guioa* occurred probably in (a part of) New Guinea, Australia and New Caledonia, perhaps already when these areas were still part of Gondwana, but not necessarily so. The Inner Melanesian Arc (New Zealand, New Caledonia, and part of New Guinea) was probably still intact. Due to the many major disturbances in New Guinea a high degree of speciation and endemism could be achieved on this island, some of it probably quite recent. When the New Guinean/Australian plate collided with the Pacific plate the island arcs of the Pacific could be invaded, a process which was accompanied by speciation. The same happened in West Malesia; as soon as the New Guinean/Australian plate contacted the island ranges dispersal commenced, and again this was accompanied by speciation. It might also have occurred that the ancestral species of the West Malesian species already rifted northwards with the early Australian fragments which later constituted Southeast Asia and the Sunda Shelf. Due to the glacial periods several species became sympatric and widespread over the Sunda Shelf.

Two critical remarks remain to be made. One concerns the way in which areas are compared with each other, the other addresses the problems of species (character) optimization in areagrams.

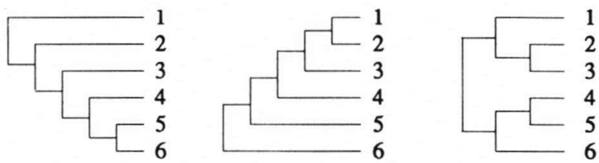
The relations among taxa are normally unique (hybridization excepted). However, the relations among areas can be several dependent on the taxa which are compared with each other (see also Cracraft, 1988). The example in figure 57 shows three taxa, all consisting of 6 species, spread over 6 areas: species 1 in area 1, 2 in 2, etc. (fig. 57a). Taxon A dispersed from area 1 to area 6 (fig. 57b), taxon B from area 6 to 1 (fig. 57c), and taxon C showed five instances of vicariance (fig. 57d). When these three taxa are compared with each other 5 generalized areagrams are the result (fig. 57e; steps: 32, consistency index: 0.938, CAFCA option: minimal steps). Of these the redundancy indices are resp. 0.466, 0.471, 0.471, 0.486, and 0.486. Based on the redundancy index the last two generalized areagrams (opposite to each other) should be selected as the best, a rather unsatisfactory result.

Five examples which compare with the above theoretical example will be shown in this paragraph: 1) The *Guioa* areagram and the Schuh & Stonedahl (1986) areagram show the same result as the two generalized areagrams at the right-hand side of figure 57e. 2) Cracraft (1986) compared several genera of Australian birds. These genera could be divided into two groups, each with its own areagram. Both areagrams had two areas (E Coast Forests and Cairns/Atherton) in common. Wiley (1988b) combined all genera and PAUP produced as many trees as was computationally possible, no tree could be chosen. 3) The position of New Guinea in the generalized areagram of Schuh & Stonedahl (1986, their fig. 12) is equivocal; one time it is included in the Oriental area, the other time in the Australian area. 4) Humphries & Parenti (1986, their figs. 4.8 and 4.9) found two connections for South America: with North America and Europe and with Australia/New Guinea. 5) Cracraft (1988) shows a nice study of two conflicting patterns in four geographical areas of South America.

In conclusion: Only those taxa should be compared with each other which a) greatly overlap in distribution, b) do not show dispersal patterns primarily, and c) originated in the same period. The latter is impossible to know in advance, but it is the cause of, for instance, the conflict in patterns in Cracraft's 1988 study: the patterns originated in different geological times.

areas species	1	2	3	4	5	6
1	1	0	0	0	0	0
2	0	1	0	0	0	0
3	0	0	1	0	0	0
4	0	0	0	1	0	0
5	0	0	0	0	1	0
6	0	0	0	0	0	1

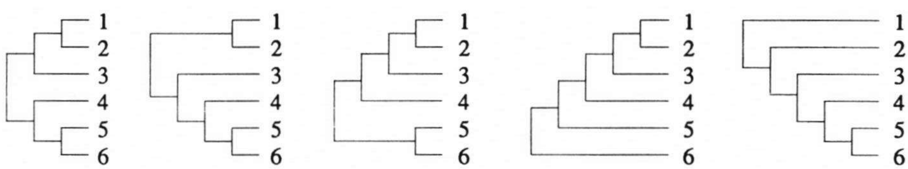
a. Equal distribution of the taxa A, B, and C over 6 areas.



b. Areagram and cladogram for taxon A.

c. Areagram and cladogram for taxon B.

d. Areagram and cladogram for taxon C.



e. Resultant generalized areagrams when taxon A, B, and C are compared with each other.

Fig. 57. Formation of a generalized areagram by comparing three hypothetical taxa, which each contain 6 species, and which are each distributed over one area.

Quite often a situation as in figure 58a is encountered in the areagrams. Here species 8 (*Guioa rigidiuscula* of New Guinea) shows two parallel events and one reversal. Normally a parallel has to be considered as an extinction or as no response to a speciation moment. However, the W Papuan Islands, the Peninsula, and the E North form a continuous distribution area. Probably *Guioa rigidiuscula* diffused over these three areas, and was primitively absent in the E Papuan Islands, the W North, and the South as these three areas are marginal to the other three in which *Guioa rigidiuscula* is found. Consequently, the parallel event and the reversal in figure 58a have to be translated into one vicariance event by ignoring the three areas in this figure as is done in figure 58b. The same applies of course to the ancestral species of *Guioa* *rigidiuscula*. This type of optimization cannot be shown in the areagrams (see for instance the areagrams of New Guinea), but should be taken into account when the distributions of the speciations are interpreted. Wiley (1988b) already pointed at the existence of difficulties in the optimization of the taxa distributions. Work in this field, especially automatization, is still badly needed.

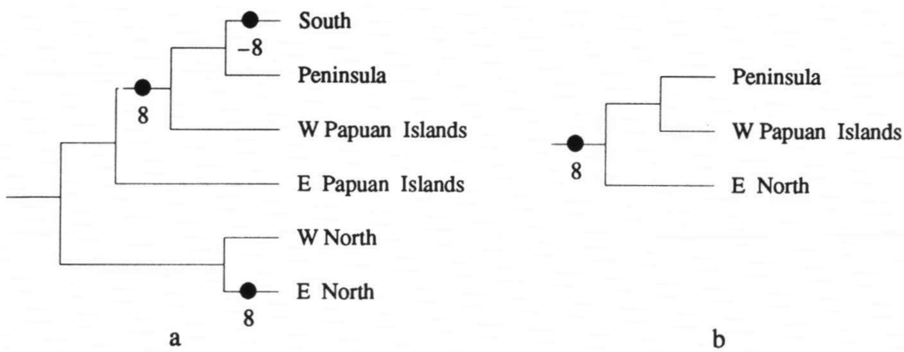


Fig. 58. Optimization of the distribution of species 8 (*Guioa rigidiuscula*) in New Guinea from two parallel events and one reversal (a) to one vicariance event (b) by ignoring the areas in which the species is primitively absent.

Conclusions:

1. CAFCA provides the best computer method for biogeographic analyses because only area components are discriminated in which taxa are present. No components are recognized on the basis of absence of taxa as the computer programs PAUP and HENNIG86 do.
2. Parsimony methods (Wiley 1988a, b; Zandee & Roos, 1987) are to be preferred above consensus methods (Nelson & Platnick, 1981; Humphries & Parenti, 1986) as they are straightforward, usually more parsimonious (a consensus tree will never be more parsimonious), and accommodate all areas.
3. Assumption 0 is to be preferred above assumption 1 and 2 as the latter two assume the existence of false distributions and allow for the creation of many trees, of which the intersection leads to the consensus tree to be accepted. The status of the consensus tree as the correct interpretation of the sequence in geological events is doubtful, because it is based on the assumption of false distributions.
4. If the historic biogeography also serves as a test of the cladograms, then the geographical analyses have to be accomplished under assumption 0. The other assumptions allow for many different cladograms with different topologies, consequently the original tree can never be tested.
5. Optimization of the species distributions in an areagram is difficult due to extinction, dispersal, primitive absence, lack of notable speciation, and sampling errors.
6. The results with *Guioa* indicate that mainly the more recent geological/climatological events have led to vicariance patterns or dispersal.

13. INFRAGENERIC CLASSIFICATION OF GUIOA

The infrageneric classification of *Guioa* serves two purposes: a) It is fully consistent with the cladogram (fig. 46a). Therefore, the classification can be considered as natural. b) The groups within the cladogram can be referred to with a name, which makes them more useful for general purposes. The criterium of recognizability of groups is not used, as it makes the groups more uninformative, see next chapter.

The already existing classification of Radlkofer (1933) is not supported and has consequently been dismissed. Radlkofer subdivided the genus into three sections: *Euguioa* (sepals dimorphic, disc complete), *Hemigyrosa* (sepals dimorphic, disc incomplete), and *Dysguioa* (sepals equal, disc complete or incomplete). Section *Dysguioa* contained one non-*Guioa* and three New Caledonian species, two of which, *Guioa crenata* and *Guioa crenulata*, are related to *Guioa villosa*, and the other, *Guioa microsepala*, to all other New Caledonian species. Radlkofer was already aware that the disc character did not provide a 100% reliable criterium to separate the sections *Euguioa* and *Hemigyrosa*. *Guioa diplopetala* in section *Euguioa* sometimes shows an incomplete disc, while *Guioa aryterifolia* in section *Hemigyrosa* has a complete disc. Historically, the division of Radlkofer is also biogeographically not supported as every area contains species of the sections *Euguioa* and *Hemigyrosa*. The cladogram (fig. 46a) shows that all three sections are polyphyletic and the classification of Radlkofer is therefore substituted by a new one.

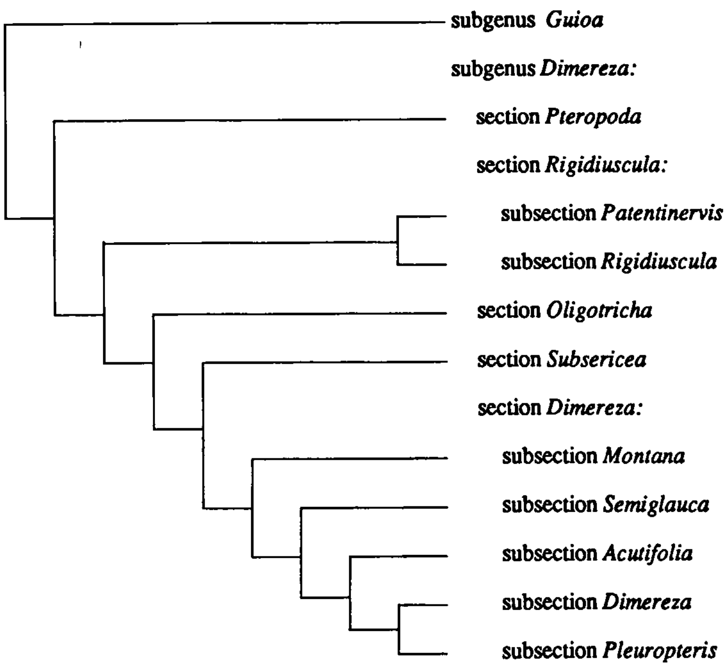


Fig. 59. Infrageneric classification of the genus *Guioa* in a cladistic perspective.

The present classification does not completely reflect the cladogram as not all nodes are recognized as taxa. There are two reasons for this decision: a) not all taxa were included in the cladogram, and b) an inflation of ranks did not seem desirable. The number of ranks was also reduced by the application of convention 3 of Wiley (1981a, chapter 6), the sequence rule: the sequence in which taxa of an equal rank are treated reflects their hierarchical relationship, the first is always the sister group of the others, then the second of the remaining groups, etc. Figure 59 displays the hierarchical groups with their rank in a cladogram.

The infrageneric groups can be keyed out as follows:

1a. Cotyledons dorsoventrally above each other (fig. 14a) 2
b. Cotyledons laterally besides each other (fig. 14b) 7

2a. Fifth petal (between two adnate large sepals) usually smaller than others. Leaflets below smooth or papillate. Fruit stiped or not 3
b. Fifth petal as large as the others. Leaflets papillate below. Fruit stiped **Guioa subgenus Guioa**

3a. Leaflets entire or with a few subapical teeth (fig. 4a, d). If leaves 1-jugate then leaflets large (more than 10 cm long) 4
b. Leaflets usually (partly) crenate (fig. 4b), if entire then leaves all 1-jugate, leaflets small (less than 7.5 cm long) . . . . **Guioa section Pteropoda**

4a. Scales mainly free from petal margin (fig. 9a–c). Leaflets below smooth or papillate 5
b. Scales folded petal margins (fig. 9d). Leaflets below papillate **Guioa section Subsericea**

5a. Petal claw short, scales reduced in length, crest absent (fig. 106b) 6
b. Petal claw normally developed, scales long, crest well-developed (fig. 99b); if crest absent and scales short then claw long (fig. 126b) **Guioa subsection Rigidiuscula**

6a. Leaves 1–3-jugate, not winged (fig. 1a). Cuticle of leaflets adaxially without thin areas in loops of undulations of anticlinal walls **Guioa section Oligotricha**
b. Leaves 2–9-jugate, usually (slightly) winged (fig. 1b, c). Cuticle of leaflets adaxially usually with thin areas in loops of undulations of anticlinal walls **Guioa subsection Patentinervis**

7a. Fruit stiped or not. Petal claw short (fig. 9c); crest glabrous, absent or clavate (fig. 10a, e–g) 8
b. Fruit stiped. Petal claw usually high (fig. 9b) except for *Guioa asquamosa* with no claw and almost no scales (fig. 8c); crest (sub)pilose, usually part of a bifid scale apex (fig. 10c), if absent then apex of scales broad (fig. 9a) **Guioa subsection Pleuropteris**

8a. Leaflets papillate below, margin entire. Fruit almost without a stipe or with a broadly cuneate stipe. Sepals inside glabrous 9
b. Leaflets smooth or papillate below, margin entire or (partly) crenate. Fruit with a slender or a broadly cuneate stipe. Sepals inside glabrous or pilose
Guioa subsection Dimereza

9a. Petals small (figs. 62b, 122b), crest normally absent. Disc complete 10
b. Petals normally developed (figs. 87b, 96b), crest clavate. Disc incomplete, either with a small slit or with a gap.......... **Guioa subsection Montana**

10a. Leaflets subglabrous below, at least some with one domatium
Guioa subsection Acutifolia
b. Leaflets shortly sericeous below, without a domatium
Guioa subsection Semiglauca

The remaining part of this chapter contains the official descriptions and typification of the infrageneric taxa as prescribed by the International Code of Botanical Nomenclature and an enumeration of the species per taxon.

Guioa subgenus Guioa

Guioa Cav., Icon. 4 (1798) 49, t. 373. — *Guioa* sect. *Euguioa* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8 (1878) 274, nom. illeg. (I.C.B.N. Art. 22.1). — Type: *Guioa lentiscifolia* Cav.

Petals: crest glabrous when present; fifth petal not or slightly reduced. *Cotyledons* dorsoventrally above each other.

Species in this subgenus: *Guioa chrysea, Guioa elliptica, Guioa lentiscifolia, Guioa megacarpa, Guioa novoëbudaënsis, Guioa punctata, Guioa rhoifolia,* and *Guioa sufusana.*

Endemics of island arcs in the Pacific.

Guioa subgenus Dimereza (Labill.) Welzen, *comb. nov., stat. nov.*

Dimereza Labill., Sert. Austr. Caled. (1825) 51, t. 51. — Type: *Guioa glauca* (Labill.) Radlk.

Petals: crest glabrous or pilose when present; fifth petal reduced. *Cotyledons* dorsoventrally above each other or secondarily laterally besides each other.

Species in this subgenus: All species mentioned below.

Guioa section Pteropoda Welzen, *sectio nov.*

Foliolis margine (pro parte) crenato infra laevibus glabris, squamis petali solite evolutis, crista glabra vel pilosa, cotyledonibus dorsoventraliter super se positis. — Typus: *Guioa pteropoda* Radlk.

Leaflets: margin (partly) crenate; below smooth, glabrous. *Petals:* scales normally developed; crest glabrous or pilose. *Cotyledons* dorsoventrally above each other.

Species in this section: *Guioa pseudoamabilis* and *Guioa pteropoda. Guioa amabilis* and *Guioa pauciflora* are tentatively placed in this section.

Endemics of New Guinea.

Guioa section **Rigidiuscula** Welzen, *sectio nov.*

Foliolis margine integro vel interdum (pro parte) serrato, infra aut laevibus plerumque glabris aut papillatis (sub)pilosis, squamis petali solite evolutis, crista plerumque bene evoluta glabra, cotyledonibus dorsoventraliter super se positis. — T y p u s: *Guioa rigidiuscula* Radlk.

Leaflets: margin entire or sometimes (partly) serrate; below either smooth and usually glabrous or papillate and (sub)pilose. *Petals:* scales normally developed; crest usually well-developed, glabrous. *Cotyledons* dorsoventrally above each other.

Species in this section: see under the two subsections.

Guioa subsection **Patentinervis** Welzen, *subsectio nov.*

Petalis sine crista, breviter unguiculatis. — T y p u s: *Guioa patentinervis* Radlk.

Petals: crest absent, claw short.

Species in this subsection: *Guioa melanopoda* and *Guioa patentinervis*. *Guioa venusta* and *Guioa waigeoensis* are tentatively placed in this subsection.

Endemics of New Guinea except *Guioa patentinervis*, which is an endemic of the S Moluccas.

Guioa subsection **Rigidiuscula** Welzen, *subsectio nov.*

Petalis crista bene evoluta spathulata vel longe unguiculatis. — T y p u s: *Guioa rigidiuscula* Radlk.

Petals: crest well-developed, spathulate or claw long.

Species in this subsection: *Guioa aryterifolia, Guioa comesperma, Guioa contracta, Guioa grandifoliola, Guioa hospita, Guioa membranifolia, Guioa misimaensis, Guioa molliuscula, Guioa normanbiensis, Guioa novobritannica, Guioa plurinervis, Guioa rigidiuscula, Guioa scalariformis,* and *Guioa unguiculata.*

Endemics of New Guinea except for *Guioa membranifolia* which is also found in the N Moluccas, and *Guioa comesperma* which also occurs in N Australia.

Guioa section **Oligotricha** Welzen, *sectio nov.*

Foliolis margine integro vel dentibus paucis subapicalibus, infra interdum papillosis pilosis, squamis petali brevibus, crista deest, cotyledonibus dorsoventraliter super se positis. — T y p u s: *Guioa oligotricha* Merr. & Perry.

Leaflets: margin entire or with a few subapical teeth; below sometimes papillate, pilose. *Petals:* scales short; crest absent. *Cotyledons* dorsoventrally above each other.

Species in this section: *Guioa oligotricha.*

Endemic of New Guinea.

Guioa section Subsericea Welzen, *sectio nov.*

Foliolis margine integro, infra papillatis pilosis, squamis petali e marginibus involutis ortis, crista plerumque deest clavata ubi adest, cotyledonibus dorsoventraliter super se positis. — T y p u s: *Guioa subsericea* Radlk.

Leaflets: margin entire; below papillate, pilose. *Petals:* scales folded margins of petal; crest normally absent otherwise clavate. *Cotyledons* dorsoventrally above each other.

Species in this section: *Guioa subsericea*. *Guioa malukuensis* is tentatively placed in this section.

Guioa subsericea is an endemic of New Guinea, *Guioa malukuensis* of the Moluccas.

Guioa section Dimereza (Labill.) Welzen, *comb. nov.*

Dimereza Labill., Sert. Austr. Caled. (1825) 51, t. 51. — *Cupania* sect. *Dimereza* G. Don, Gen. Hist. 1 (1831) 668. — T y p e: *Guioa glauca* (Labill.) Radlk.

Leaflets: margin usually entire, sometimes crenate; below either smooth and (sub-) glabrous or papillate and pilose. *Petals:* scales usually well-developed; crest glabrous or pilose. *Cotyledons* secondarily laterally besides each other.

Species in this section: see under the subsections.

Guioa subsection Montana Welzen, *subsectio nov.*

Foliolis infra papillatis pilosis, nervis distinctis, squamis petali longitudine diminutis, crista glabra bene evoluta clavata. — T y p u s: *Guioa montana* C.T. White.

Leaflets below papillate, pilose; veins distinct. *Petals:* scales reduced in length; crest glabrous, well-developed, clavate.

Species in this subsection: *Guioa lasioneura* and *Guioa montana*.

Endemics of Australia.

Guioa subsection Semiglauca Welzen, *subsectio nov.*

Foliolis infra papillatis pilosis, nervis indistinctis, squamis petali longitudine diminutis, crista glabra ubi adest. — T y p u s: *Guioa semiglauca* (F. Muell.) Radlk.

Leaflets below papillate, pilose; veins indistinct. *Petals:* scales reduced in length; crest glabrous when present.

Species in this subsection: *Guioa semiglauca*.

An endemic of Australia.

Guioa subsection Acutifolia Welzen, *subsectio nov.*

Foliolis infra papillatis subglabris, nervis indistinctis, squamis petali longitudine diminutis, crista glabra ubi adest. — T y p u s: *Guioa acutifolia* Radlk.

Leaflets below papillate, subglabrous; veins indistinct. *Petals:* scales reduced in length; crest glabrous when present.

Species in this subsection: *Guioa acutifolia.*

An endemic of Australia.

Guioa subsection **Dimereza** (Labill.) Welzen, *comb. nov.*

Dimereza Labill., Sert. Austr. Caled. (1825) 51, t. 51. — T y p e: *Guioa glauca* (Labill.) Radlk.
Guioa sect. *Dysguioa* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 615; in Engl., Pflanzenr. 98 (1933) 1174. — L e c t o t y p e (here proposed): *Guioa microsepala* Radlk.

Leaflets below either smooth and (sub)glabrous or papillate and pilose; veins distinct or indistinct. *Petals:* scales normally developed; crest glabrous, usually well-developed, clavate.

Species in this subsection: *Guioa coriacea, Guioa crenata, Guioa crenulata, Guioa fusca, Guioa glauca, Guioa gracilis, Guioa microsepala, Guioa ovalis, Guioa pectinata,* and *Guioa villosa.*

Endemics of New Caledonia except for *Guioa coriacea* which is an endemic of Lord Howe I.

Guioa subsection **Pleuropteris** (Blume) Welzen, *comb. nov.*

Cupania sect. *Pleuropteris* Blume, Rumphia 3 (1847) 158. — L e c t o t y p e (here proposed): *Cupania pleuropteris* Blume [= *Guioa pleuropteris* (Blume) Radlk.].
Hemigyrosa Blume, Rumphia 3 (1847) 165. — *Guioa* sect. *Hemigyrosa* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8 (1878) 274; in Engl., Pflanzenr. 98 (1933) 1164. — T y p e: *Hemigyrosa perrottetii* Blume [= *Guioa koelreuteria* (Blanco) Merr.].

Leaflets below either smooth and (sub)glabrous or papillate and pilose; veins distinct or indistinct. *Petals:* scales normally developed; crest pilose when present, either part of the bifid scale apex or somewhat clavate.

Species in this subsection: *Guioa acuminata, Guioa asquamosa, Guioa bijuga, Guioa diplopetala, Guioa discolor, Guioa hirsuta, Guioa koelreuteria, Guioa myriadenia, Guioa pleuropteris, Guioa pterorhachis, Guioa pubescens,* and *Guioa reticulata. Guioa bicolor, Guioa palawanica, Guioa parvifoliola,* and *Guioa truncata* are tentatively placed in this subsection.

Endemics or widespread species in West Malesia.

14. THE CLASSICAL CLASSIFICATION

This chapter will be controversial, but it is necessary to write this part as the debate between the classical school and the phylogenetical school continues. (For a comparison of the different systematic schools see Geesink, 1984; Janvier, 1984; Wiley 1981b, 1987a.) Normally, this debate only uses theoretical arguments, and from the 'classical' side quite often false ones, as the phylogenetic school is usually misunderstood (Nooteboom, 1988; Prance & White, 1988). The approach in this chapter will be different; the consequences of both schools will be demonstrated with the aid of a case study: the present revision of *Guioa*. A phylogenetic analysis has already been shown (chapter 11.13). A classical classification of *Guioa* will first be presented. It is presumed that the classical classification has to be considered as natural, i.e., that it has a phylogenetic inclination. Likewise, the phylogenetic information content of it will be discussed in relation to that of the phylogenetic classification. Finally, the consequences for the historical biogeography will be shown.

A classical classification may follow Radlkofer's classification (1933), but probably this classification will be rejected for almost the same reasons as used in the former chapter. Let us suppose that the same characters as for the cladistic analysis were used to separate *Guioa* into several groups: the crest pilosity, the position of the cotyledons, and the reduction of the fifth petal. The following groups will probably be formed:

— The West Malesian group: crest pilose, cotyledons secondarily laterally besides each other, fifth petal reduced.
— The Australian/New Caledonian group: crest glabrous, cotyledons secondarily laterally besides each other, fifth petal reduced.
— The New Guinean group: crest usually glabrous, cotyledons dorsoventrally above each other, fifth petal reduced.
— The Pacific group: crest glabrous, cotyledons dorsoventrally above each other, fifth petal not reduced.

Of these groups, the Pacific group will probably be regarded as a primitive (rest)-group as it is defined in a negative way, it will therefore be suspect of being paraphyletic (while it is monophyletic). The remaining groups will be considered as monophyletic, but in fact only the West Malesian group is monophyletic, the other two are paraphyletic. It is also possible that these four groups were not recognized as the classic dilemma exists: two characters with two character states each show all four possible combinations:

Cotyledons dorsoventrally,	crest not pilose:	Pacific group
Cotyledons dorsoventrally,	crest pilose:	*Guioa pteropoda* *Guioa unguiculata*
Cotyledons laterally,	crest not pilose:	Australian and New Caledonian group
Cotyledons laterally,	crest pilose:	West Malesian group

Consequently, one of the characters must show a homoplasy, for the above classification 'crest pilosity' has to show a parallelism. Prance & White (1988) used the existence of these incompatible characters as one of the arguments to abolish a cladistic analysis (see Geesink, 1984, for an explanation of character compatibility).

Guioa pteropoda and *Guioa coriacea* will form a separate subgroup each as they differ much from all other *Guioa* species (they possess many autapomorphies): *Guioa pteropoda:* 4 petals, filaments only basally pilose, sharply edged fruit, incomplete dissepiments; *Guioa coriacea:* scales are folded petal margins, the shape of the crest is unique, the palisade parenchyma contains 3 or 4 layers.

Quite likely the *Guioa rigidiuscula*-complex will be recognized as a separate group based on the type of petal, perhaps even subordinate to the New Guinea group, which will then be split into the *Guioa rigidiuscula* group and a restgroup of all other New Guinean species.

The following classical classification seems likely:

Guioa	section *Guioa* (Pacific group)	
	section *New Guinea*	subsection *Rigidiuscula*
		subsection *Pteropoda*
		subsection *''Rest'*
	section *Australia/New Caledonia*	subsection *Coriacea*
		subsection *'Rest'*
	section *West Malesia*	

The rest group of Australia/New Caledonia will quite likely be split into four groups: The Australian species with papillae and rather reduced petals or reduced petal scales and crests, the papillate New Caledonian species, *Guioa microsepala* (different sepals), and the remaining non-papillate New Caledonian species. Except for the Australian species all other groups are monophyletic.

When the classification above is translated into a cladogram, the differences with the phylogenetic school become apparent: compare figure 59 with figure 60. The information content of the classical tree is much less: in total the cladogram is poorly resolved. The distinction of the two basal monophyletic groups (the subgenera of fig. 60) has vanished, just like the subordination of the sections and subsections. This is because the classical school has no arguments with which they can distinguish a sequence in the splitting events. Some sections or subsections are paraphyletic (subsection *'Rest'*, subsection *Australia*, section *New Guinea* and section *Australia/New Caledonia*), the rest is monophyletic. The position of *Guioa pteropoda* and of *Guioa coriacea* in relation to the other species of their section cannot be resolved.

In the classical sense the above distinguished groups are all monophyletic (e.g., Prance & White, 1988: a group is monophyletic when the taxa are all derived from one ancestor; in a cladistic sense a group is monophyletic when not only all taxa have a common ancestral species, but all the descendants have to be included in the group as well). The consequences of accepting paraphyletic groups as 'real' groups become apparent when one starts to use these groups as terminal taxa in a phylogenetic analysis. Paraphyletic groups (classes) are defined at least by some symplesiomorphous characters, which are then considered to constitute apomorphies. As a result, the symplesiomorphous character also has to be regarded as an apomorphy for the other groups with this same character: homoplasy has to be assumed. The resultant will be a cladogram with many steps and a high amount of homoplasy. However, when the number of steps increases the chances that equally parsimonious trees exist increase too, and this is what normally happens, quite often exponentially so (e.g. Geesink, 1984). Then the phylogenetic analysis normally fails. This phenomenon (probably) plagued Geesink (1984; see also Zandee & Geesink, 1987; Geesink & Kornet, 1989), Kalkman (1988), and Prance & White (1988).

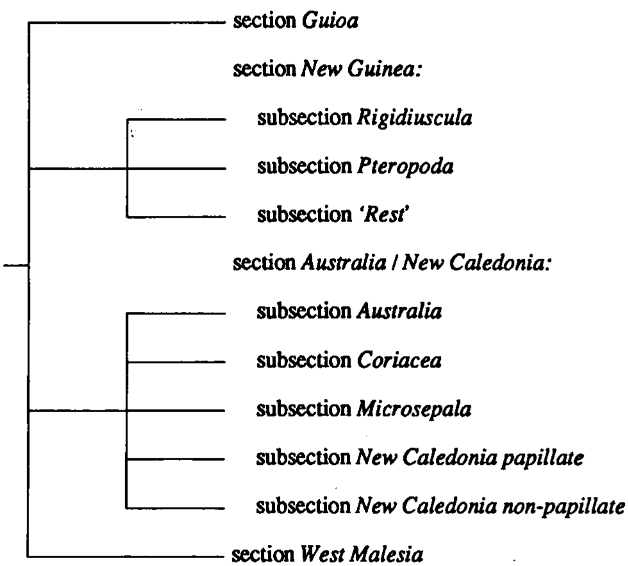


Fig. 60. Inferred cladogram from a supposed classical classification of the genus *Guioa*.

When terminal superspecific taxa are used in a phylogenetic analysis after they are first defined with the aid of phenetic techniques, a method advocated by Von Vaupel Klein (1987), then they are quite likely to be paraphyletic (or polyphyletic). This is caused by the incompatibility between the phenetic and phylogenetic methods, as their domains differ. The phenetic method bases the distinction of taxa on all available characters, the phylogenetic method only on derived characters. The phenetic method also uses plesiomorphic characters to define groups, quite often these characters are very conspicuous and handy to characterize a group with, as they often outnumber the available apomorphies. However, when plesiomorphic characters are used to characterize taxa, paraphyletic groups are usually the result; famous examples are the bone-fishes, amphibians (including Devonian fossil groups), and reptiles. The genera of Chrysobalanaceae as distinguished by Prance & White (1988) were all confirmed (with difficulty) by phenetic analyses, so some of the genera have to be paraphyletic and consequently the phylogenetic analysis had to fail.

Due to the lack of information and the amount of incorrect information in the classical system a historical biogeographical analysis cannot be performed. For instance, as the subordination of the classical groups is absent it cannot be inferred whether or not the ancestors of *Guioa* occurred in Southeast Asia or in Australia. The same applies to New Caledonia and Australia; one cannot tell whether Australia split off from New Caledonia plus other areas or New Caledonia from Australia plus other areas (or the taxa distributed from Australia to New Caledonia or the other way round). An analysis of the areas of endemism in New Guinea and in Australia will be useless due to the lack of resolution of the classical 'cladogram'.

Classifications based on a cladistic analysis are sometimes considered to destabilize the nomenclature. It is true that after a cladistic classification has been applied, names had to be changed and the number of ranks had to increase, but this is a one time occurrence only. When the branches of a cladogram show much support (many apomorphies) or when the cladogram is backed/tested by a historical biogeographic analysis it is quite likely that the nomenclature, based on a cladistic classification, will not change considerably when new facts become known. An example of the latter is the present study. An example of the first is the classification of the *Fumaria* group of the Papaveraceae (Lidén, 1986), and judging by the synonyms of the different taxa the previous classical classification has never been stable.

After finishing this chapter the reader may draw the conclusion that the cladistic method is superior to the classical method. This conclusion is of course partly caused by my bias for the cladistic method, but only partly so. Systematic, monographic work can favour immensely from the cladistic method, not only because the theoretical component is well-founded, but also because the information content of the results is much higher. Unfortunately, practical implementation of the method is still difficult, although user-friendly computer programs help considerably. However, the choices of characters, character states, and outgroups will remain difficult.

In fact, the cladistic method just goes one step further than the classical method; instead of using all characters to distinguish groups only apomorphic characters are used for the recognition of groupings. Probably there are two reasons why the switch from the classical to the phylogenetic method is not always made: 1) The bulk of theoretical papers is vast and often difficult to understand, while only a few readable summarizing papers are available. Most papers, like this one, only deal with certain aspects of the phylogenetic method. 2) Paraphyletic groups are often accepted by the classical school, because they are easy to characterize. The acceptance of species as really existing entities ('individuals') will change the view that paraphyletic groups are 'monophyletic'. Because then it logically follows that higher taxa have to comprise all descendants from an ancestral species. When a species is discussed all specimens are included, because they all constitute the species; likewise with higher taxa, a genus is only a historical, existing, natural group when all species are included.

15. REFERENCES

APPANAH, S. 1982. Pollination of androdioecious Xerospermum intermedium Radlk. (Sapindaceae) in a rain forest. Biol. J. Linn. Soc. 18: 11–34.

APPANAH, S., S.C. WILLEMSTEIN & A.G. MARSHALL. 1986. Pollen foraging by two Trigona colonies in a Malaysian rain forest. Malay. Nat. J. 39: 177–191.

AUDLEY-CHARLES, M.G. 1981. Geological history of the region of Wallace's line. In: T.C. Whitmore (ed.), Wallace's line and plate tectonics: 24–35. Oxford.

AUDLEY-CHARLES, M.G. 1987. Dispersal of Gondwanaland: relevance to evolution of angiosperms. In: T.C. Whitmore (ed.), Biogeographical evolution of the Malay Archipelago: 5–25. Oxford.

AXELIUS, B. 1987. The genus Lerchea (Rubiaceae). Blumea 32: 91–114.

BAKER, H.G. 1973. Evolutionary relationships between flowering plants and animals in American and African tropical forest. In: B.J. Meggers, E.S. Ayensu & W.D. Duckworth (eds.), Tropical forest ecosystems in Africa and South America: A comparative review: 149, 151. Washington.

BALGOOY, M.M.J. VAN. 1987. A plantgeographical analysis of Sulawesi. In: T.C. Whitmore (ed.), Biogeographical evolution of the Malay Archipelago: 94–102. Oxford.

BAWA, K.S. 1977. The reproductive biology of Cupania guatemalensis Radlk. (Sapindaceae). Evolution 31: 52–63.

BLUME, C.L. 1849. Rumphia 3: 158–160, 165, 166. Amsterdam.

BROOKS, D.R. 1981. Hennig's parasitological method: a proposed solution. Syst. Zool. 30: 229–249.

BROOKS, D.R. 1984. Quantitative parsimony. In: T. Duncan & T.F. Stuessy (eds.), Cladistics: perspectives on the reconstruction of evolutionary history: 119–132. New York.

BROOKS, D.R., & E.O. WILEY. 1985. Theories and methods in different approaches to phylogenetic systematics. Cladistics 1: 1–11.

BROOKS, D.R., & E.O. WILEY. 1988. Evolution as entropy, 2nd ed. New York.

BRYCE, D. 1986. Evolution and the new phylogeny. Llanerch.

CARPENTER, J.M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291–296.

CAVANILLES, A.I. 1798. Icones et descriptiones plantarum 4: 49, 50, tab. 373. Matriti.

CRACRAFT, J. 1983. Cladistic analysis and vicariance biogeography. Am. Scientist 71: 273–281.

CRACRAFT, J. 1986. Origin and evolution of continental biotas: speciation and historical congruence within the Australian avifauna. Evolution 40: 977–996.

CRACRAFT, J. 1988. Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. Syst. Zool. 37: 221–236.

DON, G. 1831. A general history of the dichlamydeous plants 1: 668. London.

DUFFELS, J.P. 1977. A revision of the genus Diceropyga Stål, 1870 (Homoptera, Cicadidae). Monogr. Ned. Entom. Ver. 8: 1–227.

DUFFELS, J.P. 1983a. Taxonomy, phylogeny and biogeography of the genus Cosmopsaltria, with remarks on the historic biogeograph of the subtribe Cosmopsaltriaria (Homoptera: Cicadidae). Pacif. Insects Monogr. 39: 1–127.

DUFFELS, J.P. 1983b. Distribution patterns of Oriental Cicadoidea (Homoptera) east of Wallace's line and plate tectonics. Geojournal 7: 491–498.

DUFFELS, J.P. 1986. Biogeography of Indo-Pacific Cicadoidea: a tentative recognition of areas of endemism. Cladistics 2: 381–336.

ELDREDGE, N. 1985. Time frames. New York.

ELDREDGE, N., & S.J. GOULD. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: T.J.M. Schopf, Models in Paleobiology: 82–115. San Francisco.

FAROOQUI, P. 1982. A peculiar mode of insertion of glandular hair in Sapindus laurifolia Vahl. Curr. Sc. 51: 789, 790.

FARRIS, J.S. 1979. A botanical clique. Syst. Zool. 28: 400–411.

FARRIS, J.S. 1988. Hennig86 reference, version 1.5. University of Stony Brook, New York.

FORD, E.B. 1971. Ecological genetics, 3rd ed. London.
FREE, J.B., & I.H. WILLIAMS. 1976. Insect pollination of Anacardium occidentale L., Mangifera indica L., Blighia sapida Koenig and Persae americana Mill. Trop. Agric. 53: 125–139.
GAN, Y.-Y. et al. 1977. Genetic variation in wild populations of rain-forest trees. Nature 269, no. 5626: 323, 324.
GEESINK, R. 1984. Scala Millettiearum. Leiden Bot. Series 8. Leiden.
GEESINK, R., & D.J. KORNET. 1989. Speciation and Malesian Leguminosae. In: L.B. Holm-Nielsen, I.C. Nielsen & H. Balslev, Tropical Forests: botanical dynamics, speciation and diversity: 135–151. London.
GHISELIN, M.T. 1974. A radical solution to the species problem. Syst. Zool. 23: 536–544.
GONDIM, C.J.E. 1984. Alguns aspectos da biologia reprodutiva do Guaranazeiro (Paullinia cupana var. sorbilis (Mart.) Ducke – Sapindaceae). Acta Amazonica 14: 9–38.
GOULD, J.L., & P. MARLER. 01-1987. Learning by instinct. Scient. Amer.: 62–73.
GREY-WILSON, C. 1980. Impatiens in Papuasia. Kew Bull. 34: 661–688.
HA, C.O. et al. 1988. Reproductive patterns of selected under-storey trees in the Malaysian rain forest: the sexual species. Bot. J. Linn. Soc. 97: 295–316.
HAM, R.W.J.M. VAN DER, & B.J. VAN HEUVEN. 1989. Evolutionary trends in the morphology and harmomegathy of the pollen of the genus Guioa (Sapindaceae-Cupanieae). Blumea 34: 21–60.
HAWKESWOOD, T.J. 1983. Pollination and fruit reproduction of Cupaniopsis anacardioides (A. Rich.) Radlkf. (Sapindaceae) at Townsville, North Queensland. 1. Pollination and floral biology. Vict. Nat. 100: 12–20.
HENNIPMAN, E. 1987. The relation between ontogeny and phylogeny as exemplified on ferns. In: P. Hovenkamp (ed.), Systematics and evolution: a matter of diversity: 141–157. Utrecht.
HESSE, M. 1979. Ultrastruktur und Verteilung des Pollenkitts in der insekten- und windblütigen Gattung Acer (Aceraceae). Pl. Sys. Evol. 131: 277–289.
HOLLOWAY, J.D. 1987. Lepidoptera patterns involving Sulawesi: what do they indicate of past geography? In: T.C. Whitmore (ed.), Biogeographical evolution of the Malay Archipelago: 103–118. Oxford.
HOVENKAMP, P. 1986. A monograph of the fern genus Pyrrosia. Leiden Bot. Series 9. Leiden.
HUMPHRIES, C.J., & L.R. PARENTI. 1986. Cladistic biogeography. Oxford.
JANVIER, P. 1984. Cladistics: Theory, purpose, and evolutionary implications. In: J.W. Pollard (ed.), Evolutionary theory: paths into the future: 39–75. New York.
JOHNS, R.J. 1986. The instability of the tropical ecosystem in New Guinea. Blumea 31: 341–371.
JONG, P.C. DE. 1976. Flowering and sex expression in Acer L. A biosystematic study. Belmontia 6: 1–201.
JONG, P.C. DE. 1983. Revision of the oriental genus Matapa Moore (Lepidoptera, Hesperiidae) with discussion of its phylogeny and geographic history. Zool. Meded. 57: 243–270.
JONG, P.C. DE. 1987. Biogeography – What's the question? In: P. Hovenkamp (ed.), Systematics and evolution: a matter of diversity: 251–262. Utrecht.
KALKMAN, C. 1988. The phylogeny of the Rosaceae. Bot. J. Linn. Soc. 98: 37–59.
KLUGE, A.G. 1985. Ontogeny and phylogenetic systematics. Cladistics 1: 13–27.
KOLLAR, E.J., & C. FISHER. 1980. Tooth induction in chick epithelium: expression of quiescent genes for enamel synthesis. Science 207, 29 Feb.: 993–995.
KORNET, D.J. 1988. Conventional and fundamental problems in the delimitation of genera from a phylogenetic point of view. Acta Bot. Neerl. 37: 527–529.
LABILLARDIÈRE, J.J.H. 1825. Sertum Austro-Caledonicum 1: 51, tab. 51. Paris.
LEENHOUTS, P.W. 1959. Revision of the Burseraceae of the Malaysian area in a wider sense. Xa: Canarium Stickm. Blumea 9: 275–475.
LEENHOUTS, P.W. 1978. A new species of Diploglottis (Sapindaceae) and its systematic position. Blumea 24: 173–179.
LEENHOUTS, P.W. 1988. Notes on some genera of Sapindaceae-Cupanieae. Blumea 33: 197–213.

LIDÉN, M. 1986. Synopsis of Fumarioideae (Papaveraceae) with a monograph of the tribe Fumarieae. Opera Bot. 88: 5–133.

LIN, A.L. 1984. The reproductive biology of Rambutan, Nephelium lappaceum L. (Sapindaceae). Gard. Bull. Sing. 37: 181–192.

MADDISON, W.P., M.J. DONOGHUE & D.R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

MARTINEZ DEL RIO, C., & L.E. EGUIARTE. 1987. The effect of nectar availability on the foraging behavior of the stingless bee Trigona testacea. S.W. Nat. 32: 313–319.

MERRILL, E.D., & L.M. PERRY. 1940. Plantae Papuanae Archboldianae IV. J. Arn. Arb. 21: 512–515.

METCALFE, C.R., & L. CHALK. 1950. Anatomy of the dicotyledons 1: 419–422. Oxford.

METCALFE, C.R., & L. CHALK. 1979. Anatomy of the dicotyledons 1; 2nd ed. Oxford.

MORLEY, R.J., & J.R. FLENLEY. 1987. Late Cainozoic vegetational and environmental changes in the Malay Archipelago. In: T.C. Whitmore (ed.), Biogeographical evolution of the Malay Archipelago: 50–59. Oxford.

MULLER, J., & P.W. LEENHOUTS. 1976. A general survey of pollen types of Sapindaceae in relation to taxonomy. In: I.K. Ferguson & J. Muller (eds.), The evolutionary significance of the exine. Linn. Soc. Symp. Ser. 1: 407–445.

MÜNTZING, A. 1930. Über Chromosomenvermehrung in Galeopsis-Kreuzungen und ihre phylogenetische Bedeutung. Hereditas 14: 154–172.

MUSTARD, M.J., S.-Y. LIU & R.O. NELSON. 1954. Observations of floral biology and fruit-setting in Lychee varieties. Proc. Florida Hort. Soc. 64: 212–220.

NAIR, N.C., & T. JOSEPH. 1960. Morphology and embryology of Cardiospermum halicacabum Linn. J. Ind. Bot. Soc. 39: 176–194.

NELSON, G. 1985. Outgroups and ontogeny. Cladistics 1: 29–45.

NELSON, G., & N.I. PLATNICK. 1981. Systematics and biogeography. Oxford.

NOOTEBOOM, H.P. 1988. What should botanists do with their time? Taxon 37: 134.

O'DOWD, D.J., & M.F. WILLSON. 1989. Leaf domatia and mites on Australasian plants: ecological and evolutionary implications. Biol. J. Linn. Soc. 37: 191–236.

PANNELL, C.M., & F. WHITE. 1988. Patterns of speciation in Africa, Madagascar, and the tropical far east: regional faunas and cryptic evolution in vertebrate-dispersed plants. Monogr. Syst. Bot. Missouri Bot. Gard. 25: 639–659.

PENNINGTON, T.D. 1969. Materials for a monograph of the Meliaceae I. A revision of the genus Vavaea. Blumea 17: 351–366.

PIJL, L. VAN DER. 1957. On the arilloids of Nephelium, Euphoria, Litchi and Aesculus, and the seeds of Sapindaceae in general. Acta Bot. Neerl. 6: 618–641.

PIJL, L. VAN DER. 1982. Principles of dispersal in higher plants: 35–38. Berlin.

PIMENTEL, R.A., & R. RIGGINS. 1987. The nature of cladistic taxa. Cladistics 3: 201–209.

PRANCE, G.T., & F. WHITE. 1988. The genera of Chrysobalanaceae: a study in practical and theoretical taxonomy and its relevance to evolutionary biology. Phil. Trans. R. Soc. London 320: 1–184.

PRIDDLE HOUTS, K., & G.R. HILLEBRAND. 1976. An electrophoretic and serological investigation of seed proteins in Galeopsis tetrahit L. (Labiatae) and its putative parental species. Amer. J. Bot. 63: 156–165.

RADLKOFER, L. 1879a. Ueber die Sapindaceen Holländisch-Indiens. Amsterdam.

RADLKOFER, L. 1879b. Ueber Cupania und damit verwandte Pflanzen. Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9: 457–678.

RADLKOFER, L. 1883. Ueber die Methoden in der botanischen Systematik, insbesondere die anatomische Methode. Festrede zur Vorfeier des Allerhöchsten Geburts- und Namensfestes Seiner Majestät des Königs Ludwig II: 1–64. München.

RADLKOFER, L. 1886. Ergänzungen zur Monographie der Sapindaceae-Gattung Serjania: 37–44. München.

RADLKOFER, L. 1933. Sapindaceae. In: A. Engler, Das Pflanzenreich 98: 1157–1177. Leipzig.
RAVEN, P.H., & D.I. AXELROD. 1972. Plate tectonics and Australasian paleobiogeography. Science 176: 1379–1386.
RÉNARD, A. LE. 1913. Rapports anatomiques du genre Arfeuillea. Ann. Sci. Nat. Bot. 9e ser, 17: 382.
REYNOLDS, S.T. 1984. Notes on Sapindaceae III. Austrobaileya 2: 36–39, fig. 2.
REYNOLDS, S.T. 1985. Sapindaceae. In: A.S. George, Flora of Australia 25: 47–50, fig. 11, map 56–60. Canberra.
ROOS, M.C. 1985. Phylogenetic systematics of the Drynarioideae (Polypodiaceae). Ph.D. thesis. Utrecht.
ROOS, M.C., E. HENNIPMAN & M. ZANDEE. Ontogenetic information in cladistic analysis. Msc.
SCHARLOO, W. 1987. Neo-Darwinism and transspecific evolution. In: P. Hovenkamp: Systematics and evolution: a matter of diversity: 207–217. Utrecht.
SCHUH, R.T., & G.M. STONEDAHL. 1986. Historical biogeography in the Indo-Pacific: a cladistic approach. Cladistics 2: 337–355.
SCHWENDENER, J. 1970. Experimente zur Evolution von Potentilla procumbens Sibth. Ber. Schweiz. Bot. Gesell. 79: 49–92, table I, II.
SOLEREDER, H. 1899. Systematische Anatomie der Dicotyledonen: 257–268. Stuttgart.
SOLEREDER, H. 1908. Systematische Anatomie der Dicotyledonen. Ergänzungsband: 104, 105. Stuttgart.
SPRENGEL, C. 1827. Systema vegetabilum 1: 150. Gottingae.
STANLEY, S.M. 1973. An ecological theory for the sudden origin of multicellular life in the late Precambrian. Proc. Nat. Acad. Sci. USA 70: 1486–1489.
STEENIS, C.G.G.J. VAN. 1950. The delimitation of Malaysia and its main plant geographical divisions. In: C.G.G.J. van Steenis (ed.), Flora Malesiana ser. I, 1: LXX–LXXV. Djakarta.
STEENIS, C.G.G.J. VAN. 1957. Specific and infraspecific delimitation. In: C.G.G.J. van Steenis (ed.), Flora Malesiana ser. I, 5: CLXVII–CCXXXIV. Djakarta.
STEENIS, C.G.G.J. VAN. 1962. The land-bridge theory in botany. Blumea 11: 235–542.
STEENIS, C.G.G.J. VAN. 1979. Plant-geography of East Malesia. Bot. J. Linn. Soc. 79: 97–178.
SUBBA REDDI, C. et al. 1983. Reproductive ecology of Sapindus emarginatus Vahl (Sapindaceae). Proc. Indian Natn. Sci. Acad. 49b: 57–72.
SWOFFORD, D.L. 1985. PAUP. Phylogenetic analysis using parsimony, version 2.4. Illinois Natural History Survey, Champaign, Illinois.
UJI, T. 1987. Penyerbukan pada Rambutan (Nephelium lappaceum L. var. lappaceum). Suppl. Ber. Biol. 3: 31–34.
VAUPEL KLEIN, J.C. VON. 1979. Phylogenetic analysis and its foundations. In: P. Hovenkamp (ed.), Systematics and evolution: a matter of diversity: 159–172. Utrecht.
VINK, W. 1970. The Winteraceae of the Old World. I. Pseudowintera and Drimys – Morphology and taxonomy. Blumea 18: 225–354.
VOGEL, E.F. DE. 1980. Seedlings of dicotyledons: 52–92. Wageningen.
VOGEL, E.F. DE. 1988. Revisions in Coelogyninae (Orchidaceae) III. The genus Pholidota. Orchid Mon. 3: 24.
WELZEN, P.C. VAN. 1988a. Key to the Malesian genera of Sapindaceae. Blumea 33: 215–237.
WELZEN, P.C. VAN. 1988b. Nineteen new species and a new combination in Guioa Cav. (Sapindaceae). Blumea 33: 411–421.
WELZEN, P.C. VAN, A. LAMB & W.W.W. WONG. 1988. Edible Sapindaceae in Sabah. Nat. Malays. 13 (1): 10–25.
WELZEN, P.C. VAN, & E.W.M. VERHEIJ. 1989. Nephelium lappaceum L. In: E. Westphal & P.C.M. Jansen (eds.), Plant resources of South-East Asia (P.R.O.S.E.A.). A selection: 196–200. Wageningen.
WHITMORE, T.C. (ed.). 1981. Wallace's line and plate tectonics. Oxford.
WILEY, E.O. 1981a. Phylogenetics. New York.

WILEY, E.O. 1981b. Convex groups and consistent classifications. Syst. Bot. 6: 346–358.
WILEY, E.O. 1987a. The evolutionary basis for phylogenetic classification. In: P. Hovenkamp (ed.), Systematics and evolution: a matter of diversity: 55–64. Utrecht.
WILEY, E.O. 1987b. Approaches to outgroup comparison. In: P. Hovenkamp (ed.), Systematics and evolution: a matter of diversity: 173–191. Utrecht.
WILEY, E.O. 1988a. Vicariance biogeography. Ann. Rev. Ecol. Syst. 19: 513–542.
WILEY, E.O. 1988b. Parsimony analysis and vicariance biogeography. Syst. Zool. 37: 271–290.
WILKINSON, H.P. 1979. The plant surface (mainly leaf). Part IV: Domatia. In: C.R. Metcalfe & L. Chalk. Anatomy of the dicotyledons 1, 2nd ed.: 132–140. Oxford.
ZANDEE, M. 1987. A computing environment for cladistic analysis. In: P. Hovenkamp (ed.), Systematics and evolution: a matter of diversity: 111–140. Utrecht.
ZANDEE, M. 1988. A user manual for CAFCA/PC (version 1.9.6). Institute of Theoretical Biology, University of Leiden.
ZANDEE, M., & R. GEESINK. 1987. Phylogenetics and Legumes: a desire for the impossible? In: C.H. Stirton (ed.), Advances in Legume systematics, part 3: 131–167. Kew.
ZANDEE, M., & M.C. ROOS. 1987. Component-compatibility in historical biogeography. Cladistics 3: 305–332.

16. ACKNOWLEDGEMENTS

The directors and keepers of the following herbaria are kindly thanked for a loan of their material or for enabling me to visit them: A, B, BISH, BM, BO, BRI, CANB, F, FI, K, L, LAE, M, MEL, NOU, NSW, NY, P, S, SAN, SING, U, US, and W.

I am obliged to the Greshoff Rumphius Foundation, the Society for Tropical Scientific Research, and the Rijksherbarium Foundation Professor Lam for enabling the field trip to Sabah, East Malaysia (N Borneo). The Agricultural Research Centres of Tenom and Ulu Dusun, the Herbarium of Sandakan, and Mt. Kinabalu Headquarters are thanked for their assistance during my field trip.

Susyn Andrews, Chan Chew Lun, Fui Lian-Tan, Ruurd Hoogland, Tony Lamb, Anthea Phillipps, Meg & Simon Wilkie and their children, and William Wong Wai Wah are kindly thanked for their hospitality during my trips abroad.

Sally Reynolds gave much advice and assisted in identifications.

Ed Wiley critically examined the phylogenetic and biogeographic chapters.

Caroline Pannell improved much of my English. Emma van Nieuwkoop made the lay-out and did the type-setting of the book. Jan van Os made the excellent drawings.

GUIOA

Guioa Cav., Icon. 4 (1798) 49, t. 373; Radlk. in Engl., Pflanzenr. 98 (1933) 1157. — *Cupania* sect. *Guioa* G. Don, Gen. Hist. 1 (1831) 668. — *Guioa* sect. *Euguioa* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8 (1878) 274, nom. illeg. (I.C.B.N. Art. 22.1); in Engl., Pflanzenr. 98 (1933) 1158. — Type: *Guioa lentiscifolia* Cav.

Dimereza Labill., Sert. Austr. Caled. (1825) 51, t. 51. — *Diplopetalon* Spreng., Syst. Veg. 4, 2 (1827) 146, nom. illeg. (I.C.B.N. Art. 63.1). — *Cupania* sect. *Dimereza* G. Don, Gen. Hist. 1 (1831) 668. — Type: *Dimereza glauca* Labill. [= *Guioa glauca* (Labill.) Radlk.]

Hemigyrosa Blume, Rumphia 3 (1847) 165. — *Guioa* sect. *Hemigyrosa* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8 (1878) 274; in Engl., Pflanzenr. 98 (1933) 1164. — Type: *Hemigyrosa perrottetii* Blume [= *Guioa koelreuteria* (Blanco) Merr.]

(For other species within *Hemigyrosa* see chapter 21, Excluded Taxa.)

The infrageneric classification, containing literature references, descriptions, and synonymy, can be found in chapter 13.

Shrub (to liana) to tree. *Branchlets* terete to flattened, smooth to ribbed to rough, usually sericeous when young to hirsute. *Indumentum* consisting of simple hairs only; glandular scales absent. *Leaves* spirally arranged, paripinnate, 1–9-jugate, without stipules; petiole pulvinate, not winged; rhachis usually terete to flattened above, sometimes slightly to distinctly winged; petiolules pulvinate. *Leaflets* usually subsessile, opposite (to alternate), ovate to obovate, sometimes falcate, symmetric to distinctly asymmetric (acroscopic side broader), lower leaflets smaller than to about as large as upper ones; pergamentaceous to very coriaceous, often punctate; base usually attenuate to acute; margin entire to sometimes (apically) crenate or serrate (juvenile leaflets always serrate), flat to revolute; apex retuse to caudate, very apex obtuse to mucronulate; glandular hairs usually few near midrib, very small, indistinct, white (*Guioa hirsuta* different type, distinct, red); upper surface usually darker than lower, more shiny, smooth, usually glabrous (with often a puberulous midrib) to sericeous to hirsute; lower surface differently coloured, usually dull, smooth to whitish papillate, glabrous to sericeous to hirsute, domatia absent to a single small or large sac to many pockets; venation often raised, especially on lower surface; nerves intercalated with smaller ones, larger nerves marginally looped, sometimes less distinctly so in lower half of leaflets; veins densely to laxly reticulate. *Inflorescence* a thyrse, (ramiflorous to) axillary (to pseudoterminal), laxly branching in or near axil and usually along the rhachis, usually few-flowered; first order branches oblique; cymules cincinnate (to dichasial). *Bracts* and *bracteoles* triangular, subpersistent in fruit, outside usually hirsute and inside glabrous. *Pedicels* usually sericeous, upper part above abscission zone often glabrous or less sericeous. *Flowers* zygomorphic, seemingly hermaphrodite, but presumably actually unisexual. *Sepals* 5 or seldom 6, (sub)persistent in fruit, outer 2 (slightly to) very distinctly smaller than inner 3 (except for the equal sepals of *Guioa microsepala*), usually only margin with stiff hairs, but sometimes outside sparsely hirsute and even less so inside, margin usually with glands; inner 3 sepals with a petaloid margin. *Petals* 5 (or very seldom 6), obovate to orbicular, usually distinctly clawed, margin and sometimes outside and inside pilose; scales absent to in most species well developed, part of folded margin of petal or ribbon-like and then inserted between claw and blade, either completely free or lower part of margin connate with margin of petal, margins pilose; crest absent to present as bifid apex of scales or as stiped clavate lobe on backside of scale; petal between two adjacent large sepals usually with reduced blade and scales. *Disc* incomplete with a gap near the two adjacent large sepals to complete with sometimes one or two slits at the same place, lobed, smooth, glabrous. *Stamens* 8 (or very seldom 7); filament especially basally pilose; anther basifixed in cleft, latrorsely lengthwise opening, often with few hairs. *Pistil:* ovary 3-lobed, 3-locular, smooth, subglabrous to densely hirsute, often on short gynophore; ovule one per locule, axillary, ascending, apotropous, campylotropous; stigma sessile, pyramidal, longitudinally grooved; style elongating in fruit. *Fruit* an obcordate capsule with 3 lobes, of which one to all develop, opening along margins of lobes, spreading after dehiscence, smooth to rugose to rugosely ribbed, glabrous to glabrescent, stipe narrow and high to broadly cuneate and not distinguishable, margins obtuse (only in *Guioa pteropoda* sharply edged); lobes laterally flattened; exocarp coriaceous, thin; mesocarp lighter coloured, woody, thin; endocarp brownish when dry, chartaceous, thin. *Seed* orbicular to obovoid, black when dry, laterally flattened; arilloid completely enveloping seed, apically open and lobed, basally with a rim, from the latter a long folded pseudo-funicle attaches to the basal corner of the fruit, seed dangling on the funicle in open fruit, sometimes pseudo-funicle absent, but then rim still present; hilum oval, (sub)basal; micropilar wart usually indistinct to in some species protruding; sclerotesta woody, thin; endotesta more membranaceous, whitish brown. *Embryo* notorrhizal, laterally flattened; cotyledons dorsoventrally to secondarily laterally besides each other, usually inequal, upper larger, apices often elongated, dorsoventrally flattened and then apex of lower cotyledon often recurved over that of upper one; radicle dorsoventrally flattened, inserted in pocket formed by endotesta; plumule inconspicuous.

Distribution. SE Asia (Thailand to S Vietnam as northern limit), Malesia, E Australia, Pacific up to Samoa.

Ecology. Often common. Usually found in secondary forest, but also in the under- and middle storey of primary forest. Most often found in the secondary, open edges of for instance road- or riversides, margins of forest, beaches, and plantation edges. Soil: rather indifferent, several species are (partly) found on ultrabasic (serpentine). Alt.: sea-level up to midmontane forest.

Note. Typical for *Guioa* are the lack of glandular scales; usually dimorph, petaloid sepals; petals with usually crested scales; obcordate, trilobed, reddish, inside smooth and glabrous fruits; an orange arilloid with basally a rim with usually a pseudo-funicle; and a notorrhizal embryo.

18. KEYS TO THE SPECIES OF GUIOA

This chapter contains several keys. Users are advised to have a dissecting microscope at hand, as several characters are difficult to see with the naked eye or with a handlens.

The general key will be very difficult to use for two reasons. First, material is needed with both flowers and fruits, almost impossible within the Sapindaceae. Second, for several species many leads have to be followed to find the correct name. It is better, if the region of origin of the plant is known, to use the keys for the different areas. There are keys for:

— SE Asia mainland, Sumatra, Borneo, and Java (Sunda shelf)
— Philippines
— Celebes
— Moluccas
— New Guinea
— Australia
— New Caledonia
— Solomon Islands
— Fiji

On the Lesser Sunda Islands, the New Hebrides, the Tonga Islands, and Samoa only one species of *Guioa* is found:

Lesser Sunda Islands:	*Guioa asquamosa*
New Hebrides:	*Guioa novoëbudaënsis*
Tonga Islands:	*Guioa lentiscifolia*
(Samoa:	*Guioa subfalcata*; doubtful species)

Only if the identification seems to be incorrect (by comparing the specimen with the figures), then, and only then, it is advisable to use the general key.

The terminology is explained by figs. 1–14 and in the chapter on morphological characters (chapter 6). The keys will often refer to the different drawings. Only plants with mature leaflets can be keyed out.

18.1. GENERAL KEY TO THE SPECIES OF GUIOA

1 a. Wing along rhachis more than 1.5 mm broad (fig. 1c) 2
b. Rhachis not to slightly winged, wing less than 1 mm broad (fig. 1a, b) 6

2 (1) a. Lower surface of leaflets greyish, densely papillate, (very) sparsely sericeous to hirsute 3
b. Lower surface of leaflets greenish, not to only very slightly papillate, glabrous to very sparsely sericeous 4

3 (2) a. Indumentum (very) sparsely sericeous. Leaflets elliptic (to obovate; fig. 2b, c); apex gradually acuminate to cuspidate (fig. 5e–h); domatia many sacs, hardly raised (fig. 6c); midrib below hardly raised, flat **Guioa pterorhachis**
b. Indumentum hirsute (to subsericeous). Leaflets (elliptic to) obovate (fig. 2); apex (obtuse to) abruptly acuminate (to cuspidate (fig. 5e–g, i)); domatia many pockets, sometimes sacs, raised (fig. 6a, b); midrib below raised, convex . . . . **Guioa pleuropteris**

4 (2) a. Domatia absent or sometimes a single sac. Fruit blackish when dry; stipe rather slender to broadly cuneate (fig. 13) 5
b. Domatia 2 to many sacs. Fruit reddish to reddish-black when dry; stipe slender (fig. 13a) .... **Guioa comesperma**

5 (4) a. Disc complete (fig. 12a). Apex of leaflets mucronulate. Fruits 0.9–1 cm high by 0.8–1.3 cm broad, stipe 1.5–2.5 mm high, broadly cuneate (fig. 12b) .... **Guioa melanopoda**
b. Disc incomplete (fig. 13c). Apex of leaflets not mucronulate. Fruits 1.2–2.3 cm high by 1.3–2.6 cm broad, stipe 2–5 mm high, rather slender (fig. 13a) .... **Guioa bijuga**

6 (1) a. Lower surface of leaflets smooth to at most very slightly papillate (rather shiny, greenish or brownish when dried) 7
b. Lower surface of leaflets densely papillate (dull, greyish). Use microscope! 37

7 (6) a. Sepals dimorph, outer two smaller than inner three. Leaflets glabrous to sericeous to puberulous to hirsute below.................... 8
b. Sepals all equal. Leaflets glabrous to very slightly sericeous below **Guioa microsepala**

8 (7) a. Disc complete (for discs with 1 or 2 small slits near insertion of two adjacent large sepals follow this lead; fig. 12a, b) 9
b. Disc incomplete (fig. 12c) 24

9 (8) a. Leaflets hirsute 10
b. Leaflets glabrous, sparsely pilose or sericeous 13

10 (9) a. Domatia absent to a single to many sacs (to pockets; fig. 6b, a). Lower surface of leaflets without red glands 11
b. Domatia many pockets (fig. 6a). Small red glands on lower surface of leaflets .... **Guioa hirsuta**

11 (10) a. Apex of petal scales not to slightly broadened (fig. 9b); crest either absent (fig. 10a) and then margin of leaflets usually with a few subapical teeth (fig. 4d) or crest clavate, stipitate, glabrous (fig. 10e–g), and leaflets entire (fig. 4a) 12
b. Apex of petal scales much broadened (fig. 9a); crest, if present, part of pilose bifid scale apex, not clavate (fig. 10a, c). Leaflets entire (fig. 4a) **Guioa diplopetala**

12 (11) a. Crest of petal scales absent (fig. 10a). Leaflets usually with a few subapical teeth (fig. 4d), domatia many pockets (fig. 6a) **Guioa oligotricha**
b. Crest of petal scales clavate, stipitate (fig. 10e–g). Leaflets entire (fig. 4a); domatia absent or a single sac (fig. 6b) ..... **Guioa molliuscula**

13 (9) a. Rhachis of leaves slightly winged (fig. 1b) 14
b. Rhachis of leaves terete or flattened below jugae (fig. 1a) 16

14 (13) a. Domatia absent to many. Disc complete (fig. 12a). Fruit blackish when dry, 0.7–2 cm high by 0.6–1.9 cm broad, stipe 1.5–3 mm high, slender (then fruit 0.7–0.8 cm high; fig. 11a) to broadly cuneate (fig. 13b, c) 15

b. Domatia 1 (to many). Disc with two small slits near insertion of two adjacent large sepals (fig. 12b). Fruit reddish when dry, 1.1–1.3 cm high by 0.9–1.4 cm broad, stipe 1.5–3.5 mm high, slender (fig. 13a)
Guioa gracilis

15 (14) a. Leaflets slightly crenate or sometimes entire (fig. 4b, c); apex retuse to obtuse (to acute; fig. 5a–d). Petals c. 3.4 by 1.2 mm. Fruit 1.7–1.9 cm broad . . . . **Guioa pseudoamabilis**

b. Leaflets entire, except for some subapical teeth (fig. 4d); apex acuminate (fig. 5e). Petals 0.2–1.1 by 0.1–0.2 mm. Fruit 0.6–0.9 cm broad
Guioa venusta

16 (13) a. Crest of scales clavate (fig. 10e–g) 17

b. Crest if present not clavate, but bifid part of scale apex (fig. 10a, c) . 21

17 (16) a. Scales free (fig. 9b) 18

b. Scales: auriculate and inwardly folded margins of petal (fig. 9d)
Guioa coriacea

18 (17) a. Disc incomplete, always one or two small slits present near insertion of two adjacent large sepals (fig. 12b) 19

b. Disc complete (fig. 12a) 20

19 (18) a. Petals 0.8–1.4 mm high. Fruit 1.1–1.3 cm high, stipe 1.5–3.5 mm high. Margin of leaflets entire to sometimes slightly crenate (fig. 4a, b)
Guioa gracilis

b. Petals 2–3.3 mm high. Fruit 1.7–2.4 cm high, stipe 2–6 mm high. Margin of leaflets entire (fig. 4a) . . . . **Guioa ovalis**

20 (18) a. Leaflets elliptic (fig. 2b) . . . . **Guioa aryterifolia**

b. Leaflets ovate (fig. 2a) . . . . **Guioa scalariformis**

21 (16) a. Leaflets (ovate to) elliptic (fig. 2a, b). Scales relatively long, usually more than a third of petal length (petals: 0.5–4 mm high, scales 0.3–2 mm high); crest often present 22

b. Leaflets ovate (fig. 2a). Scales relatively very short, less than a fifth of petal length (petals: 1.5–2.5 mm high, scales 0.1–0.3 mm high; fig. 8c); crest absent . . . . **Guioa asquamosa**

22 (21) a. Claw of petals 0.2–0.6(–1) mm high. Fruits 0.7–1.5 cm high by 0.7–1.8 cm broad. Domatia absent to present 23

b. Claw of petals c. 0.8 mm high. Fruits 1.5–2.2 cm high by 2–2.7 cm broad. Domatia absent . . . . **Guioa unguiculata**

23 (22) a. Apex of petal scales much broadened (fig. 9a); crest usually absent, if present, then part of bifid scale apex (fig. 10a, c) . **Guioa diplopetala**
b. Apex of petal scales very slender (fig. 9b); crest absent (fig. 10a) **Guioa patentinervis**

24 (8) a. Edges of fruits rounded; dissepiments complete. Petals (4 or) 5. Filaments completely, but especially basally pilose 25
b. Edges of fruit very sharp; dissepiments above attachment of funicle incomplete. Petals 4. Filaments only basally pilose . . **Guioa pteropoda**

25 (24) a. Leaflets glabrous, sericeous, hirsute or subvillose; domatia absent, or a single to many sacs or pockets (fig. 6a, b) 26
b. Leaflets puberulous on midrib and major nerves only (use microscope!); domatia many pockets (fig. 6a) . . . . **Guioa hospita**

26 (25) a. Scales of petal basally not auricled (fig. 9b); crest either absent, or a bifid part of scale apex or clavate (fig. 10a, c, e). Leaflets 2–30 by 0.7–13.3 cm 27
b. Scales of petal auricled basally (fig. 9c); crest linear (fig. 10d). Leaflets 5.7–14.4 by 1.6–4.1 cm . . . . **Guioa acuminata**

27 (26) a. Domatia absent. Petal crest clavate (fig. 10e–g). Fruit wall up to 3.5 mm thick; stipe 1-1.5 mm high, broadly cuneate (fig. 13c); pseudo-funicle often reduced 28
b. Domatia absent or present; if absent, then either petal crest a bifid scale apex (fig. 10c) or fruits with a 2–6 mm high, slender stipe (13a). Fruit wall c. 1 mm thick; pseudo-funicle well developed 29

28 (27) a. Leaflets ovate (fig. 2a) . . . . **Guioa grandifoliola**
b. Leaflets elliptic (fig. 2b) . . . . **Guioa contracta**

29 (27) a. Crest of petal (absent to) a pilose part of bifid scale apex (fig. 10a, c), to seldom pilose and somewhat clavate 30
b. Crest glabrous, clavate (fig. 10e–g) 32

30 (29) a. Blade of petals (elliptic to) obovate, gradually decurrent into the claw (fig. 8b) 31
b. Blade of petal orbicular, sharp transition between blade and claw (fig. 8a) **Guioa truncata**

31 (30) a. Rhachis often (slightly) winged (fig. 1b, c). Leaflets elliptic (fig. 2b); apex abruptly acuminate to cuspidate (fig. 5e, f, i); very apex obtuse (to acute) . . . . **Guioa bijuga**
b. Rhachis terete to flattened and broadened (to slightly winged; fig. 1a). Leaflets ovate (to elliptic; fig. 2a, b); apex (obtuse to) usually gradually acuminate to caudate (fig. 5c–h); very apex acute to usually mucronulate **Guioa koelreuteria**

32 (29) a. Rhachis often slightly winged (fig. 1a, b). Leaflets with (1, then rhachis slightly winged, to) 2 to many domatia 33
b. Rhachis not winged (fig. 1a). Leaflets with 0 or 1 domatium 34

33 (32) a. Rhachis not to slightly winged (fig. 1a, b). Apex of leaflets acuminate to cuspidate (to caudate; fig. 5e–g). Petals 2.1–3.8 by 0.6–1.7 mm; claw 0.3–0.8 mm high; stalk of crest long (fig. 10g) . **Guioa comesperma**
b. Rhachis slightly winged (fig. 1b). Apex of leaflets (retuse to) obtuse to acuminate (fig. 5a–e). Petals 2–2.3 by 1–1.2 mm; claw c. 0.2 mm high; stalk of crest short (fig. 10e, f) . . . . **Guioa fusca**

34 (32) a. Leaflets (ovate to) elliptic (fig. 2a, b); if ovate then 2–8.6 by 0.7–3.1 cm, surface usually finely wrinkled when dry (fig. 108b). 35
b. Leaflets ovate (fig. 2a), 7–19.3 by 2.6–6.5 cm, surface not wrinkled, smooth . . . . **Guioa normanbiensis**

35 (34) a. Fruit with a 2–4 mm high stipe; upper margin of fruit more or less flat, parallel to lower margin (fig. 13a) 36
b. Fruit without a stipe to stipe up to 2 mm high; upper margin of fruit highly convex, not parallel to lower margin (fig. 13c) . **Guioa rigidiuscula**

36 (35) a. Leaflets 3.5–16.2 by 1.5–6.4 cm; apex acute to cuspidate (fig. 5d–f), mucronulate; surface smooth, not wrinkled when dry
Guioa membranifolia
b. Leaflets 2–8.6 by 0.7–3.1 cm; apex (rounded to) obtuse (fig. 5b, c), not mucronulate; surface usually finely wrinkled when dry
Guioa pectinata

37 (6) a. Disc complete (or with 1 or 2 small slits; fig. 12a, b) 38
b. Disc incomplete (with 1 large gap; fig. 12c) 65

38 (37) a. Some leaves more than 1-jugate 39
b. All leaves 1-jugate . . . . **Guioa pauciflora**

39 (38) a. Leaflets without domatia or with small or large domatia. Petals always with scales (at least 1/8th of petal length) 40
b. Leaflets with very large domatia (fig. 6d). Petals without scales (or present as enation; fig. 8c) . . . . **Guioa lentiscifolia**

40 (39) a. Rhachis not to slightly winged (fig. 1a, b). Petals 0.3–4 mm long. Fruits 0.5–2 cm high by 0.6–2.9 cm broad. Leaflets ovate to obovate (fig. 2) 41
b. Rhachis not winged (fig. 1a). Petals 2.8–3 mm long. Fruits 2.2–2.7 cm high by 2.9–3.9 cm broad. Leaflets ovate (fig. 2a) **Guioa megacarpa**

41 (40) a. Rhachis slightly winged (fig. 1b). Margin of at least some leaflets either crenate or somewhat serrate (check carefully!; fig. 4b, c) 42
b. Rhachis not or slightly winged (fig. 1a, b), if slightly winged then margin of all leaflets entire (fig. 4a) 45

42 (41) a. Disc complete (fig. 12a). Leaflets below shortly sericeous 43
b. Disc with minute gap (fig. 12b). Leaflets below (exceptionally shortly to long sericeous to) hirsute . . . . **Guioa villosa**

43 (42) a. Domatia in at least some leaflets a single to many sacs 44
b. Domatia absent . . . . **Guioa amabilis**

44 (43) a. Leaflets 1–4.3 cm long; apex retuse to obtuse (fig. 5a–c); domatia (1 to) many sacs. Stipe of fruit 1.5–2 mm high . . . . **Guioa crenata**
b. Leaflets 1.3–2.4 cm long; apex acute (fig. 5d); domatia absent or a single sac. Stipe of fruit c. 3 mm high . . . . **Guioa waigeoensis**

45 (42) a. Plants hirsute in some part 46
b. Plants glabrous or sericeous 50

46 (45) a. Leaflets ovate to obovate (fig. 2); margin (crenate to) entire (to slightly serrate; fig. 4). Crest of petal absent to present (fig. 10). Fruit 0.8–1.9 cm high 47
b. Leaflets ovate to elliptic (fig. 2a, b); margin entire except usually for a few subapical teeth (fig. 4d). Crest of petal absent (fig. 10a). Fruit 0.6–0.8 cm high . . . . **Guioa oligotricha**

47 (46) a. Upper leaflets elliptic to obovate (fig. 2); apex (retuse to acute to) abruptly acuminate (to cuspidate; fig. 5a–g, i), if not abruptly acuminate then base and apex very asymmetric (fig. 3c) 48
b. Upper leaflets ovate (to elliptic; fig. 2a, b); apex usually gradually acute to caudate (fig. 5d–h); only base asymmetric (fig. 3b) 49

48 (47) a. Leaflets 0.9–18.7 cm long. Petals 1.3–3.5 mm long, claw 0.2–1 mm high (1/7–1/4th of petal length); crest if present part of bifid scale apex, pilose (fig. 10c) . . . . **Guioa pleuropteris**
b. Leaflets 0.5–7.5 cm long. Petals 0.8–3 mm long, claw 0.1–0.3 mm long (1/10–1/8th of petal length); crest if present linear to clavate, glabrous (fig. 10d–g) . . . . **Guioa villosa**

49 (47) a. Domatia absent to a single to many pocket-like sacs, small (fig. 6b). Crest of petal scales usually absent, sometimes well-developed, clavate (fig. 10a, e). Stipe of fruit absent to up to 4 mm high, broadly cuneate, indistinct (fig. 13b, c) . . . . **Guioa subsericea**
b. Domatia a single to many sacs, large (fig. 6d). Crest absent or a cockle (fig. 10a, b). Stipe of fruit 1–3 mm high, rather slender, distinct (fig. 13a) . . . . **Guioa chrysea**

50 (45) a. Stipe of fruit broadly cuneate (fig. 13b, c) 51
b. Stipe of fruit slender to slightly broadly cuneate (fig. 13a) 56

51 (50) a. Domatia absent. Leaflets below shortly sericeous (microscope!). Lobes of fruit not gradually decurrent into stipe (fig. 13c) 52

b. Domatia absent to present in some to all leaflets. If absent then either leaflets glabrous below, but sometimes very sparsely sericeous, lobes of fruit sharply decurrent into stipe (fig. 13a, c) or leaflets (sub)sericeous below and lobes of fruit gradually decurrent into stipe (fig. 13b) . . . 53

52 (51) a. Apex of leaflets (obtuse to) acuminate (to cuspidate; fig. 5c–f). Large sepals 2.2–3.5 mm high. Petals 2–2.5 by 0.8–1 mm; not distinctly clawed (fig. 8c). Fruit 1.2–1.6 cm high by 2–2.5 cm broad **Guioa montana**

b. Apex of leaflets retuse to acute (fig. 5a–d). Large sepals 1.3–2.5 mm high. Petals 0.5–2 by 0.2–1 mm; claw 0.2–0.7 mm high (fig. 8a). Fruit 0.6–1.1 cm high by 0.6–1.4(–1.9) cm broad **Guioa semiglauca**

53 (51) a. Scales present as inwardly folded, adnate auricles of petal (fig. 9d) . 54

b. Scales of petal free (fig. 9b) 55

54 (53) a. Rhachis never winged (fig. 1a). Leaflets usually very asymmetric (fig. 3b) **Guioa subsericea**

b. Rhachis slightly winged (fig. 1b). Leaflets ± symmetric (fig. 3d) **Guioa malukuensis**

55 (53) a. Leaves 1–3(–5)-jugate; rhachis not winged (fig. 1a). Leaflets 2.8–23.5 cm long; lower surface glabrous, but sometimes very sparsely sericeous, especially the midrib. Flower 1.5–2.5 mm in diam. Petals 0.3–1.8 mm long, claw absent to up to 0.2(–0.4) mm high; scales 0.1–1 mm long **Guioa acutifolia**

b. Leaves (3–)5–7-jugate; rhachis not to very slightly winged (fig. 1a, b). Leaflets 3.8–6.3 cm long; lower surface very sparsely subsericeous. Flower c. 2.8 mm in diam. Petals 1.5–1.7 mm long, claw c. 0.3 mm high; scales c. 1 mm long . . . . **Guioa multijuga**

56 (50) a. Rhachis not (to very slightly) winged (fig. 1a, b). Scales free or more or less present as inwardly folded auricles of the petal (fig. 9b, d) 57

b. Rhachis slightly winged (fig. 1b). Scales present as inwardly folded auricles of the petal (fig. 9d) . . . . **Guioa malukuensis**

57 (56) a. Leaflets usually punctate. Crest of petal scales absent or an enation or part of bifid scale apex (fig. 10a–c) or clavate on short stipe (fig. 10e) 58

b. Leaflets not punctate. Crest of petal clavate on a very long stipe (fig. 10g) **Guioa rhoifolia**

58 (57) a. Domatia if present small (to large); if large then domatia usually with a round opening (fig. 6d), and leaflets 2.1–8.2 cm long, falcate (fig. 3a), subsericeous below 59

b. Domatia very large, with a long opening (fig. 6e). Leaflets 3.7–16.5 cm, often slightly falcate (fig. 3b), sericeous below . . . . . . **Guioa chrysea**

59 (58) a. Leaflets ovate (fig. 2a), falcate (fig. 3a). Petals 1.8–3 mm long . . 60
b. Leaflets ovate to elliptic (fig. 2a, b), not to only somewhat falcate (fig. 3b, d), if somewhat falcate then petals 0.3–1.8 mm long 61

60 (59) a. Domatia a single, small sac with opening in the front (fig. 6b), sometimes with additional shallow pockets (fig. 6a). Petals 2.3–3 mm long, scales relatively short, 0.3–0.7 mm high . . **Guioa novoëbudaënsis**
b. Domatia 1 to many, large sacs with opening in the top (fig. 6d). Petals 1.8–2.7 mm long, scales relatively long, 0.8–1.2 mm high (N.B.: seldom scales completely wanting) . . . . **Guioa punctata**

61 (59) a. Petals 0.3–4 mm long; if overlapping in length then scales relatively long (1/3–2/3th of petal length) and apex either slender (fig. 9b) or apex very broadened (fig. 9a); crest absent to present (fig. 10). 62
b. Petals 0.7–1.3 mm long; scales relatively short (1/7–1/3th of the petal length), relatively broad (fig. 9b), apex not broadened; crest absent (fig. 10a) . . . . **Guioa sufusana**

62 (61) a. Apex of scales not broadened (fig. 9b); crest if present clavate, glabrous (fig. 10a, e) 63
b. Apex of petal scales (very) much broadened (fig. 9a); crest if present part of pilose bifid scale apex (fig. 10a, c) . . . . **Guioa diplopetala**

63 (62) a. Rhachis not to very slightly winged (fig. 1a, b). Leaflet index 1.8–4.7; domatia at least in some leaflets 1 (or seldom 2) sacs. Disc complete (fig. 12a). Scales of petals usually without a crest (fig. 10a). Fruit 0.5–1.2 cm high, stipe absent to up to 3 mm high 64
b. Rhachis not winged (fig. 1a). Leaflet index 2.9–3.5; domatia in at least some leaflets several sacs, sometimes apically a few shallow pockets. Disc with a small gap (fig. 12b). Scales of petals usually crested (fig. 10e). Fruit 1.2–1.5 cm high, stipe 3–4.5 mm high . . **Guioa elliptica**

64 (63) a. Leaves 1–3(–5)-jugate; rhachis not winged (fig. 1b). Leaflets 2.8–23.5 cm long; lower surface glabrous, or sometimes very sparsely sericeous, especially the midrib. Flower 1.5–2.5 mm in diam. Petals 0.3–1.8 mm long, claw absent to up to 0.2(–0.4) mm high; scales 0.1–1 mm long **Guioa acutifolia**
b. Leaves (3–)5–7-jugate; rhachis not to very slightly winged (fig. 1a, b). Leaflets 3.8–6.3 cm long; lower surface very sparsely subsericeous. Flower c. 2.8 mm in diam. Petals 1.5–1.7 mm long, claw c. 0.3 mm high; scales c. 1 mm long . . . . **Guioa multijuga**

65 (37) a. Plants hirsute in some part and/or the rhachis slightly winged (fig. 1b) and often shape of leaflets like fig. 3c (elliptic with asymmetric base and apex) 66
b. Plants glabrous or sericeous. Rhachis not winged (fig. 1a). Leaflets like fig. 3b, d (only base or apex asymmetric) 73

66 (65) a. Rhachis slightly winged or not (fig. 1a, b). Indumentum (at most) sericeous to hirsute. Leaflets entire (to crenate or serrate; fig. 4a–c); if not entire then domatia present 67
b. Rhachis slightly winged (fig. 1b). Indumentum sparsely shortly sericeous. Leaflets basally entire, apically crenate (fig. 4e); domatia absent **Guioa crenulata**

67 (66) a. Claw of petals 1/7–1/2th of total petal length; crest if present usually a pilose bifid part of scale apex (fig. 10c) to clavate and then either shortly stiped (fig. 10e) and (sub)glabrous or either long stiped (fig. 10g) and subglabrous 68
b. Claw of petals 1/10–1/8th of total petal length; crest if present linear to clavate, glabrous, long stiped (fig. 10d, g) . . . . **Guioa villosa**

68 (67) a. Leaflets glabrous to sericeous to hirsute. Crest absent or a bifid part of scale apex or clavate and shortly or long stiped, subglabrous (fig. 10); if clavate then petals 1.8–4 by 1–2.5 mm; fruit 1–2.3 cm high, stipe slender (fig. 13a) 69
b. Leaflets hirsute. Crest clavate, shortly stiped, glabrous (fig. 10e). Petals 1–2 by 0.4–1.2 mm. Fruit 0.7–1.2 cm high, stipe broadly cuneate (fig. 13b) . . . . **Guioa lasioneura**

69 (68) a. Indumentum glabrous to sericeous to hirsute. Blade of petal elliptic to obovate, gradually decurrent into claw (fig. 8b); crest part of bifid scale apex (to clavate; fig. 10c) 70
b. Indumentum hirsute. Blade of petal orbicular, abruptly clawed (fig. 8a); crest clavate (fig. 10e) . . . . **Guioa myriadenia**

70 (69) a. Indumentum sericeous to hirsute, especially when young. Upper leaflets either ovate (to elliptic; fig. 2a, b) and then apex usually gradually acuminate to caudate (fig. 5e–h), or leaflets (elliptic to) obovate (fig. 2b, c) and then apex (obtuse to) usually abruptly acuminate (to cuspidate; fig. 5c–g, i), leaflets asymmetric (fig. 3b); lower surface glabrous to subsericeous to hirsute, domatia absent or a single sac to many sacs or pockets (fig. 6). 71
b. Indumentum at most shortly sericeous when young. Leaflets elliptic (fig. 2b), usually symmetric (fig. 3d); apex abruptly (acuminate to) cuspidate (fig. 5e, f); lower surface glabrous to sometimes sparsely sericeous, domatia absent or a single sac (fig. 6b) . . . . **Guioa bijuga**

71 (70) a. Upper leaflets ovate (to elliptic; fig. 2a, b); apex (obtuse to) usually gradually acuminate to caudate (fig. 5c–h); lower surface glabrous to subsericeous (to hirsute), domatia absent to a single sac to many sacs (to pockets; fig. 6). Fruit blackish when dry 72

b. Upper leaflets (elliptic to) obovate (fig. 2b, c); apex (obtuse to) usually abruptly acuminate (to cuspidate; fig. 5c–f, i); lower surface (sub)sericeous to usually hirsute, domatia occasionally absent to usually many pockets (or sometimes sacs; fig. 6a). Fruit reddish (to blackish) when dry .... **Guioa pleuropteris**

72 (71) a. Rhachis not to slightly winged (fig. 1a, b). Leaflets ovate (to elliptic; fig. 2a, b); apex (obtuse to) acuminate to caudate (fig. 5c–g); veins (flat to) raised on upper side, usually not differently coloured from lamina, below raised, laxly reticulate, usually distinct. Fruit 1–2.2 cm high by 1–2.3 cm broad .... **Guioa koelreuteria**

b. Rhachis not winged (fig. 1a). Leaflets ovate (fig. 2a); apex cuspidate to caudate (fig. 5f, g); veins conspicuously raised on both sides, differently coloured from lamina, densely reticulate, very distinct. Fruit 1–1.1 cm high by 1.2–1.4 cm broad .... **Guioa reticulata**

73 (65) a. Leaflets ovate to obovate (fig. 2), coriaceous to very coriaceous; domatia absent to a single sac to many sacs or pockets, all domatia relatively small (fig. 6a–c) 74

b. Leaflets elliptic (fig. 2b), coriaceous; domatia a single, large, highly domed sac (fig. 6d) .... **Guioa novobritannica**

74 (73) a. Leaflets ovate to obovate (fig. 2). Ovary at most subhirsute. Fruits glabrous 75

b. Leaflets ovate (to elliptic; fig. 2a, b). Ovary densely hirsute. Fruits (very) sparsely sericeous, glabrescent .... **Guioa pubescens**

75 (74) a. Leaflets ovate to obovate (fig. 2); apex retuse to caudate (fig. 5). Scales more than 1/4th (usually about one half) of petal length; crest present or not (fig. 10) 76

b. Leaflets ovate (to slightly elliptic; fig. 2a, b); apex cuspidate to caudate (fig. 5f, g). Scales less than 1/4th of petal length; crest absent to occasionally an enation (fig. 10a, b) .... **Guioa novoëbudaënsis**

76 (75) a. Claw of petals 1/11–1/6(–1/4)th of total petal length; crest (absent to linear to) clavate (fig. 10a, d–g), glabrous. (Type of petal found in New Guinea and Pacific.) 77

b. Claw of petal more than 1/5th of total petal length; crest (absent to) a pilose, bifid part of scale apex to clavate and subglabrous (fig. 10a, c, e). (Type of petal found in W Malesia.) 81

77 (76) a. Leaflets ovate to obovate (fig. 2); nearly symmetric to asymmetric, seldom somewhat falcate (fig. 3); apex retuse to cuspidate (to caudate; fig. 5); domatia absent to many sacs to pockets (fig. 6). Fruits blackish or reddish when dry; stipe slender to broadly cuneate (fig. 13) 78

b. Leaflets ovate (fig. 2a), falcate (fig. 3a); apex cuspidate to caudate (fig. 5f, g); domatia absent to 1 or 2 pockets (fig. 6a). Fruit blackish when dry; stipe broadly cuneate (fig. 13b) .... **Guioa plurinervis**

78 (77) a. Apex of leaflets retuse to acuminate (fig. 5a–e); domatia either absent (or a single sac) or 1 to at least in some leaflets several sacs (fig. 6b). Fruit blackish when dry 79

b. Apex of leaflets acuminate to cuspidate (to caudate; fig. 5d–g); domatia 2 to many basally sacs to apically pockets (fig. 6a, b). Fruit reddish to reddish black when dry .... **Guioa comesperma**

79 (78) a. Leaflets elliptic to obovate (fig. 2b, c); apex retuse to acuminate (fig. 5a–e); domatia absent (or a single sac; fig. 6b) 80

b. Leaflets (ovate to) elliptic (fig. 2a, b); apex acute to acuminate (fig. 5d, e); domatia in at least some leaflets several sacs (fig. 6b) . **Guioa elliptica**

80 (79) a. Leaves 1–3-, but very often all 1-jugate. Leaflets elliptic to obovate (fig. 2b, c); apex retuse to acuminate (fig. 5a–e), not mucronulate; lower surface shortly to long sericeous, domatia absent (or a single sac; fig. 6b). Upper part of pedicel subglabrous to as sericeous as lower part. Crest of petal either linear or clavate and long stiped (fig. 10d, g) **Guioa glauca**

b. Leaves 1- or 2-jugate. Leaflets elliptic (fig. 2b); apex acute to acuminate (fig. 5d, e), mucronulate; lower surface shortly sericeous, domatia absent. Upper part of pedicel (sub)glabrous. Crest of petal clavate, shortly stiped (fig. 10e) .... **Guioa misimaensis**

81 (76) a. Blade of petal orbicular, abruptly clawed (fig. 8a) 82

b. Blade of petal elliptic to obovate, gradually decurrent into the claw (fig. 8b) 84

82 (81) a. Leaflets elliptic to obovate (fig. 2b, c), 1.6–7.6 by 0.5–2.5 cm, punctate or not; apex obtuse to acuminate (fig. 5c–e); lower surface shortly sericeous, domatia absent or 1 sac (fig. 6b). Inflorescence subsericeous to sericeous 83

b. Leaflets ovate (to elliptic; fig. 2a, b), 2.5–14.5 by 1–4.5 cm, punctate; apex (rounded to) acuminate (to cuspidate; fig. 5b–f); lower surface long sericeous, domatia (1 to many sacs to) many pockets (fig. 6a, b). Inflorescence densely sericeous .... **Guioa myriadenia**

83 (82) a. Leaflets sericeous below (microscope!), not punctate. Bracts c. 1.3 mm long; bracteoles 0.3–0.8 mm long........... **Guioa palawanica**

b. Leaflets subsericeous below, punctate. Bracts c. 2.2 mm long; bracteoles 1.3–1.6 mm long .... **Guioa parvifoliola**

84 (81) a. Leaves 1–3-jugate. Leaflets elliptic to obovate (fig. 2b, c), 1.6–7.6 cm long, very coriaceous; apex rounded to acuminate (fig. 5b–e), not mucronulate; below sericeous, domatia absent or a single sac (fig. 6b); venation on upper surface raised 85

b. Leaves 1–6-jugate. Leaflets ovate to elliptic (fig. 2a, b), 2.1–20 cm long, subcoriaceous to coriaceous; apex (obtuse to) acuminate to caudate (fig. 5c–g), often mucronulate; below glabrous to sericeous, domatia absent to a single sac to many sacs (or pockets; fig. 6a, b); venation on upper surface (slightly sunken to) flat to raised 86

85 (84) a. Leaflets sericeous below (microscope!), not punctate. Bracts c. 1.3 mm long; bracteoles 0.3–0.8 mm long . . . . **Guioa palawanica**

b. Leaflets subsericeous below, punctate. Bracts c. 2.2 mm long; bracteoles 1.3–1.6 mm long . . . . **Guioa parvifoliola**

86 (84) a. Lobes of fruit much longer than broad (c. 11 by 5 mm) 87

b. Lobes of fruit as long as broad (6.5–14 by 7–16 mm). 88

87 (86) a. Leaflets ovate to elliptic (fig. 2a, b), asymmetric but not falcate (fig. 3b); apex acuminate to caudate, with a sinus (fig. 5e–g, i); below greyish to brownish papillate when dry; venation raised on both sides, densely to laxly reticulate, rather distinct. Inner large sepals 2–3.5 by 1.8–3.5 mm . . . . **Guioa bicolor**

b. Leaflets ovate (fig. 2a), falcate (fig. 3a); apex cuspidate to caudate, gradually tapering (fig. 5f–h); below whitish papillate when dry; venation above flat (to raised), below raised, laxly reticulate, usually rather indistinct. Inner large sepals 1.5–2.2 by 1.5–2.2 mm . . . **Guioa discolor**

88 (86) a. Leaflets ovate to elliptic (fig. 2a, b), falcate to rather symmetric (fig. 3a, b); very apex rounded to acute to mucronulate; venation not raised on upper surface to raised on both sides, usually not differently coloured from lamina, especially on upper side, nerves laxly to densely reticulate, inconspicuous to conspicuous 89

b. Leaflets ovate (fig. 2a), falcate (fig. 3a); very apex usually mucronulate; venation raised on both sides, differently coloured from lamina, nerves densely reticulate, conspicuous . . . . **Guioa reticulata**

89 (88) a. Leaflets ovate (to elliptic; fig. 2a, b), usually asymmetric (fig. 3b); apex (obtuse to) usually gradually acuminate to caudate (fig. 5c–h); very apex acute to usually mucronulate; domatia absent to a single sac to many sacs (or pockets; fig. 6) 90

b. Leaflets elliptic (fig. 2b), usually symmetric (fig. 3d); apex abruptly (acuminate to) cuspidate (fig. 5e–g, i); very apex rounded to acute, not mucronulate; domatia absent or a single sac (fig. 6b) . . . . . **Guioa bijuga**

90 (89) a. Lower surface of leaflets brownish to greyish papillate, not very differently coloured from upper surface when dry. Outer small sepals 1–3.1 by 1–3.3 mm . . . . **Guioa koelreuteria**

b. Lower surface of leaflets whitish papillate, very differently coloured from upper surface when dry. Outer small sepals 1.2–1.3 by 1.1–1.3 mm **Guioa discolor**

18.2. KEY TO THE SPECIES OF SE ASIA MAINLAND, SUMATRA, BORNEO, JAVA

1 a. Rhachis of leaves slightly to distinctly winged (fig. 1b, c) 2
b. Rhachis of leaves not winged (fig. 1a) 4

2 (1) a. Jugae (1–)2–7. Upper leaflets elliptic to obovate (fig. 2b, c), lower surface densely, greyish papillate, dull; domatia many pockets or sacs (fig. 6a, b) 3
b. Jugae 1–4. Upper leaflets elliptic (fig. 2b); lower surface smooth to sometimes somewhat papillate, rather shiny; domatia absent or a single sac (fig. 6b) . . . . **Guioa bijuga**

3 (2) a. Wings along rhachis small to broad (up to 3 mm; fig. 1b, c). Apex of leaflets (obtuse to) abruptly acuminate (to cuspidate; fig. 5c–f, i); lower surface: midrib raised, convex, hairs obliquely hirsute (to sericeous), domatia many pockets (to sac-like pockets to sacs; fig. 6a–c). Mainland, Sumatra, Borneo . . . . **Guioa pleuropteris**
b. Wings along rhachis always broad, up to 4 mm broad (fig. 1c). Apex of leaflets gradually acuminate to cuspidate (fig. 5e–h); lower surface: midrib hardly raised, flat, hairs (very) sparsely sericeous, domatia many sacs (fig. 6c). E Sabah . . . . **Guioa pterorhachis**

4 (1) a. Domatia absent or a single sac. 5
b. Domatia two to many sacs or pockets 8

5 (4) a. Leaflets below smooth or papillate, glabrous or (slightly) sericeous. Petals 1.8–3.8 mm long; scales without or with a hardly broadened apex (fig. 9b); crest always present. Disc incomplete (often almost complete; fig. 12b, c). Fruit lobes either longer than broad and then usually sparsely sericeous (glabrescent) or lobes about as long as broad and then glabrous 6
b. Leaflets below usually smooth, glabrous (to slightly sericeous to subvillose). Petals 0.5–4 mm long; scales with a (very) much broadened apex (fig. 9a); crest usually absent. Disc complete (sometimes with a small slit; fig. 12a, b). Fruit lobes usually longer than broad, glabrous **Guioa diplopetala**

6 (5) a. Leaves 1–6-jugate. Leaflets ovate (to elliptic; fig. 2a, b), asymmetric (fig. 3b); apex usually gradually acuminate to caudate (fig. 5e–h), very apex acute to usually mucronulate 7
b. Leaves 1–4-jugae. Leaflets elliptic (fig. 2b), usually symmetric (fig. 3d); apex abruptly (acuminate to) cuspidate (fig. 5e, f, i), very apex usually obtuse (to sometimes acute), not mucronulate . . . . **Guioa bijuga**

7 (6) a. Leaflets below smooth, shiny, glabrous. Ovary subhirsute. Fruits glabrous . . . . **Guioa koelreuteria**

b. Leaflets below papillate, dull, (slightly) shortly sericeous. Ovary densely hirsute. Fruits (very) sparsely sericeous, glabrescent **Guioa pubescens**

8 (4) a. Upper leaflets ovate (to elliptic) to obovate (fig. 2); lower surface papillate, either hirsute and with many pockets (to sacs) or (slightly) shortly sericeous and with many sacs. Petals (elliptic to) obovate; apex of scales not to hardly broadened (fig. 9b); crest (usually) present 9

b. Upper leaflets (ovate to) elliptic (fig. 2a, b); lower surface usually smooth, glabrous (to slightly sericeous to subvillose), many sacs. Petals elliptic; scales with a (very) much broadened apex (fig. 9a); crest usually absent **Guioa diplopetala**

9 (8) a. Upper leaflets elliptic to obovate (fig. 2b, c); apex (obtuse to) abruptly acuminate (to cuspidate; fig. 5c-g, i); lower surface (sub)sericeous to hirsute, domatia pockets (to pocket-like sacs to sacs). Ovary subhirsute. Fruits glabrous. . . . . **Guioa pleuropteris**

b. Upper leaflets ovate (to elliptic; fig. 2a, b); apex gradually acuminate to cuspidate (fig. 5e, f, h); lower surface (slightly) shortly sericeous, domatia sacs. Ovary densely hirsute. Fruits (very) sparsely sericeous, glabrescent . . . . **Guioa pubescens**

18.3. KEY TO THE SPECIES OF THE PHILIPPINES

1 a. Leaflets smooth below, without papillae, rather shiny 2

b. Leaflets papillate below, dull, greyish or whitish 5

2 (1) a. Rhachis not (to slightly) winged (fig. 1a, b). Blade of petals obovate, gradually decurrent into the claw (fig. 8b) 3

b. Rhachis slightly winged (fig. 1b). Blade of petals orbicular, abruptly clawed (fig. 8a). Mindanao . . . . **Guioa truncata**

3 (2) a. Apex of leaflets (obtuse to) acuminate to cuspidate (to caudate; fig. 5 c–g). Scales of petals basically not auricled (fig. 9b), membranaceous margin along scales indistinct 4

b. Apex of leaflets (cuspidate to) caudate (fig. 5f, g). Scales of petals basally auricled (fig. 9c), membranaceous margin along scales distinct (fig. 9b) . . . . **Guioa acuminata**

4 (3) a. Rhachis often (slightly) winged (fig. 1b). Leaflets elliptic (fig. 2b), usually symmetric (fig. 3d); apex abruptly acuminate to cuspidate (fig. 5e–g, i); very apex obtuse (to acute); domatia absent or 1 sac (fig. 6b). Balabac I., Palawan I. . . . . **Guioa bijuga**

b. Rhachis terete to flattened and broadened (to slightly winged; fig. 1a, b). Leaflets ovate (to elliptic; fig. 2a, b), asymmetric (fig. 3b); apex (obtuse to) usually gradually acuminate to caudate (fig. 5c–h); very apex acute to usually mucronulate; domatia absent or a single to many sacs (to pockets; fig. 5a, b) .... **Guioa koelreuteria**

5 (1) a. Rhachis winged or not (fig. 1). Leaflets ovate to obovate (fig. 2), (sub)-coriaceous to very coriaceous, punctate or not; apex retuse to caudate (fig. 5); domatia absent to many. Inflorescence subglabrous to brown, usually shortly, sericeous to hirsute. Blade of petal obovate, gradually decurrent into claw (fig. 8b); crest if present part of bifid scale apex to seldom clavate (fig. 10a, c, e). (N.B.: the petals of *Guioa palawanica* and *Guioa parvifoliola* are unknown. Both have short sericeous hairs and very coriaceous leaflets. *Guioa palawanica* differs from *Guioa myriadenia* by the non-punctate leaflets with none or 1 domatium and rounded to acuminate apex. *Guioa parvifoliola* has leaflets with an obtuse apex and a single domatium, the inflorescence is subsericeous) 6

b. Rhachis not winged (fig. 1a). Leaflets ovate (to elliptic; fig. 2a, b), coriaceous, punctate; domatia (absent or a single sac to many sacs to) many pockets. Inflorescence long, golden (sericeous to) hirsute. Blade of petal orbicular, sharp transition with claw (fig. 8a); crest clavate, stiped (fig. 10e) .... **Guioa myriadenia**

6 (5) a. Ovary subhirsute. Fruits glabrous 7

b. Ovary densely hirsute. Fruits sericeous, glabrescent **Guioa pubescens**

7 (6) a. Upper leaflets ovate to obovate (fig. 2); apex rounded to caudate (fig. 5 b–g); below (glabrous to) sericeous to hirsute, domatia absent or a single sac to many pockets or sacs; venation usually only below conspicuously raised, above usually not differently coloured from the lamina, densely to laxly reticulate, usually rather indistinct 8

b. Upper leaflets ovate (fig. 2a); apex cuspidate to caudate (fig. 5f, g); below sericeous, domatia a single (to many) sac(s); venation conspicuously raised on both sides, differently coloured from the lamina, densely reticulate, very distinct .... **Guioa reticulata**

8 (7) a. Leaves 1–6(–7)-jugate. Upper leaflets ovate to obovate (fig. 2; obovate leaflets (sub)coriaceous), 0.9–20 by 0.5–8.4 cm, (sub)coriaceous to very coriaceous; apex (obtuse to) acuminate to caudate (fig. 5c–g), very apex usually mucronulate; lower surface glabrous to sericeous to hirsute, domatia absent to a single sac to many sacs or pockets 9

b. Leaves 1–3-jugate. Upper leaflets elliptic to obovate (fig. 2b, c), 1.6–7.6 by 0.5–2.5 cm, very coriaceous; apex rounded to acuminate (fig. 5b–e), very apex rounded to acute, not mucronulate; lower surface (sub)sericeous, domatia absent or a single sac 13

9 (8) a. Rhachis not (to slightly) winged (fig. 1a, b). Upper leaflets ovate (to elliptic; fig. 2a, b), symmetric to usually especially basally asymmetric (fig. 3d, b); apex (obtuse to) acuminate to caudate (fig. 5c–g); below glabrous to sericeous to subhirsute (Mindanao only), usually always at least some leaflets longer than 7.5 cm; major nerves marginally looped, sometimes (leaflets ovate) less distinctly so in lower half. Inflorescence (sub)sericeous (to hirsute) 10

b. Rhachis usually winged (fig. 1a, c). Upper leaflets (elliptic to) obovate (fig. 2b, c), apically and basally asymmetric (fig. 3c); apex (obtuse to) acute to acuminate (to cuspidate; fig. 5c–g); below hirsute to (sub)sericeous, the (sub)sericeous leaflets always less than 7.5 cm long; major nerves marginally looped, but less distinctly so in lower half. Inflorescence hirsute .... **Guioa pleuropteris**

10 (9) a. Lobes of fruit about as long as high. Apex of leaflets usually rather gradually narrowing (fig. 5h) 11

b. Lobes of fruit much longer than high. Apex of leaflets abruptly narrowing (fig. 5i) .... **Guioa bicolor**

11 (10) a. Leaflets ovate (to elliptic; fig. 2a, b), usually asymmetric (fig. 3b); apex (obtuse to) usually gradually acuminate to caudate (fig. 5c–h); very apex acute to usually mucronulate; domatia absent or a single sac to many sacs (or pockets; fig. 6) 12

b. Leaflets elliptic (fig. 2b), usually symmetric (fig. 3d); apex abruptly (acuminate to) cuspidate (fig. 5e–g, i); very apex rounded to acute, not mucronulate; domatia absent or a single sac (fig. 6b) ..... **Guioa bijuga**

12 (11) a. Leaflets below rather slightly papillate, dullish green or brown when dry, not very differently coloured from upper side. Outer two smaller sepals 1–3.1 by 1–3.3 mm .... **Guioa koelreuteria**

b. Leaflets below densely papillate, almost whitish when dry, very differently coloured from upper surface. Outer two smaller sepals 1.2–1.3 by 1.1–1.3 mm .... **Guioa discolor**

13 (8) a. Leaflets sericeous below (microscope!), not punctate. Bracts c. 1.3 mm long; bracteoles 0.3–0.8 mm long. Palawan .... **Guioa palawanica**

b. Leaflets subsericeous below, punctate. Bracts c. 2.2 mm long; bracteoles 1.3–1.6 mm long. Luzon (Ilocos Norte Prov.) .. **Guioa parvifoliola**

18.4. KEY TO THE SPECIES OF CELEBES

1 a. Axes and rhachises, especially when young, hirsute. Lower surface of leaflets hirsute, with many red erect glands; domatia many pockets (fig. 6a) .... **Guioa hirsuta**

b. Axes and rhachises glabrous to very subsericeous. Lower surface of leaflets glabrous, red glands absent; domatia absent or many pocket-like sacs (fig. 6b) .... **Guioa diplopetala**

18.5. KEY TO THE SPECIES OF THE MOLUCCAS

1 a. Rhachis slightly winged or not (fig. 1b, a). Lower surface of the leaflets papillate, glabrous to sericeous 2
b. Rhachis not winged (fig. 1a). Lower surface of the leaflets not papillate, smooth, glabrous 3

2 (1) a. Rhachis slightly winged (fig. 1b). Lower surface of leaflets sericeous; domatia a single to many pocket-like sacs (fig. 6b) **Guioa malukuensis**
b. Rhachis not winged (fig. 1a). Lower surface of leaflets glabrous to sometimes very sparsely sericeous; domatia 1 (or 2) sac(s) (fig. 6b) **Guioa acutifolia**

3 (1) a. Petals 1.4–3 mm high; crest of scales well-developed, clavate (fig. 10e). Disc incomplete (fig. 12c). Fruit 1.4–2.4 cm high by 1–3.6 cm broad **Guioa membranifolia**
b. Petals 0.8–1.2 mm high; crest absent (fig. 10a). Disc complete (fig. 12a). Fruit 0.7–0.9 cm high by 0.7–1.3 cm broad . . . **Guioa patentinervis**

18.6. KEY TO THE SPECIES OF NEW GUINEA

1 a. Leaflets and inflorescence hirsute or velutinous. Rhachis not winged (fig. 1a) 2
b. Leaflets and inflorescence glabrous, puberulous, tomentose, somewhat hirsute, or sericeous. If tomentose or somewhat hirsute, then rhachis winged (fig. 1c) 4

2 (1) a. Lower surface of leaflets (smooth to) papillate, domatia (absent or a single to) many pocket-like sacs or pockets (fig. 6a, b). Crest of petal scales usually absent, seldom well-developed (fig. 10a, e). If leaflets smooth then many domatia and no crest (fig. 10a) 3
b. Lower surface of leaflets smooth, without papillae, domatia absent or a single sac (fig. 6b). Crest of petal scales well-developed (fig. 10e) **Guioa molliuscula**

3 (2) a. Leaflets usually with a few subapical teeth (fig. 4d). Domatia many pockets (fig. 6a). Inflorescences axillary, 1.2–6 cm long. Petals 0.7–1 by c. 0.3 mm, margin and less so out- and inside hirsute; scales free (fig. 9b), crestless (fig. 10a). Stipe of fruit 1.5–2 mm high, slender (fig. 13a) **Guioa oligotricha**
b. Leaflets entire (fig. 4a). Domatia absent or a single sac to many pocket-like sacs (fig. 6b). Inflorescences axillary to pseudoterminal, 1–26.6 cm long. Petals 0.9–2.3 by 0.5–1.6 mm, margin and less so outside hirsute, inside (sub)glabrous; scales inwardly folded, adnate auricles of

petal (fig. 9d); crest usually absent, sometimes developed (fig. 10a, e). Stipe of fruit absent to up to 4 mm high, broadly cuneate (fig. 13b).
Guioa subsericea

4 (1) a. Lower surface of leaflets smooth to papillate. Large inner sepals 0.8–3.2 by 0.9–3.5 mm. Petals (4 or) 5 (or 6). Filaments (in lower half to) completely, but especially basally pilose. Edges of fruit rounded; dissepiments complete 5
b. Lower surface of leaflets smooth. Large, inner sepals 3–4 by 3–4.2 mm. Petals 4. Filaments only basally pilose. Edges of fruit very sharp; dissepiments above attachment of funicle incomplete . . **Guioa pteropoda**

5 (4) a. Leaves 1–9-jugate, if all 1-jugate, then leaflets usually longer than 7 cm. Leaflets ovate to obovate (fig. 2); lower surface smooth to papillate; venation usually only raised on lower surface, laxly to densely reticulate 6
b. Leaves all 1-jugate. Leaflets 1.1–6.3 cm long, elliptic to obovate (fig. 2b, c); lower surface papillate; venation raised on both sides, densely reticulate . . . . **Guioa pauciflora**

6 (5) a. Rhachis winged, wing at least 0.5 mm broad (fig. 1b, c) 7
b. Rhachis terete to flattened, not winged (fig. 1a) 13

7 (6) a. Rhachis slightly to broadly winged (fig. 1b, c); if broadly winged then 2 to many domatia present 8
b. Rhachis broadly winged (wing more than 2 mm broad; fig. 1c). Domatia absent or sometimes a single sac (fig. 6b) . . . . . . **Guioa melanopoda**

8 (7) a. Leaflets densely papillate below (dull, greyish) 9
b. Leaflets smooth below (rather shiny), no papillae 11

9 (8) a. Leaflets 1–2.4 by 0.4–0.9 cm; margin at least in some leaflets either serrate or partly crenate (fig. 4b–e); apex emarginate to acute (fig. 5 a–d) 10
b. Leaflets 3.8–6.3 by 1–1.7 cm; margin entire (fig. 4a); apex acute (fig. 5d) . . . . **Guioa multijuga**

10 9) a. Margin at least in some leaflets serrate (fig. 4c, d); domatium in some leaflets present. Waigeo I. . . . . **Guioa waigeoensis**
b. Margin entire except for the usually crenate apex (fig. 4e); domatia absent. Vogelkop . . . . **Guioa amabilis**

11 (8) a. Leaflets 0.8–6.5 by 0.5–2 cm; margin entire to usually (partly) crenate or serrate (fig. 4); domatia absent to 1 to many. Fruit blackish when dry, either 0.7–0.8 cm high with a slender stipe (fig. 13a) or 1–2 cm high with a (rather) broadly cuneate stipe (fig. 13b, c) 12
b. Leaflets 3.8–18.5 by 1.3–8.4 cm; margin entire (fig. 4a); domatia 2 to many sacs. Fruit reddish to reddish black when dry, 0.8–1.5 cm high, stipe slender (fig. 13a) . . . . **Guioa comesperma**

12 (11) a. Leaflets entire or usually slightly crenate (fig. 4a, b); apex retuse to obtuse (to acute; fig. 5a–d). Petals c. 3.4 by 1.2 mm. Fruit 1.7–1.9 cm broad **Guioa pseudoamabilis**

b. Leaflets entire, except for some subapical teeth (fig. 4d); apex acuminate (fig. 5e). Petals 0.2–1.1 by 0.1–0.2 mm. Fruit 0.6–0.9 cm broad **Guioa venusta**

13 (6) a. Lower surface of leaflets glabrous or (sub)sericeous, domatia absent, or a single sac (or single pocket to two pockets) to many pocket-like sacs (fig. 6) 14

b. Lower surface of leaflets puberulous on midrib and basal major nerves (microscope!), domatia many pockets (fig. 6a) . . . . . . **Guioa hospita**

14 (13) a. Leaflets below densely, long (greyish, dull) papillate, usually (sub)sericeous, if not sericeous then usually a single very large sac present (fig. 6d) 15

b. Leaflets below (rather shiny) smooth (or at most very shortly papillate), glabrous (to very sparsely sericeous), sacs if present small (fig. 6b). 21

15 (14) a. Leaflets glabrous to (very sparsely) sericeous, domatia absent or a single small (fig. 6b) sac (or pocket to two pockets) to many pocket-like sacs 16

b. Leaflets glabrous except for a few sericeous hairs around the domatium, latter single, very large, highly domed (fig. 6d) **Guioa novobritannica**

16 (15) a. Disc incomplete (microscope!; fig. 12c) 17

b. Disc complete (to with a small slit; fig. 12a, b) 19

17 (16) a. Domatia absent or a single to 2 pockets (fig. 6a); if 2 pockets present then fruit blackish when dry, stipe broadly cuneate (fig. 13b) 18

b. Domatia 2 to many, basally sacs to upwards pockets (fig. 6b, a). Fruit reddish to reddish black when dry, stipe slender (fig. 13a) **Guioa comesperma**

18 (17) a. Leaflets not falcate, rather symmetric (fig. 3d), about 2.6–3 times as long as broad, coriaceous. Inflorescence subsericeous. Misima I. **Guioa misimaensis**

b. Leaflets falcate, asymmetric (fig. 3a), about 3.6–4.4 times as long as broad, coriaceous to very coriaceous. Inflorescence sericeous. Rossel I. **Guioa plurinervis**

19 (16) a. Leaves either 1–3(–5)-jugate or (3–)5–7-jugate. Leaflets (ovate to) elliptic (fig. 2a, b); below glabrous to very slightly sericeous, domatia absent, or a single (or 2) sacs (fig. 6b). Scales of petals free (except for the adnate lower part; fig. 9b), often folded outwards 20

b. Leaves 1–3-jugate. Leaflets ovate (to elliptic; fig. 2a, b); below (sub)sericeous, domatia absent or a single sac to many pocket-like sacs (fig. 6b). Scales of petals present as inwardly folded, adnate auricles (fig. 9d) **Guioa subsericea**

20 (19) a. Leaves 1–3(–5)-jugate; rhachis not winged (fig. 1a). Leaflets 2.8–23.5 cm long; lower surface glabrous, but sometimes very sparsely sericeous, especially on the midrib. Flower 1.5–2.5 mm in diam. Petals 0.3–1.8 mm long, claw absent to up to 0.2(–0.4) mm; scales 0.1–1 mm long **Guioa acutifolia**

b. Leaves (3–)5–7-jugate; rhachis not to very slightly winged (fig. 1a, b). Leaflets 3.8–6.3 cm long; lower surface very sparsely sericeous. Flower c. 2.8 mm in diam. Petals 1.5–1.7 mm long, claw c. 0.3 mm high; scales c. 1 mm long .... **Guioa multijuga**

21 (14) a. Domatia absent or a single sac (fig. 6b). Fruit blackish when dry . . 22

b. Domatia 2 or more, basally sacs to upwards pockets (fig. 6a, b). Fruits reddish to reddish black when dry........... **Guioa comesperma**

22 (21) a. Some to all leaflets with a single (small) sac (fig. 6b) 23

b. All leaflets without a domatium 26

23 (22) a. Leaflets elliptic (fig. 2b). Disc incomplete to complete (fig. 12). Fruit 1.1–2.9 cm high; stipe absent or relatively short (c. 1/15–1/6th of fruit height), up to 4 mm high. Not found on Normanby I. 24

b. Leaflets ovate (fig. 2a). Disc incomplete (fig. 12c). Fruit 1.2–1.5 cm high; stipe relatively high (c. 1/4th of fruit height), 3–3.5 mm high. Normanby I. .... **Guioa normanbiensis**

24 (23) a. Disc incomplete (fig. 12c). Stipe of fruit absent to up to 4 mm long; lobes about as long as broad or broader than long (10–18 by 9–22 mm) . 25

b. Disc complete (fig. 12a). Stipe of the fruit 1–1.5 mm long; lobes much longer than broad (15–16 by 8–12.5 mm)...... **Guioa aryterifolia**

25 (24) a. Leaflets subcoriaceous. Stipe of fruit 2–4 mm high; upper margin of fruit flat to slightly convex (fig. 13a) .... **Guioa membranifolia**

b. Leaflets (sub)coriaceous. Stipe of fruit absent to up to 2 mm high; upper margin of fruit usually highly convex (lobes almost touching; fig. 13c) **Guioa rigidiuscula**

26 (22) a. Leaflets ovate (fig. 2a) 27

b. Leaflets elliptic (fig. 2b) 28

27 (26) a. Leaflets 10.9–30 by 3.8–13.3 cm, index 2.1–2.9; upper surface usually with wax. Disc incomplete (fig. 12c). Fruit wall 1–3 mm thick; stipe of fruit 1–1.5 mm high; lobes about as long as broad, 12–16 by 10–14 mm .... **Guioa grandifoliola**

b. Leaflets 11.9–22.7 by 6.1–10.7 cm, index 1.8–2.1; upper surface without wax. Disc complete (fig. 12a). Fruit wall less than 1 mm thick; stipe of fruit c. 2.5 mm high; lobes usually longer than broad, c. 17 by 12 mm .... **Guioa scalariformis**

28 (26) a. Claw of petals either c. 0.4 mm high and then the crest of the scales well-developed, clavate (fig. 10e) or the claw c. 0.8 mm high and then the crest usually absent or present as part of a bifid scale apex (fig. 10a, c). Disc (nearly) complete (fig. 12a, b). Fruit wall rather thin (c. 1 mm thick); lobes much longer than high 29

b. Claw of petals 0.2–0.4 mm high; crest well-developed, clavate (fig. 10e). Disc incomplete (fig. 12c). Fruit wall very thick (up to 3.5 mm); lobes about as high as long .... **Guioa contracta**

29 (28) a. Claw of petals c. 0.4 mm high; crest well-developed, clavate (fig. 10e). Disc complete (fig. 12a). Stipe of fruit 1–1.5 mm high **Guioa aryterifolia**

b. Claw of petals c. 0.8 mm high; crest usually absent or present as part of a bifid scale apex (fig. 10a, c). Disc (nearly) complete (fig. 12a, b). Stipe of fruit 2–3.3 mm high .... **Guioa unguiculata**

18.7. KEY TO THE SPECIES OF AUSTRALIA

1 a. Domatia (2 or) many. Disc incomplete (fig. 10.c) 2

b. Domatia absent to 1 (or seldom 2). Disc complete (sometimes with 1 or 2 small slits; fig. 12a, b) 3

2 (1) a. Axis usually shortly sericeous when young. Leaflets on lower surface smooth to seldom slightly papillate, glabrous to very sparsely sericeous, domatia basically sacs (fig. 6b). Petals 2.1–3.8 by 0.6–1.7 mm, apex acute. Fruits red to blackish red when dry; stipe slender (fig. 13a), 1.5–4.5 mm high .... **Guioa comesperma**

b. Axis hirsute when young. Leaflets on lower surface papillate, hirsute, domatia basically pockets (fig. 6a). Petals 1–2 by 0.4–1.2 mm, apex obtuse. Fruits blackish when dry; stipe broadly cuneate (fig. 13b), absent to up to 3 mm high .... **Guioa lasioneura**

3 (1) a. Lower surface of leaflets usually very densely, greyish papillate. Petals small or large, 0.3–2.5 by 0.2–1 mm; if large (2–2.5 mm high) then scales not present as inwardly folded margins, scales free (fig. 9b). Fruits 0.5–1.6 cm high by 0.6–2.5 cm broad. Queensland and New South Wales 4

b. Lower surface of leaflets smooth. Petals large, 2–3.5 by 1.7–3 mm; scales present as inwardly folded margins (fig. 9d). Fruits 1.5–2.7 cm high by 2.1–3.4 cm broad. Lord Howe I. .... **Guioa coriacea**

4 (3) a. Leaflets elliptic to obovate (fig. 2b, c), coriaceous to very coriaceous; margin (flat to) revolute; apex retuse to acuminate (to cuspidate; fig. 5 a–f); lower surface sericeous, domatia absent 5

b. Leaflets (ovate to) elliptic (fig. 2a, b), subcoriaceous (to very coriaceous); margin flat; apex (obtuse to) acute to cuspidate (to caudate; fig. 5c–g); lower surface glabrous to very sparsely sericeous, a single domatium usually present in some to all leaflets .... **Guioa acutifolia**

5 (4) a. Apex of leaflets (obtuse to) acuminate (to cuspidate; fig. 5c–f). Large sepals 2.2–3.5 mm high. Petals 2–2.5 by 0.8–1 mm; not distinctly clawed. Fruit 1.2–1.6 cm high by 2–2.5 cm broad. NE Queensland **Guioa montana**

b. Apex of leaflets retuse to acute (fig. 5a–d). Large sepals 1.3–2.5 mm high. Petals 0.5–2 by 0.2–1 mm; claw 0.2–0.7 mm high. Fruit 0.6–1.1 cm high by 0.6–1.4(–1.9) cm broad. Mid E Queensland, SE Queensland to NE New South Wales .... **Guioa semiglauca**

18.8. KEY TO THE SPECIES OF NEW CALEDONIA

1 a. Lower surface of leaflets greyish papillate, dull, sericeous (microscope!) to villose 2

b. Lower surface of leaflets smooth, more or less shiny, glabrous (to very sparsely sericeous) 5

2 (1) a. Disc incomplete (gap sometimes minute; fig. 12a, b). Rhachis slightly winged or not (fig. 1a, b). Lower surface of leaflets shortly sericeous to villose, domatia absent to many; if rhachis winged and indumentum shortly sericeous then no domatia present or if many domatia present then indumentum long, sericeous to usually hirsute 3

b. Disc complete (fig. 12a). Rhachis slightly winged (fig. 1b). Lower surface of leaflets shortly sericeous, domatia (1 to) many . **Guioa crenata**

3 (2) a. Domatia absent or 1 sac (fig. 6b). Indumentum shortly to long sericeous 4

b. Domatia (exceptionally 1 sac to) many large to often very shallow pockets (fig. 6a). Indumentum (short to long sericeous to) hirsute **Guioa villosa**

4 (3) a. Domatia absent or 1 sac (fig. 6b). Rhachis never winged (fig. 1a). Leaflets 1.6–19.8 by 0.6–7.8 cm; margin entire (fig. 4a) .. **Guioa glauca**

b. Domatia absent. Rhachis slightly winged (fig. 1b). Leaflets 0.8–3.6 by 0.3–0.9 cm; margin basically entire to apically crenate (fig. 4e) **Guioa crenulata**

5 (1) a. Sepals distinctly dimorph, largest sepals (1.2–)1.9–3.7 mm high. Disc incomplete either with one large gap or with one or two small slits (latter appearing as complete; fig. 12b, c). Leaflets thin to very coriaceous . 6

b. Sepals equal, 0.6–1.7 mm high. Disc complete (very occasionally with a small gap; fig. 12a, b). Leaflets very coriaceous **Guioa microsepala**

6 (5) a. Rhachis slightly winged or not (fig. 1a, b). Leaflets ovate to elliptic (fig. 2a, b), thin to coriaceous; domatia 1 to many. Petals 0.8–2.3 by 0.4–1.3 mm. Fruit 1.1–1.3 cm high by 0.9–1.8 cm broad 7

b. Rhachis not winged (fig. 1a). Leaflets (ovate to) elliptic (fig. 2a, b), coriaceous to very coriaceous; domatia absent or a single sac. Petals 2–3.5 by 1–3.1 mm. Fruit 1.6–2.4 cm high by 1.6–2.9 cm broad. . . 8

7 (6) a. Rhachis not (to slightly) winged (fig. 1a, b). Leaflets ovate (fig. 2a); domatia 1(–many). Petals 0.8–1.4 by 0.4–1.3 mm. Disc with two minute slits (fig. 12b) . . . . **Guioa gracilis**

b. Rhachis slightly winged (fig. 1b). Leaflets (ovate to) elliptic (fig. 2a, b); domatia (1–)many. Petals 2–2.3 by 1–1.2 mm. Disc with one large gap (fig. 12c) . . . . **Guioa fusca**

8 (6) a. Leaflets 2–8.6 by 0.7–3.1 cm, usually finely wrinkled when dry. Fruits c. 1.6 cm high, 1.6–1.9 cm broad. Disc with a distinct gap (fig. 12c) **Guioa pectinata**

b. Leaflets 4.3–22.7 by 1.5–7.9 cm, not wrinkled when dry. Fruits 1.7–2.4 cm high, 1.7–2.9 cm broad. Disc with 1 or 2 small slits (fig. 12b) **Guioa ovalis**

18.9. KEY TO THE SPECIES OF THE SOLOMON ISLANDS

1 a. Leaflets ovate to elliptic (fig. 2a, b), 3.6–18.3 by 1–8.4 cm. Petals either 0.7–1.3 mm high or 2.8–3 mm high. Disc complete (fig. 12a) 2

b. Leaflets (ovate to) elliptic (fig. 2a, b), 3.8–9.9 by 1.3–3.4 cm. Petals 1.8–2.1 mm high. Disc with a small gap (fig. 12b) . . **Guioa elliptica**

2 (1) a. Leaflets 8.5–18.3 by 2.3–8.4 cm. Petals 0.7–1.3 by 0.5–0.8 mm. Fruits 1.3–1.5 cm high, 1.6–2.1 cm broad. . . . . . . **Guioa sufusana**

b. Leaflets 3.6–11.2 by 1–3.2 cm. Petals 2.8–3 by 1.2–1.4 mm. Fruits 2.2–2.7 cm high, 2.9–3.9 cm broad . . . . **Guioa megacarpa**

18.10. KEY TO THE SPECIES OF THE FIJI ISLANDS

1 a. Leaflets papillate below. Disc complete (fig. 12a) 2

b. Leaflets smooth below, without papillae. Disc incomplete with 1 or 2 small slits (fig. 12b) . . . . **Guioa ovalis**

2 (1) a. Leaflets punctate. Scales of petals 0.5–1.2 mm long; crest not developed to small (fig. 10a, b, e) 3

b. Leaflets not punctate. Scales of petals 0.3–0.5 mm long; crest well-developed, large (fig. 10g) . . . . **Guioa rhoifolia**

3 (2) a. Indumentum sericeous (to hirsute). Leaflets often slightly falcate (fig. 3a, b), rather large, 3.7–16.5 by 1.4–5.7 cm. Scales of petals 0.5–1 mm long, crest not to slighty developed as a cockle (fig. 10a, b) **Guioa chrysea**

b. Indumentum sericeous. Leaflets falcate (fig. 3a), rather small, 2.1–8.2 by 0.6–3.3 cm. Scales of petals 0.8–1.2 mm long, crest usually developed, then small, stiped, clavate (fig. 10e) .... **Guioa punctata**

19. SPECIES DESCRIPTIONS

(The species are described in alphabetical order)

Guioa acuminata Radlk. – Fig. 61a–c.

Guioa acuminata Radlk., Philip. J. Sc. 8, Bot. (1914) 463; Merr., Enum. Philip. 2 (1923) 506; Radlk. in Engl., Pflanzenr. 98 (1933) 1172; Salvosa, Lex. Philip. Pl. (1963) 104. — Lectotype (here proposed): *BS (Ramos) 10916* (M, holo; iso in US), Philippines, Luzon, Laguna Prov., San Antonio.

Guioa perrottetii auct. non Radlk.: Sasaki, Cat. Gov. Herb. (1930) 328, p.p. (*Ramos 10916*).

Tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 2–4 mm thick. *Leaves* 1–3-jugate; rhachis 1.9–12 cm long, basally terete to upwards flattened, not winged, (sub)glabrous, petiole 1.5–8.2 cm long; petiolules up to 0.7 cm long. *Leaflets* not subsessile, opposite to subopposite, ovate to elliptic, somewhat falcate, 5.7–14.4 by 1.6–4.1 cm, index 2.6–4.2, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, flat (to revolute); apex (cuspidate to) caudate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, not papillate, glabrous (to some sparse hairs), domatia a single sac on basiscopic side in axil of second nerve; venation raised;

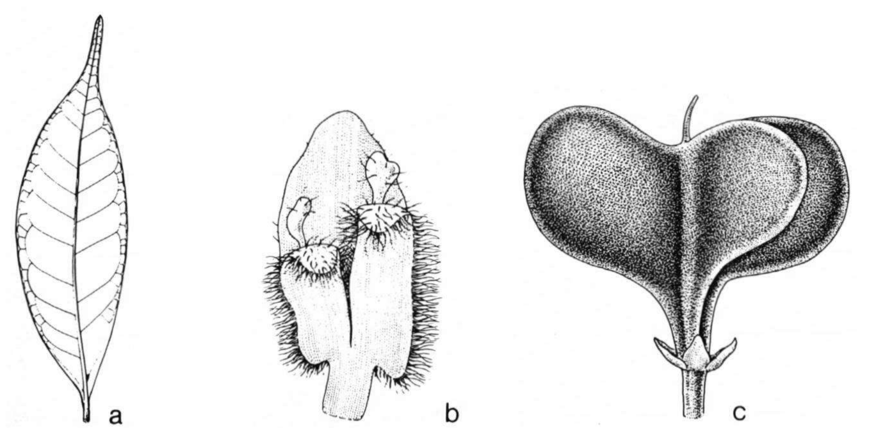


Fig. 61. *Guioa acuminata* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, b: *FPRI (Lagrimas) 523*, L; c: *FB (Miranda) 21144*, A).

nerves 0.4–1.9 cm apart, marginally looped; veins laxly reticulate, indistinct. *Inflorescences* axillary, branching in or near axil to mainly along rhachis; latter flattened, 2.8–16.5 cm long, sericeous; first order branches up to 7.7 cm long; cymules cincinnate, c. 3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.7–2 mm long; bracteoles 0.5–0.8 mm long. *Pedicels* 3–4.4 mm long, sericeous except for the (sub)glabrous 0.5–0.8 mm long upper part. *Flowers* 4–4.3 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1.5–2.3 by 1.2–2.6 mm; 3 inner larger ones 2.2–3.3 by 2.2–3.7 mm, margin petaloid. *Petals* 5, obovate, 3.3–3.7 by 1.2–1.3 mm, blade elliptic, gradually decurrent into the claw, latter 0.4–0.8 mm high, margin pilose, outside and inside glabrous, apex obtuse; scales 2.3–3.2 mm long, free, basally auricled, membranaceous margin distinct; crest a linear appendage, (sub)glabrous. *Disc* incomplete. *Stamens* 8; filament 2–5 mm long, especially basally pilose; anther c. 0.5 mm long, glabrous. *Pistil:* ovary 0.4–2.1 mm long, smooth, subhirsute; style and stigma 0.3–1.5 mm long, elongating in fruit up to 2.7 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 2 or 3 well-developed lobes, c. 1.3 cm high by 1.5 cm broad, rugose-ruminate, glabrous, stipe c. 4 mm long, slender, edge of margin rounded, angle between lobes 90–100°, blackish when dry; dissepiments complete; lobes c. 8 by 8 mm. *Seed* immature.

Field notes. Tree, 6–8 m high, d.b.h. up to 12.5 cm. Twigs brownish. Inflorescences pseudoterminal and axillary. Flowers white.

Distribution. Philippines (Central & E Luzon, Polillo I.).

Ecology. Secondary forest. Alt.: sea-level up to 100 m. Flowering: throughout the whole year.

Vernacular names. Pasi (Bikol), salag (Dumagat); anayen, salab (Tagalog).

Note. This species is characterized by the long leaftip, slightly raised venation on lower leaf surface, single domatium, absence of papillae, elliptic petals with linear, non-pilose crest, and interrupted disc. Fruiting specimens are hardly distinguishable from *Guioa koelreuteria,* only the leaf characteristics remain, which are often difficult to interpret.

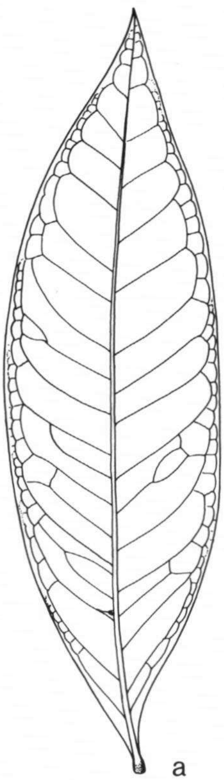
Specimens studied:
PHILIPPINES. Luzon: *BS (Ramos) 10916, 16585,* Laguna Prov., San Antonio; *FB (Tamesis) 15356,* Laguna Prov.; *(Miranda) 21144,* Camarines Prov.; *FPRI (Lagrimas) 525,* Quezon Prov. — Polillo I.: *PNH (Fox) 9186,* Polillo.

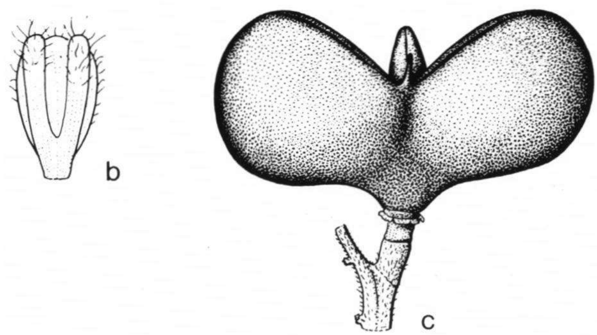
Guioa acutifolia Radlk. – Fig. 62a–c, 63.

Guioa acutifolia Radlk., [Sapind. Holl.-Ind. (1879) 11, nom. nud.] Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 608; Bot. Jahrb. 56 (1921) 278; Domin, Bibl. Bot. 22 (1927) 903; Radlk. in Engl., Pflanzenr. 98 (1933) 1159; C.T. White, Contr. Arn. Arbor. 4 (1933) 60; J.G. Tracey, Veget. Humid Trop. Region N. Queensl. (1982) 106; Reynolds in Stanley & Ross, Fl. S.E. Queensl. 1 (1983) 511, f. 80a; McDonald, Queensl. Bot. Bull. 2 (1984) 53; Reynolds, Austrobaileya 2 (1984) 53; Fl. Austr. 25 (1985) 48, fig. 11d–f, map 58. — [*Cupania semiglauca* var. *acutifolia* F. Muell. ex Radlk., Sapind. Holl.-Ind. (1879) 11, nom. nud.] — *Nephelium semiglaucum* var. *acutifolium* F. Muell. ex Bailey & White, Bot. Bull. Queensl. Dep. Agr. 18 (1916) 9. — Lectotype (here proposed): *Dallachy s.n.* (M, holo; iso in K, L, M, MEL, NSW), Australia, Rockingham Bay. See note 1.

Cupania sericolignis auct. non Bailey: Bailey, Bot. Bull. Queensl. Dep. Agr. 5 (1892) 11, p.p. (Bailey Bellenden Kerr Exp. s.n.); Queensl. Fl. 1 (1899) 294, p.p. See note 2.

(Shrub to) tree. *Branchlets* glabrous, at most sparsely sericeous when young; flowering twigs 1–5(–15) mm thick. *Leaves* 1–3(–5)-jugate (1–6-jugate in vegetative parts); rhachis 1–25 cm long, basally terete to sometimes upwards somewhat flattened, not winged (except for juvenile specimens), glabrous, petiole 0.5–6.6(–8.8) cm long; petiolules up to 0.9 cm long. *Leaflets* usually subsessile, opposite to alternate, (ovate to) elliptic, sometimes slightly falcate, 2.8–23.5 by 1.2–8.7 cm, index 1.8–4.7, usually symmetric, (thin when juvenile to) subcoriaceous (to very coriaceous), usually punctate; base attenuate; margin entire (juvenile leaflets with a few teeth), flat; apex (obtuse to) acute to cuspidate (to caudate), usually mucronulate; upper surface smooth, glabrous except for the sometimes sparsely pilose midrib, sometimes covered with a thick waxy layer; lower surface differently coloured, dull, papillate (often smooth when juvenile), glabrous but sometimes very sparsely sericeous especially on the midrib, domatia usually present in some to all leaflets, 1 (seldom 2) often rather small sacs on basiscopic side in axil of second or third nerve (for exception see note 5); venation of upper surface flat except for the basally raised midrib, on lower surface raised; nerves 0.2–3.9 cm apart, marginally looped, sometimes less so in lower part of leaflets; veins laxly reticulate. *Inflorescences* axillary to rarely pseudoterminal, not branching to branching in or near axil to also along rhachis; latter terete, 0.4–16.8 cm long, usually sericeous; first order branches up to 6 cm long; cymules cincinnate to dichasial, 1–7(–10)-flowered. *Bracts* and *bracteoles* deltoid, outside sericeous, inside glabrous; bracts (0.2–)0.4–1.4 mm long; bracteoles 0.2–0.9 mm long. *Pedicels* 0.5–4 mm long, usually sericeous, except for the (sub)glabrous, 0.3–1.7 mm long upper part. *Flowers* 1.5–2.5 mm in diam. *Sepals* 5 (or 6), broadly ovate to orbicular, margin pilose, with glands, outside sometimes sericeous, inside glabrous; 2 outer smaller ones 0.5–1.7 by 0.5–1.9 mm; 3 (or 4) inner larger ones 1–2.3 by 0.9–2.3 mm, margin petaloid. *Petals* 5, (rhomboid to) obovate, 0.3–1.8 by 0.2–0.8 mm, claw absent to up to 0.2(–0.4) mm high, margin pilose, outside and inside glabrous, apex obtuse to somewhat fimbriate; scales 0.1–1 mm long, free, apex not broadened; crest sometimes developed, then clavate on slender short stipe, glabrous. *Disc* complete. *Stamens* 8; filament 0.7–3 mm long, completely but especially basally pilose; anther 0.2–0.7 mm long, glabrous to papillate. *Pistil:* ovary 0.2–1.3 mm high, smooth, sparsely hirsute; stigma and style 0.1–0.7(–2) mm long, both elongating up to 2 mm in fruit, then upper c. 0.5 mm stigmatic. *Fruit* with 1–2(–3) well-developed lobes, 0.5–1.2 cm high by 0.8–2 cm broad, smooth to rugose-ruminate, glabrous, stipe absent to up to 3 mm high, resp. broadly cuneate to slender, edge of margin rounded, angle between lobes 45–135°, blackish when dry; dissepiments complete; lobes 5.5–12 by 5–8 mm. *Seed* obovoid, 4–8 by 3–5 mm; hilum 0.7–1.7 mm long. *Embryo* 3.8–7.1 by 3–4.6 mm; cotyledons secondarily laterally besides each other, inequal, upper larger, both apices usually elongated, especially of upper, that of lower not recurved over that of upper cotyledon; radicle 1–2.8 mm long.





a

Fig. 62. *Guioa acutifolia* Radlk. a. Leaflet, × 0.5; b. petal, × 25; c. fruit, × 3 (a, b: *A. & M. Thorsborne & Travers 462*, BRI; c: *Van Balgooy 5087*, L).

F i e l d n o t e s. (Shrub to) tree, 2.5–25 m high, d.b.h. 10–45 cm, spindly. Outer bark nondescript, smooth to with small pustules and furrows, blotched variously grey to plum coloured; middle bark green to pink outside; inner bark cream to pink to wine red to light brown, with white fibrous vertical stripes. Wood cream to light straw. Leaves light to usually glossy dark green above; below dull, rather glaucous to grey-green. Flowers sweet scented. Petals creamy green to white to tinged pinkish. Anthers pink. Fruit pink or red.

D i s t r i b u t i o n. Moluccas; Irian Jaya (Vogelkop, Geelvink Bay); Papua New Guinea (Western and Southern Highlands, Central Prov.); NE Australia: N Queensland (Cook, N Kennedy and Wide Bay District). See fig. 63.

E c o l o g y. Scarce to common understorey tree; found in disturbed rain forests, secondary bamboo forests, tall secondary montane forests, regrowth thickets, *Araucaria* vine thickets, along margins of forests, beach forests, water, mangroves, *Melaleuca* swamps. Vegetation types (Tracey, 1982): Usually found in Mesophyll vine forest, Complex notophyll vine forest with emergent *Agathis robusta*; less common in Complex notophyll vine forest, Semideciduous mesophyll vine forest, Simple notophyll vine forest; once recorded in Mesophyll fan-palm vine forest; for a more detailed description of coastal vegetations see McDonald (1984). Humidity: (dry to) moist to very wet. Soil material: (basalt), sand, granite, alluvials and metamorphics (Tracey, 1982). Alt.: sea-level up to 1800 m. Flowering: (March–)May–Sept.(–Oct.). Fruiting: Nov.–Jan.

V e r n a c u l a r n a m e. Mampias (Biak).

N o t e s. 1. Radlkofer as well as Bailey and White referred to F. Mueller as the person who described *Cupania semiglauca* var. *acutifolia* in Fragm. 9 (1875) 98. The word 'varietas' as used by Mueller was falsely interpreted; Mueller did not de-

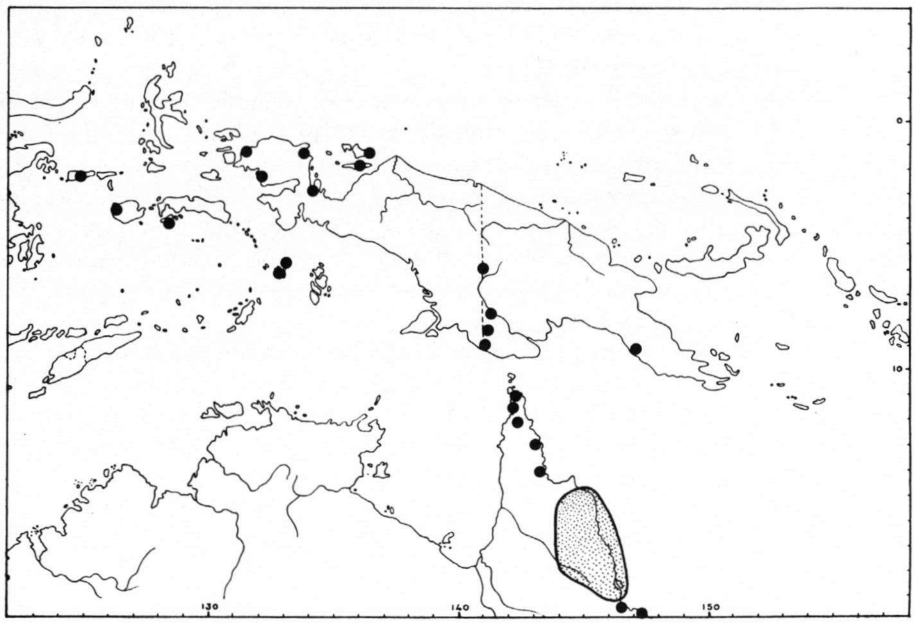


Fig. 63. Distribution map of *Guioa acutifolia* Radlk.

scribe a variety, he did not provide a new name, he merely referred to some 'exceptional specimens'. So, Radlkofer himself was the first to use the non-existing name *Cupania semiglauca* var. *acutifolia,* which he directly placed into the synonymy of *Guioa acutifolia* (1879, Sapind. Holl.-Ind.), he only referred to Von Mueller, he did not mention the publication; in the same year he gave a full description of *Guioa acutifolia,* which made the name valid (1879, Sitzungsber.). Because of the invalid reference to Von Mueller (I.C.B.N. art. 32.3) the specimens mentioned by Radlkofer in the latter publication have to be regarded as the types, not those mentioned by Von Mueller. Of these *Dallachy s.n.* is chosen as lectotype.

2. Bailey described *Cupania sericolignis* on a mixtum, part of it (*Bailey s.n.*, Mulgrave River) belongs to *Guioa acutifolia,* the other part (*Cowley 69a*) is *Lepiderema sericolignis.* The description of Bailey (adhered to the Cowley specimen) only fits the latter, therefore the lectotypification by Radlkofer (Fedde Rep. 20, 1924, 29) of *Cupania sericolignis* with *Cowley 69a* is correct.

3. Tracey (1982) records lowland and highland forms of *Guioa acutifolia,* but he did not explain on which criteria these forms can be recognized. Some possible reasons for the distinction are discussed below:

The material showed a more or less diminishing size of the leaflets with rising altitude, the leaflets also became somewhat more coriaceous. No disjunctions in dimensions were found, so no taxonomic distinction has been made.

There are more or less two fruit forms, of which the most common form almost lacks a stipe, while the other form has somewhat larger fruits and a slender stipe (examples: *Hyland 3695, 6889*).

A different reason for Tracey's opinion could have been the specimen *Webb & Tracey 13251*. This specimen was originally identified as *Guioa acutifolia*, but it actually is a New Guinea species, *Guioa comesperma*. This species is new for Australia. The fruits are different (with a high stipe, red colour, and slender lobes, instead of usually no stipe, black fruits, and lobes which are about as long as broad); the leaflets show many domatia instead of 1 and no papillae (*Guioa acutifolia* is papillate); the petals are well-developed instead of reduced as in *Guioa acutifolia*.

Another reason can be found in note 4.

4. Specimens found in the neighbourhood of salty water (along creeks, beaches, or on small islands) are sclerophilous with a thick waxy layer on the upper leaf surface. The same phenomenon can be observed in specimens of *Guioa bijuga* from poor sandy soil in Borneo. Examples: *Epps 61; Petrie 119a, 167; Sharpe 2073; Tracey 14455; Webb & Tracey 13253; C.T. White 12306.*

5. *Beccari FI 2810* is an exceptional specimen; the leaflets sometimes possess a small subapical tooth, like *Guioa oligotricha*, and instead of a single sac several pockets are present. This specimen may belong to another, new species; for this reason it was not selected as lectotype of *Guioa acutifolia*. Unfortunately, no more material was present; therefore it is still contained in *Guioa acutifolia*.

6. Several specimens in New Guinea possess very long leaflet apices, which make them look different from the more 'normal' specimens of *Guioa acutifolia*. Especially *BW (Versteegh & Vink) 8295* is strange, because the fruits are also slightly different in shape.

7. See also note under *Guioa patentinervis*.

Specimens studied:

MOLUCCAS. *Balgooy 5087*, NW Buru, Waeduna River mouth; *Beccari FI 2808*, Key, Tural; *FI 2809*, idem; *Hulstijn 92*, Taliaboe I., G. Bena, Atje; *Jaheri 435*, Key I.; *Moseley s.n.*, IX-1874, Ki I.

NEW GUINEA. Irian Jaya: *Beccari FI 2810*, Geelvinkbaai, Wandammen; *FI 2811*, Arfak Mts., Putat; *Branderhorst 183*; *Brass 7513*, Lake Daviumbu; *7739*, idem; *BW (Versteegh & Vink) 8295*, Son Biak, Div. Geelvinkbaai; *NIFS bb (van Dijk) 30953*, Seroei, Miosnoem; *Warburg s.n.*, VI-1890, Sigar; *20538*. — Papua New Guinea: Western Prov.: *NGF (Henty et al.) 33216*, Ingembit village; *(Ridsdale & Galore) 33500*, Weam; *(Ridsdale & Galore) 33709*, Junction Bensbach & Tarl rivers. — Central Prov.: *MacGregor s.n.*, s.d., Port Moresby to Kalo.

AUSTRALIA. Queensland: 137 specimens.

Guioa amabilis Kaneh. & Hatus. – Fig. 64 a, b.

Guioa amabilis Kaneh. & Hatus., Bot. Mag. Tokyo 57 (1943) 76, f. 11. — Type: *Kanehira & Hatusima 13999* (TI, holo, n.v.; iso in A), Irian Jaya, Arfak Mts., Anggi.

Shrub. *Branchlets* terete, smooth to rough, shortly sericeous, especially when young; flowering twigs 1–3.5 mm thick. *Leaves* 3–5-jugate; rhachis 0.6–5.4 cm long, terete, slightly winged, wing at most 1 mm broad, slightly pilose, petiole 0.6–1.7 cm long. *Leaflets* subsessile, opposite to alternate, elliptic to obovate, 1–1.9 by

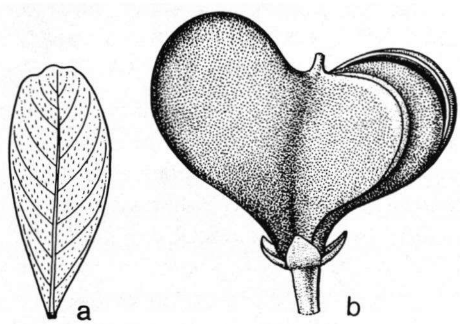


Fig. 64. *Guioa amabilis* Kaneh. & Hatus. a. Leaflet, × 1.5; b. fruit, × 3 (*BW (Sleumer & Vink) 14124*, L).

0.5–0.9 cm, index 1.7–2.4, often asymmetric, then acroscopic side broader, very coriaceous, usually punctate; base attenuate; margin entire, except for the usually crenate apex, revolute; apex emarginate to acute, sometimes mucronulate; upper surface smooth, glabrous except for the sometimes puberulous midrib, often covered with wax; lower surface differently coloured, duller, papillate, sericeous, domatia absent; venation on upper surface flat to slightly raised, raised below; major nerves 0.1–0.4 cm apart, marginally looped; veins densely reticulate, inconspicuous. *Inflorescences* axillary to pseudoterminal, not to at most branching along the rhachis; latter terete, 0.6–9.7 cm long, sericeous; first order branches up to 0.5 cm long; cymules cincinnate, 1- or 2-flowered. *Bracts* and *bracteoles*
0.5–1.3 mm long; bracteoles 0.3–0.6 mm long. *Pedicels* 2–4 mm long, sericeous; upper part less pilose, 0.8–1.8 mm long. *Flowers* in bud. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1.4–2 by 1.6–2.2 mm; 3 inner larger ones 2.2–3 by 2.2–3 mm, margin petaloid. *Petals* still immature, 5, clawed, margin pilose, outside and inside glabrous; scales still small. *Disc* complete. *Stamens* 8; filament 1.7–2 mm long, completely but especially basally pilose; anther c. 0.6 mm long, glabrous. *Pistil:* ovary c. 0.5 mm high, smooth, subhirsute; style and stigma c. 0.2 mm long, elongating in fruit up to 3.7 mm long, then upper 0.5 mm stigmatic. *Fruit* with 2 or 3 well-developed lobes, 1–1.2 cm high by 1.1–1.4 cm broad, smooth to slightly rugose, glabrous, stipe 1.5–2 mm high, broadly cuneate, edge of margin rounded, angle between lobes 135–160°, blackish when dry; dissepiments complete; lobes 7–9 by 7–9 mm. *Seed* immature.

Field notes. Shrub, 1–5 m high. Buds light green, tinged with red. Sepals light green. Petals white. Filaments light green; anther pink. Fruits brownish red.

Distribution. Irian Jaya (Vogelkop).

Ecology. Scarce to common. Found at mountain forest edges and in occasionally burned scrubs. Soil: grey clay. Alt.: 2300–2500 m. Flowering: Jan.

Note. See notes under *Guioa pseudoamabilis* and *Guioa venusta*.

Specimens studied:
NEW GUINEA. Irian Jaya: *BW (Sleumer & Vink) 14124*, Mt. Mobreimot (Koebre), above Testega, Anggi Lakes; *14202*, Mt. Sensenemes, Anggi Gigi Lake; *Kanehira & Hatusima 13999*, Arfak Mts., Anggi.

Guioa aryterifolia Radlk. – Fig. 65 a–c.

Guioa aryterifolia Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20 (1890) 357; Bot. Jahrb. 56 (1921) 282; Baker in Rendle, J. Bot. 61, Suppl. (1923) 11; Radlk. in

Engl., Pflanzenr. 98 (1933) 1174; P. van Royen, Man. For. Trees Papua & N.G. 2 (1964) 24, f. 11; Streimann, Pl. Upper Watut Watershed (1983) 169. — Lectotype (here proposed): *Forbes 870* (M, holo; iso in BM, MEL, P), Papua New Guinea, Owen Stanley Range.

Shrub to tree. *Branchlets* terete, smooth, usually sericeous when young; flowering twigs 3–10 mm thick. *Leaves* 2–4-jugate; rhachis 4–21 cm long, terete, not winged, glabrous, petiole 2.6–7.3 cm long. *Leaflets* subsessile, opposite to alternate, elliptic, 6.3–19.2 by 2.5–7.1 cm, index 2.2–3, usually rather symmetric, sometimes acroscopic side broader, coriaceous, usually punctate; base attenuate; margin entire, flat; apex acute to cuspidate, often mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous (to sparsely sericeous), domatia absent or at least in some leaflets a single small sac on basiscopic side in axil of second major nerve; venation on upper side flat (to raised), raised on lower; major nerves 0.3–2.9 cm apart, usually marginally indistinctly looped, especially in the lower part of the leaflets; veins laxly reticulate, often distinct. *Inflorescences* axillary to ramiflorous, not branching to branching in axil and especially along rhachis; latter flattened to terete when in fruit, 3–13 cm long, sericeous, glabrescent; first order branches up to 3.9 cm long; cymules cincinnate, c. 2-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.7–0.9 mm long; bracteoles 0.2–0.6 mm long. *Pedicels* 3.3–5.5 mm long, sericeous; upper part 1.8–3.2 mm long. *Flowers* c. 3.2 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside sometimes sparsely pilose, inside glabrous; 2 outer smaller ones 1–1.7 by 1.2–2 mm; 3 inner larger ones 1.8–2.5 by 1.8–2.8 mm, margin petaloid. *Petals* 5, obovate, 1.8–1.9 by 0.6–0.9 mm, claw c. 0.4 mm high, margin pilose, outside and inside subglabrous, apex acute; scales c. 1 mm long, free; crest clavate, stiped, apex lobed. *Disc* complete. *Stamens* 8; filament 2.6–2.8 mm long, completely but especially basally pilose; anther c. 0.5 mm

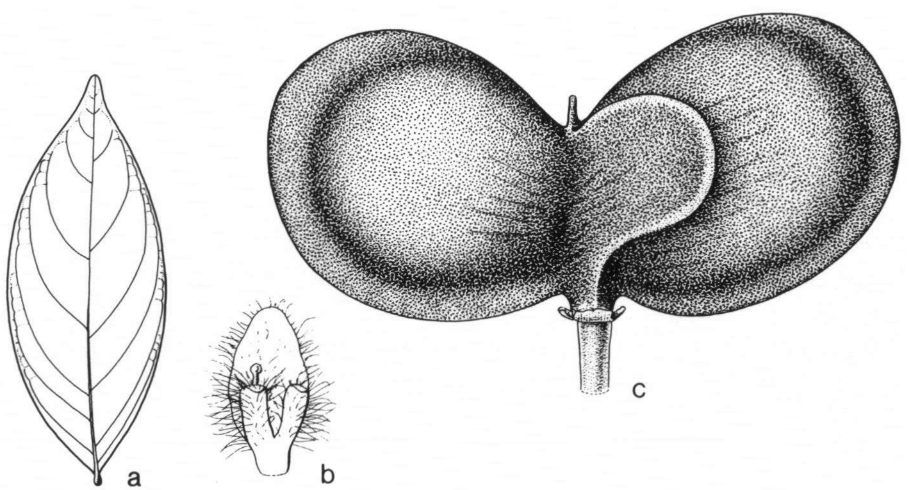


Fig. 65. *Guioa aryterifolia* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *Brass 614*, L; b: *NGF (Sayers) 19394*, L).

long, glabrous. *Pistil:* ovary c. 0.3 mm long, smooth, subhirsute; style and stigma c. 0.1 mm long, elongating in fruit up to 1.5 mm long, then upper c. 0.4 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.3–1.6 cm high by 1.6–3.3 cm broad, rough to slightly rugose or ribbed, glabrous, stipe 1–1.5 mm high, slender, edge of margin rounded, angle between lobes 90–125°, black when dry; dissepiments complete; lobes 15–16 by 8–12.5 mm, broadly spreading; wall thin to rather thick, not exceeding 1 mm. *Seed* globose to obovoid, c. 10 by 7 mm; arilloid without or with a small pseudo-funicle, but always with a basal rim; hilum c. 1.5 mm long. *Embryo* c. 8.5 by 5.5 mm; cotyledons dorsoventrally above each other, about equal in size, apex of upper one elongated, straight; radicle c. 3.3 mm long.

Field notes. Shrub to tree, 5–20 m high, d.b.h. up to 45 cm. Bark grey, thin. Leaflets shiny dark green above. Flowers tasting sweet and faintly smelling. Petals white. Fruits brown when old.

Distribution. Papua New Guinea (Central Prov.).

Ecology. Common. Found in lowland rain forest, the edge of the forest, and in secondary forest. Alt.: 50–1330 m. Flowering: April.

Notes. 1. This species is part of the *Guioa rigidiuscula*-complex (characterized by the type of petal). Typical are the complete disc; fruits with a short slender stipe, a thin wall, and lobes which almost spread over 180°; the lobes are longer than broad; the venation, with rather hardly arching major nerves, is characteristic too. The differences between this species and the other species of the *Guioa rigidiuscula*-complex are discussed in chapter 9.

2. Surprising is the complete disc. Most other species within the *Guioa rigidiuscula*-complex have an interrupted disc. Radlkofer (1933) placed *Guioa aryterifolia* in the subgenus *Hemigyrosa* (defined by its incomplete disc), presumably to retain an indication of the relationship with the other species of this complex. Young buds of *Guioa aryterifolia* may still show a small gap in the disc. So the ontogeny shows that in this species the complete disc is an autapomorphy (it does not necessarily mean that a complete disc is apomorphous for all species).

3. *Guioa molliuscula, Guioa scalariformis,* and *Guioa unguiculata* also have a complete disc. The first is hirsute, the others are sericeous at most. *Guioa scalariformis* has much larger broader leaflets (11.9–22.7 by 6.1–10.7 cm, index 1.8–2.1; *Guioa aryterifolia:* 6.3–19.2 by 2.5–7.1 cm, index 2.2–3) with a rather closed venation and much larger petals (2.5–3.8 mm long; *Guioa aryterifolia:* 1.8–1.9 mm). *Guioa unguiculata* has long clawed petals (petals 2–3.2 mm, claw c. 0.8 mm long; *Guioa aryterifolia:* claw c. 0.4 mm) with at least several scales without a crest.

Specimens studied:

PAPUA NEW GUINEA. Central Prov.: *Brass 614,* Bisiatabu?; *Carr 13410,* Boridi; *Forbes 870,* Owen Stanley's Range; *NGF (Sayers) 19594,* Cape Rodney; *Sayer s.n.,* s.d. (M), Mt. Obree. — Unknown: *Anonymous 2* (MEL 31986).

Guioa asquamosa Welzen – Fig. 66 a–c.

Guioa asquamosa Welzen, Blumea 33 (1988) 411. — Type: *Metzner 227* (L, holo), Lesser Sunda Islands, Timor, 1200 m alt.

Guioa spec.: Verheijen, Dict. Manggarai Pl., Pac. Ling. ser. D, 43 (1982) 104.

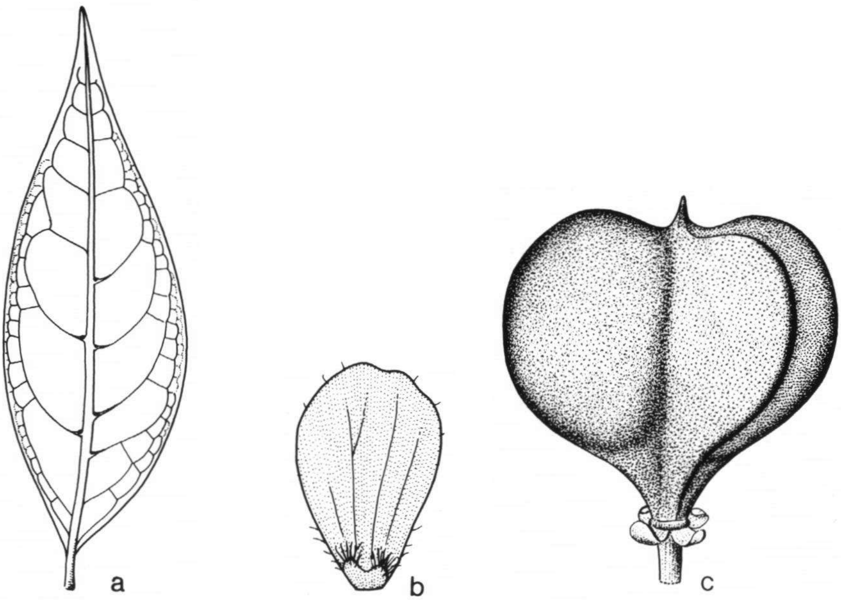


Fig. 66. *Guioa asquamosa* Welzen. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, b: *Metzner 226*, L; c: *Schmutz 595*, L).

Tree. *Branchlets* terete, smooth, usually sericeous when young; flowering twigs 1.5–3 mm thick. *Leaves* 2–4-jugate; rhachis 4.6–19 cm long, terete to upwards flattened above, not winged, subglabrous, petiole 2.8–8 cm long; petiolules up to 0.9 cm long. *Leaflets* not subsessile, opposite (to alternate), ovate, 2.9–10.8 by 0.9–3.3 cm, index 2.9–3.9, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, flat; apex acuminate to cuspidate, not mucronulate; upper surface smooth, glabrous, sometimes wax layer present; lower surface differently coloured, more dull, smooth, no papillae, glabrous to very sparsely pilose, domatia (absent to) a single to many sac(s), in axil of basiscopic second nerve to in axils of the major nerves; venation on upper side flat to raised, raised below; nerves 0.3–1.6 cm apart, marginally looped; veins laxly reticulate, rather distinct. *Inflorescences* axillary, mainly only branching along rhachis; latter terete to somewhat flattened, 2.2–13.2 cm long, subsericeous; first order branches up to 4.2 cm long; cymules cincinnate, 2- or 3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.7–0.9 mm long; bracteoles 0.3–0.6 mm long. *Pedicels* 3–6 mm long, subsericeous, upper part less pilose, 2–3.4 mm long. *Flowers* c. 4 mm in diam. *Sepals* 5, ovate, margin pilose, without glands, outside and inside glabrous; 2 outer smaller ones 1.3–1.8 by 1.3–1.8 mm; 3 inner larger ones 2.2–2.7 by 2.2–2.7 mm, margin petaloid. *Petals* 5, (elliptic to) obovate, 1.5–2.5 by 1.1–1.7 mm, claw 0.1–0.2 mm high, margin pilose, outside and inside glabrous, apex retuse to acute; scales free, very short, 0.1–0.3 mm high; crest absent.

Disc complete. *Stamens* 8; filament 1.4–3.5 mm long, especially basally pilose; anther 0.4–0.7 mm long, glabrous. *Pistil:* ovary 0.5–1.5 mm high, smooth, subhirsute; style and stigma 0.2–1.5 mm long, elongating in fruit up to 2 mm, then upper c. 0.4 mm stigmatic. *Fruit* with 1 or 2 well-developed lobes, c. 1.4 cm high by 1–1.4 cm broad, smooth, glabrous, stipe c. 2 mm high, broadly cuneate, angle between lobes c. 120°, blackish when dry; lobes c. 9 by 9 mm. *Seed* not mature.

Field notes. Medium-sized tree.

Distribution. Lesser Sunda Islands (Flores, Timor).

Ecology. Alt.: 800–1200 m. Flowering: May to June.

Vernacular names. W Flores: simpar (Manggarai, Denge dial.; Verheijen, 1982).

Note. Typical are the ovate leaflets (like in *Guioa pubescens*), the reduced scales on the petals (only remnants remain, often only a tuft of hairs), and the rather large fruits (like in *Guioa bijuga, Guioa pubescens,* but unlike the smaller ones of *Guioa diplopetala*). This species is closely related to *Guioa diplopetala,* because the leaflets lack papillae and the disc is complete. It differs from *Guioa diplopetala* by the shape of the leaflets, the almost absent scales, and the size of the fruits.

Specimens studied:

LESSER SUNDA ISLANDS. Flores: *Schmutz 595, 3547; Verheijen 1621, 1622.* — Timor: *Metzner 226, 227.*

Guioa bicolor Merr. – Fig. 67 a, b.

Guioa bicolor Merr., Philip. J. Sc. 17 (1920) 279; En. Philip. 2 (1923) 507; Radlk. in Engl., Pflanzenr. 98 (1933) 1170; Salvosa, Lex. Philip. Pl. (1963) 104. — Type: *BS (Ramos & Pascasio) 34487* (PNH, holo, †; iso in A, K, P), Philippines, Mindanao, Surigao Prov.

Tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 1–6 mm thick. *Leaves* 2–5-jugate; rhachis 2.8–20.5 cm long, basally terete to upwards flattened above, not winged, glabrous, petiole 2.1–9.1 cm long; petiolules up to 1 cm long. *Leaflets* not subsessile, opposite to subopposite, ovate to elliptic, 3.7–11.3 by 0.8–4.8 cm, index 2.4–4.6, asymmetric, not falcate, acroscopic side broader, coriaceous to very coriaceous, punctate; base attenuate; margin entire, flat to revolute; apex acuminate to caudate, usually abruptly narrowing (with a sinus), usually mucronulate; upper surface smooth, glabrous except for the sometimes puberulous midrib; lower surface differently coloured, dull, brownish to greyish papillate, glabrous to shortly subsericeous, domatia absent to a single small sac on basiscopic side in axil of second nerve; venation raised, above not differently coloured from lamina; veins 0.2–2.3 cm apart, marginally looped, but often less distinctly so in lower part of leaflets; nerves densely to laxly reticulate, rather distinct. *Inflorescences* axillary, not branching to branching in or near axil and along rhachis; latter flattened, 1.9–14.4 cm long, subsericeous, glabrescent; first order branches up to 6.4 cm long; cymules cincinnate, c. 3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.6–1.3 mm long; bracteoles 0.3–0.9 mm long. *Pedicels* 2.5–4.9 mm long, sericeous, glabrescent, upper part 0.7–2.5 mm long. *Sepals* 5, ovate, margin pilose, with glands, outside and inside (sub)glabrous; 2 outer

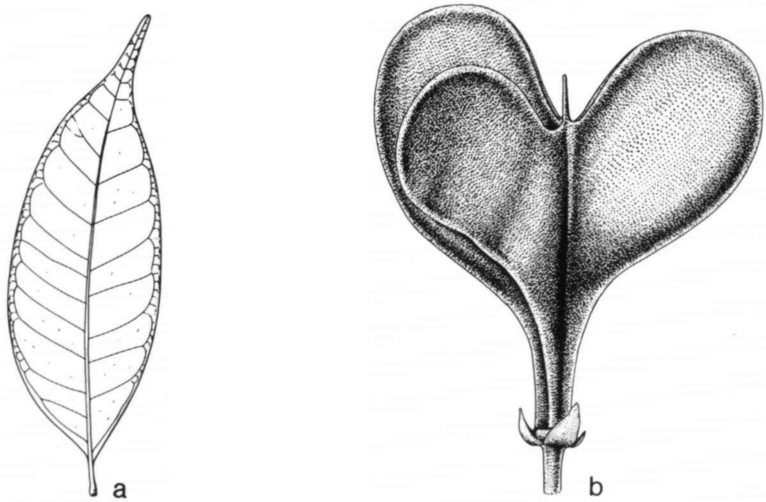


Fig. 67. *Guioa bicolor* Merr. a. Leaflet, × 0.5; b. fruit, × 3 (*BS (Ramos & Edaño) 33798*, A).

smaller ones 0.9–1.5 by 1.3–1.5 mm; 3 inner larger ones 2–3.5 by 1.8–3.5 mm, margin petaloid. *Petals* 5, immature, margin pilose, outside and inside glabrous, blade obovate, gradually decurrent into stipe; scales free; crest present as pilose flat part of bifid scale apex. *Disc* incomplete. *Stamens* 8, immature; filament especially basally pilose; anther glabrous. *Pistil:* ovary immature, smooth, subhirsute; style and stigma elongating in fruit up to 2 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, c. 1.5 cm high by 1.5–2.1 cm broad, smooth, glabrous, stipe c. 3.5 mm high, slender, angle between lobes 90–120°, blackish when dry; lobes c. 11 by 5 mm. *Seed* obovoid, c. 9 by 5 mm; hilum c. 1.4 mm long. *Embryo* c. 8.6 by 4.8 mm; cotyledons secondarily laterally besides each other, lower larger, only apex of upper elongated, straight; radicle c. 2.5 mm long.

Field notes. Tree, 1–15 m high, d.b.h. at least 4 cm. Bark grey. Wood white, hard. Leaflets submembranaceous, tough, dark green above, glaucous or light grey below, flat and horizontally spreading. Inflorescence ascending. Buds dark wine red. Calyx pink. Corolla pinkish on outside, creamy white inside. Stamens light pink.

Distribution. Philippines (Luzon, Mindanao, Sabtang I.).

Ecology. On ridges, in woods, cut forest. Soil: iron deposits present. Alt.: 130–850 m. Bud: April. Fruiting: May.

Vernacular names. Uyos (Cebu Bisaya); canilum (Palawan I.).

Note. Typical for this species are the leaflets with many veins, an apex with a sinus, a lower surface with none or 1 domatium, papillae, shortly sericeous indumentum, and the fruits with a long stipe and long narrow lobes.

See also note undei *Guioa discolor*.

S p e c i m e n s   s t u d i e d:
PHILIPPINES. Luzon: *BS (Yates) 25450*, Tayabas Prov.; *(Yates) 25469*, Mt. Cadig; *(Ramos & Edaño) 33798*, Camarines Prov., Paracale; *(Ramos & Edaño) 45664*, Tayabas Prov., Mt. Alzapan. — Mindanao: *BS (Ramos & Pascasio) 34487*, Surigao Prov. — Sabtang I.: *BS (Ramos) 79891*, Sabtang.

Guioa bijuga (Hiern) Radlk. – **Fig. 68a–c, 69.**

Guioa bijuga (Hiern) Radlk., Sapind. Holl.-Ind. (1879) 38; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 521, 611; Craib, Fl. Siam. En. 1 (1926) 332; Radlk. in Engl., Pflanzenr. 98 (1933) 1165; Corner, Gard. Bull. Str. Settl. 10 (1939) 44; Ways. Trees (1940) 588; Desch, Mal. For. Rec. 15 (1954) 526; Meijer, Bot. News Bull. 9 (1967) 74; Brünig, Heidewald Sarawak Brunei (1968) 372; Corner, Gard. Bull. Suppl. 1 (1978) 153. — *Cupania pleuropteris* Blume var. *bijuga* Hiern in Hook. f., Fl. Br. Ind. 1 (1875) 677. — *Guioa pleuropteris* Radlk. var. *bijuga* King, J. As. Soc. Beng. 65, II (1896) 444; Ridley, Fl. Mal. Pen. 1 (1922) 505. — T y p e: *Wallich 8094* (K, holo; iso in BM, K), Malaya, Penang.

[*Guioa rubrofusca* Radlk. ex Merr., Pl. Elm. Born. (1929) 175, nom. nud.; Radlk. in Engl., Pflanzenr. 98 (1933) 1177; Masamune, En. Phan. Born. (1942) 427. Based on *Elmer 21392*.] See note 2.

Tree. *Branchlets* terete, smooth (to somewhat ribbed to rough), usually glabrous, at most shortly sericeous when young; flowering twigs 1–7.5 mm thick. *Leaves* 1–4-jugate; rhachis 0.8–16.8 cm long, usually above flattened, not to often (slightly) winged, wing up to 2 mm broad, rhachis at most puberulous, petiole 0.7–11 cm long. *Leaflets* subsessile, opposite to subopposite (to alternate), elliptic, 2.1–20 by 1.1–8.4 cm, index 1.2–4, usually symmetric, subcoriaceous to very coriaceous,

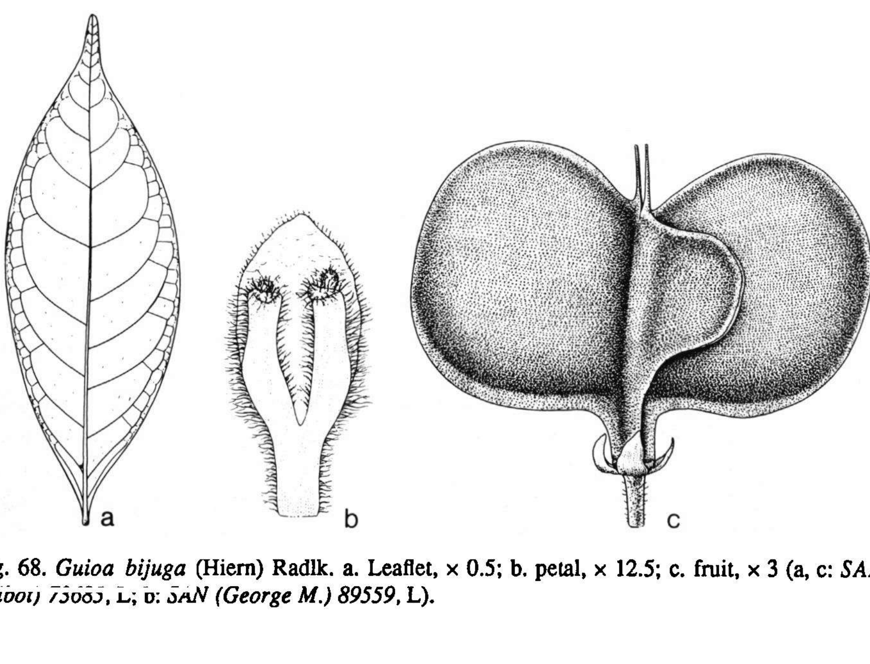


Fig. 68. *Guioa bijuga* (Hiern) Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *SAN (Gibot) 73683*, L; b: *SAN (George M.) 89559*, L).

punctate; base sharply attenuate; margin entire (except juvenile leaflets with a few teeth), flat to seldom revolute; apex abruptly (acuminate to) cuspidate, very apex obtuse (to acute), not mucronulate; upper surface smooth, glabrous (except sometimes sparsely puberulous on the midrib) to slightly sericeous; lower surface differently coloured, duller, smooth to sometimes slightly papillate, glabrous to sometimes sparsely sericeous especially on the midrib, domatia absent or a single small sac on basiscopic side in axil of second or third nerve (see also note 3); venation on upper surface (slightly sunken to) flat to raised, not differently coloured from lamina, below raised; nerves 0.3–4.2 cm apart, marginally looped, sometimes less so in lower third of leaflets; veins laxly reticulate, rather indistinct. *Inflorescences* axillary (to pseudoterminal), (not branching to) branching in or near axil to especially along rhachis; latter terete to triangular to flattened, 0.7–16.5 cm long, glabrous to sericeous (to shortly hirsute); first order branches up to 7.4 cm long; cymules cincinnate, 1–3(–6)-flowered. *Bracts* and *bracteoles* deltoid to triangular, outside sericeous, inside (sub)glabrous; bracts 0.5–1.9 mm long; bracteoles 0.2–1 mm long. *Pedicels* 2.2–10 mm long, sericeous, upper part sometimes less pilose, 0.8–3.3 mm long. *Flowers* 3.5–4.2 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside (sub)glabrous; 2 outer smaller ones 1–2.8 by 1–2.3 mm; 3 inner larger ones 1.4–3.4 by 1.2–3.8 mm, margin petaloid. *Petals* 5, obovate, 1.8–3.8 by 0.7–1.7 mm, blade orbicular, gradually decurrent into the claw, latter 0.4–1.2 mm high, margin pilose, outside and inside (sub)glabrous, apex emarginate to acute; scales (0.8–)1.2–2 mm long, free, basally without auricles, membranaceous margin indistinct, apex not to hardly broadened; crest present as a pilose flat part of the bifid scale apex. *Disc* incomplete. *Stamens* 8; filament 1.6–5 mm long, especially basally pilose; anther 0.2–0.4 mm long, glabrous. *Pistil:* ovary 0.3–1.8 mm high, sparsely hirsute; style and stigma 0.2–2.5 mm long, elongated in fruit up to 3.2 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.2–2.3 cm high by 1.3–2.6 cm broad, smooth to somewhat ribbed or rugose-ruminate, glabrous, stipe 2–5 mm high, rather slender, edge of margin rounded, angle between lobes 95–150°, blackish when dry; dissepiments complete; lobes 8.5–14 by 8–16 mm. *Seed* (globose to) obovoid, 8–9.8 by 7–7.8 mm; hilum 1.1–2 mm long. *Embryo* 7–8.9 by 5–6.9 mm; cotyledons secondarily laterally besides each other, upper larger, apices (not elongated to) elongated, upper usually straight, lower recurved; radicle 2.8–4 mm long.

Field notes. Tree, 3–30 m high, d.b.h. 5 cm to 1 m; bole straight. Outer bark smooth to somewhat finely fissured, usually hard, usually whitish to (dark) grey, with dark patches, but also red-brown to brown, c. 0.15 cm thick; inner bark yellow to pink to red to brown, sometimes fibrous, 0.25–0.5 cm thick. Cambium white to yellow, sometimes pink to red. Sapwood brown to usually white with brown growth rings; heartwood pinkish brown. Leaves shiny dark green above; light green below. Inflorescence light green. Sepals green. Petals white to yellow.

Distribution. Thailand, Malaysia, Sumatra, Borneo, Philippines (Balabac I., Palawan). See fig. 69.

Ecology. Often common. Found in lower and middle storey of primary and especially secondary forest, savannah (kerangas), along roads, rivers, margin of

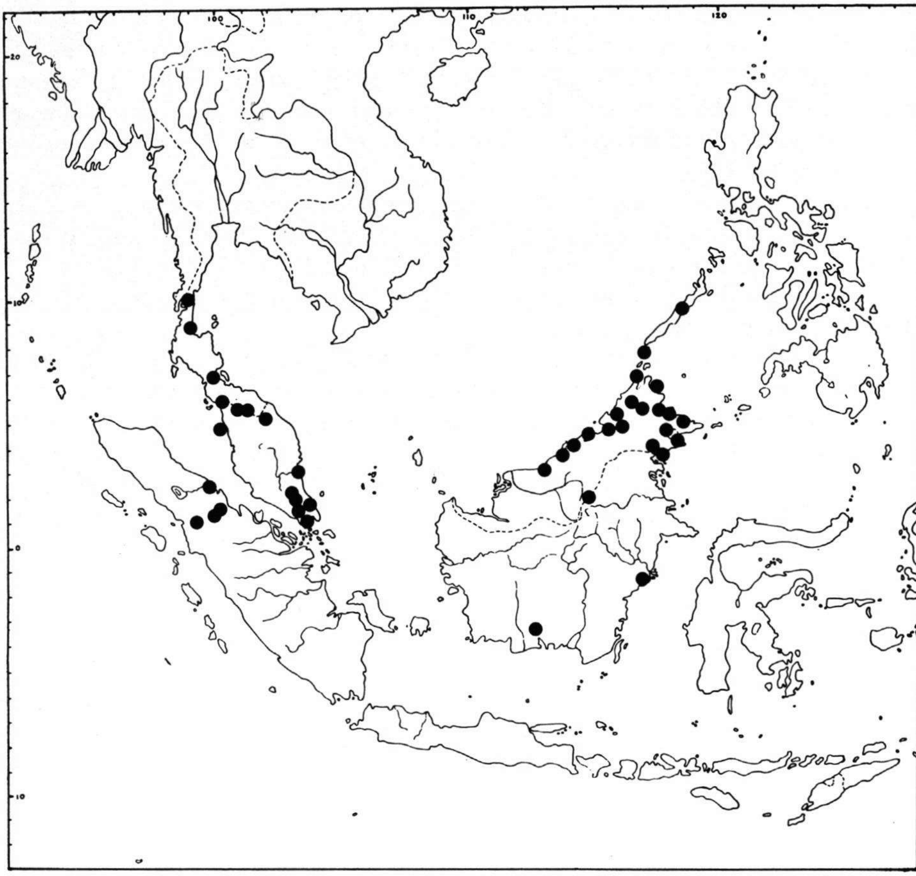


Fig. 69. Distribution map of *Guioa bijuga* (Hiern) Radlk.

forest, mangrove, in peat swamp, sometimes in cultivated fields. Soil: sandstone, podsolized white sand, ultrabasic, red-yellow loam. Alt.: sea-level up to 1525 m. Flowering season: mainly (Nov.–)Febr.–March(–April), less so in Aug.–Sept. Fruiting season: mainly March–June, less so in Sept. and Oct.

W o o d. Weight and hardness: soft and light. Grain straight; texture fine and even. Sapwood and heartwood not differentiated; light brown with pink tinge. Durability variable from unlikely to resist decay and termite attack to resistant to powder-post beetles or sap-stain fungi. Growth rings distinct to the naked eye, narrow layer of terminal parenchyma present. Vessels moderately small to medium-sized; moderately few to numerous; solitary and in radial groups of 2 or 3 or several, the groups of several vessels often with one medium-sized vessel followed by two radial rows of moderately small vessels, sometimes a medium-sized vessel at either end of two radial rows of chains of small vessels, groups predominating over solitary vessels; vessels open. Wood parenchyma sparse, in narrow terminal layers and occasionally diffuse strands scattered throughout the fibres. Rays extremely fine or very fine, extremely low; visible only with a lens on transverse and tangential surfaces, inconspicuous on radial surface. Ripple marks absent. Intercellular canals not observed. (After Desch, 1954.)

Vernacular names. Malaysia: pena-pena, sempayan ulur, senyamak (Kelantan); medang. E coast Sumatra: kaju assibang, kaju langsat, kaju si margalagala, kaju pinggol-pinggol. Borneo: buah sungket (Kedaya); lapak lapak (Murut); tinggal asam (Murut Tenom); rupag (Sungei Kinabatangan); bengkulat (Dusun Labuk). Philippines: busikag (Sulu).

Notes. 1. Several specimens, growing on poor white sand, have smaller leaflets (3.2–14 by 1.5–7.9 cm) which are very thick and scleromorphic (resp. 3.9–19.6 by 1.8–8.4 cm and thinner, less scleromorphic in specimens on richer soils). Examples of the more scleromorphic specimens: *BRUN 5083, 5426, 5427, Jacobs 5667, Keith 2620, Van Niel 3498, 4311, S 2233, SAN 16110, 78048, 80015.*

2. Due to the 'premature' death of Radlkofer (see Merrill, 1929, 173) a description of *Guioa rubrofusca* is not provided (see also in Engler, 1933, 1177). The field notes, as cited by Merrill, cannot be considered as a description as Merrill always provides Latin descriptions of his new species. Masamune, who also refers to this species, does not provide a Latin description either, therefore the name is a mere nomen nudum.

3. One specimen is exceptional: *S 32186:* leaflets with many pockets, lower side very papillate and somewhat sericeous.

4. The difference between *Guioa bijuga* and *Guioa pubescens* is often rather vague in Borneo. Usually, *Guioa bijuga* has elliptic leaflets which are smooth and usually glabrous below; the fruits are glabrous too. *Guioa pubescens* usually has ovate leaflets which are papillate below and sericeous, the fruits are glabrescent. In Borneo *Guioa bijuga* can be papillate and somewhat sericeous, while *Guioa pubescens* can have rather elliptic and more glabrous leaflets, especially in Sarawak and on the Kinabalu. Then the more ovate shape of the leaflets and the few hairs on the fruit remain always indicative for *Guioa pubescens* and the above flattened to winged rhachis for *Guioa bijuga*. There also remain anatomical differences: *Guioa bijuga* always possesses secretory idioblasts which *Guioa pubescens* always lacks.

Specimens studied:
THAILAND: 6 specimens. — MALAY PENINSULA: 38 specimens. — SUMATRA: 8 specimens. — BORNEO: 79 specimens. — PHILIPPINES: *BS (Mangubat) 463*, Balabac I.; *Ebalo 483*, Palawan, Mt. Salacat.

Guioa chrysea A.C. Smith – Fig. 70a–c.

Guioa chrysea A.C. Smith, Sargentia 1 (1942) 54; J. Arn. Arbor. 31 (1950) 292; Parham, Pl. Fiji Is. (1964) 174; Pl. Fiji Is., rev. ed. (1972) 247; A.C. Smith, Fl. Viti. 3 (1985) 599, fig. 144a–c. — Type: *Degener 14398* (A, holo; iso in K, NY), Fiji, Viti Levu, Tholo North Prov., vicinity of Nandarivatu.

Guioa capillacea A.C. Smith, J. Arn. Arbor. 31 (1950) 293; Parham, Pl. Fiji Is. (1964) 174; Pl. Fiji Is., rev. ed. (1972) 247; A.C. Smith, Fl. Viti. 3 (1985) 599, fig. 144d. — Type: *A.C. Smith 1715* (A, holo; iso in BO, K, NY, P), Fiji, Vanua Levu, Mbua Prov., Lower Wainunu River valley.

Shrub to tree. *Branchlets* terete, smooth (to ribbed to rough), sericeous (to hirsute), especially when young; flowering twigs 2–5 mm thick. *Leaves* 2–4-jugate; rhachis 2.7–16.7 cm long, especially upwards somewhat dorsoventrally flattened, not winged, subsericeous (to hirsute), petiole 1.4–6.2 cm long; petiolules up to 1 cm long. *Leaflets* not subsessile, (opposite to) subopposite (to alternate), ovate (to elliptic), often slightly falcate, 3.7–16.5 by 1.4–5.7 cm, index 2–3.8, base somewhat asymmetric, acroscopic side broader, coriaceous (to very coriaceous), punctate; base attenuate; margin entire, flat (to revolute); apex acute to gradually cuspidate, not mucronulate; upper surface smooth, subglabrous to puberulous on the venation; lower surface differently coloured, dull, papillate, sericeous (to hirsute), domatia a single to many large sac(s) in axils of nerves, opening long; venation usually raised, especially on lower side; nerves 0.3–2.7 cm apart, marginally looped; veins usually densely reticulate, conspicuous. *Inflorescences* axillary to pseudoterminal, only branching along rhachis; latter somewhat flattened, 1.1–16.5 cm long, sericeous (to hirsute); first order branches up to 8.7 cm long; cymules (cincinnate to) dichasial, 4–8-flowered. *Bracts* and *bracteoles* deltoid to triangular, outside sericeous, inside only basally pilose; bracts 0.5–1.9 mm long; bracteoles 0.2–1 mm long. *Pedicels* 2–7 mm long, sericeous (to hirsute), also the 0.9–3.9 mm long upper part. *Flowers* 3–3.8 mm in diam. *Sepals* 5, ovate, margin pilose, without glands, outside basally slightly pilose, inside glabrous; 2 outer smaller ones 0.5–1.3 by 0.7–1.6 mm; 3 inner larger ones 1.4–2.5 by 1.4–2.4 mm, margin petaloid. *Petals* 5, elliptic, 1.2–2.3 by 0.3–1.3 mm, claw 0.1–0.3 mm high, margin pilose, outside and inside very

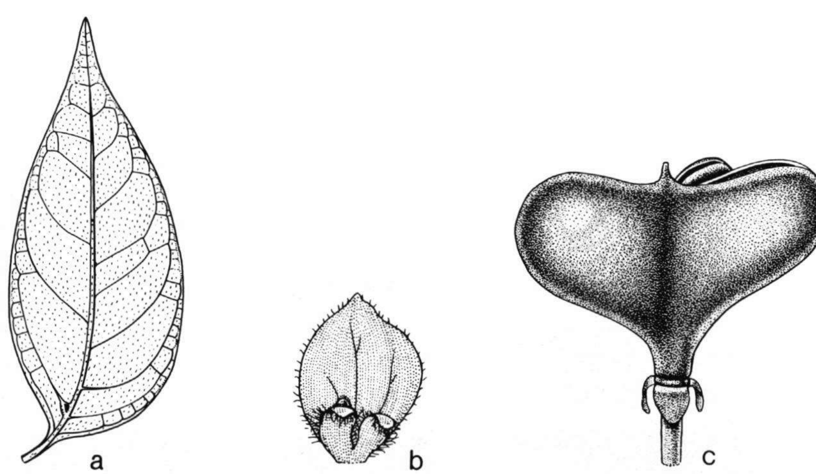


Fig. 70. *Guioa chrysea* A.C. Smith a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (*Damanu 57*, L).

sparsely so, apex retusely obtuse; scales 0.5–1 mm long, free; crest not to very slightly developed as a cockle; petal between two adjacent large sepals not reduced. *Disc* complete. *Stamens* 8; filament 0.3–3 mm long, especially basally pilose; anther 0.2–0.5 mm long, pilose. *Pistil:* ovary 0.2–2 mm long, sparsely hirsute; style and stigma 0.1–1 mm long, elongating in fruit up to 1.5 mm, then upper c. 0.4 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1–1.6 cm high by 1.1–2.1 cm broad, smooth (to rough), glabrous, stipe 1–3 mm high, rather slender, angle between lobes 125–140°, blackish when dry; lobes 8–11 by 6–9 mm. *Seed* obovoid, 5.6–8 by 4.6–5.5 mm; hilum 1–1.2 mm long. *Embryo* 4.8–6 by 4–5 mm; cotyledons dorsoventrally above each other, upper larger, apices not elongated; radicle 1–1.1 mm long.

Field notes. Shrub to tree, 4–20 m high, d.b.h. up to 35 cm. Wood pale brown. Buds white. Sepals white. Petals white. Disk pale yellow. Filaments white; anthers pink to dark red.

Distribution. Fiji: Ovalau, Vanua Levu, Viti Levu.

Ecology. Common; found in dense to open forest, margin of forest, open hillsides. Alt.: 70–1075 m. Flowering: Jan.–Aug. Fruiting: (March–)May–Dec.

Vernacular names. Ovalau: baka ni vudi, Marasa, Wive. Vanua Levu: ndrau-sasa. Viti Levu: kaula (Naitasiri); marasa levu (After A.C. Smith, 1985).

Uses. Wood is used for construction.

Notes. 1. This species differs from *Guioa punctata* by its larger leaflets and from *Guioa rhoifolia* by its punctate leaflets and different crest on the scales.

2. *A.C. Smith 1715* was described as *Guioa capillacea* because of its hirsute instead of sericeous indumentum. However, the specimens *A.C. Smith 4632* and less so *Koroiveibau & Vodonaivalu 16668* form a transition between *'Guioa capillacea'* and *Guioa chrysea*. Several other species of *Guioa* also have exceptional specimens with a different indumentum: e.g. *Guioa pleuropteris, Guioa reticulata, Guioa subsericea, Guioa villosa.*

Specimens studied:
FIJI: 29 specimens.

Guioa comesperma Radlk. – Fig. 71a–c.

Guioa comesperma Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20 (1870) 357; Bot. Jahrb. 50 (1914) 77; Bot. Jahrb. 56 (1921) 281; in Engl., Pflanzenr. 98 (1933) 1173; Hartley et al., Lloydia 36 (1973) 270 (p.p.: *Hartley 9788*); Peekel, Fl. Bismarck-Arch. (1984) 337, fig. 545. — Lectotype (present author): *McGregor s.n.*, 1889, p.p. (M, holo; iso in MEL), New Guinea, Louisiades. See note 1.

Nephelium winterianum Bailey, Queensl. Agr. J. 3 (1898) 283. — Type: *Bailey s.n.* (BRI, holo; iso in K), New Guinea, Bay at foot of Mt. Trafalgar.

Guioa rigidiuscula auct. non Radlk.: Hartley et al., Lloydia 36 (1973) 270.

Guioa subsericea auct. non Radlk.: Streimann, Pl. Upper Watut Watershed (1983) 169 (p.p.: *NGF 9176, 14484*).

Guioa spec.: Streimann, Pl. Upper Watut Watershed (1983) 169 (p.p.: *NGF 14494*).

(Shrub to) tree. *Branchlets* terete, smooth to somewhat ribbed, usually shortly sericeous when young; flowering twigs 1.5–8 mm thick. *Leaves* 1–4-jugate;

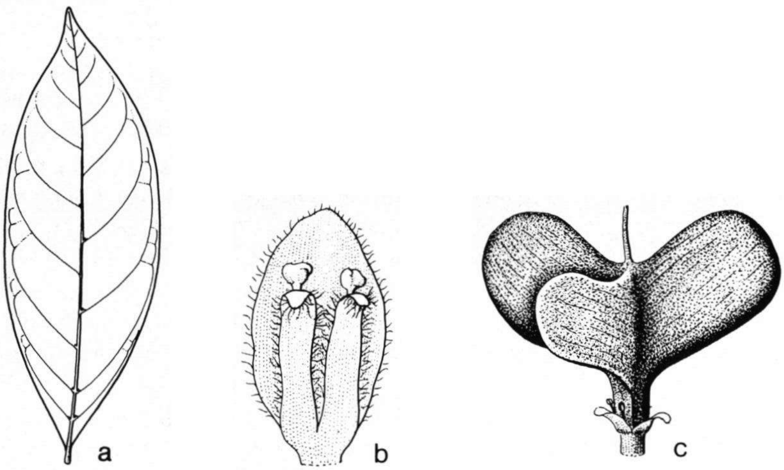


Fig. 71. *Guioa comesperma* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *NGF (Henty & Streimann) 38816*, L; b: *NGF (Womersley) 15384*, L).

rhachis 1.8–14.8 cm long, terete to winged, wing up to 3 mm broad, subglabrous, petiole 0.9–6.6 cm long; petiolules up to 0.7 cm long. *Leaflets* usually subsessile, opposite to alternate, ovate to elliptic, 3.8–18.5 by 1.3–8.4 cm, index 2–3.8, often asymmetric, acroscopic side broader, subcoriaceous, punctate; base attenuate; margin entire, flat; apex acuminate to cuspidate (to caudate), usually mucronulate; upper surface smooth, glabrous, except for the sometimes sparsely puberulous midrib; lower surface differently coloured, duller, smooth to seldom papillate (never papillate when winged), glabrous to very sparsely sericeous, domatia small, 2 to many, basally small sacs to upwards pockets, on both sides of midrib in axils of major nerves; venation on upper side (slightly sunken to) flat (to raised), raised below; major nerves 0.2–2.5(–3.5) cm apart, marginally looped, but often less distinctly so in lower part of leaflets; nerves laxly reticulate, often distinct; young leaflets dangling, reddish. *Inflorescences* axillary to pseudoterminal, branching in axils and along rhachis; latter terete to ribbed, 1–17.6 cm long, subglabrous to sericeous; first order branches up to 7.8 cm long; cymules cincinnate (to dichasial), 2–4(–7)-flowered. *Bracts* and *bracteoles* deltoid to triangular, outside sericeous, inside glabrous; bracts 0.4–1.3 mm long; bracteoles 0.2–0.6 mm long. *Pedicels* 1.1–4.5 mm long, sericeous except for the subglabrous, 0.8–2.2 mm long upper part. *Flowers* 4–4.5 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 0.7–2 by 0.6–1.8 mm; 3 inner larger ones 1.8–3.2 by 1.7–3.5 mm, margin petaloid. *Petals* (4 or) 5, elliptic, 2.1–3.8 by 0.6–1.7 mm, claw 0.3–0.8 mm high, margin and less so outside pilose, inside (sub)glabrous, apex acute; scales 0.7–2 mm long, free, basally not auricled; crest clavate, long stiped, apex lobed, glabrous. *Disc* incomplete. *Stamens* 8; filament 1.1–4.5 mm long, completely but especially basally pilose; anther 0.3–

0.8 mm long, sparsely pilose. *Pistil:* ovary 0.2–2 mm long, smooth, subhirsute; style and stigma 0.1–2 mm long, elongating in fruit up to 4 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 0.8–1.5 cm high by 0.9–2 cm broad, smooth to rugosely ribbed, glabrous, stipe 1.5–4.5 mm high, slender, edge of margin rounded, angle between lobes (50–)90–145°, reddish to reddish black when dry; dissepiments complete; lobes 7–11 by 5.5–11 mm. *Seed* obovoid, 6–8.5 by 4.3–6.5(–8) mm; hilum 0.8–1.4 mm long. *Embryo* 5.5–7 by 3.5–5.5 mm; cotyledons (obliquely) dorsoventrally above each other, upper larger in size, sometimes apex of upper elongated, straight; radicle 1–2.5(–3.5) mm long.

Field notes. (Shrub to) tree, 2–18 m high, d.b.h. 7–30 cm, bole 2–5 m high; crown usually regular, spreading. Bark c. 5 mm thick; outer bark smooth to finely vertically fissured to fluted, reddish brown to grey, usually patched; middle bark yellow-green to green; inner bark straw coloured to pink to dark orange-red. Sapwood surface may be corrugated, white to pale pink; heartwood pinkish. Leaves above dull to glossy light to dark green; paler and duller below. Sepals green to pinkish. Petals white to pale pink; crest yellow. Anthers pink to purplish pink. Fruit red; arilloid orange; seed glossy dark brown.

Distribution. Papua New Guinea (Southern Highlands, Western Highlands, Madang, Morobe, W & E New Britain, New Ireland, Manus, Northern, Milne Bay, Central Prov.); Australia (Queensland: Cook Dist.).

Ecology. Often found in savannah, secondary forest, lower montane forest on steep slopes or ridges, sometimes in primary lowland rain forest; along banks of rivers, lakes, mangrove, beach. Usually found in more open vegetations. Vegetation type in Australia: Semideciduous mesophyll vine forest. Dominant plants in vegetation: *Casuarina, Eucalyptus deglupta.* Soil: alluvial, sand, limestone, rock, ultrabasic. Alt.: sea-level up to 900 m. Flowering: (April–)May–Oct.(–Dec.). Fruiting: Jan.–Oct.

Metabolites. Hartley et al. (1973) reported that the leaves and bark of *Hartley 9788* and *12221* did not contain alkaloids.

Vernacular names. Milne Bay: kairag (Onjob); kwairoro (Minufia); seagwat (Daga). New Britain: rapakir.

Notes. 1. A lectotype is chosen, because the other types mentioned by Radlkofer appeared to be *Guioa rigidiuscula.*

2. A topocline can be found from the Central Prov. via Milne Bay towards the other northern provinces. In Central Prov. the specimens have winged leaves without papillae and highly stiped, small fruits with slender lobes (examples: *Carr 12291, 12694, Schodde 2928*). In Milne Bay the fruits are still the same, but the wing is seldom present and then usually very small (examples with wing: *Kanis 1298, NGF (Gillison) 25369, (Streimann & Katik) 34110*; all others wingless). In Morobe Prov. and the other more northern and western provinces wingless specimens are found with sometimes papillate leaflets and usually with larger fruits (lobes broad and stipe small).

3. *Guioa comesperma* belongs to the *Guioa rigidiuscula*-complex. The differences between the species in this complex are discussed in chapter 9.

4. The differentiation between *Guioa comesperma* and *Guioa subsericea* can be difficult if specimens of *Guioa comesperma* possess the large type of fruits and have leaflets with papillae and a subsericeous indumentum. The major remaining difference is the disc: incomplete in *Guioa comesperma,* complete in *Guioa subsericea.* Flowering specimens show a different type of petal, those in *Guioa comesperma* are large (2.1–3.8 mm long) with long, broad, free scales with big crests, while in *Guioa subsericea* the petals are much smaller (0.9–2.1 mm long), have infolded auricles as scales, and the crest is usually absent but can be as well-developed as in *Guioa comesperma.*

Specimens studied:
PAPUA NEW GUINEA: 48 specimens studied.
AUSTRALIA. Queensland: *Webb & Tracey 13251,* Cook Dist., Quintil Creek, Lockhart River Aboriginal Reserve.

Guioa contracta Radlk. – Fig. 72a–c.

Guioa contracta Radlk., Bot. Jahrb. 50 (1914) 77; Bot. Jahrb. 56 (1921) 283; in Engl., Pflanzenr. 98 (1933) 1174. — Type: *Schlechter 18269* (B, holo, †; iso in K, P), New Guinea, Kani Mts.
Guioa aryterifolia auct. non Radlk.: Hartley et al., Lloydia 36 (1973) 269.
Guioa comesperma auct. non Radlk.: Hartley et al., Lloydia 36 (1973) 270 (p.p.: *Hartley 10976, 12635*).

Tree. *Branchlets*
mm thick. *Leaves* 1–3-jugate; rhachis 2.3–19.2 cm long, terete, not winged, (sub)-glabrous, petiole 2–8.5 cm long; petiolule up to 1.1 cm long. *Leaflets* usually subsessile, subopposite to alternate, elliptic, 7.6–24.2 by 3–8.9 cm, index 2.1–3.3, ± symmetric, otherwise acroscopic side broader, subcoriaceous, punctate; base attenuate; margin entire, flat; apex acuminate to cuspidate, very apex obtuse, sometimes mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous to often very sparsely sericeous, domatia absent; venation on upper side flat, raised on lower; major nerves 0.3–3.3 cm apart, marginally looped, but less distinctly so in lower part of leaflets; veins laxly reticulate, rather indistinct. *Inflorescence* ramiflorous (to axillary), branching in axil to mainly along rhachis; latter terete, 1.3–18 cm long, subsericeous; first order branches up to 8.3 cm long; cymules cincinnate, (1–)3–4-flowered. *Bracts* and *bracteoles* triangular, outside hirsute, inside glabrous; bracts 0.5–1 mm long; bracteoles 0.2–0.5 mm long. *Pedicels* 1.8–5 mm long, completely sericeous, upper part 1–3.1 mm long. *Flowers* 3.5–4 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 0.7–1.4 by 1.1–2 mm; 3 inner larger ones 1.8–2.8 by 1.5–3 mm, margin petaloid. *Petals* 5, ovate to elliptic (to obovate), 1.7–2.8 by 0.5–1.3 mm, claw 0.2–0.4 mm high, margin and less so outside pilose, inside glabrous, apex rounded to acute; scales 0.7–1.6 mm long, free, basally not auricled; crest clavate, stiped, apex lobed. *Disc* incomplete. *Stamens* 8; filament 1.2–3.5 mm long, completely but especially basally pilose; anther 0.4–0.6 mm long, glabrous to subpilose. *Pistil:* ovary 0.3–0.6 mm long,

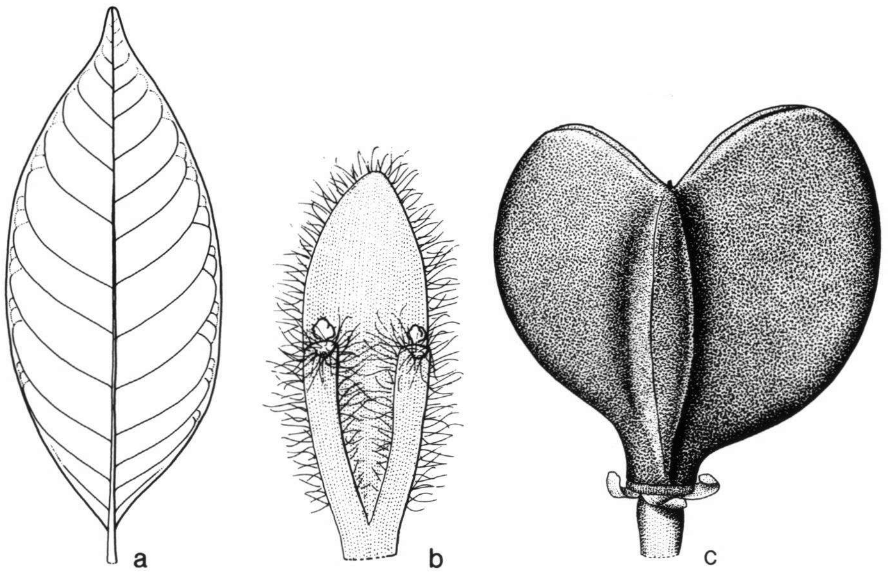


Fig. 72. *Guioa contracta* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *Hartley 12635*, L; b: *Clemens 430*, L).

smooth, subhirsute; style and stigma 0.2–0.6 mm long, elongating in fruit up to 3 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.4–1.9 cm high by 1.3–2.4 cm broad, smooth to rugose, glabrous, not dehiscing to only (partly) dehiscing when completely ripe, stipe 1–1.5 mm high, broadly cuneate, wall at edge up to 3.5 mm thick, edge rounded, angle between lobes 70–145°, blackish when dry; dissepiments complete; lobes 11–15 by 9–15 mm, widening, not narrowing towards axis. *Seed* obovoid, c. 8 by 7.5 mm; arilloid without a pseudofunicle, but a basal rim present; hilum c. 1 mm long. *Embryo* c. 7 by 7 mm; cotyledons dorsoventrally above each other, upper larger in size, apex of upper somewhat elongated, straight; radicle c. 3.5 mm long.

Field notes. Tree, 5–27 m high, d.b.h. 8–20 cm. Outer bark smooth to faintly longitudinally fissured, light grey to reddish brown to dark blackish green; inner light straw to pale brown, c. 6 mm thick. Wood soft, white to straw-white. Leaves pale to medium green, shiny above. Flowers cauliflorous to axillary. Calyx pale green. Corolla white. Filaments white. Disk lobes yellow. Fruit cream when immature to red when mature.

Distribution. Papua New Guinea (Madang, Morobe, Northern, and Central Prov.).

Ecology. Lowland and montane rain forest, secondary forest bordering oak forest, scrubby forest along creeks and mangrove, along roadsides. Alt.: sea-level up to 1500 m. Many twigs hollow with ants. Flowering: Aug.–Oct. Fruiting: July.

M e t a b o l i t e s. Hartley et al. (1973) record an absence of alkaloids in bark and leaflets (*Hartley 10976, 12208* and *12635*).

V e r n a c u l a r   n a m e s. Lagasam (Amele); ongo (Orokaiva: Mumuni).

N o t e s. 1. Typical for this species are the rather large, almost glabrous, elliptic leaflets without papillae and domatia, and the exceptional fruits. The fruits are hardly lobed, the lobes do not narrow towards the axis, but widen; the wall is very thick (the fruits dehisce late and presumably only partly); the pseudo-funicle is reduced to a rim only.

2. *Guioa contracta* is part of the *Guioa rigidiuscula*-complex. The differences among the species of this complex are discussed in chapter 9.

S p e c i m e n s   s t u d i e d:

PAPUA NEW GUINEA. Madang Prov.: *Schlechter 18269*, Bismarck Mts. — Morobe Prov.: *Clemens 430, 1003, 8054*, Sattelberg; *41653*, Boana; *Hartley 10976*, Zenag; *12208*, Butibum River; *12635*, Bakaia; *NGF (Native Collector) 4646, (MacDonald) 5145*, Lae; *(White) 10327*, Oomsis Creek; *(Millar) 18858*, Lae; *(Streimann) 45076*, Kipu; *Okada & Katik 4305*. — Northern Prov.: *Carr 16039*, Isurava; *Darbyshire 1216*, Fiobobo, near Naro resthouse; *Hoogland 3969*, Arumu River, S of Botue Village. — Central Prov.: *Frodin 846*, Motupore I.

Guioa coriacea (Radlk.) Radlk. - Fig. 73a–c.

Guioa coriacea (Radlk.) Radlk., Abhand. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 16 (1886) 60; in Engl., Pflanzenr. 98 (1933) 1161; Reynolds, Austrobaileya 2 (1984) 38, fig. 2b, c. — *Atalaya coriacea* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1878) 326. — T y p e: *Fullagan s.n.*, August 1874 (M, holo; iso in BM, BO, G, K, MEL, NSW), Australia, Lord Howe I.

Cupania howeana Maiden, Proc. Linn. Soc. N.S.W. 23 (1898) 126, pl. 1. — L e c t o t y p e (present author): *J.H. Maiden s.n.*, IV-1898 (NSW, holo; iso in BM, MEL), Australia, Lord Howe I.

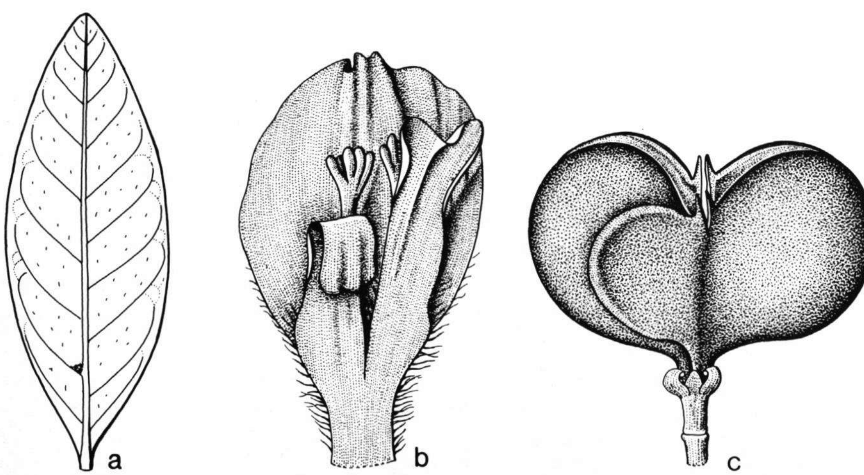


Fig. 73. *Guioa coriacea* (Radlk.) Radlk. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 1.5 (a, b: *E. King NSW 168623*; c: *Maiden NSW 168624*).

Tree. *Branchlets* terete to usually flattened, usually smooth, shortly sericeous when young; flowering twigs 3.5–7 mm thick. *Leaves* 1–4-jugate; rhachis 1.3–13 (–18 in vegetative parts) cm long, terete, upwards broadly furrowed and somewhat dorsoventrally flattened, not winged, sericeous, petiole 1–4.5 cm long; petiolule if present up to 0.7 cm long. *Leaflets* usually subsessile, opposite to alternate, elliptic, 3.8–13.2 by 2–5.3 cm, index 1.7–3.3, asymmetric, acroscopic side broader than basiscopic side, thick coriaceous, young leaflets punctate; base (cuneate to) attenuate; margin entire, revolute; apex retuse to obtuse (to acute), not mucronulate; upper surface smooth, sparsely sericeous when young; lower surface differently coloured, duller, smooth, without papillae, sparsely sericeous, domatia usually absent, otherwise a single sac on basiscopic side in axil of second major nerve; venation usually raised on both sides; nerves 0.3–2 cm apart, marginally looped; veins laxly reticulate, indistinct. *Inflorescences* axillary to pseudoterminal, branching along rhachis and first order branches, very sturdy; rhachis flattened, 2.5–16.6 cm long, sericeous; first order branches up to 12.5 cm long; cymules cincinnate, 2–3-flowered. *Bracts* and *bracteoles* deltoid, outside pubescent, inside glabrous; bracts 0.7–0.8 mm long; bracteoles 0.2–0.7 mm long. *Pedicels* 2.3–8 mm long, sericeous except for the glabrous, 1.4–3.3 mm long upper part. *Flowers* 4–6 mm in diam. *Sepals* 5, broadly ovate to orbicular, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1.5–2.5 by 1.8–3 mm; 3 inner larger ones 2.7–3.8 by 2.5–4 mm, margin petaloid. *Petals* 5, rhomboid to orbicular, 2–3.5 by 1.7–3 mm, claw 0.5–0.7 mm long, margins pilose, outside and inside glabrous, apex obtuse; basal part of margins auriculate and folded inwards as scales, 1.2–2.8 mm long, margin pilose; crest clavate, on slender stipe, lobed; petal between two adjacent larger sepals sometimes without auricles. *Disc* complete. *Stamens* 8; filament 1.3–4 mm long, pilose; anther 0.5–1.3 mm long, glabrous to pilose. *Pistil:* ovary 0.4–1.8 mm high, smooth, very sparsely pilose; stigma and style 0.2–1.2 mm high, both elongating in fruit up to 2 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.5–2.7 cm high by 2.1–3.4 cm broad, smooth to rough, glabrous, stipe 3–5 mm high, slender, angle between lobes 90–120°, blackish when dry; lobes 1.6–2.4 by 1.4–1.8 cm. *Seed* obovoid, 1.2–1.4 by 1–1.2 cm; hilum 2.2–2.8 mm long. *Embryo* 10–15 by c. 10 mm; cotyledons secondarily laterally besides each other, equal to inequal (upper larger) in size, apices usually elongated, especially that of the upper cotyledon, both apices bended towards radicle; latter 3.5–4 mm long. *Seedling* epigeal. *Taproot* terete, with many branching sideroots. *Hypocotyl* terete, 6.7–10.4 cm long, hirsute. *Cotyledons* already fallen. *Axis* flattened, hirsute, c. 5 cm high up to first leaves. *Leaves* first pair opposite, later on alternate; 3- or 4-jugate; rhachis slightly winged. *Leaflets* 1.5–3.4 by 0.9–1.5 cm, thin, punctate; margin serrate, flat; upper surface hirsute.

Field notes. Tree, 8–20 m high, d.b.h. 30–45 cm. Young shoots densely rust-coloured pilose. Outer bark reddish, flaky. Sapwood pale yellow; heartwood reddish brown, not easy to split.

Distribution. Australia: Lord Howe I.

Ecology. Often common. Reported from forests on low grounds and on slopes. Soil: basalt. Alt.: sea-level up to 185 m. Flowering: Jan. Fruiting: Sept.–Jan.

Pickard (Biol. Cons. 27, 1983, 125–139) did not mention *Guioa coriacea* as a rare or endangered species of Lord Howe I.

W o o d. One of the best soft woods of Lord Howe I. (*Boorman s.n.*, V-1920, NSW 178952).

N o t e. *Guioa coriacea* differs in several characters from other species of *Guioa:* a) The inflorescence is very sturdy, thick (usually more slender in other species of *Guioa*). b) The petals have folded margins, instead of almost free scales. However, the fruit and arilloid are typical for *Guioa* and were not encountered among other Australian genera.

S p e c i m e n s s t u d i e d:
AUSTRALIA. Lord Howe I.: 15 specimens.

Guioa crenata Radlk. – Fig. 74 a–c.

Guioa crenata Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 615; Guillaumin, Bull. Soc. Bot. Fr. 79 (1932) 338; Radlk. in Engl., Pflanzenr. 98 (1933) 1174; Guillaumin, Fl. Nouv.-Caléd. (1948) 199; Mém. Mus. Nat. Hist. Nat. B, 15 (1967) 110; Morat et al., Bull. Mus. Nat. Hist. Nat. 4e sér., 8, B (1986) 174. — L e c t o t y p e (here proposed): *Balansa 2840* (M, holo; iso in P), New Caledonia, Mt. Mu.

Treelet to tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 1.2–3 mm thick. *Leaves* 1–7-jugate; rhachis 0.7–7.8 cm long, terete, slightly winged, slightly sericeous, petiole 0.5–2.3 cm long. *Leaflets* subsessile, opposite to alternate, elliptic (to obovate), 1–4.3 by 0.3–1.3 cm, index 2.3–3.3, slightly asymmetric, acroscopic side somewhat broader, very coriaceous, punctate; base attenuate; margin in at least some leaflets crenate (to serrate), especially near the apex, revolute; apex retuse to obtuse, not mucronulate; upper surface smooth, sericeous, especially the midrib; lower surface differently coloured, lighter, dull, papillate, shortly sericeous, domatia (either a single sac or) many sacs in axils of major nerves; venation flat to raised on upper side, raised on lower; nerves 0.1–0.6 cm apart, marginally looped; veins ± densely reticulate, indistinct. *Inflorescences* axillary, branching along rhachis, not in or near axil; rhachis flattened, 0.6–10.3 cm long, sericeous; first order branches up to 2.7 cm long; cymules cincinnate, 2-flowered. *Bracts* and *brac-*

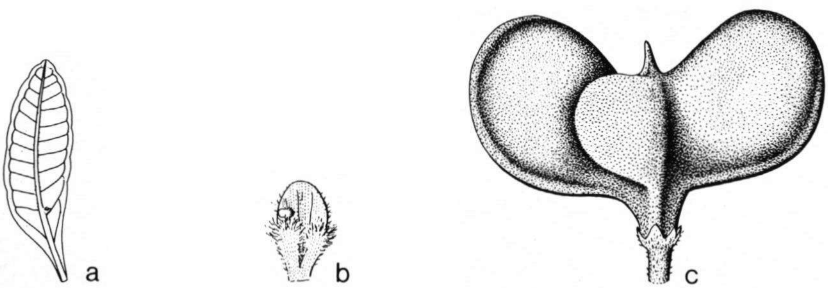


Fig. 74. *Guioa crenata* Radlk. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, c: *MacKee 23695*, L; b: *MacKee 22910*, L).

teoles triangular, completely sericeous; bracts 0.5–1.3 mm long; bracteoles 0.3–0.6 mm long. *Pedicels* 1.9–4.1 mm long, sericeous; upper part usually as sericeous as lower part, 0.7–2.5 mm long. *Flowers* c. 1.8 mm in diam. *Sepals* 5, hardly dimorph, triangular, completely sericeous, with glands along margin; 2 outer smaller ones 0.7–1.1 by 0.5–1 mm; 3 inner larger ones 1.1–1.6 by 0.8–1.2 mm, margin petaloid. *Petals* 5, obovate, 1.2–1.5 by 0.5–0.8 mm, claw 0.1–0.3 mm high, completely sparsely pilose, apex obtuse to acute; scales 0.5–0.7 mm long, free; crest sometimes present, clavate on slender stipe. *Disc* complete. *Stamens* 8; filament 1.3–2.3 mm long, pilose; anther 0.5–0.6 mm long, pilose. *Pistil:* ovary 0.4–1.2 mm high, smooth, hirsute; stigma and style 0.1–1.7 mm long, both elongating up to 3 mm in fruit, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1–1.2 cm high by 1.6–1.8 cm broad, smooth, glabrous, stipe 1.5–2 mm high, slender, angle between lobes 90–125°, blackish when dry; lobes 8.5–9 by 7–8.5 mm. *Seed* obovoid, 8–8.8 by 4.5–7 mm; hilum c. 1.2 mm long. *Embryo* 7–7.8 by 4.2–5 mm; cotyledons secondarily laterally besides each other, about equal in size, apices elongated, that of lower recurved; radicle 1.5–2.8 mm long.

Field notes. Treelet to tree, 1–4(–12) m high. Leaflets shiny green above, greyish below. Sepals green. Petals and filaments white. Anthers red. Arilloid yellow.

Distribution. New Caledonia.

Ecology. Found in *Auracaria-Nothofagus* forest, moss forest, maquis. Soil: ultrabasic (serpentine), calcareous. Alt.: 750–1450 m. (Partly after Morat et al., 1986.) Flowering: Nov. Fruiting: May–Aug.

Notes. Typical for *Guioa crenata* are the slightly winged rhachis; small, crenate leaflets with below papillae and short appressed indumentum; small flowers with hardly dimorphic sepals and complete disc.

See also note 2 and 3d under *Guioa villosa.*

Specimens studied:
NEW CALEDONIA: 19 specimens.

Guioa crenulata Radlk. – Fig. 75a, b.

Guioa crenulata Radlk., Bot. Jahrb. 39 (1906) 176; Guillaumin, Bull. Soc. Bot. Fr. 79 (1932) 338; Radlk. in Engl., Pflanzenr. 98 (1933) 1175; Guillaumin, Fl. Nouv.-Caléd. (1948) 199. — Type: *Schlechter 15413* (M, holo; iso in BM, K, L, M, P, W), New Caledonia, Oubatche.

Treelet. *Branchlets* terete, smooth, sericeous when young; flowering branchlets 1.5–2 mm thick. *Leaves* 2–5-jugate; rhachis 1.6–8.6 cm long, terete, slightly winged, subsericeous, petiole 0.8–2.8 cm long. *Leaflets* subsessile, opposite to alternate, elliptic, 0.8–3.6 by 0.3–0.9 cm, index 2.7–4.2, ± symmetric, very coriaceous, punctate; base attenuate; margin basically entire to apically crenate, revolute; apex obtuse to acute, not mucronulate; upper surface smooth, very sparsely sericeous to glabrous; lower surface differently coloured, lighter, dull, papillate, sparsely shortly sericeous, domatia absent; venation on upper surface flat to raised, raised on lower side; nerves 0.1–0.4 cm apart, marginally looped; veins densely reticulate, indistinct. *Inflorescences* axillary, branching in or near axil to also along

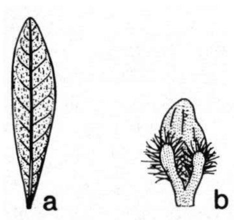


Fig. 75. *Guioa crenulata* Radlk. a. Leaflet, × 1; b. petal, × 12.5 (*MacPherson 4534*, L).

rhachis; latter flattened, 0.8–5.3 cm long, sericeous; first order branches up to 2.6 cm long; cymules cincinnate, 2- or 3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.6–1.1 mm long; bracteoles 0.2–0.5 mm long. *Pedicels* 1.6–2.8 mm long, sericeous, just like the 0.7–1.3 mm long upper part. *Flowers* c. 2 mm in diam. *Sepals* 5, ovate, completely (sub)sericeous, margin with glands; 2 outer smaller ones 0.8–1.1 by 0.9–1.2 mm; 3 inner larger ones 1.3–1.8 by 1.1–1.5 mm, margin petaloid. *Petals* 5, elliptic, 1–1.3 by c. 0.5 mm, claw 0.1–0.2 mm high, margin pilose, outside and inside glabrous; apex acute; scales 0.5–0.8 mm long, free; crest sometimes developed, linear, not clavate. *Disc* incomplete. *Stamens* 8; filament 1.8–2.2 mm long, especially basically pilose; anther c. 0.4 mm long, very sparsely pilose. *Pistil:* ovary 0.2–0.6 mm high, smooth, hirsute; stigma and style 0.1–0.4 mm high. *Fruit* unknown.

Field notes. Treelet, 2–6 m high. Leaflets shiny green above, dull greyish below. Corolla white.

Distribution. NW New Caledonia.

Ecology. Humid forest. Soil: micaschist. Alt.: 500–700 m. Flowering: Dec.

Note. *Guioa crenulata* is well recognizable by its winged rhachis, very small, partly crenate leaflets, absence of domatia, subsericeousness of lower surface of leaflets (short hairs), and small flowers.

See also note 2 and 3e under *Guioa villosa*.

Specimens studied:

NEW CALEDONIA: *McKee 19989*, Upper Diahot, Tende; *McPherson 4534*, Mandjelia; *Schlechter 15413*, Oubatche.

Guioa diplopetala (Hassk.) Radlk. – Fig. 76 a–c, 77 a–h.

Guioa diplopetala (Hassk.) Radlk., Sapind. Holl.-Ind. (1879) 88; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 514, 521, 543, 610; Val., Bull. Inst. Bot. Btzg. 15 (1902) 10; Koord. & Val., Bijdr. Boomsoort. Java 9 (1903) 207; Radlk. in Perk., Fragm. Fl. Philip. 1 (1904) 63; de Clercq, Nieuw Plantk. Woordenb. (1909) 251, nr. 1710; Backer, Schoolfl. (1911) 268; Moll & Janss., Mikrogr. Holz. 2 (1911) 377; Koord., Exk. Fl. Java 2 (1912) 542; Koord.-Schum., Syst. Verz. (1912) fam. 165, 11; Radlk., Philip. J. Sc. 8, Bot. (1913) 446; Merr., En. Philip. 2 (1923) 507; Pl. Elm. Born. (1929) 175; Radlk. in Engl., Pflanzenr. 98 (1933) 1162; Corner, Gard. Bull. Str. Settl. 10 (1939) 43 (sub *Guioa fuscidula*); Masamune, En. Phan. Born. (1942) 426; Desch, Mal. For. Rec. 15 (1954) 526; Salvosa, Lex. Philip. Pl. (1963) 104; Backer & Bakh. f., Fl. Java 2 (1965) 140. — *Cupania diplopetala* Hassk., Flora 25, 2, Beibl. (1842) 39; Cat. Hort. Bog. (1844) 224; Walp., Rep. 5 (1845) 363; Hassk., Pl. Jav. Rar. (1848) 286; Filet, Plantk. Woordenb. ed. 2 (1888) 171, nr. 4454 c. — *Guioa diplopetala* f. *genuina* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 610, nom. illeg. (I.C.B.N. art. 26.1); in Engl., Pflanzenr. 98 (1933) 1162. — Type: not indicated, either Herbarium Hasskarl or Herbarium Bogoriense (n.v.), Java.

Guioa squamosa Radlk., [Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8 (1878) 303, nom. nud.] Sapind. Holl.-Ind. (1879) 38; Sitzungsber. Math.-Phys. Cl. Königl.

Bayer. Akad. Wiss. München 9 (1879) 544, 609; King, J. As. Soc. Beng. 65, II (1896) 444; Ridley, J. Str. Br. R. As. Soc. 33 (1900) 66; Brandis, Ind. Trees (1906) 186; Lec., Fl. Gén. I.-C. 1 (1912) 1025; Ridley, Fl. Mal. Pen. 1 (1922) 506; Radlk. in Engl., Pflanzenr. 98 (1933) 1161; Gagnep., Fl. Gén. I.-C. Suppl. 1 (1950) 981. — [*Sapindus squamosa* Wall., non Roxb., Cat. (1847) 8097, nom. nud., nom. inval. (I.C.B.N. art. 32.1.c).] — *Guioa squamosa* f. *genuina* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 609, nom. illeg. (I.C.B.N. art. 26.1); in Engl., Pflanzenr. 98 (1933) 1161. — T y p e: *Wallich 8097* (K, holo; iso in A, BM, FI, P), Malaya, Penang.

Cupania regularis Blume, Rumphia 3 (1847) 159; Walp., Ann. 2 (1851/2) 214; Filet, Plantk. Woordenb. ed. 2 (1888) 277, nr. 8115. — *Guioa regularis* Radlk., Sapind. Holl.-Ind. (1879) 12, 41; Masamune, En. Phan. Born. (1942) 427. — *Guioa diplopetala* f. *borneensis* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 610; in Engl., Pflanzenr. 98 (1933) 1162. — *Guioa diplopetala* var. *borneensis* Radlk., Bot. Jahrb. 49 (1913) 370. — L e c t o t y p e (present author): *Korthals s.n.*, s.d. (L, sh.no. 908.269-309), Borneo. See note 2.

Cupania minjalilen Blume, Rumphia 3 (1847) 162; Walp., Ann. 2 (1851/2) 214; Filet, Plantk. Woordenb. ed. 2 (1888) 218, nr. 5987. — *Guioa minjalilen* Radlk., Sapind. Holl.-Ind. (1879) 10, 37; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 609. — L e c t o t y p e (here proposed): *Waitz s.n.* (L, holo, sh.no. 908.269-779; iso in L, P), Java, Murion.

Arytera karang Miq., Sumatra (1861) 510; Filet, Plantk. Woordenb. ed. 2 (1888) 151, nr. 3862 b. — T y p e: *Diepenhorst HB 2487* (U, holo; iso in BO), Sumatra, Priaman Prov.

Cupania fuscidula Kurz, J. As. Soc. Beng. 41, II (1872) 302; J. As. Soc. Beng. 44, II (1875) 188, 189 (type); Hiern in Hook. f., Fl. Br. Ind. 1 (1875) 676; Kurz, Fl. Burm. 1 (1877) 284. — *Guioa fuscidula* Radlk., Sapind. Holl.-Ind. (1879) 38; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 515, 609; King, J. As. Soc. Beng. 65, II (1896) 445; Brandis, Ind. Trees (1906) 186; Ridley, Fl. Mal. Pen. 1 (1922) 506; Burk. & Hend., Gard. Bull. Str. Settl. 3 (1925) 363; Radlk. in Engl., Pflanzenr. 98 (1933) 1161; Corner, Gard. Bull. Str. Settl. 10 (1939) 44; Ways. Trees (1940) 588; Gagnep., Fl. Gén. I.-C. Suppl. 1 (1950) 979; Meijer, Bot. News Bull. 9 (1967) 75. — T y p e: *Helfer 993* (K, holo; iso in A, L, M, P, W), Burma, Tenasserim.

Guioa squamosa Radlk. f. *lineolata-punctata* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 609; in Engl., Pflanzenr. 98 (1933) 1161. — T y p e: *Helfer 983* (K, holo; iso in A, P), Burma, Tenasserim.

Guioa diplopetala f. *microcarpa* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 610; in Engl., Pflanzenr. 98 (1933) 1162. — T y p e: *Beccari FI 2812* (FI, holo, cited by Radlkofer as *Beccari 6*), Celebes, Prov. Kandari, Lepo-lepo.

Guioa leptoneura Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 611, 618; in Engl., Pflanzenr. 98 (1933) 1163. — S y n t y p e s: *Beccari FI 2807* (FI, cited by Radlkofer as *Beccari 7'''*), Celebes, Kandari Prov., Lepo-lepo; *Riedel s.n.* (BO, K, W), Celebes, Gorontalo.

Guioa cambodiana Pierre, Fl. Coch. 4 (1894) t. 317a; Lec., Fl. Gén. I.-C. 1 (1912) 1025, fig. 127: 7; Craib, Fl. Siam. En. 1 (1926) 332; Radlk. in Engl., Pflanzenr. 98 (1933) 1176; Gagnep., Fl. Gén. I.-C. Suppl. 1 (1950) 981; Pételot, Pl. Medic. Cambodge, Laos, Viet-Nam 1 (1952) 201. — T y p e: *Pierre 884* (P, holo; iso in K), Cambodia, Tpong Prov., Mt. Knang-repoeu, 800 m.

Guioa fuscidula (Kurz) Radlk. var. *glabrescens* King, J. As. Soc. Beng. 65, II (1896) 445; Ridley, Fl. Mal. Pen. 1 (1922) 506. — T y p e: *Scortechini 1714* (K, holo), Malaya.

Guioa microphylla Radlk., Rec. Bot. Surv. Ind. 3 (1908) 354; Ridley, Fl. Mal. Pen. 1 (1922) 506; Radlk. in Engl., Pflanzenr. 98 (1933) 1161; Corner, Gard. Bull. Str. Settl. 10 (1939) 43. — T y p e: *C. Curtis 1346* (K, holo), Malaya, Perak, l'Hermitage hill, 2000 ft.

Guioa bullata Radlk., Fedde Rep. 18 (1922) 342; in Engl., Pflanzenr. 98 (1933) 1164; Masamune, En. Phan. Born. (1942) 426. — L e c t o t y p e (here proposed): *Haviland 1003* (K, holo; iso in M), Borneo, Kuching (cited by Radlkofer as *Haviland 1063*).

Arytera montana auct. non Blume: Miq., Sumatra (1861) 510.

Cupania glabrata auct. non Kurz: Hiern in Hook. f., Fl. Br. Ind. 1 (1875) 676, p.p. (*Wallich 8097, 8550*).

Cupania griffithiana auct. non Kurz: Kurz, J. As. Soc. Beng. 44, II (1875) 188, p.p. (*Helfer 983*); Fl. Burm. 1 (1877) 284. See note 3 under *Guioa pleuropteris*.

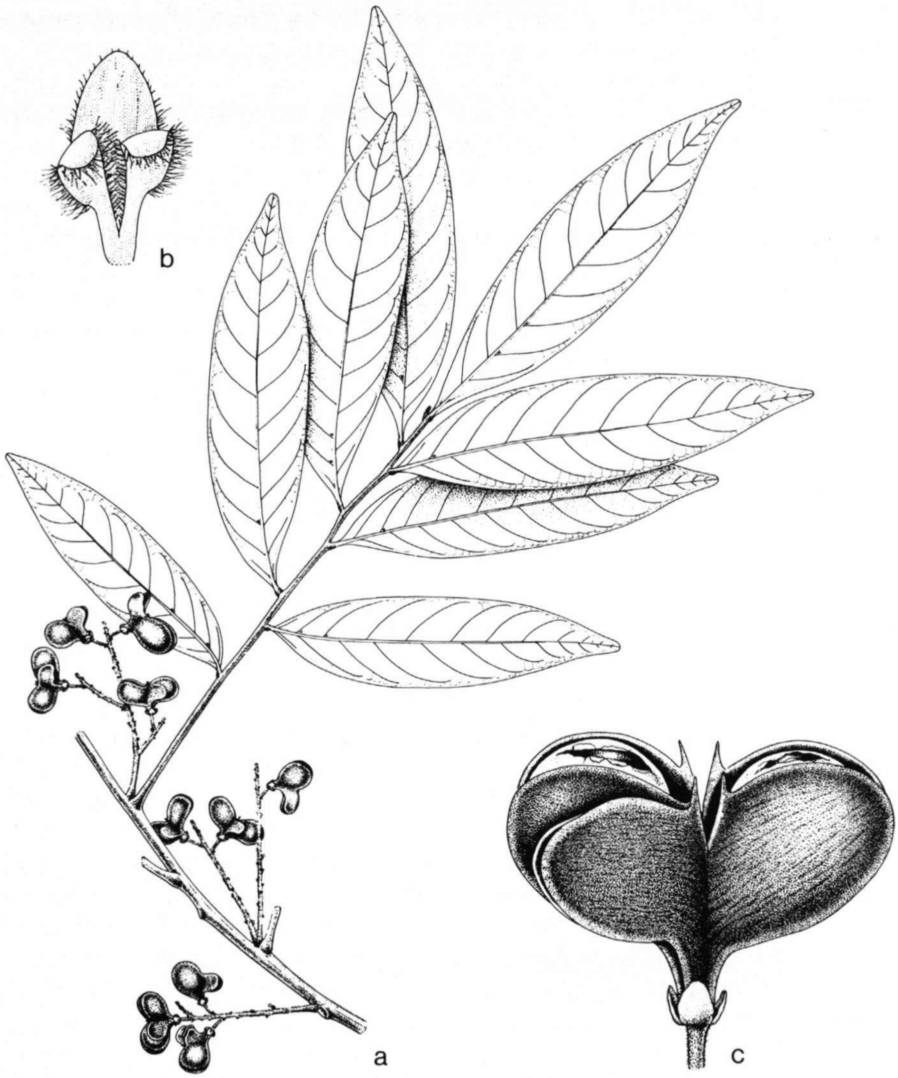


Fig. 76. *Guioa diplopetala* (Hassk.) Radlk. a. Habit, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *Ranayu & Maskura 340*, BO; b: *Beumée A 765*, L).

Shrub to tree. *Branchlets* (somewhat flattened to) terete, smooth (to somewhat ribbed to rough), usually sericeous when young; flowering twigs 1.5–25 mm thick. *Leaves* 1–9-jugate; rhachis 2.3–33.5 cm long, terete to upwards flattened above, not winged (except slightly winged when juvenile), glabrous to subsericeous, petiole 1.4–13.5 cm long; petiolules if present up to 0.9 cm long. *Leaflets* usually subsessile, opposite to alternate, (ovate to) elliptic, 2.3–24.3 by 0.8–7.8 cm, index (1.1–) 2.5–5.9, (slightly) asymmetric, especially basally, the acroscopic side broader, coriaceous, usually punctate; base attenuate; margin entire (to crenate, latter presumably together with serrate only in juvenile ones), flat (to revolute); apex (obtuse to) acuminate to cuspidate (to caudate), usually not mucronulate; upper surface smooth, usually glabrous to puberulous on the midrib to slightly sericeous; lower surface differently coloured, dull, smooth, very seldom papillate (then indumentum at most sericeous), glabrous (to slightly sericeous to subvillose; subvillose leaves without papillae), red glands absent, domatia (absent to a single sac to) many small sacs (to pockets), in axils of major nerves; venation on upper surface (slightly sunken to) flat to raised, raised on lower side; nerves 0.2–3.7 cm apart, marginally looped, sometimes less distinctly so in lower part of leaflets; veins laxly reticulate, usually indistinct. *Inflorescences* (ramiflorous to) axillary (to pseudoterminal), (not branching to) branching in or near axil to also along rhachis; latter terete to somewhat flattened, 0.4–18 cm long, subsericeous (to subhirsute); first order branches up to 9 cm long; cymules cincinnate (to dichasial), 2–6-flowered. *Bracts* and *bracteoles* deltoid to triangular, outside sericeous, inside (sub)glabrous; bracts 0.5–2 mm long; bracteoles 0.2–0.9 mm long. *Pedicels* 1.8–7.3 mm long, completely sericeous, upper part 0.9–3.5 mm long. *Flowers* 3–4.5 mm in diam. *Sepals* 5, ovate, margin and sometimes outside pilose, margin with glands, inside glabrous; 2 outer smaller ones 0.9–2.8 by 0.8–2.1 mm; 3 inner larger ones 1.4–3.4 by 1.2–3.6 mm, margin petaloid. *Petals* 5, elliptic to obovate, 0.5–4 by 0.3–2.2 mm, claw 0.2–1 mm high, margin pilose, outside and inside (sub)glabrous, apex rounded to acute; scales 0.3–2 mm long, free, apex (very) much broadened; crest usually absent, if present a pilose flat part of the bifid scale apex. *Disc* complete, often with a small slit. *Stamens* 8; filament 1.2–5 mm long, especially basally pilose; anther 0.3–0.8 mm long, glabrous to slightly pilose. *Pistil:* ovary 0.2–2 mm long, smooth, subhirsute; style and stigma 0.1–2 mm long, elongating in fruit up to 3.2 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 0.7–1.5 cm high by 0.7–1.8 cm broad, smooth to somewhat ribbed, glabrous, stipe 2–5 mm high, slender, angle between lobes 90–150°, blackish when dry; lobes 5–10 by 4–9.5 mm. *Seed* obovoid, 5–9 by 4.1–7.3 mm; hilum 0.8–2 mm long. *Embryo* 4–7.8 by 3–6 mm; cotyledons secondarily laterally besides each other, upper larger, apices often elongated, upper usually straight, lower (re)curved; radicle 1.5–3.7 mm long.

Field notes. Shrub to tree, 1–18.5 m high, d.b.h. 3 cm to 1.3 m; bole up to 5 m high. Outer bark smooth, grey-brown to grey-white to black; inner bark pink to reddish to pale brown, c. 5 mm thick. Sapwood white to light yellow. Leaves bright green. Inflorescence green with brown hairs. Flowers without scent. Sepals green, 3 larger ones with white margin. Petals white. Disc yellow. Filaments white;

anthers pink. Ovary light green to white, with few golden-brown hairs. Fruit pink to red; arilloid white, sour; seed black. Plant is recorded to be poisonous.

Distribution. Burma, Thailand, Cambodia, Vietnam, Malay Peninsula, Sumatra, Java, Borneo, Celebes.

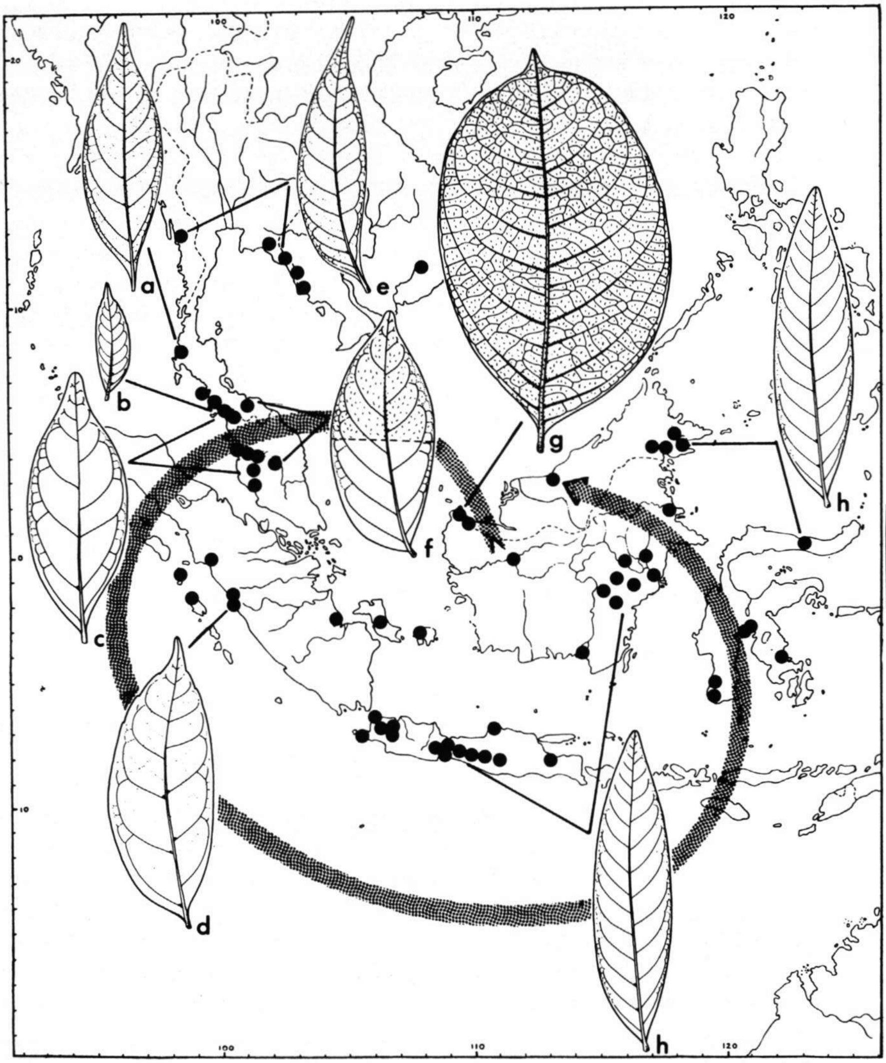


Fig. 77. Distribution map of *Guioa diplopetala* (Hassk.) Radlk., showing the change in leaflet forms from W Borneo to E Borneo (all leaflets x 0.5). – a. '*Guioa squamosa*' form (*Geesink et al. 7688*, L); b. '*Guioa microphylla*' form (*Curtis 1346*, K); c. '*Guioa squamosa*' form (*Curtis 1041*, K); d. intermediate form between the '*Guioa squamosa*' form and the *Guioa diplopetala* form (*Iboet 304*, L); e. '*Guioa squamosa*' form (*Put 3024*, L); f. upper half '*Guioa fuscidula*' form, pilose (*Helfer 993*, L); lower half '*Guioa fuscidula* var. *glabrescens*' form, glabrous (*Scortechini 1714*, K); g. '*Guioa bullata*' form (*Haviland 2137*, L); h. *Guioa diplopetala* form (*Rahayu & Maskura 540*, BO).

E c o l o g y. Regularly encountered, not common. Found in primary and especially in secondary forest, in heath forest, submontane forest, edge of forest, along rivers, roads, seashore, in deserted cultivated fields, savannah (belukar). Soil: granitic sand, basalt, clay, loam on sandstone, limestone, marshy sand. Alt.: sea-level up to 1700 m. Flowering: Sept.–April. Fruiting: Dec.–April.

W o o d. As that of *Guioa bijuga* (see there), but with an abundance of confluent parenchyma absent in *Guioa bijuga* and *Guioa koelreuteria* (Desch, 1954).

V e r n a c u l a r n a m e s. Cambodia: ko dang bai; chran, mpat, se xet, tap yor (Moi). Malay Peninsula: senyamok. Sumatra: karang-karang, kenenem, kongkiel, pulas (Malay). Java: minjalilen, pendjalinan, songga langit, walik elar (Javanese); kihowe, ki bajawak, ki huut, salam andjung (Sunda); pisitan bodas. Borneo: Sabah: belimbing talun (Bajau); gulambir ayam; kayu lulus (Tidong); Kalimantan Timur: mentuga, n'tuga (Tundjung Dajak). Celebes: sosareu (Tobelas: Tokoronsie dial.).

U s e s. Boiled roots act against blennorrhea (suppurating inflammation of mucous membranes; Pételot, 1952). The wood is used for house construction (De Clercq, 1909); it is resistant against termites and is used as poles (Gagnepain, 1950). N.B.: The wood of *Guioa bijuga,* which is quite similar to that of *Guioa diplopetala,* is said to be of poor quality as it is very vulnerable to insect attack.

N o t e s. 1. *Guioa diplopetala* is a very widespread and variable species, with a peculiar, almost circular distribution of forms. See fig. 77. On Borneo two well-distinguishable forms are present (fig. 77 g, h); specimens which link these two forms are found on the Malay Peninsula, Sumatra, and Java (see arrow on map). The form *'Guioa bullata'* has been described for the west point of Borneo (S Sarawak and SW Kalimantan; fig. 77 g shows an extreme form): the leaflets are broad, have a low leaf-index, an asymmetric base and are slightly villose below. The same form has been described for the Malay Peninsula as *'Guioa fuscidula'* (fig. 77 f upper half), of which the base can be even more asymmetric, the indumentum is somewhat more hirsute. The latter form is connected to another form of the Peninsula: *'Guioa squamosa'* (fig. 77 a, c, e; synonym: *Guioa cambodiana*), and to a form with very small leaflets: *Guioa microphylla* (fig. 77 b) through *'Guioa fuscidula* var. *glabrescens'* (fig. 77 f, lower half). The form *'Guioa squamosa'* has smaller asymmetric leaflets with a somewhat higher leaf-index and lacks the hirsute indumentum. Intermediate forms between the *'Guioa fuscidula/Guioa squamosa'* form and the typical *Guioa diplopetala* form (synonym: *Guioa regularis*) are found in Sumatra (fig. 77 d). The typical *Guioa diplopetala* form is especially found in Sumatra, Java, E Borneo (the other form of Borneo!) and Celebes (fig. 77 h): the leaflets are rather symmetric, long, narrow (high leaf-index), and lack hairs (sometimes the leaflets are very sparsely pilose below).

Examples of ranges: From the small-leaved, asymmetric *'Guioa microphylla'* (perhaps this form, of which two specimens are known, only represents flowering juveniles) to the long-leaved, more symmetric *Guioa diplopetala: Curtis 1346, SF 11151* (hairy, small leaflets, Malay Peninsula: *Guioa microphylla*), *Thorel 1490* (Malay Peninsula), *Wallich 8097* ('glabrous', longer leaflets, Malay Peninsula: *Guioa squamosa*), *Boden Kloss 14594, Iboet 304* (long leaflets, Sumatra), *Korthals s.n.* (Java: *Guioa diplopetala*).

From the broad, hairy '*Guioa bullata*' to the more slender, glabrous *Guioa diplopetala: Haviland 1003, 2137* ('villose', Borneo: *Guioa bullata*), *Helfer 993, King's collector 2452, 3818* ('hirsute', Malay Peninsula: *Guioa fuscidula*), *Scortechini 1714* (glabrous, Malay Peninsula: *Guioa fuscidula* var. *glabrescens*), *Iboet 304, Exposition Paris 1578, Riedel s.n.*, X-1876 (glabrous, smaller, Sumatra), *Korthals s.n.* (Java: *Guioa diplopetala*).

In Borneo both forms are spatially separated by the geologically old (dating from before the glacial periods) Lupar River system in W Borneo. This river is a border for more species, also from other families, e.g. 57 species of Dipterocarpaceae occur either E or W of it (Ashton, Ann. Missouri Bot. Gard. 64, 1977, 694–705). The presence of the central mountain range in Borneo may have prevented a further mingling of both forms; however, few collections have been made in Central Borneo and it is therefore possible that intermediates exist in Borneo itself. From Java northwards to Borneo and Celebes the fruits gradually become somewhat smaller; examples: *SAN 62371* (Borneo), *Ramlanto 223* (Celebes).

At first sight *Riedel s.n.* (Celebes; one of the types of *Guioa leptoneura*) appeared to be rather different from *Guioa diplopetala*, as it did not show any domatia and had very coriaceous leaflets and rather large, *Guioa bijuga*-like fruits. However, for instance the specimens *Kjellberg 2780* and *Teijsmann HB 12443* form transitions between both species and undo any delimitation: *Kjellberg 2780* possesses no domatia either (but it has thinner leaflets and small fruits) and *Teijsmann HB 12443* also has very coriaceous leaflets, but it possesses domatia and its fruits are intermediate in size. The other type of *Guioa leptoneura, Beccari FI 2807*, has very small fruits and domatia. Specimens without domatia tend to have a very slightly raised venation on the lower surface.

Typical for *Guioa diplopetala* are the elliptic leaflets, absence of papillae on the lower surface, many domatia, and small slender fruits.

2. *Cupania regularis* had to be lectotypified as Radlkofer only used part of the syntypes of *Cupania regularis* to describe *Guioa diplopetala* f. *borneensis*.

3. For the differences between *Guioa diplopetala* and *Guioa asquamosa* see the note under the latter, while the differences among *Guioa diplopetala, Guioa hirsuta,* and *Guioa patentinervis* are discussed in the note under *Guioa hirsuta*.

4. *Kooy 366* of the Lesser Sunda Islands resembles *Guioa diplopetala* macromorphologically, but anatomically (see chapter 7.6) and palynologically (Van der Ham & Van Heuven, pers. comm.) this specimen is quite unlike any *Guioa*.

Specimens studied:
BURMA: 2 specimens. — THAILAND: 5 specimens. — CAMBODIA: 7 specimens. — VIETNAM: 5 specimens. — MALAY PENINSULA: 26 specimens. — SUMATRA: 29 specimens. — JAVA: 69 specimens. — BORNEO: 51 specimens. — CELEBES: 8 specimens.

Guioa discolor Radlk. – **Fig. 78a, b.**

Guioa discolor Radlk., Elmer Leafl. Philip. Bot. 5 (1913) 1609; Philip. J. Sc. 8, Bot. (1914) 446; Merr., En. Philip. 2 (1923) 507; Radlk. in Engl., Pflanzenr. 98 (1933) 1168; Salvosa, Lex. Philip. Pl. (1963) 105. — Lectotype (here proposed): *Elmer 7493* (M, holo; iso in A, BM, FI, K, L, NY, W), Philippines, Luzon, Tayabas Prov., Lucban.

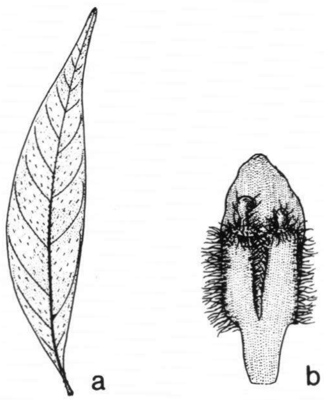


Fig. 78. *Guioa discolor* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5 (*Allen 259-81*, BISH).

Tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 3–8.5 mm in diam. *Leaves* 3–5-jugate; rhachis 4.3–22 cm long, basally terete to upwards flattened, not winged, subglabrous, petiole 1.8–8.3 cm long; petiolules up to 1 cm long. *Leaflets* not subsessile, opposite to subopposite, ovate, falcate, 4.9–14.4 by 1–3.6 cm, index 3.5–5, asymmetric, acroscopic side broader, coriaceous to very coriaceous, not punctate; base attenuate; margin entire, flat to revolute; apex cuspidate to caudate, gradually narrowing, usually mucronulate; upper surface smooth, glabrous; lower surface very differently coloured, dull, densely whitish papillate, sericeous, domatia absent to a single small sac on basiscopic side in axil of second nerve; venation on upper surface flat (to raised), not differently coloured from lamina, below raised; nerves 0.2–1.8 cm apart, marginally looped; veins laxly reticulate, usually rather indistinct. *Inflorescences* axillary, branching in or near axil and along rhachis; latter usually flattened, 1.3–9.5 cm long, brown sericeous; first order branches up to 3.3 cm long; cymules cincinnate, c. 2-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.8–1.2 mm long; bracteoles 0.7–0.8 mm long. *Pedicels* 1.8–4.5 mm long, sericeous except for the subglabrous, 0.9–1.5 mm long upper part. *Flowers* c. 4.2 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside (sub)glabrous; 2 outer smaller ones 1.2–1.3 by 1.1–1.3 mm; 3 inner larger ones 1.5–2.2 by 1.5–2.2 mm, margin petaloid. *Petals* 5, elliptic to obovate, 2.5–2.7 by 0.6–1 mm, blade obovate, gradually decurrent into claw, latter 0.7–1 mm high, margin pilose, outside and inside glabrous, apex obtuse to acute; scales 1.1–1.7 mm long, free; crest present as a pilose flat part of the bifid scale apex to rather glabrous and clavate. *Disc* incomplete. *Stamens* 8; filament 2.8–3.7 mm long, especially basally pilose; anther c. 0.3 mm long, glabrous. *Pistil:* ovary 0.4–0.7 mm long, smooth, subhirsute; style and stigma 0.4–0.5 mm long. *Fruit* immature.

Field notes. Tree, 6–13 m high, d.b.h. 15–20 cm. Outer bark grey. Wood white, hard. Leaves membranaceous, tough, dark green above; glaucous or grey below. Inflorescence ascending. Buds dark wine red. Sepals green to pink. Petals white to pink. Anthers pink.

Distribution. Philippines (Luzon, Samar).

Ecology. Primary dipterocarp forest. Alt.: 90–850 m. Flowering: May–June.

Vernacular name. Alahan-puti (Filipino).

Note. This species looks like *Guioa bicolor*, but the lower surface of the leaflets has in a dried state a lighter colour, the veins are less raised, the leaflets are smaller, and the apex is tapering or at most with a slight sinus. The fruit is still unknown; the shape of the latter is typical for *Guioa bicolor*.

S p e c i m e n s   s t u d i e d:
PHILIPPINES. Luzon: *M.S. Allen 259-81*, Cagayan Prov., Bagio cave; *Elmer 7493, 9321*, Tayabas Prov., Lucban. — Samar: *PNH (Madulid et al.) 118348.*

Guioa elliptica Welzen – Fig. 79a–c.

Guioa elliptica Welzen, Blumea 33 (1988) 411, pl. 3a–c. — T y p e: *BSIP (Gafui et al.) 16776* (L, holo; iso in BSIP, K; LAE, n.v.), Solomon Islands, Mockolonga area, Small Nggela.
Guioa koelreuteria auct. non Merr.: Merr. & Perry, J. Arn. Arbor. 21 (1940) 515.

Tree. *Branchlets* terete, smooth, sericeous especially when young; flowering twigs 2–3.5 mm thick. *Leaves* 1–3-jugate; rhachis 1.4–6.8 cm long, especially upwards above slightly flattened, not winged, subsericeous, petiole 0.8–2.5 cm long. *Leaflets* usually subsessile, opposite to subopposite, (ovate to) elliptic, 3.8–9.9 by 1.3–3.4 cm, index 2.9–3.5, asymmetric, not falcate, acroscopic side slightly broader, coriaceous, punctate; base attenuate; margin entire, mainly revolute; apex acute to acuminate, often mucronulate; upper surface smooth, glabrous, midrib usually basally puberulous; lower surface differently coloured, dull, papillate, (sub)-sericeous, domatia at least in some leaflets several relatively small sacs in axils of nerves, sometimes apically a few shallow pockets; venation on upper side flat, raised on lower; nerves 0.4–1.9 cm apart, marginally looped; veins laxly reticulate, indistinct. *Inflorescences* axillary to pseudoterminal, only branching along rhachis; latter somewhat flattened or grooved, 4–11.6 cm long, sericeous; first order branches up to 4.9 cm long; cymules cincinnate, 2–7-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.6–1.2 mm long; bracteoles 0.3–0.5 mm long. *Pedicels* 3.3–5.3 mm long, sericeous except for the subglabrous, 0.3–0.5 mm long upper part. *Flowers* 3–3.5 mm in diam. *Sepals* 5, ovate, margin pilose, outside and inside glabrous; 2 outer smaller ones 0.9–1.6 by 1–1.7 mm, margin with glands; 3 inner larger ones 1.5–2.3 by 1.5–3.2 mm, margin petaloid, without

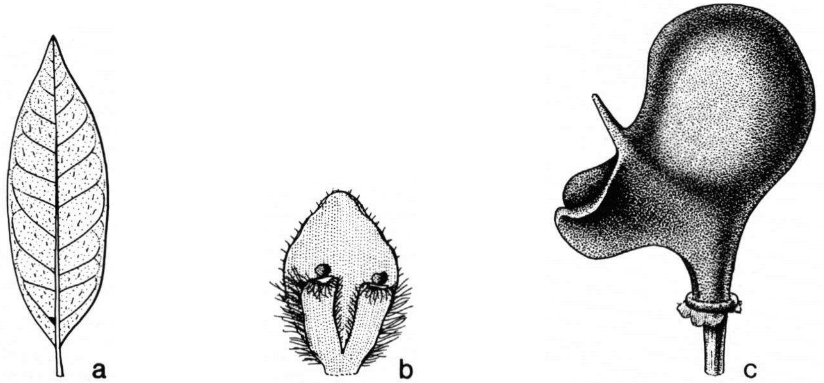


Fig. 79. *Guioa elliptica* Welzen. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, b: *BSIP (Gafui et al.) 16776*, L; c: *Brass 2884*, BW).

glands. *Petals* 5, elliptic, 1.8–2.1 by 0.9–1.1 mm, claw c. 0.2 mm high, margin pilose, outside and inside very sparsely pilose, apex obtuse; scales 0.5–0.7 mm long, free, apex not broadened; crest usually present, shortly stiped, apex clavate, somewhat pustular, glabrous; petal between two adjacent larger sepals not reduced. *Disc* incomplete, gap small. *Stamens* 8; filament 3–3.3 mm long, especially basally pilose; anther c. 0.7 mm long, glabrous. *Pistil:* ovary 0.3–0.5 mm high, very sparsely hirsute; style and stigma c. 0.2 mm long, elongating in fruit up to 2 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1 well-developed lobe, 1.2–1.5 cm high by 1.2–1.7 cm broad, smooth, glabrous, stipe 3–4.5 mm high, rather slender, angle between lobes 125–150°, blackish when dry; lobes 8.5–10 by 8–9 mm. *Seed* obovoid, c. 8 by 7 mm; hilum c. 1.3 mm long. *Embryo* c. 7.2 by 5.2 mm; cotyledons dorsoventrally above each other, upper larger, apices not elongated.

Field notes. Tree, 1–7 m high, d.b.h. 15–33 cm; bole straight, no buttresses. Outer bark dark brown, smooth. Wood white, soft. Leaves grey-green below. Bud cream. Flowers white. Fruits pink.

Distribution. W Solomon Islands: Guadalcanal, San Cristobal, San Jorge, Santa Ysabel, Small Nggela.

Ecology. Common, found in well-drained often secondary forest and in *Casuarina* forest on ultrabasic. Alt.: 800–1200 m. Flowering: July–Oct. Fruiting: Aug.–Oct.

Vernacular names. Sufusana (Kwara'ae; name also for *Guioa sufusana* and *Guioa megacarpa*). San Jorge: felo-felongwani. Guadalcanal: punga punga.

Note. *Guioa elliptica* differs from *Guioa sufusana* by its smaller leaflets and from *Guioa megacarpa* by its elliptic non-falcate leaflets and smaller fruits. *Guioa elliptica* has an incomplete disc, while the other two have complete discs.

Specimens studied:
SOLOMON ISLANDS. Guadalcanal: *Kajewski 2592*, Mt. Intuve?. — San Cristobal: *Brass 2884*, Hinuahaoro; *Whitmore 6274*, Warahito River Valley. — San Jorge: *Corner 2713*, Astrolabe Bay. — Santa Ysabel: *BSIP (Whitmore) 2410*, Maringa Lagoon. — Small Nggela: *BSIP (Gafui et al.) 16776*, Mockolonga area.

Guioa fusca Radlk. – Fig. 80 a–c.

Guioa fusca Radlk., Sapind. Holl.-Ind. (1879) 40, 41; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 614; Guillaumin, Bull. Soc. Bot. Fr. 79 (1932) 337; Radlk. in Engl., Pflanzenr. 98 (1933) 1171; Guillaumin, Fl. Nouv.-Caléd. (1948) 199; Mém. Mus. Nat. Hist. Nat. B, 15 (1967) 110 (p.p.: *Hürlimann 62*). — Type: *Baudouin 219* (P, holo), New Caledonia, Port de France.

Guioa gracilis auct. non Radlk.: Guillaumin et al., Un. Iowa Stud. Nat. Hist. 20, 7 (1965) 36 (*Thorne 28396*).

Treelet. *Branchlets* terete, smooth, sericeous when young; flowering twigs 1.5–5 mm thick. *Leaves* 1–5-jugate; rhachis 0.7–11.6 cm long, basally terete to upwards especially above flattened, slightly winged, subglabrous, petiole 0.6–3.3 cm long. *Leaflets* subsessile, opposite to subopposite, (ovate to) elliptic, 2.2–9.2 by 0.7–3.7 cm, index 2–3.5, ± symmetric, thin to coriaceous, punctate; base attenuate; margin entire, flat; apex (retuse to) obtuse to acuminate, not mucronulate; upper surface

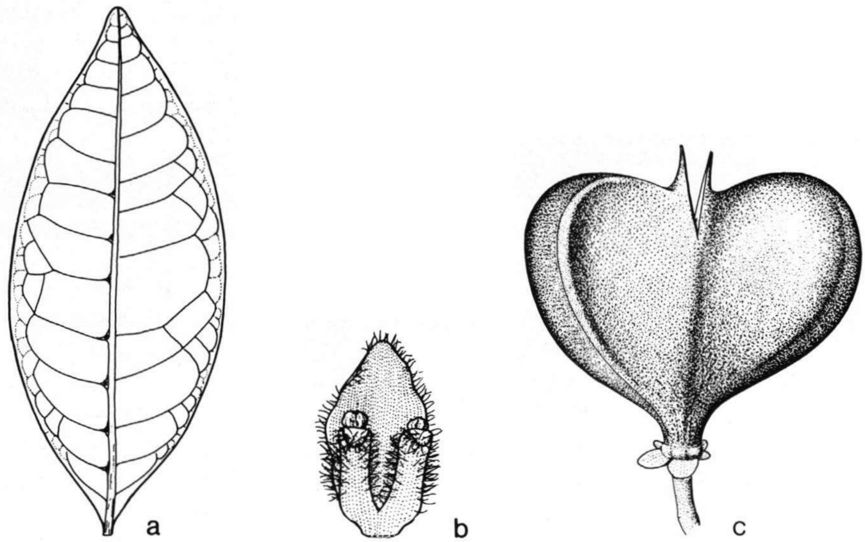


Fig. 80. *Guioa fusca* Radlk. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, b: *Balansa 152*, W; c: *Thorne 28396*, L).

smooth, glabrous; lower surface differently coloured, lighter, more dull, smooth, glabrous, domatia (1 to) many sac(s) in axils of nerves; venation on upper surface flat to raised, on lower raised; nerves 0.2–1.3 cm apart, marginally looped; veins laxly reticulate, distinct. *Inflorescences* axillary, branching in or near axil to racemosely along rhachis too; rhachis flattened, 0.8–11.9 cm long, subglabrous; first order branches up to 4.7 cm long; cymules usually cincinnate, 2–4-flowered *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.4–1.2 mm long; bracteoles 0.2–0.5 mm long. *Pedicels* 2.3–5.1 mm long, subglabrous except for the glabrous, 1.3–2.8 mm long upper part. *Flowers* c. 3 mm in diam. *Sepals* 5, ovate, margin pilose, without glands, outside and inside glabrous; 2 outer smaller ones 0.9–1.8 by 1–1.8 mm; 3 inner larger ones 1.9–3 by 1.9–3.1 mm, margin petaloid. *Petals* 5, elliptic to obovate, 2–2.3 by 1–1.2 mm, claw c. 0.2 mm high, margin pilose, outside and inside subglabrous, apex rounded to acute; scales 1–1.5 mm long, free, basally not auricled; crest clavate, lobed, on very short stalk. *Disc* incomplete. *Stamens* 8; filament 3–4.3 mm long, especially basally pilose; anther 0.5–0.7 mm long, glabrous. *Pistil:* ovary 0.3–0.7 mm high, smooth, subglabrous; stigma and style 0.2–0.3 mm high, elongating up to 1.5 mm in fruit, then upper c. 0.4 mm stigmatic. *Fruit* with 1–3 well-developed lobes, c. 1.3 cm high by 1.3–1.8 cm broad, smooth (to rough), glabrous, stipe c. 2 mm high, slender, edge of margin rounded, angle between lobes 120–145°, reddish when dry; dissepiments complete; lobes 9–10 by 8–8.5 mm. *Seed* and *embryo* immature.

Field notes. Treelet, 3–7.5 m high. Bark white, smooth. Leaflets green, shiny above. Flowers white, smelling like the egg-plant.

D i s t r i b u t i o n. SE New Caledonia and the islands N of New Caledonia.

E c o l o g y. Often common in forest. Soil: basalt. Alt.: 50–150 m. Flowering: Oct.

N o t e. The species *Guioa fusca, Guioa gracilis* and *Guioa pectinata* look rather alike; the following table lists the differences:

	Guioa gracilis	*Guioa fusca*	*Guioa pectinata*
Rhachis winged	–	+	–
Leaflet shape	ovate(-elliptic)	(ovate-)elliptic	elliptic
Leaflet thickness	thin	thin	thick
Domatia	1(–many)	(1–)many	(0–)1
Pedicel	subglabrous	subglabrous	sericeous
Petal height	0.8–1.4 mm	2–2.3 mm	2.5–3.5 mm
Disc	2 minute gaps	big gap	big gap

Some exceptions exist. One specimen of *Guioa gracilis* showed sometimes 2 and another one many domatia; also several specimens show a slight tendency towards a winged rhachis. Two specimens of *Guioa fusca* usually showed 1 large domatium, sometimes 2 (*Balansa 2274; Nicholson 73*).

S p e c i m e n s   s t u d i e d:
NEW CALEDONIA: 21 specimens, mainly in the South.

Guioa glauca (Labill.) Radlk. – Fig. 81 a–e.

Guioa glauca (Labill.) Radlk., Sapind. Holl.-Ind. (1879) 38; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 513, 516, 530, 531, 612; Guillaumin & Beauvis, Ann. Soc. Bot. Lyon 38 (1914) 86; Guillaumin, Bull. Soc. Bot. Fr. 79 (1932) 337; Radlk. in Engl., Pflanzenr. 98 (1933) 1170; Guillaumin, Fl. Nouv.-Caléd. (1948) 199; Guillaumin & Virot, Mém. Mus. Nat. Hist. Nat. B, 4 (1953) 18; Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 8 (1959) 134; ibid. 15 (1967) 110; Morat et al., Bull. Mus. Nat. Hist. Nat. sér. 4, B, 8 (1986) 174. — *Dimereza glauca* Labill., Sert. Austr.-Caled. (1825) 51, t. 51. — *Diplopetalon glaucum* Spreng., Syst. Veg. 4, 2 (1827) 150, nom. superfl. (I.C.B.N. art. 63.1). — *Cupania glauca* Cambess., Mém. Mus. Hist. Nat. 18 (1829) 28; Seem., Fl. Vit. (1865) 46; Séb., Not. Bois Nouv.-Caléd. (1874) 231. — *Cupania dimereza* Steud., Nom. Bot. 2 (1840) 433, nom. superfl. (I.C.B.N. art. 63.1). — For other references and typification see under var. *glauca*.
For further synonyms see under the varieties.

Shrub to treelet. *Branchlets* terete, smooth (to ribbed to rough), sericeous especially when young; flowering twigs 1–5(–13) mm thick. *Leaves* 1–3-jugate, very often all 1-jugate; rhachis 0.3–7.8(–13.3) cm long, basally terete to upwards adaxially somewhat flattened, not winged (see note 5 for an exception), subsericeous, petiole 0.3–9 cm long. *Leaflets* subsessile, opposite (to alternate), elliptic to obovate, 1.6–19.8 by 0.6–7.8 cm, index 1.7–4.9, ± symmetric, very coriaceous, usually punctate; base attenuate; margin entire, revolute; apex retuse to acuminate, not mucronulate; upper surface smooth, glabrous except for the basally pilose midrib to sericeous, sometimes covered with wax; lower surface differently coloured, dull, papillate, short to long sericeous, domatia absent (or a single, slightly domed sac on basiscopic side in axil of usually the second nerve); venation usually raised on both

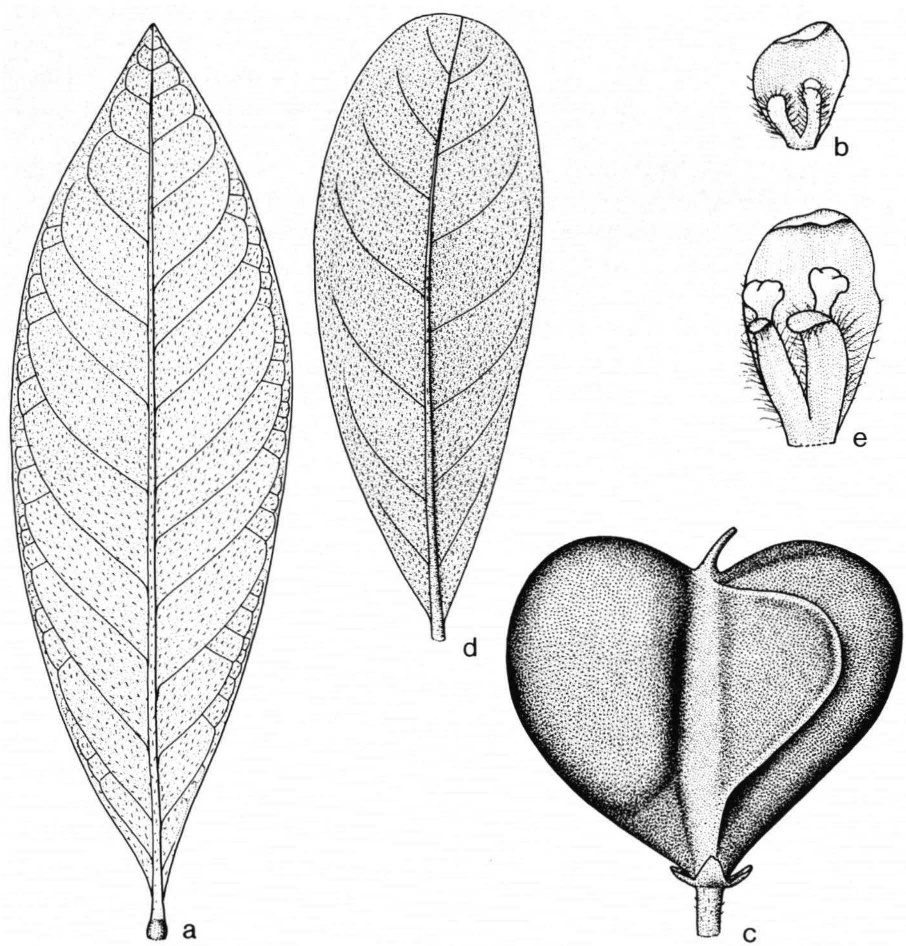


Fig. 81. *Guioa glauca* (Labill.) Radlk. – a–c: var. *glauca*. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, c: *Balansa 2266*, K; b: *Balansa 2843*, M). – d, e: var. *vulgaris* Welzen: d. leaflet, × 1 ; e. petal, × 12.5 (d: *MacKee 14365*, L; e: *MacKee 28736*, L).

sides, especially on lower; nerves 0.2–3 cm apart, marginally looped; veins laxly reticulate, indistinct. *Inflorescences* axillary, branching sometimes in or near axil to sometimes also along rhachis; rhachis somewhat flattened, 0.4–12.6 cm long, sericeous; first order branches up to 4.5 cm long; cymules cincinnate, 1–4-flowered. *Bracts* and *bracteoles* triangular, completely sericeous; bracts 0.5–1.3 mm long; bracteoles 0.2–1 mm long. Pedicels 1.5–9 mm long, sericeous, upper part subglabrous to as sericeous as the basal part, 0.5–7 mm long. *Flowers* 3–5 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside subglabrous to sericeous; 2 outer smaller ones 0.7–3.5 by 0.7–3 mm; 3 inner larger ones 1.7–

4.8 by 1.1–4.5 mm, margin petaloid. *Petals* 5, elliptic, 1.1–4.7 by 0.5–3.3 mm, claw 0.1–0.5 mm high, margin and sometimes outside and inside pilose, apex rounded to obtuse; scales 0.7–2.5 mm long, free; crest sometimes developed as a linear appendix or completely developed, then longly stiped, apex clavate, lobed, glabrous. *Disc* incomplete. *Stamens* 8; filament 1.2–5.7 mm long, especially basally pilose; anther 0.3–1.1 mm long, glabrous to pilose. *Pistil:* ovary 0.2–2 mm high, sparsely hirsute; style and stigma 0.1–2 mm high, elongating in fruit up to 4 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-devoloped lobes, 1–2.1 by 0.9–2.6 cm, smooth (to occasionally rugose), glabrous, stipe 0.5–5 mm high, slender to broadly cuneate, angle between lobes 80–160°, blackish when dry; lobes 7–12 by 7–12 mm. *Seed* obovoid, 6.7–9.2 by 4.8–6.5 mm; hilum 0.8–1.3 mm long. *Embryo* 5.8–8.2 by 4–5.8 mm; cotyledons secondarily laterally besides each other, about equal in size, apices elongated, recurved; radicle 1.2–2.8 mm long.

Field notes. Shrub to treelet, 0.6–15 m high, d.b.h. up to 25 cm. Bark smooth to slightly rough, brown with grey stripes to grey. Wood reddish. Leaflets above yellowish green to light green to dark green; below light green to glaucous to greyish green to yellowish. Buds white to pink. Pedicels tinged red. Flowers sweet scented. Sepals green to white to red. Petals white to pink; crest yellow. Disc yellow. Filaments white to pink; stamens pink to dark purple; pollen yellow. Pistil light green to pink. Fruits purple; arilloid yellow to orange; seed shiny brown to black.

Distribution. New Caledonia.

Ecology. Rare to common. Found in rain forest to savannah, often along water (gallery forest, sea shore, sometimes in tidal zone), edge of forest or along roads. Soil: ultrabasic (serpentine), vulcanic, calcareous, (mica)schist, peridotite. Alt.: sea-level up to 1200 m. Seeds eaten by parakeets.

Notes. 1. The difference between the two varieties is correlated with ecological circumstances. The variety *glauca* is found on calcareous soil and along the coast (also a lime-rich environment). The other variety is mainly found in more acid surroundings. Within the variety *vulgaris* three indistinct groups can be found:

a. A group of plants only found on serpentine in the south of the island. Typical are the long petioles, of which the upper part is (sub)glabrous, and the large flowers. Examples are: *Baumann-Bodenheim 14341; Bernardi 9843; Däniker 240; Franc A 7; Green 1196; MacKee 42277, 42779, 42781, 42788, 42929; Morat 7548; Pancher 281; Thorne 28600; Webster & Hildreth 14943.*
b. The second (and third) group have shorter petioles and smaller flowers. The second group was known as forma *trachycalyx*. The leaflets and sepals are very hairy. This group is found on all types of soil. Examples: *Balansa 1444; Bernardi 10248, 12550; Compton 691; Deplanche 278; MacKee 2637, 4261, 4566, 4661, 4854; MacMillan 5065a; MacPherson 3877, 4655; Schlechter 15199, 15503; Vieillard 776.*
c. The third group was known as forma *psilocalyx*. These plants have subsericeous leaflets and subglabrous sepals. They are found in the same habitat as the former group. Examples: *Balansa 3305; Franc 1515, 1922; Guillaumin & Baumann-Bodenheim 11392; Hürlimann 1621; MacKee 4738, 11681; MacMillan 5063; MacPherson 2725, 5540; Vieillard 219, 314.*

2. On Mt. Koniambo specimens were collected which, at first look, resembled each other very closely and looked different from *Guioa glauca* as well as *Guioa villosa*. However, some specimens (*MacKee 4261; Schmid 115; Veillon 6076, 6109*) appeared to have the same characters as *Guioa glauca* (one domatium, short appressed hairs), while the other specimens possessed the characteristics of *Guioa villosa* (more domatia of a different type, long subappressed to patent hairs: *Bernardi 10162, 10163; Jaffré 910, 2351; MacKee 4296; Suprin 670; Webster & Jaffré 19263*). This is a nice example of convergence between two species. See also note 1 and 3f under *Guioa villosa*.

3. Lectotypes are proposed for the formae *psilocalyx* and *trachycalyx*, now synonyms of var. *vulgaris*, because not all syntypes appeared to belong to these two morphotypes (see note 1 for definition of the morphotypes).

4. See also the notes under *Guioa villosa* (note 3f), *Guioa semiglauca*, and *Guioa palawanica*.

5. *Jaffré 857* looks very atypical, the leaflets are very small (about 4.6 by 0.8 cm) and they have a glabrous lower surface. The rhachis of the leaves is slightly winged.

KEY TO THE VARIETIES

1a. Leaflets large, 4–19.8 by 1.2–7.8 cm; apex (obtuse to) acute to acuminata. Petals 1.1–2.3 by 0.5–1.9 mm, crest if present a linear appendage, not clavate. Stipe of fruit 0.5–2 mm high, broadly cuneate .... **a. var. glauca**

b. Leaflets small to large, 1.6–15.8 by 0.6–5.3 cm; apex retuse to acuminate. Petals 1.7–4.7 by 1–3.3 mm; crests clavate (exceptionally linear). Stipe of fruit 1–5 mm high, usually slender .... **b. var. vulgaris**

a. var. glauca – Fig. 81a–c.

Guioa glauca f. *genuina* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 612, nom. illeg. (I.C.B.N. art. 26.1); in Engl., Pflanzenr. 98 (1933) 1170. — *Guioa glauca* var. *glauca:* Welzen, Blumea 33 (1988) pl. 11c, d. — Type: *Labillardière s.n.* (FI, holo; iso in P), New Caledonia.

Guioa glauca f. *dendroides* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 612; in Engl., Pflanzenr. 98 (1933) 1170. — Lectotype (here proposed): *Balansa 2266* (M, holo; iso in BM, K, NY, P), New Caledonia, Port-Bouquet.

Leaves 1- or 2-jugate. *Leaflets* 4–19.8 by 1.2–7.8 cm; apex (obtuse to) acute to acuminate. *Petals* 1.1–2.3 by 0.5–1.9 mm; scales 0.7–1.6 mm long; crest absent to slightly developed as a linear appendage, not clavate. *Fruit:* stipe 0.5–2 mm high, broadly divergent.

Ecology. Mainly found on calcareous soil. Alt.: sea-level up to 500 m. Flowering: March–May. Fruiting: Sept.–Oct.

Specimens studied:
NEW CALEDONIA: 48 specimens.

b. var. vulgaris Welzen – Fig. 7a, c; 81d, e.

Guioa glauca var. *vulgaris* Welzen, Blumea 33 (1988) 411, pl. 11a–e. — *Guioa glauca* f. *trachycalyx* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 613; in Engl., Pflanzenr. 98 (1933) 1171. — L e c t o t y p e: *Balansa 1444* (P, holo; iso in P), New Caledonia, Bourail.

Guioa glauca f. *psilocalyx* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 612; in Engl., Pflanzenr. 98 (1933) 1170. — L e c t o t y p e (here proposed): *Balansa 3305*, p.p. (M, holo; iso in A, P), New Caledonia, Poum.

Guioa aryteroides Guillaumin, Acta Horti Gotob. 19 (1952) 21, pl. 14; Morat et al., Bull. Mus. Nat. Hist. Nat. Paris 4e sér., 8, B (1986) 174. — T y p e: *Selling 228* (S, holo; iso in P), New Caledonia, Montagne des Sources.

Guioa koniamboensis Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 8 (1959) 134; ibid. 15 (1967) 110; Morat et al., Bull. Mus. Nat. Hist. Nat. 4e sér., 8, B (1986) 174. — T y p e: *MacKee 4261* (P, holo; iso in K, L), New Caledonia, Mt. Koniambo.

Leaves 1–3-jugate. *Leaflets* 1.6–15.8 by 0.6–5.3 cm; apex retuse to acuminate. *Petals* 1.7–4.7 by 1–3.3 mm; scales 0.7–2.5 mm long; crest well-developed, clavate, stiped, lobed, very occasionally a linear appendage. *Fruit:* stipe 1–5 mm high, usually slender.

E c o l o g y. Mainly found on ultrabasic and vulcanic soil. Alt.: sea-level up to 1200 m. Flowering: Dec.–Oct. Fruiting: mainly Aug.–Oct.

S p e c i m e n s   s t u d i e d:
NEW CALEDONIA: 208 specimens.

Guioa gracilis (Panch. & Séb.) Radlk. – Fig. 82a–c.

Guioa gracilis (Panch. & Séb.) Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 609, 617; Guillaumin, Not. Syst. 1 (1909) 330; Bull. Soc. Bot. Fr. 79 (1932) 337; Radlk. in Engl., Pflanzenr. 98 (1933) 1161; Guillaumin, Fl. Nouv.-Caléd. (1948) 199; Guillaumin & Virot, Mém. Mus. Nat. Hist. Nat. B, 4 (1953) 18. — *Cupania gracilis* Panch. & Séb., Rév. Marit. Colon. 41 (IV-1874) 207; in Séb., Not. Bois Nouv.-Caléd. (1874) 231, 270. — L e c t o t y p e (here proposed): *Vieillard 226*, p.p. (M, holo; iso in L, P), New Caledonia.

Guioa mareensis Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 15 (1967) 111. — S y n t y p e s: New Caledonia, Maré, Pénélo: *Baumann-Bodenheim 14782* (A, BRI, NY, P); *14787* (cited as *14789*; A, NY, P).

Guioa fusca auct. non Radlk.: Guillaumin & Virot, Mém. Mus. Nat. Hist. Nat. B, 4 (1953) 18.

Tree(let). *Branchlets* terete, smooth (to slightly rough), only sericeous when young; flowering twigs 1–4 mm thick. *Leaves* 1–4-jugate; rhachis 0.6–11.6 cm long, basally terete to upwards somewhat dorsoventrally flattened, not winged (to slightly winged), glabrous, petiole 0.5–3.4 cm long; petiolules when present up to 0.8 cm long. *Leaflets* usually subsessile, opposite to subopposite, ovate, 1.6–12.1 by 0.6–3.8 cm, index 2.1–4.6, usually symmetric, thin to coriaceous, punctate; base attenuate; margin entire to sometimes slightly crenate, flat; apex obtuse to acute (to acuminate), not mucronulate; upper surface smooth, glabrous; lower surface differently coloured, more dull, smooth, (sub)glabrous, domatia usually a single sac on basiscopic side in axil of second nerve to very exceptionally many sacs in axils of nerves; venation on upper surface flat to raised, raised on lower side; nerves 0.2–1.9 cm apart, marginally looped; veins laxly reticulate, not very distinct. *Inflorescences* axillary, branch-

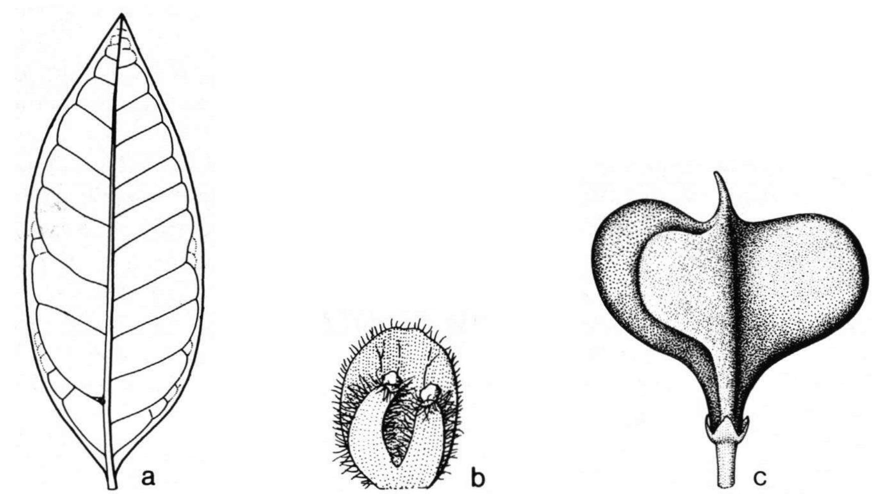


Fig. 82. *Guioa gracilis* (Panch. & Séb.) Radlk. a. leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a: *Mac Pherson 4663*, L; b: *MacKee 33585*, L; c: *MacKee 36497*, L).

ing along rhachis (to in or near axil too); rhachis somewhat flattened, 0.7–10.5 cm long, subsericeous; first order branches up to 4.8 cm long; cymules usually dichasial, 2–5-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.3–1 mm long; bracteoles 0.2–0.4 mm long. *Pedicels* 1.3–3.8 mm long, subglabrous, except for the glabrous, 0.8–2.5 mm long upper part. *Flowers* 2–4 mm in diam. *Sepals* 5, ovate to orbicular, margin pilose, without glands, outside and inside glabrous; 2 outer smaller ones 0.7–1.8 by 0.7–2 mm; 3 inner larger ones 1.2–2.8 by 0.8–2.5 mm, margin petaloid. *Petals* 5, obovate, 0.8–1.4 by 0.4–1.3 mm, claw 0.1–0.2 mm high, margin pilose, inside less so, outside glabrous, apex retuse to truncate; scales 0.6–1.2 mm long, free; crest clavate on short stumpy stipe, lobed. *Disc* incomplete, with 2 small slits near insertion of two adjacent large sepals. *Stamens* 8; filament 1–3.4 mm long, especially basally pilose; anther 0.3–0.7 mm long, pilose. *Pistil*: ovary 0.2–2 mm high, smooth, very sparsely hirsute; stigma and style 0.1–2 mm long, elongating up to 3.3 mm in fruit, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.1–1.3 by 0.9–1.4 cm, smooth (to rugose), glabrous, stipe 1.5–3.5 mm high, slender, angle between lobes 135–150°, reddish when dry; lobes 7.5–8 by 7–8.5 mm. *Seed* obovoid, 6.9–8 by 4.6–6 mm; hilum 0.8–1.2 mm long. *Embryo* 6.3–7.2 by 4–5.8 mm; cotyledons secondarily laterally besides each other, upper larger, both apices elongated, usually recurved, especially that of lower cotyledon; radicle 2–3.5 mm long.

Field notes. Tree(let), 1.5–10 m high; d.b.h. up to 10 cm. Bark almost smooth, (brown tinged) grey. Leaflets (light) green, shiny above; light green, shiny below. Flowers white, fragrant. Anthers pink to purple.

D i s t r i b u t i o n. NW and SE New Caledonia, and the islands N of New Caledonia.

E c o l o g y. Found in gallery forest, degradated forest, littoral. Soil: lime rich, schists, (ultrabasic). Alt.: sea-level up to 300 m. Flowers visited by bees. Flowering: July–Aug. Fruiting: Oct.–Jan.

N o t e s. 1. Radlkofer was unaware of the fact that Pancher and Sébert already described *Guioa gracilis* (as *Cupania gracilis*), he just used the epitheton, which was present on the sheeths and thereby created the correct combination within *Guioa*.

2. Two specimens have somewhat exceptional features: *MacPherson 4863* has sometimes 2 domatia and *Whitmee s.n.* (from Lifu) has many domatia. *Whitmee s.n.* is also special because of the smaller rugose fruits. Several specimens show a tendency towards winged rhachises.

3. For the differences among *Guioa fusca, Guioa gracilis,* and *Guioa pectinata,* see the note under *Guioa fusca.*

S p e c i m e n s s t u d i e d:
NEW CALEDONIA: 48 specimens.

Guioa grandifoliola Welzen – Fig. 83a, b.

Guioa grandifoliola Welzen, Blumea 33 (1988) 412, pl. 4a, b. — T y p e: *NGF (Streimann) 45154* (L, holo; iso in BRI, K; LAE, n.v.), Papua New Guinea, Morobe Prov., Buso.

Tree. *Branchlets* terete, smooth (to slightly rough), shortly sericeous when young; flowering twigs 5–19 mm thick. *Leaves* 2- or 3-jugate; rhachis 5.8–21 cm long, terete, not winged, glabrous, petiole 1.7–9.5 cm long. *Leaflets* subsessile, opposite to subopposite, ovate, 10.9–30 by 3.8–13.3 cm, index 2.1–2.9, ± symmetric, otherwise acroscopic side broader, coriaceous, not punctate; base attenuate; margin entire, flat; apex acute to cuspidate, mucronulate; upper surface smooth, glabrous, usually with wax; lower surface differently coloured, duller, smooth, no papillae, glabrous, domatia absent; venation on upper side flat (to raised), raised on lower; major nerves 0.4–4.3 cm apart, marginally looped, but less distinctly so in lower part of leaflets; veins laxly reticulate, indistinct. *Inflorescences* ramiflorous (to axillary), not branching to branching in axil and along rhachis; latter flattened to terete when in fruit, 0.7–12.7 cm long, (sub)sericeous; first order branches up to 8.5 cm long; cymules cincinnate. *Bracts* and *bracteoles* triangular, outside hirsute, inside glabrous; bracts 0.9–1 mm long; bracteoles 0.3–0.6 mm long. *Pedicels* 4–5.6 mm long, sericeous except for the subglabrous 2–2.5 mm long upper part. *Flowers* unknown. *Sepals* 5, ovate, margin pilose, outside and inside glabrous; 2 outer smaller ones 0.8–1.7 by 1.5–1.8 mm, margin with glands; 3 inner larger ones 1.9–3 by 2–3 mm, margin petaloid, without glands. *Petals* unknown. *Disc* incomplete. *Stamens* unknown. *Pistil*: ovary unknown; style and stigma elongating in fruit up to 3 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.2–1.6 cm high by 2–2.7 cm broad, smooth to slightly rugose or ribbed, glabrous, stipe 1–1.5 mm high, broadly cuneate, wall 1–3 mm thick near edge, latter rounded, angle between lobes 45–95°, black when dry; dissepiments complete; lobes 12–16

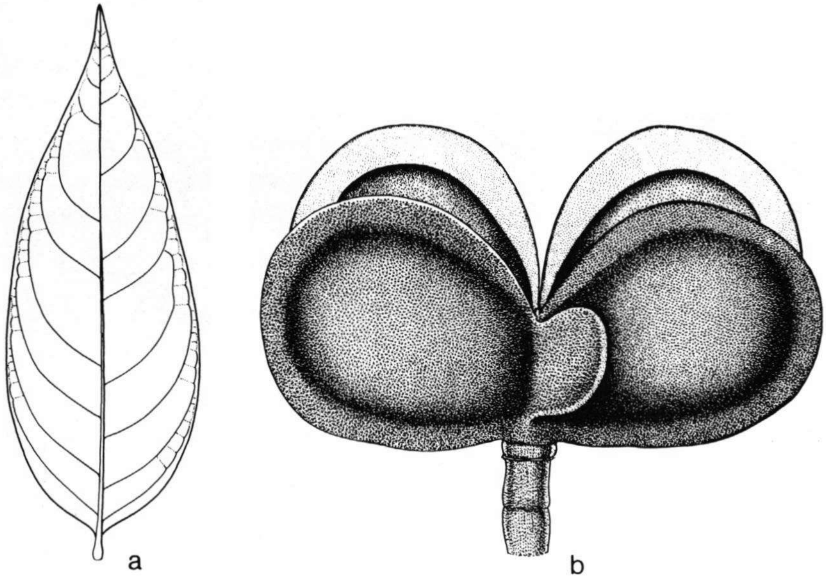


Fig. 83. *Guioa grandifoliola* Welzen. a. Leaflet, × 0.25; b. fruit, × 3 (*NGF (Streimann) 45154*, L).

by 10–14 mm. *Seed* obovoid, c. 7.5 by 5.5 mm; pseudofunicle often reduced in size, sometimes only a basal rim present on arilloid; hilum c. 1.1 mm long. *Embryo* c. 6.3 by 4.3 mm; cotyledons dorsoventrally above each other, upper larger, apex of upper somewhat elongated, straight; radicle c. 1.5 mm long.

Field notes. Tree, 5–25 m high, d.b.h. 5–30 cm; bole 3–20 m. Outer bark slightly pustular, grey to grey-brown to light brown to red-brown; middle olive green; inner red-orange. Wood of moderate weight and hardness, cream. Leaves glossy to dull dark green above, dull lighter green to yellow-green below. Calyx light green. Fruit yellow turning orange.

Distribution. Papua New Guinea (Morobe, Northern Prov.).

Ecology. Found in lowland rain forest (Dipterocarp dominated), advanced secondary forest and gallery forest. Alt.: sea-level up to 400 m. Fruiting: Aug.

Notes. 1. Typical for this species are the very large, ovate leaflets without indumentum and domatia and with on the uooer side usually wax. The fruits are like those of *Guioa rigidiuscula*, only usually smaller.

2. *Guioa grandifoliola* is part of the *Guioa rigidiuscula*-complex. The differences among the species within this complex are discussed in chapter 9.

Specimens studied:

PAPUA NEW GUINEA. Morobe Prov.: *Conn 319*, & *Students 195*, Buso River; *NGF (Streimann) 24299*, Ana; *(Streimann) 45154*, Buso River. — Northern Prov.: *NGF (Ridsdale) 31715*, Ioma.

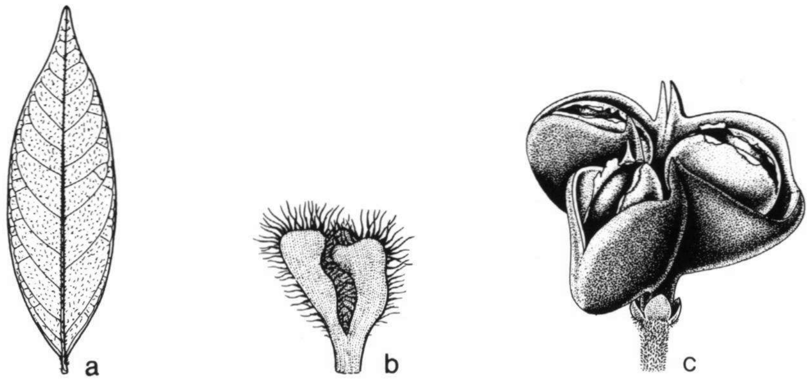


Fig. 84. *Guioa hirsuta* Welzen. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *Curran 3426*, A; b: *Meijer 9706*, L).

Guioa hirsuta Welzen – Fig. 84 a–c.

Guioa hirsuta Welzen, Blumea 33 (1988) 412, pl. 1a–c. — Type: *Van Balgooy 3658* (L, holo; iso in K; BO, n.v.), S Celebes, hills W of Soroako.

Shrub to treelet. *Branchlets* terete, smooth, hirsute; flowering twigs 2.2–7 mm thick. *Leaves* 2–7-jugate; rhachis 1.8–15.5 cm long, terete to upwards flattened above, not winged (except slightly winged when juvenile), hirsute, petiole 1.1–6.2 cm long. *Leaflets* subsessile, subopposite to alternate, (ovate to) elliptic, 3–10.7 by 1–3.5 cm, index 2.4–3.8, usually somewhat asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire (serrate in juvenile ones), flat (to revolute); apex acuminate to cuspidate, usually not mucronulate; upper surface smooth, hirsute; lower surface differently coloured, duller, smooth, no papillae, hirsute, small red erect glands abundant, domatia many pockets in axils of major nerves; venation on upper side flat, raised on lower; nerves 0.3–1.6 cm apart, marginally looped; veins laxly reticulate, rather indistinct. *Inflorescences* axillary, branching in or near axil and along rhachis; latter terete to somewhat flattened, 1.5–17 cm long, hirsute; first order branches up to 5 cm long; cymules cincinnate, 2- or 3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.7–1 mm long; bracteoles 0.3–0.5 mm long. *Pedicels* 1.8–4 mm long, sericeous, except for the less sericeous, 0.8–2 mm long upper part. *Flowers* 3.2–3.5 mm in diam. *Sepals* 5, ovate, margin and basally the outside pilose, margin with glands, inside glabrous; 2 outer smaller ones 1–1.8 by 1–1.8 mm; 3 inner larger ones 1.8–2.8 by 1.4–3.2 mm, margin petaloid. *Petals* 5, elliptic, 1–1.9 by 0.3–0.7 mm, claw 0.4–0.8 mm high, margin pilose, outside and inside (sub)glabrous, apex obtuse; scales 0.9–1.3 mm long, free; crest sometimes present as the slender pilose part of a bifid scale apex. *Disc* complete. *Stamens* 8; filament 3.8–4.3 mm long, especially basally pilose;

anther 0.4–0.5 mm long, glabrous. *Pistil*: ovary 0.3–0.5 mm long, smooth, subhirsute; stigma and style 0.1–0.6 mm long, elongating in fruit up to 2.5 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 0.7–1.1 cm high by 0.7–1.5 cm broad, smooth to sometimes somewhat rugose-ruminate, glabrous, stipe c. 1.5 mm high, slender, angle between lobes 135–145°, blackish when dry; lobes 5–8 by 6.5–8 mm. *Seed* obovoid, 5.2–5.3 by 2.9–4.2 mm; hilum 1–1.1 mm long. *Embryo* 4.3–5.8 by 3.3–4 mm; coteledons secondarily laterally besides each other, about equal in size, apices elongated, that of upper straight, of lower recurved; radicle 1.5–1.8 mm long.

Field notes. Shrub to tree, 2–15 m high, d.b.h. up to 19 cm, ornamental; flutes up to 1.5 m high, c. 5 cm deep, c. 10 cm wide. Outer bark brownish grey, not fissured, not peeling off, with many small elevated lenticels, c. 0.3 mm thick; middle and inner bark c. 4.5 mm thick, middle pale reddish, inner cream coloured, without exudate. Sapwood pale reddish cream; heartwood reddish ochre. Leaves dark green above, below lighter green with brown indumentum. Buds light green to pale green-yellow. Flowers white. Fruit red; seed brown.

Distribution. Celebes.

Ecology. Found in swamp forest, disturbed forest, belukar, and along lakes. Vegetation usually with *Gleichenia* ferns, *Imperata, Melastoma*. Soil: usually ultrabasic, sometimes siliceous or clayey. Alt.: sea-level up to 1200 m. Flowering: April–July. Fruiting: March–June.

Note. The differences among *Guioa diplopetala, Guioa hirsuta*, and *Guioa patentinervis* are listed below:

	Guioa diplopetala	*Guioa hirsuta*	*Guioa patentinervis*
Pilosity	glabrous (Borneo + Celebes)	hirsute	glabrous
Glands	absent	present	absent
Domatia	absent to many sacs (to pockets), at least basally a sac	many pockets	absent to a single sac to many sacs
Flowers	3–4.5 mm in diam.	3.2–3.5 mm	c. 2 mm
Petals	0.5–4 by 0.3–2.2 mm	1–1.9 by 0.3–0.7 mm	0.8–1.2 by 0.3–0.4 mm
Fruits	0.7–1.5 cm high by 0.7–1.8 cm broad	0.7–1.1 cm by 0.7–1.5 cm	0.7–0.9 cm by 0.7–1.3 cm
Cotyledons	secondarily laterally besides each other	secondarily laterally besides each other	dorsoventrally above each other

Specimens studied:

CELEBES. *Van Balgooy 3658*, Soroako; *3942*, between Soroako and Nickel plant; *3995*, between Tabarano and Ranteloka; *Curran 3426*, Kulawi; *Meijer 9706, 9930*, Mt. Nokilalaki; *11420*, Matano Lake near Soroako; *NIFS Cel./IV-93, NIFS Cel./IV-156*, Malili; *De Vogel 6202*, NE shore of Lake Matano, Seluro.

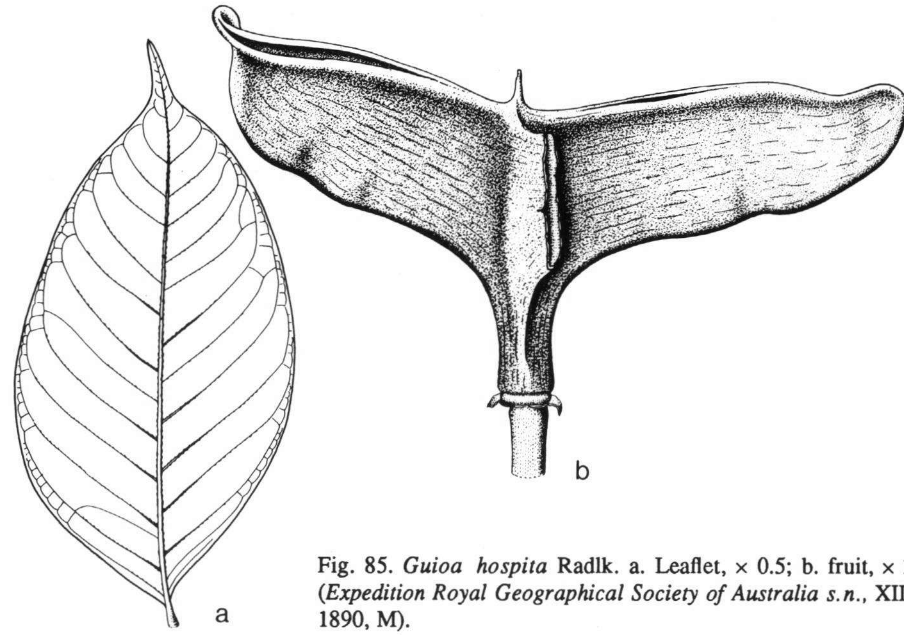


Fig. 85. *Guioa hospita* Radlk. a. Leaflet, × 0.5; b. fruit, × 3 (*Expedition Royal Geographical Society of Australia s.n.*, XII-1890, M).

Guioa hospita Radlk. – Fig. 85 a, b.

Guioa hospita Radlk. [in E. & P., Nat. Pflanzenfam. 3, 5 (1895) 346, nom. nud.], Bot. Jahrb. 56 (1921) 281; in Engl., Pflanzenr. 98 (1933) 1173. — Type: *Expedition Royal Geographical Society of Australia s.n.*, XII-1890 (M, holo), New Guinea, Mt. Yule.

Tree? *Branchlets* terete, swollen beneath the nodes (see note 2), smooth, puberulous when young; flowering twigs c. 5 mm thick. *Leaves* 1- or 2-jugate; rhachis 6.8–16.5 cm long, terete, not winged, slightly puberulous, petiole 6.5–9.5 cm long. *Leaflets* subsessile, opposite, ovate, 15.4–22.5 by 7.4–9 cm, index 2.1–2.5, subbasally asymmetric, acroscopic side broader, subcoriaceous, punctate; base attenuate; margin entire, flat; apex acuminate to cuspidate, mucronulate; upper surface smooth, puberulous on midrib and basal major nerves; lower surface differently coloured, duller, smooth, no papillae, puberulous on venation, domatia many pockets in axils of major nerves; venation on upper side flat, raised below; major nerves 0.3–2.2 cm apart, marginally looped, but less distinctly so in lower part of leaflets; veins laxly reticulate, rather inconspicuous. *Infructescence* axillary, branching along rhachis; latter terete, c. 11 cm long, puberulous; first order branches up to 4.4 cm long. *Bracts* and *bracteoles* caducous. *Pedicels* 6–6.5 mm long, puberulous; upper part 2.5–3 mm long. *Flowers* absent. *Sepals* and *petals* caducous. *Disc* incomplete. *Stamens* and *pistil* absent. *Fruit* immature, with 1 or 2 developing lobes, c. 1.8 cm high by c. 2.8 cm broad, slightly ribbed, glabrous, stipe c. 6 mm high, slightly cuneate, edge of margin rounded, angle between lobes c. 135°, blackish when dry; dissepiments complete; lobes c. 16 by 7 mm. *Seed* unknown.

Distribution. Papua New Guinea (Gulf Prov.).

Notes. 1. This species is part of the *Guioa rigidiuscula*-complex. It is distinct from the other species of this complex by its puberulous leaflets with many pockets, many and dense major nerves, and highly stiped fruits with slender long lobes. The differences between *Guioa hospita* and the other species in the *Guioa rigidiuscula*-complex are discussed in chapter 9.

2. The name *hospita* (the hospitable *Guioa*) refers to the insect (ants?) nests in the swollen nodes. It is not clear whether the nodes are normally swollen or, more probably, whether this is a reaction to nestling insects.

Specimen studied:
PAPUA NEW GUINEA. Gulf Prov.: *Expedition Geographical Society of Australia s.n.*, XII-1890, Mt. Yule.

Guioa koelreuteria (Blanco) Merr. – Fig. 7b; 86a–e.

Guioa koelreuteria (Blanco) Merr., Sp. Blanc. (1918) 241; Brown, Min. Prod. Philip. For. 3 (1921) 204; Merr., En. Philip. 2 (1923) 507; Radlk. in Engl., Pflanzenr. 98 (1933) 1172 (footnote); Brown, Useful Pl. Philip. 2 (1950) 363; Desch, Mal. For. Rec. 15 (1954) 526; Salvosa, Lex. Philip. Pl. (1963) 105; Guzman et al., Guide Phil. Fl. Fauna 3 (1986) 300, fig. 218. — *Sapindus koelreuteria* Blanco, Fl. Filip. (1837) 289, *'kolreuteria'*. — *Koelreuteria arborea* Blanco, Fl. Filip. ed. 2 (1845) 202. — Neotype: *Merrill 644* (PNH, holo, †; iso in BM, F, K, L, NY, P, W), Philippines, Luzon, Rizal Prov.

Hemigyrosa perrottetii Blume, Rumphia 3 (1847) 165; Walp., Ann. 2 (1851/2) 212; Gray, U.S. Expl. Exp. Bot. 1 (1854) 251; Miq., Fl. Ind. Bat. 1, 2 (1859) 568; F.-Vill., Nov. App. (1883) 349. — *Guioa perrottetii* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8 (1878) 273; Sapind. Holl.-Ind. (1879) 39; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 614; Vidal, Rev. Pl. Vasc. Philip. (1886) 95; Ceron, Cat. Pl. Herb. Manila (1892) 53; Radlk. in Perk., Fragm. Fl. Philip. 1 (1904) 63; Merr., Philip. J. Sc. 1, Suppl. (1906) 87; Philip. J. Sc. 3, Bot. (1908) 79; Fl. Manila (1912) 306; Radlk., Philip. J. Sc. 8, Bot. (1913) 446; Sasaki, Cat. Gov. Herb. (1930) 328; Radlk. in Engl., Pflanzenr. 98 (1933) 1172. — Lectotype (here proposed): *Perrottet s.n.*, s.d. (L, holo, sh. no. 908.270-339; iso in Fl, L, P), Philippines, Manila.

Guioa salicifolia Radlk., Elmer Leafl. Philip. Bot. 5 (1913) 1608; Philip. J. Sc. 8, Bot. (1913) 446; Merr., En. Philip. 2 (1923) 509; Radlk. in Engl., Pflanzenr. 98 (1933) 1165; Salvosa, Lex. Philip. Pl. (1963) 105. — Type: *Elmer 12286* (M, holo; iso in A, BM, F, Fl, K, L, NY, P, U, W), Philippines, Capiz Prov., Sibuyan I., Magallanes, Mt. Giting-giting.

Guioa mindorensis Merr., Philip. J. Sc. 20 (1922) 404; En. Philip. 2 (1923) 508; Radlk. in Engl., Pflanzenr. 98 (1933) 1165; Salvosa, Lex. Philip. Pl. (1963) 105. — Type: *BS (Ramos) 39639* (PNH, holo, †; iso in A, K), Philippines, Mindoro, Paluan.

Guioa spec.: Vidal, Rev. Pl. Vasc. Philip. (1886) 95, p.p. (*Vidal 1226, 1230*).

Quassia simaruba auct. non L.: Blanco, Fl. Filip. ed. 2 (1845) 247; Merr., Sp. Blanc. (1918) 241 (in synonymy).

Sapindus pubescens auct. non Zoll. & Mor.: Zoll. & Mor. in Mor., Syst. Verz. (1846) 22, p.p. (*Perrottet s.n.*).

Cupania regularis auct. non Blume: Vidal, Sinopsis (1883) 21, fig. 34 b.

Guioa rigidiuscula auct. non Radlk.: Vidal, Rev. Pl. Vasc. Philip. (1886) 95; Ceron, Cat. Pl. Herb. Manila (1892) 53.

Guioa diplopetala auct. non Radlk.: Meijer, Bot. News Bull. 9 (1967) 75.

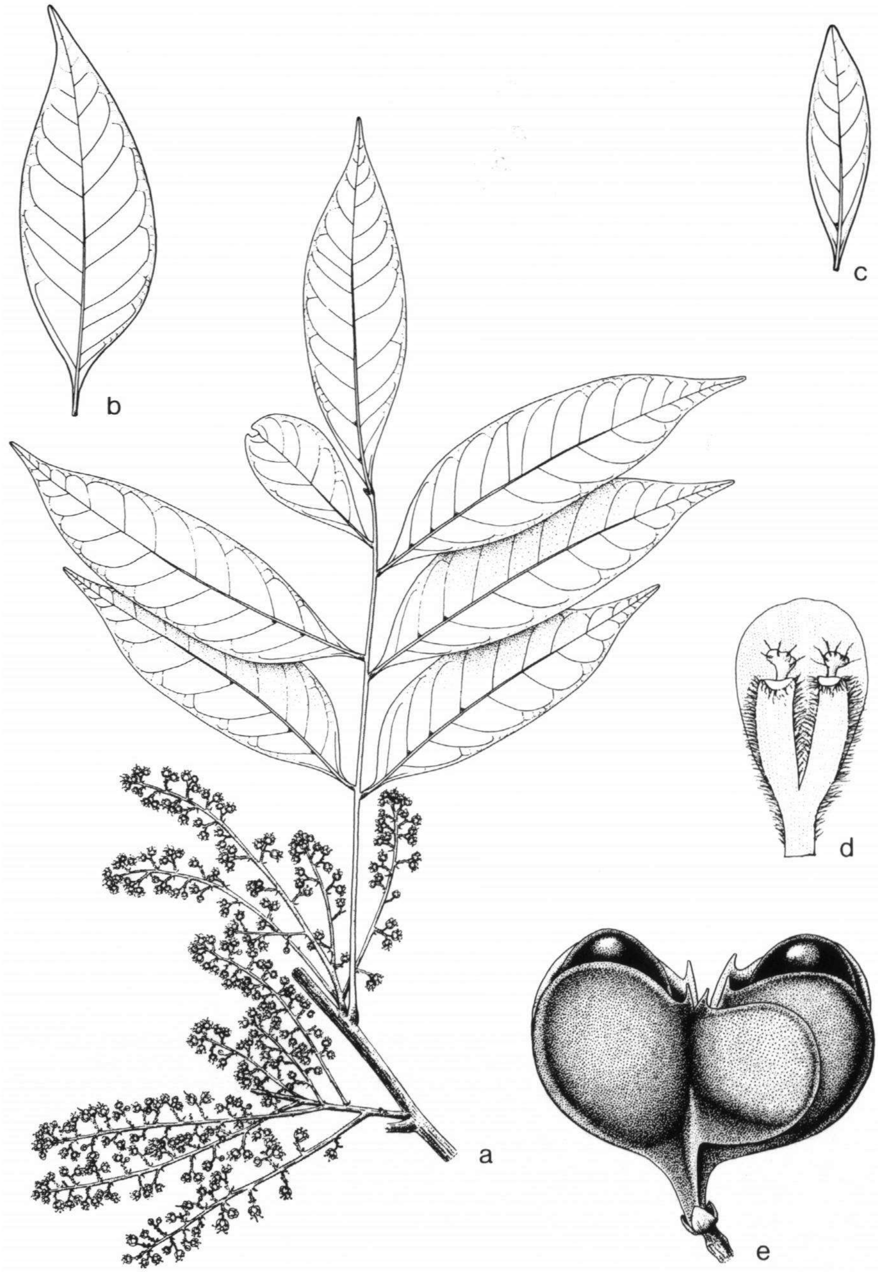


Fig. 86. *Guioa koelreuteria* (Blanco) Merr. a. Habit, × 0.5; b. leaflet, typical form, × 0.5; c. leaflet, *'Guioa mindorensis'* form, × 0.5; d. petal, × 12.5; e. fruit, × 3 (a, d: *BS (Ramos) 88*, M; b: *Valera 10259*, L; c: *BS (Ramos) 39639*, A; e: *Addura 43*, A).

Shrub to tree. *Branchlets* terete, smooth (to seldom rough), especially sericeous (to hirsute) when young; flowering twigs 1–7 mm thick. *Leaves* 1–6-jugate; rhachis 2.4–20.5 cm long, terete to flattened and broadened (to slightly winged), subglabrous (to subhirsute), petiole 1–8 cm long; petiolules if present up to 0.7 cm long. *Leaflets* usually subsessile, opposite to alternate, ovate (to elliptic), 2.8–17.8 by 0.9–5.4 cm, index 1.7–5.7, usually asymmetric, acroscopic side broader, coriaceous to very coriaceous, usually punctate; base attenuate; margin entire (juvenile leaflets with a few teeth), flat (to revolute); apex (obtuse to) usually gradually acuminate to caudate, very apex acute to usually mucronulate; upper surface smooth, glabrous to puberulous on the midrib to subhirsute; lower surface somewhat differently coloured, duller, smooth to seldom slightly (greyish, brownish) papillate, glabrous to subsericeous (to hirsute), domatia absent to a single sac to many sacs (to pockets) on basiscopic side in axil of ± second nerve to in axils of major nerves; venation on upper surface (flat to) raised, usually not differently coloured from lamina, below raised; nerves 0.2–2.5 cm apart, marginally looped; veins laxly reticulate, usually distinct. *Inflorescences* axillary (to pseudoterminal), not branching to branching in or near axil and along rhachis; latter slightly flattened, 0.8–20.5 cm long, brown (sub)-sericeous (to hirsute); first order branches up to 9.8 cm long; cymules cincinnate (see also note 4), 2–5(–8)-flowered. *Bracts* and *bracteoles*
inside subglabrous; bracts 0.5–1.5 mm long; bracteoles 0.2–1 mm long. *Pedicels* 1.4–7 mm long, sericeous, except for the usually subglabrous 0.5–3.5 mm long upper part. *Flowers* 3.2–4 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside (sub)glabrous; 2 outer smaller ones 1–3.1 by 1–3.3 mm; 3 inner larger ones 1.5–3.8 by 1.2–4 mm, margin petaloid. *Petals* 5, (elliptic to) obovate, 1.8–3.8 by 1–2.5 mm (see also note 4), blade obovate, gradually decurrent into the claw, latter 0.4–1.3 mm high, margin and seldom outside pilose, inside (sub)glabrous, apex retuse to acute; scales 0.9–2.1 mm long, free, basally not auricled, membranaceous margin indistinct, apex not to hardly broadened; crest seldom absent, usually a pilose, flat part of the bifid scale apex (to somewhat swollen and clavate). *Disc* incomplete. *Stamens* 8 (or very seldom 9); filament 1.2–5 mm long, especially basally pilose; anther 0.3–0.6 mm long, glabrous to pilose. *Pistil:* ovary 0.2–2.4 mm long, smooth, subhirsute; style and stigma 0.1–2.7 mm long, elongating in fruit up to 5 mm long, then upper c. 0.6 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1–2.2 cm high by 1–2.3 cm broad, smooth, glabrous, stipe 2–5.5 mm high, slender, edge of margin rounded, angle between lobes 30–140°, blackish when dry; dissepiments complete; lobes 6.5–13 by 7–12 mm. *Seed* (globose to) obovoid, 5.3–8.5 by 5–7.5 mm; hilum 1–2.3 mm long. *Embryo* 5–7.8 by 3.8–6 mm; cotyledons secondarily laterally besides each other, upper larger, apices usually elongated, upper straight, lower recurved; radicle 0.6–2 mm long.

Field notes. Shrub to tree, sometimes scandent, 2–16 m high, d.b.h. 2–50 cm. Outer bark brown to dark greyish, smooth (to rough); inner pink to red-brown, fibrous, c. 5 mm thick. Sapwood white to straw coloured to brownish, odourless, tasteless, annual rings slightly visible. Young branchlets yellow-green; older dark shiny green above, paler green below, tip recurved and conduplicate above. Inflorescence erect, green. Flowers usually with a sweet scent. Sepals pink. Petals creamy white (to somewhat reddish). Either scales, crests, or stamens yellow. Fruit pink to red, edible.

D i s t r i b u t i o n. Borneo (islands NE of Sabah); Philippines.

E c o l o g y. Common. Found in primary and especially in secondary forest, in ridge forest, thickets, on heath, along the seashore, roads, streams, edge of plantations. Soil: sand, gravel, limestone, ultrabasic. Alt.: sea-level up to 1350 m. Flowering: (Aug.–)Nov.–Febr.(–March). Fruiting: March–Oct.

W o o d. Reddish, straight-grained and fine textured, heavy, hard, and tough. Growth rings marked by terminal parenchyma and dense latewood, spaced from a fraction of 1 mm to 2 mm apart. Vessels mostly isolated. Wood parenchyma terminal and diffuse; terminal parenchyma appears as a very fine line at the end of a growth ring; diffuse parenchyma occurs as light-coloured dots with the tendency to align in concentric metatracheal bands. Rays uniseriate, very narrow, very numerous; exceedingly low; homogeneous (Reyes, cited in Desch, 1954).

U s e s. The wood is used for agricultural implements and tool handles (Reyes, cited in Desch, 1954). Oil extracted from the seeds can be used in the cure of certain skin diseases (Guerrero, cited in Brown, 1921, 1950).

V e r n a c u l a r n a m e s. Borneo: saasa, saksah, sasah (Bajan East Coast). Philippines: alahan (main name); pasi, salab (Bikol); comotan (Cebuano); uyos (Cebu Bisaya); alahan-mangyan (Fil.); ulas (Igorot); kaninging (Mangyan); basai, kasai, paksion, talimanok (Panay Bisaya); kamotelen, pamotelen, salab, salap (Pangasinan); angset (Iloko); alahabi, bangil, gisi-gisi, nisi-nisi (Sambali); alahan, alasan, anayen, anoyen, hualis, malasabe, malasanki, malauas, ngisi-ngisi, salab, salap, salub (Tagalog); dangalis, maimtok, marintok, tupsan (Tagbanua); babae-baoy (on Mindoro).

N o t e s. 1. *Guioa koelreuteria* is rather variable as can be expected of island populations. For instance, the leaflets differ much in size, most are small, but some can become rather large. The leaflets are usually rather thin, but some have thick coriaceous leaflets. On Mindanao, Davao Prov. and occasionally on Guimaras Island a rather distinguishable form can be found of which the leaflets always possess many domatia and short (combined with a few long) hairs sparsely all over the lower surface. The inflorescence is patently pilose. The fruits are usually smaller, although the size of the fruits of the more northern specimens is the same as there is a vague geographical cline in the size of the fruits. Examples of the hairy form are: *Copeland 406; Elmer 11264, 12012; FB 28255; PNH 11083, 11137, 11499; Vidal 1226.*

2. The specimens which were described as *Guioa salicifolia* differ only slightly from the normal appearance of *Guioa koelreuteria,* the leaflets are more coriaceous than more typical *Guioa koelreuteria* and relatively narrower.

3. Neither can *Guioa mindorensis* be distinguished. The characters mentioned by Merrill (small leaflets, winged rhachis) can also be found among more typical specimens of *Guioa koelreuteria.* On Mindoro two forms can be found, the typical *Guioa koelreuteria* with no papillae and usually with a long cuspidate apex of the leaflets and the *'Guioa mindorensis'* form with papillae and a short, rather obtuse apex of the leaflets (see fig. 86c). The latter form is presumably found at higher altitudes.

Two specimens, *Coode & Ridsdale 5674 & 5732*, examples of *'Guioa mindorensis'*, even have more or less reduced petals with very short crestless scales. Intermediates between both forms are: *PNH 17632* (*'Guioa mindorensis'*), *37868, 37869* (*Guioa koelreuteria*).

4. One exceptional specimen was found, *ANU 1652* from Mindanao, Mt. Apo. The cymes are dichasia instead of monochasia and the petals are almost completely reduced (the flowers are still young and might have opened prematurely because of drying). As no other specimens with these characteristics were found (Mt. Apo has been visited several times), *ANU 16523* is just regarded as an extraordinary specimen and not as a distinct species.

5. See notes under *Guioa pubescens* and *Guioa acuminata*.

Specimens studied:
BORNEO: 11 specimens on islands N and NE of Sabah.
PHILIPPINES: 223 specimens all over the Philippines.

Guioa lasioneura Radlk. – Fig. 87a–c.

Guioa lasioneura Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 608; Domin, Bibl. Bot. 22 (1927) 903; Radlk. in Engl., Pflanzenr. 98 (1933) 1160; C.T. White, Contr. Arn. Arbor. 4 (1933) 60; J.G. Tracey, Veget. Humid Trop. Region N. Queensl. (1982) 106; Reynolds, Austrobaileya 2 (1984) 37, fig. 2m, n; Fl. Austr. 25 (1985) 48, map 57. — Type: *Dallachy s.n.* (M, holo; iso in K, L, MEL, NSW, W), Australia, Rockingham Bay. Epitheton based on manuscript of F. Mueller (*Cupania semiglauca* var. *lasioneura*).

Tree. *Branchlets* terete, smooth (to ribbed to rough), hirsute, especially when young; flowering twigs 1.2–4 mm thick. *Leaves* 1–2(–4 in vegetative parts)-jugate; rhachis 0.4–8(–23 in vegetative parts) cm long, terete, not winged, hirsute, petiole 0.3–2.8(–9 in vegetative parts) cm long. *Leaflets* subsessile, opposite to alternate, elliptic, 3.2–12.8(–24.8 in vegetative parts) by 1.1–4.8(–7.3 in vegetative parts) cm, index 1.9–3.5, usually symmetric, coriaceous, punctate; base attenuate; margin entire, flat (to revolute); apex acute to caudate, mucronulate; upper surface smooth, usually hirsute, especially on midrib and nerves; lower surface differently coloured, dull, papillate, hirsute, domatia many pockets in axils of nerves in especially lower part of leaflets; venation on upper surface (slightly sunken to) flat (to raised), except for the basically raised midrib, raised on lower surface; nerves 0.2–3.1 cm apart, marginally looped in upper part of leaflets; veins densely reticulate, conspicuous. *Inflorescences* axillary, seldom pseudoterminal, usually only branching in or near axil, seldom along rhachis too; rhachis terete, 0.7–6.6 cm long, hirsute; first order branches up to 2.3 cm long; cymules cincinnate, 2–4-flowered. *Bracts* and *bracteoles* (triangular to) narrowly triangular, outside hirsute, inside glabrous; bracts 1.1–3 mm long; bracteoles 0.5–1.8 mm long. *Pedicels* 1.7–4.8 mm long, hirsute except for the slightly pilose, 0.5–1.8 mm long upper part. *Flowers* 2.5–3 mm in diam. *Sepals* 5, broadly ovate to triangular, margin pilose, with glands, outside hispid, sometimes also inside; 2 outer smaller ones 1–2.1 by 1–1.5 mm; 3 inner larger

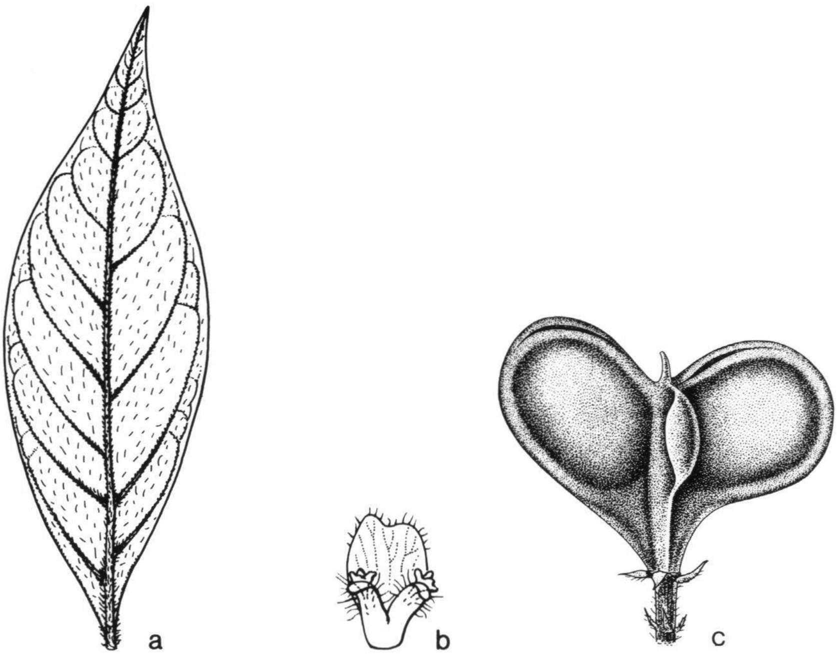


Fig. 87. *Guioa lasioneura* Radlk. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, b: *K.A.W. Williams 77216*, CANB; c: *Stocker 959*, LAE).

ones 1.5–2.4 by 1.4–2 mm, margin petaloid. *Petals* 5, rhomboid to obovate, 1–2 by 0.4–1.2 mm, claw 0.3–0.7 mm long, margin and outside pilose, inside glabrous, apex obtuse; scales 0.5–1.2 mm long, free; crest clavate on short slender stipe, glabrous. *Disc* incomplete. *Stamens* 8; filament (0.8–)1.8–2.8 mm long, usually basically pilose; anther 0.3–0.6 mm long, glabrous. *Pistil:* ovary 0.2–0.4 (–2) mm high, smooth, very sparsely hirsute; stigma and style 0.1–0.5(–2) mm high, both elongating up to 2 mm in fruit, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 0.7–1.2 cm high by 1.1–2 cm broad, smooth (to rugose), glabrous, stipe broadly cuneate, absent to up to 3 mm high, angle between lobes 75–135°, blackish when dry; lobes 8–11 by 7–9 mm. *Seed* globose to obovoid, 7.1–8.5 by 4–4.8 mm; hilum 1–1.2 mm long. *Embryo* 4.5–5.5 by 2.2–4.5 mm; cotyledons secondarily laterally besides each other, inequal, upper larger, both apices elongated, apex of lower cotyledon recurved over apex of upper one; radicle 2–2.5 mm long.

F i e l d n o t e s. Tree 4–16 m high, d.b.h. 15–20 cm; crown dense. Terminal twigs covered with rusty hairs. Outer bark brown; middle bark cream whitish to green, granular; inner bark cream to dull pinkish brown. Wood whitish. Branchlets light green. Petals white. Filaments cream; anthers violet. Fruits red to pink; aril orange; seeds brown.

D i s t r i b u t i o n. Australia, Queensland (Cook Dist.: Atherton tableland). *Webb & Tracey 10051* from N Kennedy Dist. and *K.A. Williams s.n.*, 17-IX-1983 from Moreton Dist., are found outside the Cook Dist. Especially the latter can be due to introduction (ornamental plant).

E c o l o g y. Common. Found in rain forest, often as a regrowth, in logged forest, on cultivated land, along edges of forest. Vegetation types: common in Complex mesophyll vine forest and Mesophyll vine forest, once found in Mesophyll fan-palm vine forest, Complex notophyll vine forest and Low microphyll fern thickets (Tracey, 1982). Humidity: moist to usually very wet. Soil parent material: (granite) basalt, metamorphics and alluvials (Tracey, 1982). Alt.: sea-level up to 1000 m. Flowering: July–Nov. Fruiting: Oct.–Jan.

N o t e. See note 1 under *Guioa oligotricha.*

S p e c i m e n s s t u d i e d:
AUSTRALIA. Queensland: 32 specimens.

Guioa lentiscifolia Cav. – Fig. 88 a – c.

Guioa lentiscifolia Cav., Icon. 4 (1798) 50, t. 373; Jaume St.-Hill., Expos. Fam. 2 (1805) 12; Steudel, Nom. Bot. (1821) 367 (*'Giroa'*), 385; Radlk., Sapind. Holl.-Ind. (1879) 37; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 608; in Engl., Pflanzenr. 98 (1933) 1158; A.C. Smith in Yuncker, Bull. Bish. Mus. 220 (1959) 174. — *Cupania lentiscifolia* Pers., Syn. Pl. 1 (1805) 413; Steudel, Nom. Bot. (1821) 245 (*'Gouioa'* in synon.); Cambess., Mém. Mus. Hist. Nat. 18 (1829) 28; Don, Gen. Hist. 1 (1831) 668. — T y p e: *Neé s.n.* (Hb. Cavanilles), 21–31 May 1792 (MA, 3 sheets; photos in L), Tonga I., Babao (= Vavau).

Guaiacum dubium auct. non Forst.: Forst., Fl. Ins. Austr. Prod. (1786) 32, p.p.: fruits. See note 2.

Guioa glauca auct. non Radlk.: Burkill, J. Linn. Soc. Bot. 55 (1901) 33.

Shrub to treelet. *Branchlets* terete, smooth to ribbed, sericeous when young; flowering twigs 1–4 mm thick. *Leaves* 1–4-jugate; rhachis 2–5.8 cm long, dorso-ventrally flattened, usually slightly winged, subsericeous, petiole 0.7–3.1 cm long; petiolules up to 0.7 cm long. *Leaflets* usually subsessile, opposite to alternate, (ovate to) elliptic, slightly falcate, 1.2–8.2 by 0.7–3.3 cm, index 1.7–3.4, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, flat (to revolute); apex rounded to acute, not mucronulate; upper surface smooth, subsericeous on venation; lower surface differently coloured, dull, papillate, very subsericeous, domatia 1 (or 2) large sac(s), with apical opening, on basiscopic side in axil of usually the second nerve; venation on lower surface more raised than on upper; nerves 0.8–1.6 cm apart, marginally looped; veins laxly reticulate, not very distinct. *Inflorescences* axillary, only branching along rhachis; latter somewhat flattened, 1.3–10.3 cm long, subsericeous; first order branches up to 3.7 cm long; cymules usually dichasial, 3–8-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside only basally pilose; bracts 0.6–1.3 mm long; bracteoles 0.4–0.7 mm long. *Pedicels* 2–6 mm long, sericeous, upper part usually less pilose, 1.1–2.1 mm long. *Flowers* c. 3 mm in diam. *Sepals* 5, ovate, margin pilose, without glands, outside and inside (sub)glabrous; 2 outer smaller ones 1.3–1.9 by 1.4–2.3 mm; 3 inner larger ones 2.1–3 by 2.1–3 mm, margin petaloid. *Petals* 5, (elliptic to) obovate,

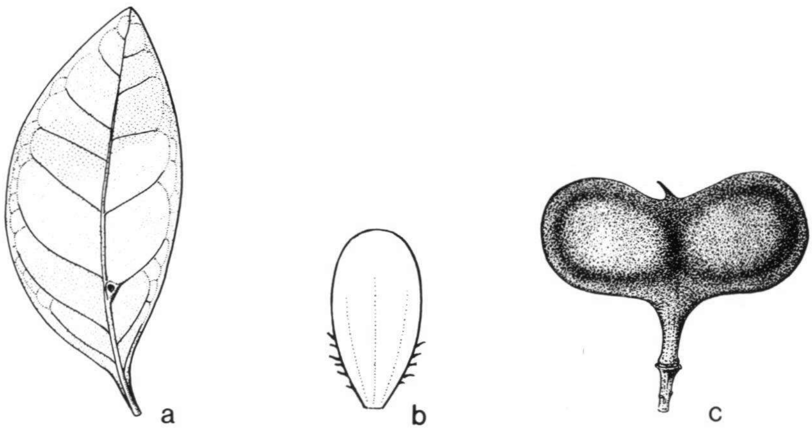


Fig. 88. *Guioa lentiscifolia* Cav. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 1.5 (*Crosby 29*, MEL).

1.2–2.8 by 0.6–2 mm, claw absent (to up to 0.4 mm), margin pilose, outside and inside subglabrous, apex rounded to obtuse; scales absent (to present as enation); crest absent; petal between two adjacent large sepals usually not reduced in size. *Disc* complete. *Stamens* 8; filament 1.4–3.5 mm long, especially basally pilose; anther 0.4–0.7 mm long, glabrous. *Pistil:* ovary 0.3–0.5 mm high, slightly hirsute; style and stigma 0.2–0.3 mm long, elongating in fruit up to 2 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.5–2.1 cm high by 1.9–2.8 cm broad, smooth (to slightly ribbed), glabrous, stipe 2.5–5 mm long, slender, angle between lobes 100–150°, blackish when dry; lobes 13–17 by 11–14 mm. *Seed* obovoid, c. 11.2 by 9.5 mm; hilum c. 4 mm long. *Embryo* c. 8.9 by 7.5 mm; cotyledons dorsoventrally above each other, upper larger, apices not elongated; radicle c. 2 mm long.

Field notes. Shrub to treelet, up to 5.5 m high, d.b.h. up to 25 cm. Flowers white. Fruit red.

Distribution. Tonga I.: Eua, Vavau. According to Hotta (Acta Phytotax. Geobot. 20, 1962, 184), 33% of the flora of the Tonga Islands is found on Tonga, Samoa and Fiji, 10% of the flora is endemic; of the flowering plants 25% is common with continental Asia, just like 33% of the ferns. On generic level *Guioa* belongs to the group of plants 'distributed' from continental Asia to the Tonga Islands, while on specific level *Guioa lentiscifolia* is endemic.

Ecology. Found at margins of forest, along paths. Alt.: sea-level up to 160 m. Flowering: March–May. Fruiting: March–Dec.

Vernacular name. Olive (Tonga).

Notes. 1. *Guioa lentiscifolia,* type species of *Guioa,* is an obscure species. Misidentifications and wrong interpretations are regularly encountered. *Guioa lentiscifolia* is an endemic of the Tonga Islands. Consequently the following synonyms of

Guioa lentiscifolia, found in the literature, are interpreted as misidentifications, as this species does not occur on the islands where these so-called synonyms are found:

Aporetica pinnata auct. non DC.: Hook. & Arn., Bot. Capt. Beechey Voy. (1832) 61 (Society I.).

Ratonia stipitata auct. non Benth.: Seem., Fl. Viti. (1865) 47 (Samoa).

2. A different problem is presented by *Guaiacum dubium* of the Tonga Islands. The epithet is older than *lentiscifolia*. However, the type specimen of *Guaiacum dubium* consists of a mixtum: the fruits are *Guioa lentiscifolia*, the leaves have not been identified yet. Following A.C. Smith (1959) it is proposed to lectotypify *Guaiacum dubium* with the leaves, as this is the only part described by Forster. This solution is in accordance with Forster's concept of his 'species' and it leaves the name *Guioa lentiscifolia* untouched (stability of names).

Specimens studied:

TONGA ISLANDS: *Forster s.n.* — Eua: *Lister s.n.*, XII-1899; *Parks 16156, 16162; Soakai 347; Yuncker 15503, 15545.* — Vavau: *Cavanilles (Ne) s.n.; Crosby 29; Yuncker 16106.*

Guioa malukuensis Welzen – **Fig. 89.**

Guioa malukuensis Welzen, Blumea 33 (1988) 418, pl. 5. — Type: *Kostermans 1206* (L, holo; iso in BRI, K, P; BO, n.v.), Moluccas, Morotai, Mt. Parew.

Tree. *Branchlets* terete, somewhat rough, shortly sericeous, especially when young; flowering twigs 3–3.5 mm in diam. *Leaves* 2–4-jugate; rhachis 0.7–6 cm long, terete, slightly winged, subsericeous, petiole 0.7–3 cm long. *Leaflets* subsessile, opposite to subopposite, elliptic, 3.4–7.2 by 1–2.2 cm, index 2.4–3.7, ± symmetric, coriaceous, punctate; base attenuate; margin entire, flat; apex acuminate, not mucronulate; upper surface smooth, subsericeous, especially the venation; lower surface differently coloured, dull, papillate, sericeous, domatia a single to many pocket-like sac(s) in axils of major nerves; venation on upper side flat, raised on lower; major nerves 0.3–1.3 cm apart, marginally looped; veins densely reticulate, distinct. *Inflorescences* axillary, branching in axil and along rhachis; latter somewhat flattened, 3.3–12.2 cm long, sericeous; first order branches up to 3.3 cm long; cymules cincinnate. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts c. 0.9 mm long; bracteoles 0.3–0.4 mm long. *Pedicels* 3.5–3.8 mm long, sericeous except for the (sub)glabrous 1.8–2 mm long upper part. *Flowers* c. 3 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones c. 1.2 by 1.2 mm; 3 inner larger ones 1.8–2.2 by 1.8–2.2 mm, margin petaloid. *Petals* 5, elliptic, c. 1.4 by 1 mm, claw c. 0.2 mm high, margin and less so outside pilose, inside (sub)glabrous, apex retuse to rounded; scales present as inwardly folded auricles of the petal, c. 0.4 mm

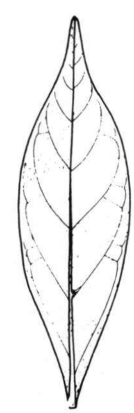


Fig. 89. *Guioa malukuensis* Welzen, leaflet, × 1 (*Kostermans 1275*, L).

long; crest absent. *Disc* complete. *Stamens* 8; filament c. 2.4 mm long, especially basally pilose; anther c. 0.4 mm long, glabrous. *Pistil* in young state. *Fruit* unknown.

Field notes. Tree, c. 13 m high, d.b.h. up to 20 cm. Bark grey. Wood hard. Flowers white.

Distribution. Moluccas (Morotai I.).

Ecology. Found at 1000 m alt.

Notes. 1. Typical for this species are the symmetric leaflets with on the lower side papillae, a sericeous indumentum, and 1 to many pocket-like sac(s); and the somewhat reduced petals with the crestless scales present as folded auricles.

2. This species strongly resembles *Guioa subsericea*, but the latter has a wingless rhachis and asymmetric leaflets with a cuspidate to caudate apex instead of a winged rhachis, symmetric leaflets, and an acuminate apex.

Specimens studied:
MOLUCCAS. Morotai I., Mt. Parew: *Kostermans 1206, 1275.*

Guioa megacarpa Welzen – Fig. 90 a–c.

Guioa megacarpa Welzen, Blumea 33 (1988) 418, pl. 10a–c. — Type: *BSIP (Leggate) 338* (L, holo; iso in A, CANB, K, LAE; BSIP, n.v.), Solomon I., Sta. Cruz Group, Vanikoro I., alongside main bush road S.P. 10.

Tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 2–4.5 mm thick. *Leaves* 2–5-jugate; rhachis 4.4–15.6 cm long, basally terete to upwards above somewhat flattened, not winged, subsericeous, petiole 2.3–6.2 cm long; petiolules up to 0.6 cm long. *Leaflets* not subsessile, opposite to subopposite, ovate, falcate, 3.6–11.2 by 1–3.2 cm, index 2.9–4.6, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, revolute; apex acuminate to caudate, very apex acute, not mucronulate; upper surface smooth, (sub)glabrous, midrib basally often puberulous; lower surface differently coloured, dull, papillate, subsericeous, domatia a single small sac with the opening in the front, on basiscopic side in axil of ± second nerve, sometimes also a pocket present; venation on upper surface flat to raised, raised on lower; nerves 0.3–2 cm apart, marginally looped; veins rather densely reticulate, conspicuous. *Inflorescences* axillary, branching along rhachis; latter somewhat flattened or grooved, 5.5–15.9 cm long, sericeous; first order branches up to 7.4 cm long; cymules cincinnate, 3- or 4-flowered. *Bracts* and *bracteoles* triangular, sericeous outside, subglabrous inside; bracts 1–1.1 mm long; bracteoles 0.5–0.8 mm long. *Pedicels* 5–17 mm long, sericeous; upper part less sericeous, 2.8–5 mm long. *Flowers* c. 3.5 mm in diam. *Sepals* 5, ovate, only margin pilose, other parts glabrous; 2 outer smaller ones 1.7–2 by 1.8–2 mm, margin with few glands; 3 inner larger ones 2.3–3 by 2.7–3.2 mm, margin petaloid, without glands. *Petals* 5, elliptic, 2.8–3 by 1.2–1.4 mm, claw c. 0.2 mm high, margin and basally the outside and inside pilose, apex obtusely acute; scales 1.2–1.3 mm long, free; crest usually present, slenderly clavate, not lobed, stipe pilose; petal between two adjacent large sepals not reduced. *Disc* complete. *Stamens* 8; filaments 2.2–3.7 mm long, especially basally pilose; anthers 0.6–0.8 mm long, glabrous.

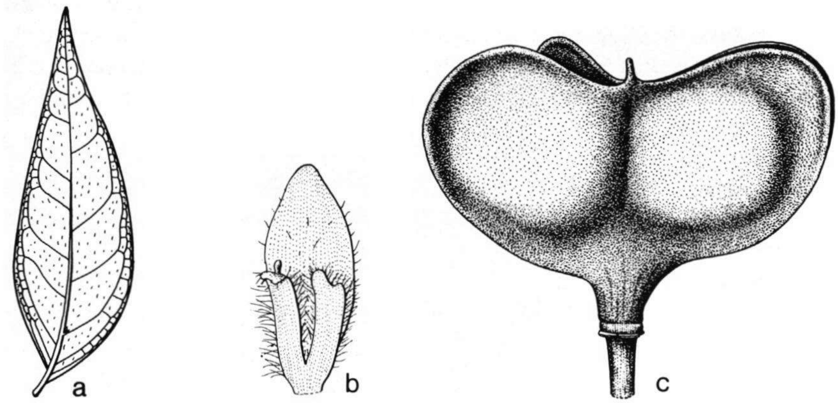


Fig. 90. *Guioa megacarpa* Welzen. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 1.5 (a, c: *BSIP (Walker) 216*, BRI; b: *BSIP (Whitmore) 1670*, L).

Pistil: ovary 0.3–0.5 mm high, sparsely hirsute; style and stigma up to 0.2–0.7 mm high, elongating in fruit up to 2 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 2.2–2.7 cm high by 2.9–3.9 cm broad, smooth (to rough), glabrous, stipe 5–7 mm high, somewhat broadly cuneate, angle between lobes 130–135°, blackish when dry; lobes 18.5–20 by 16–17 mm. *Seed* obovoid, 7–9 by 6–7 mm; hilum 1.2–2 mm long. *Embryo* 5.8–6 by c. 5 mm; cotyledons dorsoventrally above each other, about as large, apices not elongated; radicle 1.2–2 mm long.

Field notes. Tree, 7–20 m high, d.b.h. up to 100 cm; buttresses absent to present, if present thin, equal, 0.6 m high; bole straight; crown diffuse, flattish. Bark brown to grey, smooth to slightly longitudinally cracked, with small orange-brown lenticels, thin, papery; inner bark c. 0.6 cm thick, green to pink, fleshy texture. Sapwood straw coloured, 3.8–5 cm thick; heartwood reddish brown. Leaflets light green to dark green above; lighter green to glaucous to grey-green below, horizontally arranged. Flowers white, with a heavy sweet smell. Fruits pendulous, green.

Distribution. Solomons, Santa Cruz Group, Vanikoro I.

Ecology. In secondary, often exploited or occasionally burned forest, with *Agathis* and *Macaranga*. Soil: red clay. Alt.: 170–500 m. Flowering: March–April. Fruiting: April.

Wood. A moderately hard wood of possible use in small sizes for temporary buildings. Pores small to very small, moderately numerous (5–6/mm^2), in short radial multiples. Rays narrower than the pores. Ground tissue surrounding the pores and in regular bands, wider than the pores. After *BSIP (Walker) 216*.

Vernacular names. Nganuanbua (Vanikoro: Nambula name); sufusane (Kwara'ae: Malita name; also used for *Guioa sufusana* and *Guioa elliptica*).

N o t e s. 1. This species is very closely related to *Guioa novoëbudaënsis* and *Guioa punctata*; the differences are small as can be seen below. Delimitative characters among the species are marked with an asterisk between the columns, for example the character domatium can be used to separate *Guioa punctata* from the other two, while the measures for the scales are different for all three:

Guioa	*megacarpa*		*novoëbudaënsis*		*punctata*
Leaflet length	3.6–11.1 cm		2.5–9.8 cm		2.1–8.2 cm
Leaflet very apex	acute		acute	*	obtuse
Number of sacs	1		1	*	1 to many
Size of sacs	hardly visible by eye		hardly visible by eye	*	large
Opening in sac	front		front	*	top
Height of smaller sepals	1.7–2 mm	*	1.3–1.7 mm		0.8–2 mm
Petal width	1.2–1.4 mm	*	1.6–2 mm		0.9–1.8 mm
Scale length	1.2–1.3 mm	*	0.3–0.7 mm	*	0.8–1.2 mm[1]
Fruit size	2.2–2.7 by 2.9–3.9 cm	*	1.8–2 by 1.8–2.3 cm		1.1–2 by 1.1–2.9 cm
Stipe height	5–7 mm	*	c. 3.5 mm		1.5–5 mm
Fruit lobe size	18.5–20 by 16–17 mm	*	c. 12 by 12.5 mm		8.7–14 by 7–13 mm

[1] The specimen *A.C. Smith 1123 (Guioa punctata)* lacks the scales.

It is possible that further collections may confuse this delimitation, as it is mainly based on differences in measures. The distinction between *Guioa punctata* on the one and the other two on the other hand is rather sharp because of the differences in domatium. However, one specimen of *Guioa punctata, A.C. Smith 1477,* tends to have smaller domatia with the opening on the front, but these are still well visible with the naked eye; moreover, several leaflets possess larger domatia with the opening in the top of the sac.

2. For the differences between *Guioa elliptica, Guioa megacarpa,* and *Guioa sufusana* see note under *Guioa elliptica.*

S p e c i m e n s s t u d i e d:

SOLOMONS. Santa Cruz Group, Vanikoro I.: *BSIP (Walker) 216; (Leggate) 338; (Whitmore) 1566; (Whitmore) 1670; (Whitmore) 1690; (Piaito) 7012; (Mauriasi et al.) 17023.*

Guioa melanopoda Merr. & Perry – **Fig. 91a, b.**

Guioa melanopoda Merr. & Perry, J. Arn. Arbor. 21 (1940) 514. — T y p e: *Brass 13699* (A, holo; iso in BM, K, L), Irian Jaya, Idenburg River, Bernhard Camp.

Tree. *Branchlets* terete, smooth to slightly ribbed, glabrous except for some tomentose hairs on nodes; flowering twigs 3–6 mm thick. *Leaves* 3- or 4-jugate; rhachis 3.2–20.5 cm long, terete, winged, wing 2.5–3 mm broad, subtomentose, petiole 2.7–7.7 cm long. *Leaflets* subsessile, subopposite to alternate, (ovate to) elliptic, 8–16.4 by 2.4–5.6 cm, index 2.7–3.5, slightly asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, flat; apex cuspidate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous to sparsely sericeous, domatia absent to sometimes a single pocket on basiscopic side in axil of ± second major nerve; venation on upper side slightly sunken to flat, raised below; major nerves 0.3–2.2 cm apart, marginally looped, less distinctly so in lower part of leaflets; veins densely reticulate, rather conspicuous. *Infructescences* axillary (to pseudoterminal), branching in axil and along rhachis; latter terete, 2.7–6 cm long, subtomentose; first order branches up to 4 cm long. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.7–0.9 mm long; bracteoles 0.4–0.5 mm long. *Pedicels* 1.8–2.2 mm long, completely slightly sericeous, upper part 0.7–1 mm long. *Flowers* unknown. *Sepals* 5, ovate, margin pilose, without glands, outside and inside glabrous; 2 outer smaller ones 1–1.2 by 0.9–1.2 mm; 3 inner larger ones c. 1.5 by 1.5 mm, margin petaloid. *Petals* see note 2. *Disc* complete. *Stamens* and *pistil* unknown. *Fruit* with 1 or 2 well-developed lobes, 0.9–1 cm high by 0.8–1.3 cm broad, rugose, glabrous, stipe 1.5–2.5 mm high, broadly cuneate, edge of margin rounded, angle between lobes 45–105°, blackish when dry; dissepiments complete; lobes 8–9 by 6–6.5 mm. *Seed* obovoid, c. 6.5 by 5 mm; hilum c. 1.1 mm long. *Embryo* c. 5.7 by 5 mm; cotyledons dorsoventrally above each other, about equal in size, apices not elongated; radicle c. 2.1 mm long.

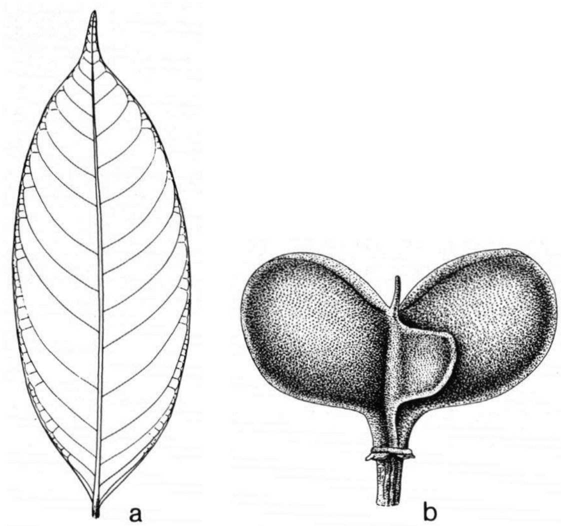


Fig. 91. *Guioa melanopoda* Merr. & Perry. a. Leaflet, × 0.5; b. fruit, × 3 (*Brass 13699*, L).

Field notes. Tree, 8–15 m high. Fruit red.

Distribution. Irian Jaya (Jayapura Prov.).

Ecology. Rain forest substage to seral rain forest of river banks. Alt.: 850–1200 m. Fruiting: Febr.–March.

Notes. 1. Several specimens of *Guioa comesperma* also have winged rhachises, but *Guioa comesperma* has less major veins in its leaflets, many sac-like domatia, and an incomplete disc.

2. One petal has been found, but it is not known whether this is one of the well-developed petals or the usually more reduced one between the two adjacent large

sepals. The petal is ovate, c. 2.8 by 1 mm, claw c. 0.2 mm high, margin slightly pilose, outside and inside glabrous; scales c. 0.6 mm long, free; crest absent.

Specimens studied:
NEW GUINEA. Irian Jaya, Jayapura, Idenburg River, Bernhard Camp: *Brass 12783, 13699.*

Guioa membranifolia Radlk. – Fig. 92a–c.

Guioa membranifolia Radlk., Sapind. Holl.-Ind. (1879) 11, 40; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 614 (typification); in Rech., Denkschr. K. Ak. Wiss. M.-N. Kl. Wien 89 (1913) 573, t. 6a, fig. 11; Bot. Jahrb. 56 (1921) 282; Lauterb., Bot. Jahrb. 62 (1929) 555; Radlk. in Engl., Pflanzenr. 98 (1933) 1174; Kaneh. & Hatus., Bot. Mag. Tokyo 57 (1947) 77. — Type: *Beccari PP 807* (FI, holo, cited by Radlkofer as *Beccari 9*), New Guinea, Mt. Arfak a Putat.

Tree. ***Branchlets*** terete, smooth (to slightly rough), shortly sericeous when young; flowering twigs 2.5–8 mm long. *Leaves* 1–3-jugate; rhachis 4.2–19.5 cm long, terete, not winged, glabrous, petiole 1.7–6.4 cm long. *Leaflets* subsessile, opposite to alternate, elliptic, 3.5–16.2 by 1.5–6.4 cm, index 2.3–3.8, usually slightly asymmetric, acroscopic side broader, subcoriaceous, punctate; base attenuate; margin entire, flat; apex acute to cuspidate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous, domatia a single small sac on basiscopic side in axil of ± second major nerve; venation on upper side flat, raised below; major nerves 0.2–2.3 cm apart, marginally looped, but less distinctly so in lower part of leaflets; veins laxly to densely reticulate, rather inconspicuous. *Inflorescences* ramiflorous to axillary, branching in axil and along rhachis; latter flattened to terete in fruit, 1.9–12.3 cm long, sericeous; first order branches up to 5.2 cm long; cymules cincinnate, 3- or 4-flowered. *Bracts* and

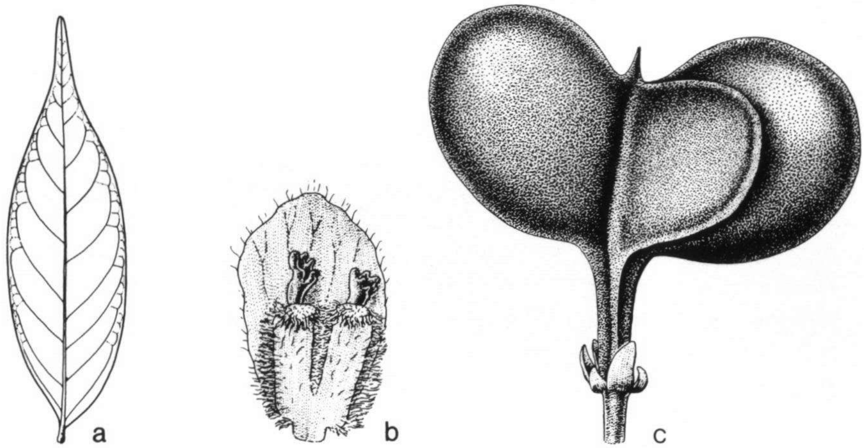


Fig. 92. *Guioa membranifolia* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, b: *Kostermans 805*, L; c: *Anang 655*, L).

bracteoles triangular, outside hirsute, inside glabrous; bracts 0.5–0.8 mm long; bracteoles 0.2–0.4 mm long. *Pedicels* 2–5.7 mm long, sericeous except for the subglabrous 1.4–3.7 mm long upper part. *Flowers* 3.5–4 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1–1.5 by 1–1.8 mm, 3 inner larger ones 1.4–3.2 by 1.4–3 mm, margin petaloid. *Petals* 5, elliptic, 1.4–3 by 0.7–1.4 mm, claw 0.2–0.3 mm high, margin pilose, outside and inside subglabrous, apex acute; scales 0.8–2 mm long, free, basally not auricled; crest clavate, stiped, apex lobed, pilose. *Disc* incomplete. *Stamens* 8; filament 1.8–3.5 mm long, completely but especially basally pilose; anther 0.4–0.8 mm long, glabrous. *Pistil:* ovary 0.2–0.8 mm long, smooth, subhirsute; style and stigma 0.1–0.7 mm long, elongating in fruit up to 2 mm long, then upper c. 0.4 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.4–2.4 cm high by 1–3.6 cm broad, smooth to slightly rugose or ribbed, glabrous, stipe 2–4 mm high, slender, upper margin about flat to slightly convex, edge of margin rounded, angle between lobes basally 65–135°, black when dry; dissepiments complete; lobes 10.5–16 by 10–13 mm. *Seed* obovoid, 8.5–9.7 by 6.5–7.2 mm; hilum c. 1.7 mm long. *Embryo* 7–8 by c. 6 mm; cotyledons dorsoventrally above each other, upper larger, apex of upper somewhat elongated, straight; radicle 1.8–2.5 mm long.

Field notes. Tree, 6–10 m high, d.b.h. up to 10 cm. Bark grey. Leaves green. Flowers white, fragrant. Fruit red.

Distribution. Moluccas (Halmaheira, Morotai); Irian Jaya (Vogelkop, Geelvink Bay, Jayapura).

Ecology. Found in fringing rain forest. Alt.: 30–600 m. Flowering: May–Aug. Fruiting: March–May.

Notes. 1. Typical for this species are the elliptic leaflets without papillae and hairs, and with a single sac. The fruit is always clearly stiped and the upper margin of the lobes is at most slightly convex.

2. This species strongly resembles *Guioa rigidiuscula* but differs from the latter by the above mentioned fruit characters and by its thinner leaflets (in *Guioa rigidiuscula* the stipe is almost absent, and the upper margin of the lobes is usually strongly convex).

3. *Guioa membranifolia* is part of the *Guioa rigidiuscula*-complex. The differences among the species within this complex are discussed in chapter 9.

Specimens studied:

MOLUCCAS. Halmaheira: *Anang 655*, S Peninsula, Weda. — Morotai: *Kostermans 805*, Tjaw.
IRIAN JAYA. Vogelkop: *Beccari PP 807*, Arfak Mts., Putat; *Van Royen & Sleumer 7332*, Kebar Valley, 'Aer Panas'; *Tuyama 1892*, Hattam. — Geelvink Bay: *Kanehira & Hatusima 12658*, Slieber, Nabire. — Jayapura: *Docters van Leeuwen 9737*, Rouffaer River.

Guioa microsepala Radlk. – Fig. 93a–c.

Guioa microsepala Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 613; Guillaumin, Bull. Soc. Bot. Fr. 79 (1932) 338; Radlk. in Engl., Pflanzenr. 98 (1933) 1175; Guillaumin, Fl. Nouv.-Caléd. (1948) 199; Mém. Mus. Nat. Hist. Nat. B, 15 (1967) 111. — Lectotype (here proposed): *Balansa 2265* (M, holo; iso in NY, P), New Caledonia, Canala.

Cupaniopsis guioides Guillaumin, Bull. Mus. Nat. Hist. Nat. sér. 2, 15 (1943) 218. — Type: *Vieillard s.n.* (P, holo; iso in P), New Caledonia, Kanala.

Guioa pectinata auct. non Radlk.: Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 8 (1959) 135 (*MacKee 3637*).

Guioa fusca auct. non Radlk.: Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 15 (1967) 110 (p.p.: *Baumann-Bodenheim 15637*).

Shrub to tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 1–4.2 mm thick. *Leaves* 1–3-jugate; rhachis 0.6–10.5 cm long, basally terete to upwards above somewhat flattened, not winged, subglabrous, petiole 0.5–5.3 cm long; petiolules if present up to 1.7 cm long. *Leaflets* usually subsessile, opposite to subopposite, elliptic, 1.2–11.5 by 0.4–5.1 cm, index 2–4.5, ± symmetric, very coriaceous, usually punctate; base attenuate; margin entire, revolute; apex acute to acuminate, very apex obtuse, not mucronulate; upper surface smooth, glabrous except for the basically pilose midrib, often with a wax layer; lower surface differently coloured, duller, smooth, not papillate, glabrous to very sparsely sericeous, domatium a single sac on basiscopic side in axil of second nerve; young leaflets golden sericeous; venation on upper surface flat to raised, on lower raised; nerves 0.2–1.9 cm apart, marginally looped; veins laxly reticulate, indistinct. *Inflorescences* axillary, seldom branching; rhachis flattened to triangular to terete, 0.4–6.4 cm long, subsericeous; first order branches when present up to 3.2 cm long; cymules cincinnate, 2(–4)-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.7–1.7 mm long; bracteoles 0.2–0.9 mm long. *Pedicels* 2–7 mm long, sericeous, also the 1–3.5 mm long upper part. *Flowers* c. 2 mm in diam. *Sepals* 5, all equal, triangular, 0.6–1.7 by 0.5–1.3 mm, completely sericeous, margin not petaloid, with glands. *Petals* 5, elliptic, 0.5–1.2 by 0.3–0.7 mm, claw 0.1–0.2 mm high, completely subpilose, apex obtusely acute; scales 0.5–1.2 mm long, free; crest absent to usually slightly developed as a thickened, lobed, apical part of the scale, to sometimes clavate and slightly stiped. *Disc* complete (see also note 2). *Stamens* 8; filament 1.1–2.8 mm long, especially basically pilose; anther 0.3–0.8 mm long, glabrous. *Pistil:* ovary 0.3–1.2 mm high, densely hirsute; style and stigma 0.1–1.8

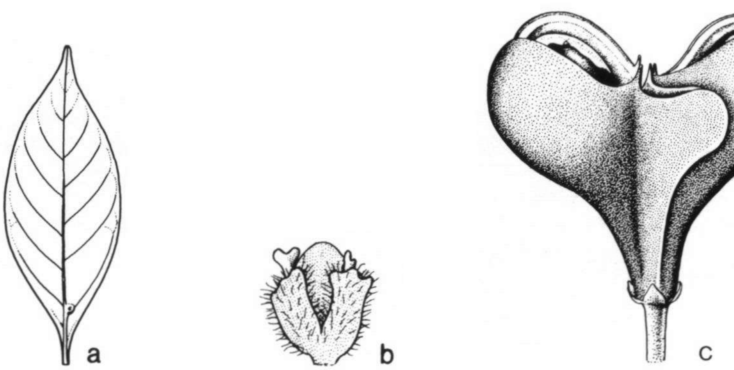


Fig. 93. *Guioa microsepala* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, b: *Schodde 5233*, L; c: *MacPherson 5147*, L).

mm high, elongated in fruit up to 2 mm, then upper c. 0.5 mm stigmatic. Fruit with 1–3 well-developed lobes, 1.2–1.7 cm high by 1–1.7 cm broad, smooth (to rugose), glabrous, stipe broadly cuneate, 2.5–5 mm high, angle between lobes 70–125°, (reddish brown to) black when dry; lobes 8–11 by 7–9.5 mm, wall rather thick, up to 1 mm. *Seed* obovoid, 6.8–10 by 5–6.5 mm; hilum 1–2 mm long. *Embryo* 6–8.5 by 4.2–5.8 mm; cotyledons secondarily laterally besides each other, about equal in size, apices elongated, that of upper usually straight, but sometimes together with lower recurved; radicle 2.4–3.5 mm long.

Field notes. Shrub to tree, 2–11 m high. Bark smooth, brown to midgrey to grey-reddish, striate. Leaves light to rather dull dark green above, yellow-green to light green below. Buds white. Flowers greenish to white to pink, fragrant. Filaments white; anthers yellow-brown to red.

Distribution. New Caledonia.

Ecology. Often abundantly present. Found in and along wet montane and moss forest on ultrabasic (serpentine), schists, gneiss. Dominant trees: *Agathis, Araucaria, Metrosideros, Nothofagus baumanniae, Piliocalyx.* Alt. 350–1500 m. Flowering: Jan.–Aug. Fruiting: Sept.–Nov.

Notes. 1. This species can be recognized by its very thick leaflets with one large domatium; small, equal sepals; fruits with a broadly divergent stipe.

2. The specimen *Hürlimann 1882* has a disc with a small gap.

Specimens studied:
NEW CALEDONIA: 55 specimens.

Guioa misimaensis Welzen – Fig. 94.

Guioa misimaensis Welzen, Blumea 33 (1988) 418, pl. 9. — Type: *Brass 27661* (L, holo; iso in K; LAE, n.v.), Papua New Guinea, Misima I., Quartz Mountain.

Tree. *Branchlets* terete, smooth, shortly sericeous when young; flowering twigs c. 4 mm thick. *Leaves* 1- or 2-jugate; rhachis 4.2–7.6 cm long, flattened above, not winged, subsericeous, petiole 2.7–4.7 cm long; petiolules up to 0.9 cm long. *Leaflets* not subsessile, subopposite, elliptic, 10.2–13.9 by 3.9–4.7 cm, index 2.6–3, symmetric, coriaceous, punctate; base attenuate; margin entire, flat; apex acute to acuminate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, dull, papillate, short sericeous, domatia absent; venation raised on both sides; nerves 0.4–1.8 cm apart, marginally looped; veins laxly reticulate, indistinct. *Inflorescences* axillary, branching along rhachis; latter flattened, 4.6–13.7 cm long, subsericeous; first order branches up to 4.9 cm long; cymules cincinnate, c. 3-flowered. *Bracts* and *bracteoles* triangular, outside subsericeous, inside glabrous; bracts c. 0.7 mm

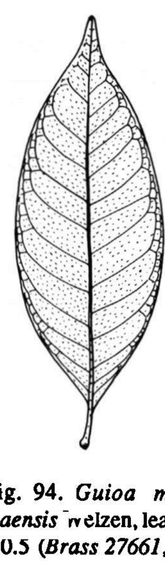


Fig. 94. *Guioa misimaensis* Welzen, leaflet, × 0.5 (*Brass 27661*, L).

long; bracteoles c. 0.3 mm long. *Pedicels* 2.5–3 mm long,subsericeous except for the (sub)glabrous, 1–1.5 mm long upper part. *Flowers* in bud. *Sepals* 5, ovate, margin pilose, outside and inside glabrous; 2 outer smaller ones 1–1.3 by c. 1.3 mm, margin with glands; 3 inner larger ones 1.8–2 by 2–2.2 mm, margin petaloid, without glands. *Petals* 5, immature, elliptic, margin pilose, outside and inside glabrous, apex acute; scales free; crest clavate, shortly stiped, glabrous. *Disc* incomplete. *Stamens* 8, immature; filament completely but especially basally pilose; anther glabrous. *Pistil:* ovary smooth, subhirsute. *Fruit* unknown.

Field notes. Tree up to 20 m high, d.b.h. up to 30 cm. Leaflets grey below. Flowers white.

Distribution. Papua New Guinea (Milne Bay Prov.: Misima I.).

Ecology. Common. Found in subcanopy of rain forest. Alt.: c. 150 m.

Notes. 1. Typical for this species are: the symmetric leaflets with papillae and short subsericeous hairs, the crested scales, and an incomplete disc.

2. This species together with *Guioa plurinervis* and *Guioa novobritannica* are the only species within the *Guioa rigidiuscula*-complex with leaflets with a papillate lower surface. The differences among the species of this complex are discussed in chapter 9.

3. Differences between this species and the *Guioa rigidiuscula*-complex, *Guioa plurinervis*, and *Guioa subsericea* are discussed in note 3 under *Guioa plurinervis*.

Specimens studied:
PAPUA NEW GUINEA. Milne Bay Prov., Misima I.: *Brass 27661*.

Guioa molliuscula Radlk. – Fig. 95.

Guioa molliuscula Radlk., Bot. Jahrb. 50 (1914) 76; Bot. Jahrb. 56 (1921) 280; in Engl., Pflanzenr. 98 (1933) 1163. — Type: *Schlechter 19521* (B, holo, †; iso in K, P), Papua New Guinea, Meboro.

Tree. *Branchlets* terete, smooth, velutinous; flowering twigs 2–4 mm thick. *Leaves* 1- or 2-jugate; rhachis 2.2–9.5 cm long, terete, not winged, velutinous, petiole 1.1–4.8 cm long; petiolules up to 0.9 cm long. *Leaflets* usually subsessile, subopposite, ovate (to elliptic), 6.6–17.8 by 3.4–8.2 cm, index 1.9–2.3, ± symmetric, coriaceous, punctate; base attenuate; margin entire, flat; apex acuminate to cuspidate, mucronulate; upper surface smooth, especially hirsute on the venation; lower surface differently coloured, duller, smooth, not papillate, hirsute, domatia absent or a single sac on basiscopic side in axil of second major nerve; venation on upper side flat, raised on lower; major nerves 0.4–2.5 cm apart, marginally looped, somewhat less distinctly so in lower part of leaflets; veins laxly reticulate, indistinct. *Inflorescences* axillary, hirsute, with very young buds. *Sepals* 5, dimorph, margin with glands. *Petals* 5, elliptic, apex acute; scales free, apex not broadened; crest cla-

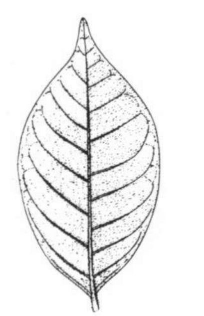


Fig. 95. *Guioa molliuscula* Radlk., leaflet, × 0.5 (*Schlechter 19521*, K).

clavate, stiped, glabrous. *Disc* complete. *Stamens* 8; filament pilose; anther glabrous. *Pistil:* ovary smooth, subhirsute. *Fruit* unknown.

Field notes. Tree, c. 10 m high. Leaves uniform midgreen. Flowers white.

Distribution. Papua New Guinea (Morobe Prov.).

Ecology. Understorey tree in alluvial swamp. Alt.: c. 10 m. Buds in January and May.

Notes. 1. This species is only known from two collections, which do look rather different at first sight, as *NGF 31702* has much larger and less pilose leaflets. Distinctive are the velutinous leaflets without papillae, the type of petals, and the complete disc. The type of petal is recognizable in spite of the fact that the petals are still immature. This type points to a relationship with the *Guioa rigidiuscula*-complex. The differences among the species in this complex are discussed in chapter 9.

Within the complex several species (*Guioa aryterifolia, Guioa molliuscula, Guioa scalariformis,* and *Guioa unguiculata*) have a complete disc; their differences are discussed in note 3 under *Guioa aryterifolia.*

2. The shape of the leaflets, and even the hirsute appearance remind of *Guioa subsericea,* where specimens with a hirsute indumentum are occasionally encountered. The absence of papillae and the type of petal are characters not found in *Guioa subsericea.*

3. *Guioa molliuscula* also resembles *Guioa oligotricha*; both have a hirsute indumentum, lack papillae (some specimens of *Guioa oligotricha* excepted), and have a complete disc. However, *Guioa oligotricha* has a different type of petals, it has leaflets with many pockets instead of no domatia or a single sac, and often shows leaflets with subapical teeth.

Specimens studied:
NEW GUINEA. Papua New Guinea, Morobe Prov.: *NGF (Ridsdale) 31702*, Maiama; *Schlechter 19521*, Meboro.

Guioa montana C.T. White – Fig. 96a–c.

Guioa montana C.T. White, Contr. Arn. Arbor. 4 (1933) 61; J.G. Tracey, Veget. Humid Trop. Region N. Queensl. (1982) 106; Reynolds, Austrobaileya 2 (1984) 39, fig. 2h–j; Fl. Austr. 25 (1985) 50, fig. 11a–c, map 60. — Type: *Kajewski 1286* (A, holo; iso in K, NSW, NY), Australia, N Queensland, Mt. Bartle Frere.

Tree. *Branchlets* terete, smooth (to somewhat rough), shortly sericeous when young; flowering twigs 2–3 mm thick. *Leaves* 1–2(–4 in vegetative parts)-jugate; rhachis 1.5–5.5(–21.5 in vegetative parts) cm long, flattened above, not winged, glabrous, petiole 0.9–5.7 cm long. *Leaflets* subsessile, subopposite (to alternate), elliptic (to obovate), 3.3–10.3 by 1.1–3.6 cm, index 2.4–3.3, ± symmetric, pergamentaceous when young to very coriaceous when mature, punctate; base attenuate; margin entire, (flat to) revolute; apex (obtuse to) acuminate (to cuspidate), mucronulate; upper surface smooth, glabrous except for the sometimes puberulous midrib; lower surface differently coloured, lighter, dull, papillate, sericeous, domatia absent; venation raised; nerves 0.2–1.2 cm apart, marginally looped; veins laxly reticulate, distinct. *Inflorescences* axillary, branching in or near axil and racemosely along

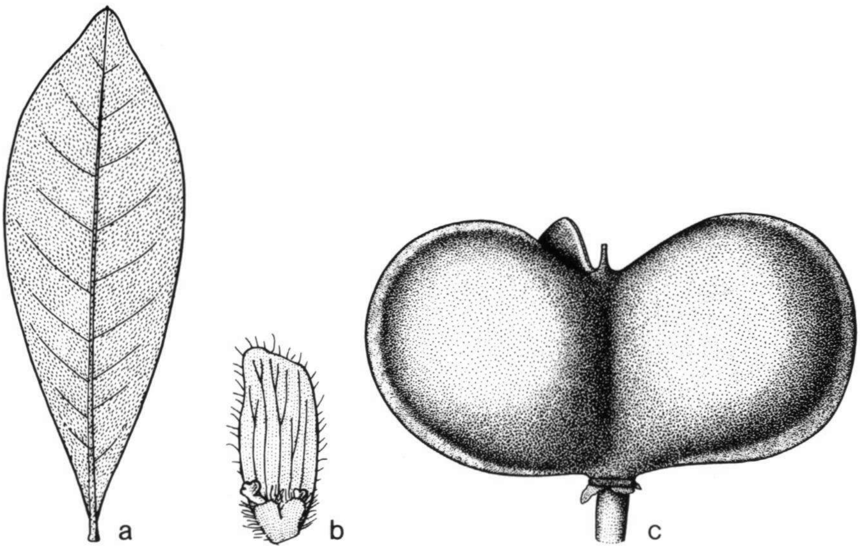


Fig. 96. *Guioa montana* C.T. White. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, b: *Hyland 7021*, L; c: *Hyland 1628*, BRI).

rhachis too; rhachis terete, 1.2–7.5 cm long, sericous; first order branches up to 2.6 cm long; cymules cincinnate, 1–4-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 1.1–1.7 mm long; bracteoles 0.7–0.9 mm long. *Pedicels* 3.2–4.8 mm long, sericeous, also the 1.7–2.5 mm long upper part. *Flowers* c. 6 mm in diam. *Sepals* 5, broadly ovate to ovate, margin and outside pilose, margin with glands, inside (sub)glabrous; 2 outer smaller ones 1.6–2.5 by 1.4–2 mm; 3 inner larger ones 2.2–3.5 by 2–3 mm, margin petaloid. *Petals* 5, obovate, 2–2.5 by 0.8–1 mm, not distinctly nailed, margin pilose, outside and inside glabrous, apex obtuse; scales free, 0.7–0.9 mm long; crest well developed, clavate on thin stipe, top lobed. *Disc* complete, with 1 or 2 slits near reduced petal. *Stamens* 8; filament 1.5–3 mm long, especially basally pilose; anther 0.5–0.8 mm long, glabrous to sparsely pilose. *Pistil:* ovary c. 0.6 mm high, smooth, sparsely hirsute; stigma 0.2–0.3 mm high; style elongating in fruit. *Fruit* with usually 2 or 3 well developed lobes, 1.2–1.6 cm high by 2–2.5 cm broad, smooth, glabrous, stipe inconspicuous, angle between lobes c. 90°, black when dry; lobes c. 13 by 11 mm (see note 1). *Seed* unknown.

Field notes. Tree up to 20 m high, d.b.h. c. 30 cm. Flowers cream.

Distribution. Australia, N Queensland (S Cook Dist.).

Ecology. Commonly found in understorey of rain forest. Vegetation type: Simple notophyll vine forest (Tracey, 1982) and Mixed notophyll vine forest: emergents: *Agathis microstachya* and *Eucalyptus grandis*. Humidity: very wet. Soil material: granite. Alt.: 1000–1300 m. Flowering: Oct. Fruiting: July.

N o t e s. 1. The fruits of *Guioa montana* were still unknown. The collection *Hyland 1628* only contained fallen-off fruits, no branchlets and leaves were present. These fallen-off fruits are much larger than those of the other Queensland species of *Guioa*, therefore they can only belong to *Guioa montana* and are likewise described above.

2. See also note 1 under *Guioa semiglauca*.

S p e c i m e n s s t u d i e d:
AUSTRALIA. Queensland: *Hyland 1628, 7021; Kajewski 1286; L.S. Smith 14729; Webb & Tracey 13119, 13120, 13240, 13241, 13242; K.J. White 888.*

Guioa multijuga Welzen – Fig. 97 a, b.

Guioa multijuga Welzen, Blumea 33 (1988) 418, pl. 7a, b. — T y p e: *BW (van der Sijde) 4061* (L, holo; iso in K, P; MAN, n.v.), Irian Jaya, Hollandia, 'Dok 5'.

Small tree. *Branchlets* terete, smooth to somewhat ribbed, shortly sericeous when young; flowering twigs 2.5–4.5 mm thick. *Leaves* (3–)5–7-jugate; rhachis 7.3–14.7 cm long, terete, not to very slightly winged, subglabrous to subsericeous, petiole 1.6–4.5 cm long; petiolules up to 0.6 cm long. *Leaflets* not subsessile, opposite to subopposite, (ovate to) elliptic, 3.8–6.3 by 1–1.7 cm, index 3.7–4.7, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, flat; apex acute to cuspidate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, dull, papillate, very sparsely subsericeous, domatia at least in some leaflets a single small sac on basiscopic side in axil of second major nerve; venation on upper side flat, except for the raised midrib, raised below; major nerves 0.2–0.9 cm apart, marginally looped, sometimes less distinctly so in lower part of leaflets; veins laxly reticulate, indistinct. *Inflorescences* axillary, branching in axil and along rhachis; latter terete, 0.5–6.5 cm long, slightly sericeous; first order branches up to 0.9 cm long; cymules cincinnate, 2-flowered. *Bracts* and *bracteoles* triangular, outside pilose, inside glabrous; bracts c. 1 mm long; bracteoles c. 0.4 mm long. *Pedicels* 2.1–2.5 mm long, sericeous except for the subglabrous, 0.9–1.1 mm long upper part. *Flowers* c. 2.8 mm in diam. *Sepals* 5, ovate, margin pilose, outside and inside glabrous; 2 outer smaller ones 1.2–1.5 by 0.8–0.9 mm, margin with glands; 3 inner larger ones 1.5–1.8 by 1.3–1.5 mm, margin petaloid, without glands. *Petals* 5, obovate, 1.5–1.7 by 0.3–0.5 mm, claw c. 0.3 mm high, margin densely pilose, outside and inside (sub)glabrous, apex acute; scales c. 1 mm long, free, folded outwards, apex not broadened; crest absent; petal between two adjacent large sepals not

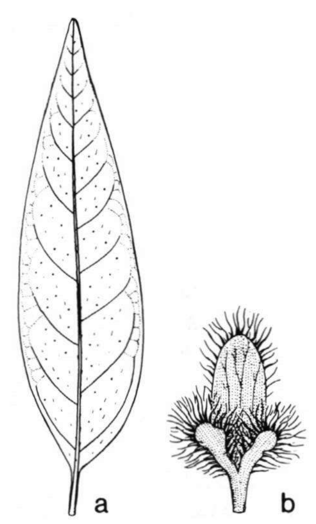


Fig. 97. *Guioa multijuga* Welzen. a. Leaflet, × 1; b. petal, × 12.5 (*BW (Van der Sijde) 4061*, L).

reduced. *Disc* complete. *Stamens* 8; filament c. 2.3 mm long, completely but especially basally pilose; anther 0.3–0.4 mm long, sparsely pilose. *Pistil:* ovary c. 0.7 mm high, smooth, subhirsute; style and stigma c. 0.5 mm long. *Fruit* unknown.

F i e l d n o t e s. Small tree, up to 5 m high. Flowers white, sweet smelling.

D i s t r i b u t i o n. Irian Jaya, around Jayapura.

E c o l o g y. Rare; found in old secondary forest and at edge rain forest-savannah on steep terrain. Soil: once recorded from clayey sand. Alt.: 100–185 m. Bud: March. Flowering: Sept.

N o t e s. 1. Typical are the many jugae; small, papillate, almost glabrous leaflets; small petals with outwardly folded scales, and complete disc.

2. *Guioa subsericea* looks much alike, see also note 3 under the latter.

3. Merrill identified this species as *Guioa koelreuteria*, the most commonly found species of *Guioa* in the Philippines. The latter has very different petals, with the scales folded inwards instead of outwards. Moreover, *Guioa koelreuteria* only very exceptionally possesses papillae.

S p e c i m e n s s t u d i e d:
NEW GUINEA. Irian Jaya, Jayapura: *BW (van der Sijde) 4061*, 'Dok 5'; *Sigafoos 108*, N of Simboror Strait of Sentani Lake.

Guioa myriadenia Radlk. – Fig. 98a–d.

Guioa myriadenia Radlk., Elmer Leafl. Philip. Bot. 5 (1913) 1610; Philip. J. Sc. 8, Bot. (1914) 446; Merr., En. Philip. 2 (1923) 508; Radlk. in Engl., Pflanzenr. 98 (1933) 1168; Salvosa, Lex. Philip. Pl. (1963) 105. — L e c t o t y p e (here proposed): *Elmer 8704* (M, holo; iso in FI, K, L, NY, W), Philippines, Luzon, Benguet Prov., Baguio.

Guioa falcata Radlk., Philip. J. Sc. 8, Bot. (1914) 446, 461; Merr., En. Philip. 2 (1923) 507; Radlk. in Engl., Pflanzenr. 98 (1933) 1167; Salvosa, Lex. Philip. Pl. (1963) 105. — T y p e: *Elmer 5869* (M, holo; iso in K, NSW, NY, P), Philippines, Luzon, Benguet Prov., Baguio.

Guioa obtusa Merr., Philip. J. Sc. 12, Bot. (1917) 276; En. Philip. 2 (1923) 508; Radlk. in Engl., Pflanzenr. 98 (1933) 1170; Salvosa, Lex. Philip. Pl. (1963) 105. — T y p e: *BS (Ramos & Edaño) 26636* (PNH, holo, †; iso in A, K, NY, P), Philippines, Luzon, Tayabas Prov., Mt. Dingalan.

[*Guioa ferruginea* Merr. ex Salvosa, Lex. Philip. Pl. (1963) 105, nom. nud., based on *BS (Ramos) 42181*.]

Shrub to tree. *Branchlets* terete, smooth (to slightly ribbed), golden (sericeous to) hirsute, especially when young; flowering twigs 1.5–6 mm thick. *Leaves* 2–5-jugate; rhachis 1.8–16.2 cm long, basally terete to upwards dorsoventrally flattened, not winged, subsericeous to hirsute, petiole 1–6.3 cm long; petiolules up to 0.9 cm long. *Leaflets* usually not subsessile, opposite (to subopposite), ovate (to elliptic), often falcate, 2.5–14.5 by 1–4.5 cm, index 2.3–4.2, usually asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, (flat to) revolute; apex (rounded to) acuminate (to cuspidate), usually mucronulate; upper surface smooth, usually subsericeous to appressedly hirsute; lower surface differently coloured, dull, papillate, long sericeous to hirsute, domatia (a single to many sacs to) many pockets in axils of major nerves; venation on upper side (slightly sunken to) flat (to raised), below raised; nerves 0.2–1.8 cm apart, marginally looped; veins

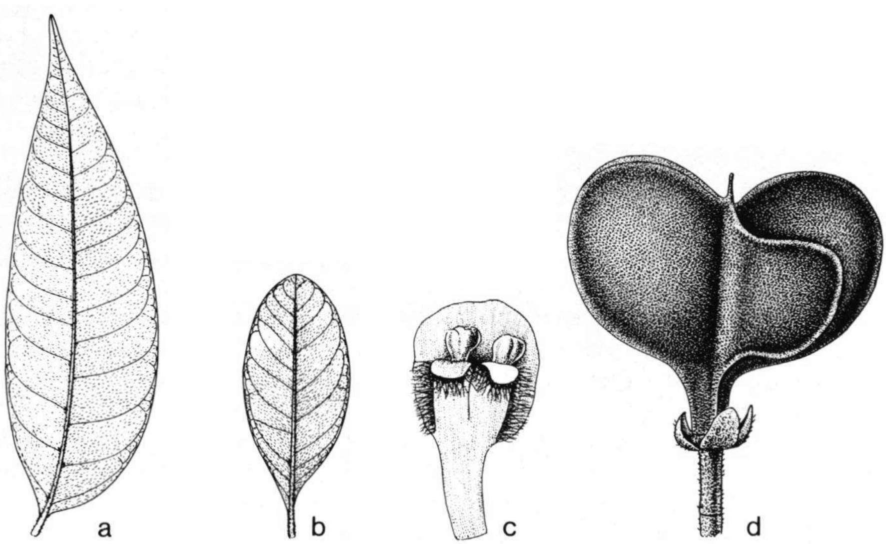


Fig. 98. *Guioa myriadenia* Radlk. a. Leaflet, typical form, × 0.5; b. leaflet, '*Guioa obtusa*' form, × 0.5; c. petal, × 12.5; d. fruit, × 3 (a, c: *Vanoverbergh 2706*, L; b: *BS (Ramos & Edaño) 26636*, A; d: *FB (Rontanilla) 29453*, A).

densely reticulate, distinct. *Inflorescences* axillary to pseudoterminal, branching in or near axil and along rhachis, often dense and many-flowered; rhachis flattened, 1.7–15.7 cm long, densely golden (sericeous to) hirsute; first order branches up to 7.6 cm long; cymules cincinnate, 2–4-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 1.5–2.5 mm long; bracteoles 0.5–1.8 mm long. *Pedicels* 2.8–8 mm long, sericeous; upper part 1–3.5 mm long, often less pilose. *Flowers* 3.5–4 mm in diam. *Sepals* 5, ovate, margin and outside pilose, margin with glands, inside glabrous; 2 outer smaller ones 1.6–2.5 by 1.1–2.4 mm; 3 inner larger ones 2–3.2 by 2–3.2 mm, margin petaloid. *Petals* 5, obovate, 2.5–4 by 1.3–1.7 mm, blade orbicular, abruptly clawed, latter 0.8–2 mm high, margin pilose, outside and inside (sub)glabrous, apex retuse to obtuse; scales 1.2–1.7 mm long, free; crest clavate, shortly stiped, apex lobed, subglabrous. *Disc* incomplete. *Stamens* 8; filament 2–4.4 mm long, especially basally pilose; anther 0.3–0.6 mm long, glabrous. *Pistil:* ovary 0.4–2.3 mm long, smooth, subhirsute; style and stigma 0.1–1.5 mm long, elongating in fruit up to 2.5 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.1–1.4 cm high by 1.1–1.8 cm broad, smooth, glabrous, stipe 2.5–4 mm high, slender, angle between lobes 135–140°, blackish when dry; lobes 8–9 by 7–10 mm. *Seed* obovoid, c. 6.2 by 4.8 mm; hilum c. 1.9 mm long. *Embryo* c. 5.2 by 4.5 mm; cotyledons secondarily laterally besides each other, upper larger, apices elongated, that of upper straight, of lower recurved; radicle c. 1.8 mm long.

F i e l d n o t e s. Shrub to tree, 2–9 m high, d.b.h. up to 6 cm, branches widely spreading. Bark greyish white to mottled, hard. Sapwood white, very hard. Leaflets submembranaceous; below glaucous green. Inflorescence suberect, olive-green. Flowers without scent. Sepals whitish. Petals white to red; scales or crests yellow. Filaments white; anthers light red, later blackish. Disc greenish yellow.

D i s t r i b u t i o n. Philippines (Luzon).

E c o l o g y. Found in primary forest, forested slopes, mossy forest, along pine crest. Alt.: 270–1700 m. Flowering: Dec.–April. Fruiting: July.

V e r n a c u l a r n a m e s. Philippines: ulas (Igorot); ulas-lilik (Tagalog); alahan-kalauang, alahan-silangan (Filipino).

N o t e s. 1. This species can be distinguished by its ovate leaflets, reticulate venation, lower surface with sericeous to hirsute hairs, usually many pockets, punctation, sepals with sericeous outside, petals with a long stipe and orbicular blade, clavate stiped crests.

Several forms can be found, three of which are rather distinct: One form with leaflets with a sericeous lower surface in the Benguet and Mountain Prov. (this form may be subdivided; some specimens have rather symmetric leaflets, viz. *Guioa myriadenia* s. s., others have more falcate leaflets, viz. *'Guioa falcata'*).

Another form, with hirsute indumentum, occurs in the Rizal Prov. Two specimens form a transition between both forms, viz. *Elmer 8769* and *Loher 13714*, and therefore no taxonomic status has been attributed to these two forms, although Radlkofer suggested a separation by introducing a different name (*'Guioa subferruginea'*) on his labels for the hirsute form. The latter name has never been published.

The third form was known as *Guioa obtusa* (Tayabas Prov.) and has leaflets with a densely sericeous lower surface and obtuse apex. The former two forms possess acute to cuspidate leaflet apices. However, the southern hirsute form has a far less elongated apex than the northern sericeous form (N.B.: Tayabas Prov. is south of Rizal Prov.). The name *Guioa obtusa* has been placed in the synonymy, because the apex is the only distinctive character and this character is usually a rather poor one.

2. See for the distinction between *Guioa myriadenia, Guioa palawanica,* and *Guioa parvifoliola* the note under the latter.

3. The rather glabrous falcate form of *Guioa myriadenia* looks very similar to *Guioa reticulata*. The latter has usually far less pilose inflorescences (use naked eye) and the shape of the petals is different, the blade is elliptic to obovate and gradually decurrent into the stipe, not orbicular and with an abrupt transition from blade to stipe.

4. Some forms of *Guioa myriadenia* look remarkably like the *'Guioa lasiothyrsa'* form of *Guioa pleuropteris*. *Guioa myriadenia* has always a rather golden indumentum, not dull brown like *Guioa pleuropteris,* while the venation is denser and usually more distinct. The crest is also different; that of *Guioa pleuropteris,* if present, is like that of *Guioa reticulata* (see former note). The fruits of *Guioa pleuropteris* can be reddish when dry, those of *Guioa myriadenia* are black.

S p e c i m e n s s t u d i e d:
PHILIPPINES. Luzon: 19 specimens.

Guioa normanbiensis Welzen – **Fig. 99a–c.**

Guioa normanbiensis Welzen, Blumea 33 (1988) 418, pl. 6a–c. — T y p e: *Brass 25521* (L, holo; iso in K), Papua New Guinea, Milne Bay Prov., Esa'ala Subprov., Sewa Bay, Normanby I.

Tree. *Branchlets* terete, smooth to slightly ribbed or rough, at most only sericeous when young; flowering twigs 3–13 mm thick. *Leaves* 2–4-jugate; rhachis 4–17.7 cm long, terete, not winged, glabrous, petiole 3.5–7 cm long. *Leaflets* subsessile, opposite to alternate, ovate, 7–19.3 by 2.6–6.5 cm, index 2.7–3.2, ± symmetric, otherwise acroscopic side broader, coriaceous, seldom punctate; base attenuate; margin entire, flat; apex acuminate to cuspidate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous to seldom very sparsely sericeous, domatia a single small sac on basiscopic side in axil of second major nerve; venation on upper side flat (to raised), raised below; major nerves 0.3–3.3 cm apart, marginally looped, but less distinctly so in lower part of leaflets; veins laxly reticulate, indistinct. *Inflorescences* ramiflorous to axillary, branching in axil and along rhachis; latter flat to terete in fruit, 1.5–6.8 cm long, subglabrous; first order branches up to 2 cm long; cymules cincinnate, c. 3-flower-
Bracts and *bracteoles* triangular, outside hirsute, inside glabrous; bracts 0.7–1.1 mm long; bracteoles 0.3–0.8 mm long. *Pedicels* 1.8–4 mm long, subglabrous, except for the glabrous 0.8–1.6 mm long upper part. *Flowers* c. 3.5 mm in diam. *Sepals* 5, ovate, margin pilose, outside and inside glabrous; 2 outer smaller ones 1–1.6 by 1.2–1.3 mm, margin with glands; 3 inner larger ones 1.9–2.8 by 1.7–2.7 mm, margin petaloid, without glands. *Petals* 5, obovate, c. 2 by 0.6–0.8 mm, claw c. 0.3 mm high, margin pilose, outside and inside (sub)glabrous, apex acute; scales 1.2–1.3 mm long, free, basally not auricled; crest clavate, stiped, apex lobed. *Disc* incomplete. *Stamens* 8; filament 2.7–3.1 mm long, completely but especially basally pilose; anther c. 0.6 mm long, glabrous. *Pistil:* ovary c. 0.3 mm long, smooth, subhirsute; style and stigma c. 0.2 mm long, elongating in fruit up to 3 mm long, then

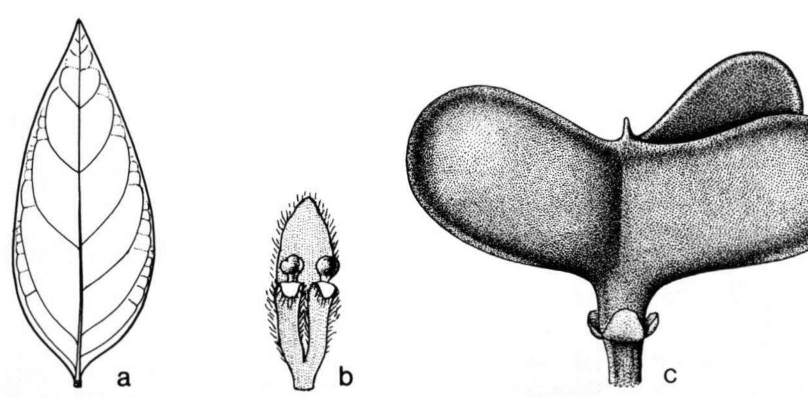


Fig. 99. *Guioa normanbiensis* Welzen. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, b: *NGF (Buderus) 24061*, L; c: *Brass 25521*, L).

upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.2–1.5 cm high by 1.3–2.2 cm broad, smooth to somewhat ribbed, glabrous, stipe 3–3.5 mm high, slender, edge of margin rounded, angle between lobes 75–110°, blackish when dry; dissepiments complete; lobes 11–15 by 7.5–9.5 mm. *Seed* immature.

Field notes. Tree, 7–20 m high, d.b.h. at least 5 cm; bole c. 3 m. Bark brown. Wood medium hard. Leaves dull dark green above, green below. Flowers white.

Distribution. Papua New Guinea (Milne Bay Prov., Normanby I.).

Ecology. Frequently found in lowland rain forest, along gullies. Alt.: sea-level up to 200 m. Flowering: Sept.

Notes. 1. Typical for this species are the ovate leaflets (almost) without indumentum and without papillae, the presence of a single sac, and the fruits with a high slender stipe and slender lobes.

2. *Guioa normanbiensis* is part of the *Guioa rigidiuscula*-complex. The differences among the species within this complex are discussed in chapter 9.

Specimens studied:
PAPUA NEW GUINEA. Milne Bay Prov., Normanby I.: *Brass 25521*, Lebudowa River; *LAE (Lelean & Streimann) 52521*, Sewa Bay; *NGF (Womersley & Brass) 8671*, Waikaiuna Bay; *(Buderus) 24061*, Sewa Bay.

Guioa novobritannica Welzen – Fig. 100 a, b.

Guioa novobritannica Welzen, Blumea 33 (1988) 419, pl. 17a, b. — Type: *NGF (Frodin) 26918* (L, holo; iso in BM, BRI, CANB; LAE, n.v.), Papua New Guinea, West New Britain, Talasea, Mt. Tangis, NW slope.

Tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 2–2.5 mm thick. *Leaves* 1- or 2-jugate; rhachis 1.2–4.3 cm long, flattened above, not winged, glabrous, petiole 1.3–2.7 cm long. *Leaflets* subsessile, opposite to subopposite, elliptic, 4.2–4.9 by 1.1–1.7 cm, index 2.9–3.8, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, flat; apex acuminate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, dull, papillate, glabrous except for a few hairs near domatium, latter a single, large, highly domed sac on basiscopic side in axil of ± second major nerve; venation on upper side flat, raised below; major nerves 0.2–0.8 cm apart, marginally looped, but less distinctly so in lower part of leaflets; veins densely reticulate, distinct. *Inflorescences* axillary, branching along rhachis; latter flattened, 3–10 cm long, subsericeous; first order branches up to

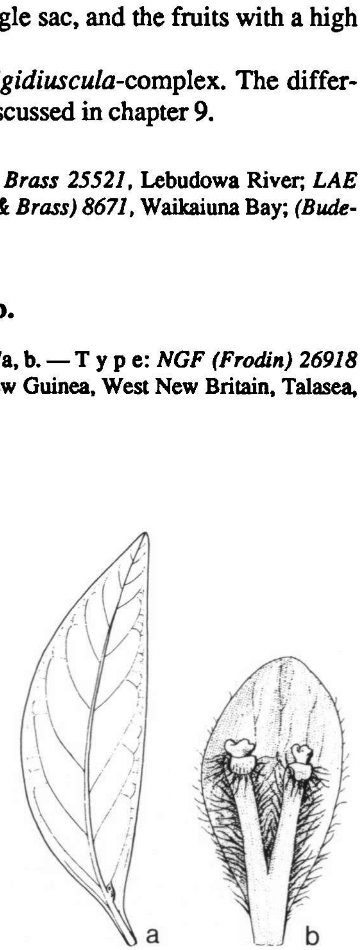


Fig. 100. *Guioa novobritannica* Welzen. a. Leaflet, × 1; b. petal, × 12.5 (*NGF (Frodin) 26918*, L).

4.8 cm long; cymules cincinnate, c. 2-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.7–0.8 mm long; bracteoles 0.2–0.4 mm long. *Pedicels* c. 3 mm long, sericeous except for the (sub)glabrous, c. 1.9 mm long upper part. *Flowers* c. 3.5 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones c. 1.5 by 1.7 mm; 3 inner larger ones 1.8–2.5 by c. 1.8 mm, margin petaloid. *Petals* 5, elliptic, 3–3.2 by 1.2–1.3 mm, claw c. 0.8 mm high, margin pilose, outside and inside glabrous, apex obtuse to acute; scales 1.5–1.8 mm long, free; crest clavate, stiped, apex lobed; petal between two adjacent large sepals not reduced in size. *Disc* incomplete. *Stamens* 8; filament 1.7–1.8 mm long, completely but especially basally pilose; anther c. 0.4 mm long, glabrous. *Pistil:* ovary c. 1.7 mm long, smooth, subhirsute; style and stigma c. 1.8 mm long. *Fruit* unknown.

Field notes. Tree, c. 20 m high, d.b.h. up to 20 cm; buttresses absent. Bark brown, moderately fissured, slightly scaly in places, lenticels absent; blaze red-brown. Wood straw. Odour and exudate absent. Leaves dark green above, light green below. Flowers white.

Distribution. Papua New Guinea (West New Britain Prov.).

Ecology. Found in montane forest with dominant *Casuarina rumphiana*. Alt.: c. 800 m. Flowering: May.

Vernacular name. Nasigaga.

Notes. 1. Typical for this species are the small papillate leaflets with a single large sac.

2. This species, together with *Guioa plurinervis* and *Guioa misimaensis* are the only species with papillate leaflets in the *Guioa rigidiuscula*-complex. The differences among the species of this complex are discussed in chapter 9.

Specimens studied:
PAPUA NEW GUINEA. West New Britain Prov.: *NGF (Frodin) 26918*, Talasea, Mt. Tangis.

Guioa novoëbudaënsis Welzen – Fig. 101a–c.

Guioa novoëbudaënsis Welzen, Blumea 33 (1988) 419, pl. 14a–c. — Type: *Bernardi 13284* (L, holo; iso in K, M, NOU, NY, P, W), New Hebrides, Erromango I., Baie Dillon (Oupongkor) at Happy Land.

Tree. *Branchlets* terete, smooth (to ribbed), sericeous when young; flowering twigs 2–4 mm thick. *Leaves* 4–6-jugate; rhachis 7.7–19.3 cm long, basally terete to upwards above somewhat flattened, not winged, subsericeous, petiole 3–7.1 cm long; petiolules up to 0.7 cm long. *Leaflets* not subsessile, opposite to subopposite, ovate (to somewhat elliptic), falcate, 2.5–9.8 by 0.6–3.2 cm, index 2.7–4.4, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, flat (to revolute); apex cuspidate to caudate, very apex acute, not mucronulate; upper surface smooth, (sub)glabrous, midrib basally often puberulous; lower surface differently coloured, dull, papillate, subsericeous, domatia a single small sac with the opening in the front, on basiscopic side in axil of ± second vein, sometimes additional shallow pockets present; venation on upper surface (flat to) raised, raised on lower; nerves 0.5–2.8 cm apart, marginally looped; veins rather densely reticulate,

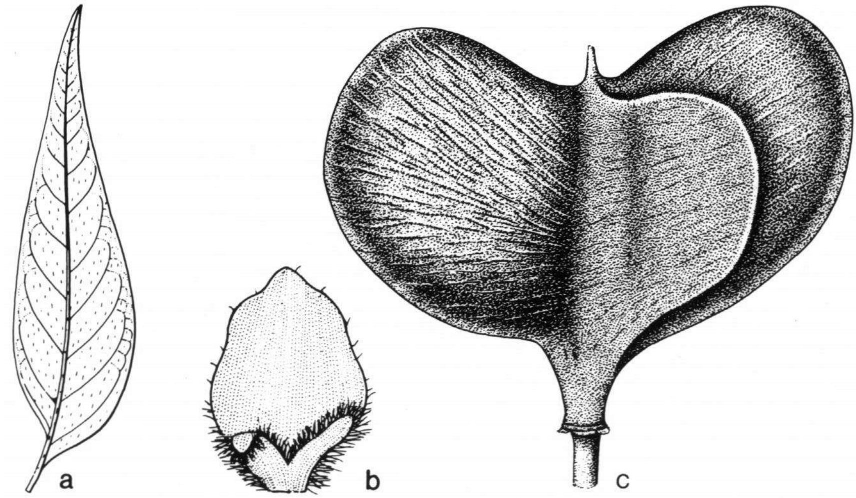


Fig. 101. *Guioa novoëbudaënsis* Welzen. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, c: *Cabalion 2182*, K; b: *Morrison s.n.*, 28-V-1896, L).

conspicuous. *Inflorescences* axillary, branching along rhachis; latter somewhat flattened or grooved, 5.4–21.2 cm long, sericeous; first order branches up to 9.2 cm long; cymules cincinnate, c. 3-flowered. *Bracts* and *bracteoles* triangular, sericeous outside, inside subglabrous; bracts 0.7–1.1 mm long; bracteoles 0.3–0.7 mm long. *Pedicels* 3.7–9 mm long, sericeous; upper part less sericeous, 2–3 mm long. *Flowers* c. 3.5 mm in diam. *Sepals* 5, ovate, only margin pilose, other parts glabrous; 2 outer smaller ones 1.3–1.7 by 1.3–2 mm, margin with few glands; 3 inner larger ones 2.4–2.9 by 2.4–3 mm, margin petaloid, without glands. *Petals* 5, elliptic, 2.3–3 by 1.6–2 mm, claw 0.1–0.2 mm high, margin and basally the outside and inside pilose, apex obtusely acute to acute; scales 0.3–0.7 mm long, free; crest not present to occasionally present as an enation, not stiped, not clavate; petal between two adjacent large sepals not reduced. *Disc* incomplete to complete with a thin part near insertion of two adjacent large sepals. *Stamens* 8; filament 2–4.3 mm long, especially basally pilose; anther 0.6–0.8 mm long, glabrous. *Pistil:* ovary 0.3–0.5 mm high, sparsely hirsute; style and stigma 0.2–0.3 mm high, elongating in fruit up to 2.5 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.8–2 cm high by 1.8–2.3 cm broad, smooth, glabrous, stipe c. 3.5 mm high, somewhat broadly cuneate, angle between lobes c. 130°, blackish when dry; lobes c. 12 by 12.5 mm. *Seed* obovoid, c. 11.8 by 8.2 mm; hilum c. 2 mm long. *Embryo* c. 8.7 by 7.8 mm; cotyledons dorsoventrally above each other, upper larger, apices not elongated; radicle c. 1 mm long.

Field notes. Tree, 6–12 m high. Leaves membranaceous, glaucous below. Sepals and petals white. Stamens pink.

Distribution. New Hebrides: Erromanga I., Pentecote I.

E c o l o g y. Found mainly on savannah, some in forest remnants. Alt.: 100–430 m. Buds: March. Flowering: May–June. Fruiting: July.

N o t e. See note under *Guioa megacarpa* for differences among *Guioa novo-ebudaënsis, Guioa megacarpa,* and *Guioa punctata.*

S p e c i m e n s   s t u d i e d:
NEW HEBRIDES. Erromango I.: *Bernardi 13284; Cabaliou 2182; Morrison s.n.*, 18-VII-1896; *Schmid 3299.* — Pentecote I.: *Morrison s.n.*, 28-V-1896. — Santo I.: *Suprin 321.*

Guioa oligotricha Merr. & Perry – Fig. 102a, b.

Guioa oligotricha Merr. & Perry, J. Arn. Arbor. 21 (1940) 512. — T y p e: *Brass 8290* (A, holo; iso in BM, L), Papua New Guinea, Lower Fly River, Gaima.

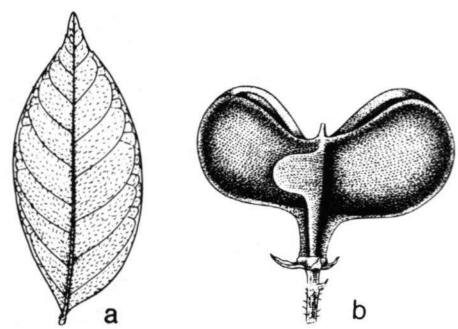


Fig. 102. *Guioa oligotricha* Merr. & Perry. a. Leaflet, × 0.5; b. fruit, × 3 (*LAE (Streimann) 51732*, L).

Small tree. *Branchlets* terete, smooth to slightly rough, hirsute when young; flowering twigs 2.5–11 mm thick. *Leaves* 1–3-jugate; rhachis 2.1–8.5 cm long, terete, not winged, hirsute, petiole 1–2.7 cm long. *Leaflets* subsessile, opposite to alternate, ovate to elliptic, 4.1–9.1 by 2–4 cm, index 2.1–2.5, symmetric, subcoriaceous, punctate; base acute; margin entire except usually for a few subapical teeth, flat to somewhat revolute; apex acuminate to cuspidate, sometimes mucronulate; upper surface smooth, glabrous to sparsely hirsute, the midrib densely hirsute; lower surface lower surface differently coloured, duller, smooth to papillate, hirsute, red glands absent, domatia many pockets in axils of major nerves; venation on upper side slightly sunken (except for the raised midrib), raised below; nerves 0.3–1.3 cm apart, marginally looped, but less distinctly so in lower third of leaflets; veins laxly scalariform to densely reticulate, rather distinct. *Inflorescences* axillary, not branching to branching in or near axil; rhachis terete, 1.2–6 cm long, hirsute; first order branches up to 1.5 cm long; cymules cincinnate, 1- or 2-flowered. *Bracts* and *bracteoles* narrowly triangular, outside hirsute, inside subglabrous; bracts c. 1 mm long; bracteoles 0.4–0.8 mm long. *Pedicels* 1–3.2 mm long, hirsute except for the (sub)glabrous, 0.5–1.2 mm long upper part. *Flowers* c. 3 mm in diam. *Sepals* 5, ovate, margin and outside pilose, margin with few glands, inside glabrous; 2 outer smaller ones 1–1.3 by 0.8–1 mm; 3 inner larger ones 1.4–2.2 by 1.1–1.5 mm, margin petaloid. *Petals* 5, obovate, 0.7–1 by c. 0.3 mm, claw 0–0.3 mm high, margin and less so outside and inside hirsute, apex acute; scales 0.6–0.7 mm long, free, apex not broadened; crest absent. *Disc* complete. *Stamens* 8; filament 1.1–1.8 mm long, especially basally pilose; anther c. 0.3 mm long, glabrous. *Pistil:* ovary c. 0.3 mm long, smooth, subhirsute; style and stigma c. 0.2 mm long, elongating in fruit up to 2.1 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 0.6–0.8 cm high by 0.8–1.2 cm broad, smooth to rugose, glabrous, stipe 1.5–2 mm high, slender, angle between lobes 90–130°, blackish when dry; lobes 7.5–8 by 6–6.5 mm. *Seed* obovoid, 5–6 by 3–4 mm; hilum c. 1 mm long. *Embryo* 4.3–5.3 by 2.2–3.5 mm; cotyledons dorsoventrally above each other, upper larger, apex of upper slightly elongated, straight; radicle 1.5–1.8 mm long.

Field notes. Small bushy tree, 5–7.5 m high, d.b.h. c. 10 cm. Leaves dull dark green above, green below. Corolla white. Fruits smooth, red.

Distribution. New Guinea: Irian Jaya (Southern Div.) and Papua New Guinea (Western Prov.).

Ecology. Common, found in secondary forest to light rain forest, along edge of forest, riverbanks. Soil: once recorded from clayey soil. Alt.: 50–150 m. Flowering: March. Fruiting: Aug.–Nov.

Notes. 1. This species looks like *Guioa lasioneura*. Differences are:

	Guioa lasioneura	*Guioa oligotricha*
Leaflets	elliptic	ovate to elliptic
Margin of leaflets	entire	often subapically a few teeth
Disc	incomplete	complete
Fruit	0.7–1.2 cm high by 1.1–2 cm broad	0.6–0.8 cm high by 0.8–1.2 cm broad

2. See note 3 under *Guioa molliuscula* for the differences between *Guioa oligotricha* and *Guioa molliuscula*.

3. *Beccari FI 2810* (*Guioa acutifolia*) resembles *Guioa oligotricha*, because it also possesses leaflets with subapical teeth and several pockets. However, this specimen totally lacks indumentum; therefore it has been identified as *Guioa acutifolia*, also because some W New Guinea specimens of *Guioa acutifolia* tend to have more than one domatium.

Specimens studied:

NEW GUINEA. Irian Jaya, Southern Div.: *BW (Kalkman) 6412*, Jibi, 5 km N from Ninati. — Papua New Guinea, Western Prov.: *Brass 8290*, Lower Fly River, Gaima; *LAE (Streimann) 51732*, Kiunga.

Guioa ovalis Radlk. — Fig. 103a–c.

Guioa ovalis Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 610; Guillaumin, Bull. Soc. Bot. Fr. 79 (1932) 337; Radlk. in Engl., Pflanzenr. 98 (1933) 1162; Guillaumin, Fl. Nouv.-Caléd. (1948) 199. — Type: *Balansa 1448* (P, holo), New Caledonia, Bourail.

Tree(let). *Branchlets* terete, smooth, sericeous when young; flowering twigs 2–8 mm thick. *Leaves* 1–6-jugate; rhachis 1.8–25 cm long, basally terete to apically somewhat flattened, not winged, subglabrous, petiole 1.6–11.8 cm long; petiolules if present up to 1.7 cm long. *Leaflets* usually subsessile, opposite to alternate, elliptic, 4.3–22.7 by 1.5–7.9 cm, index 1.8–3.7, ± symmetric, coriaceous to very coriaceous, usually punctate; base attenuate; margin entire, (flat to) revolute; apex (retuse to) obtuse to acuminate, sometimes mucronulate; upper surface smooth, gla-

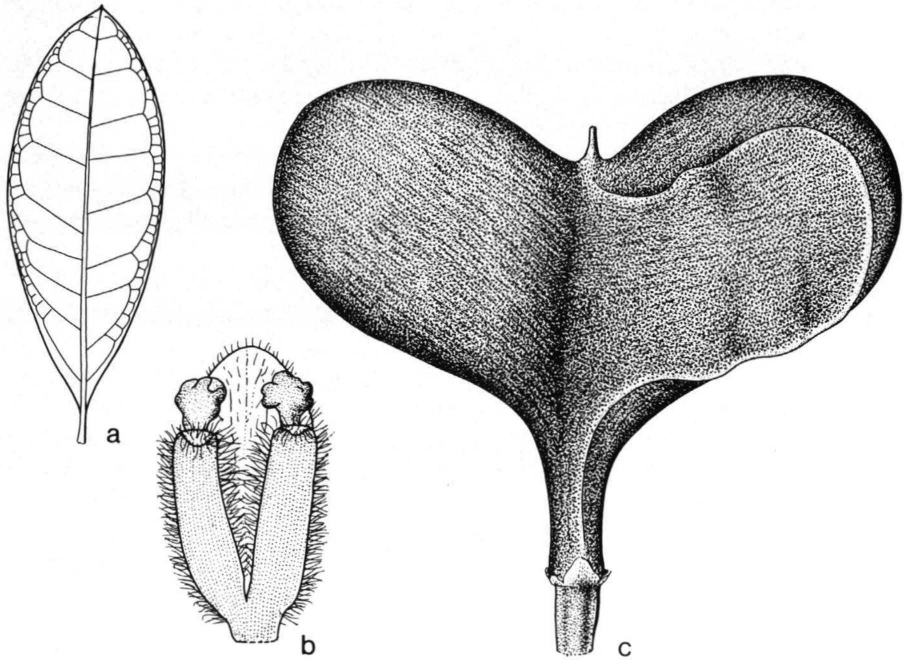


Fig. 103. *Guioa ovalis* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *MacPherson 3193*, L; b: *MacKee 23795*, L).

brous, sometimes with wax; lower surface differently coloured, more dull, smooth, no papillae, glabrous (to very sparsely sericeous), domatia absent or a single sac on basiscopic side in axil of second nerve; venation raised; nerves 0.2–3 cm apart, marginally looped; veins laxly indistinctly reticulate. *Inflorescences* axillary to pseudoterminal, branching along rhachis and sometimes in or near axil too; rhachis terete to slightly flattened, 0.8–32 cm long, subglabrous; first order branches up to 14.6 cm long; cymules cincinnate, 1–3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.6–1.3 mm long; bracteoles 0.3–0.8 mm long. *Pedicels* 1.2–7 cm long, slightly sericeous except for the glabrous 0.4–3.5 mm long upper part. *Flowers* c. 4 mm in diam. *Sepals* 5, ovate, margin pilose, without glands, outside and inside glabrous; 2 smaller outer ones 1.2–2.2 by 1.2–2.3 mm; 3 larger inner ones 2.1–3.7 by 1.8–3.7 mm, margin petaloid. *Petals* 5, elliptic, 2–3.3 by 1–3.1 mm, claw 0.1–0.3 mm high, completely pilose, apex truncate to obtuse; scales 1.3–2.1 mm long, free; crest clavate, flat, lobed. *Disc* incomplete with 1 or 2 small slits. *Stamens* 8; filament 1.8–4.3 mm long, especially basally pilose; anther 0.4–1 mm long, pilose. *Pistil:* ovary 0.2–1.8 mm high, smooth, sparsely hirsute; stigma and style 0.2–2 mm long, elongated in fruit and then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.7–2.4 cm high by 1.7–

2.9 cm broad, smooth, glabrous, stipe 2–6 mm high, slender, angle between lobes 90–135°, blackish when dry; lobes 15–17 by 10–13 mm. *Seed* obovoid, 14–15 by 10–10.8 mm; hilum 2.5–5 mm long. *Embryo* 9.5–12.5 by 7.2–9 mm; cotyledons secondarily laterally besides each other, upper larger, apices elongated, that of upper straight, that of lower recurved; radicle 4.6–5.5 mm long.

Field notes. Tree(let), 2.5–8 m high, d.b.h. up to 25 cm. Bark smooth to slightly rough, brown (with grey veins) to grey. Leaflets dark green above, light green below. Flowers white. Crests yellow. Filaments white; anthers red. Aril yellow to red-orange; seed black.

Distribution. New Caledonia and perhaps Fiji (Viti Levu; see note 2).

Ecology. In humid forest. Soil: schist, calcareous, ultrabasic. Alt.: 30–700 m. Flowering: Febr.–Aug. Fruiting: Sept.–Dec.

Notes. 1. In New Caledonia this species is readily recognizable by its large, smooth (no papillae) leaflets and very large fruits.

2. One specimen from Fiji (*Linney 860626-2*) closely resembles *Guioa ovalis* and is tentatively treated as belonging to this species. There are some small differences. The specimen of Fiji has a thicker disc and slightly larger sepals. The (still immature) fruits are somewhat different in shape and thickness.

3. Two specimens (*Jaffré 880* and *MacKee 22428*) are flowering juveniles, the rhachises are slightly winged and the margins of the leaflets of *MacKee 22428* are serrate.

Specimens studied:
NEW CALEDONIA: 33 specimens.
FIJI: *Linney 860626-2*, Viti Levu, NW of cement factory at Lami (see note 2).

Guioa palawanica Welzen – Fig. 104 a, b.

Guioa palawanica Welzen, Blumea 33 (1988) 419, pl. 15a, b. — Type: *BS (Foxworthy) 697* (L, holo; iso in M), Philippines, Palawan, Mt. Victoria.

Guioa glauca auct. non Radlk.: Radlk., Philip. J. Sc. 8, Bot. (1913) 446; Merr., En. Philip. 2 (1923) 507; Radlk. in Engl., Pflanzenr. 98 (1933) 1171, p.p. (Philippine plants); Salvosa, Lex. Philip. Pl. (1963) 105.

Shrub to tree. *Branchlets* terete, smooth to rough, sericeous when young; flowering twigs 2.5–4.5 mm thick. *Leaves* 1–3-jugate; rhachis 1.1–9.2 cm long, dorsally flattened, not winged, subglabrous (to sericeous), petiole 1–3.3 cm long; petiolules up to 1 cm long. *Leaflets* not subsessile, opposite to subopposite, elliptic (to obovate), 2.5–7.6 by 1–2.5 cm, index 2.1–3.4, rather symmetric, very coriaceous, punctate; base attenuate; margin entire, revolute; apex rounded to acuminate, very apex rounded to acute, not mucronulate; upper surface smooth, glabrous except for the basally puberulous midrib; lower surface differently coloured, dull, papillate, shortly sericeous, domatia absent or a single sac on basiscopic side in axil of ± second nerve; venation raised; nerves 0.3–1.7 cm apart, marginally looped; veins laxly reticulate, rather distinct. *Inflorescences* axillary, branching along rhachis; latter flattened, 1.2–9.8 cm long, sericeous, glabrescent: first order branches up to 3.9 cm long; cymules cincinnate. *Bracts* and *bracteoles* triangular, outside sericeous, inside

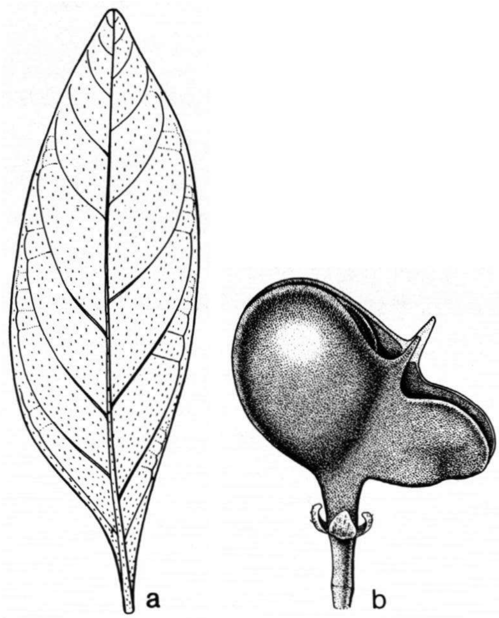


Fig. 104. *Guioa palawanica* Welzen. a. Leaflet, × 0.5; b. fruit, × 3 (a: *BS (Foxworthy) 562*, M; b: *BS (Foxworthy) 697*, M).

glabrous; bracts c. 1.3 mm long; bracteoles 0.3–0.8 mm long. *Pedicels* 3.2–6.3 mm long, sericeous, upper part 2–3.4 mm long. *Flowers* unknown. *Sepals* 5, ovate, margin and outside sericeous, inside glabrous, glands along margin unknown; 2 outer smaller ones 1.4–2.2 by 1.9–2 mm; 3 inner larger ones c. 2.3 by 2–2.2 mm, margin petaloid. *Disc* incomplete. *Fruit* with 1–3 well-developed lobes, 1.2–1.4 cm high by 1.1–1.9 cm broad, smooth to rugose-ruminate to rough, glabrous, the stipe 2–3 mm high, slender, angle between lobes 110–140°, blackish when dry; the lobes 8–10 by 7–10 mm. *Seed* obovoid, 7.5–8.5 by 6.2–6.8 mm; hilum 1–1.3 mm long. *Embryo* 6.5–7.5 by 5–5.5 mm; cotyledons secondarily laterally besides each other, upper larger, apex of the latter elongated, straight (to curved); radicle c. 2.3 mm long.

Field notes. Shrub to tree, 1–8 m high, d.b.h. 15 cm. Leaves bluish green.

Distribution. Philippines (Palawan).

Ecology. Found in lowland forest on ultrabasic, in stunted montane rain forest with many epiphytes, and along rivers. Alt.: 200–815 m. Fruiting: Nov.–March.

Vernacular names. Bunsikag (Tagnanua); bunsikag-puti (Filipino).

Notes. 1. *Guioa palawanica* has always been confused with *Guioa glauca* from New Caledonia. The resemblance between the two is striking; however, the punctation of the leaflets, the type of petal (that of *Guioa palawanica* is still unknown, but the type of *Guioa glauca* has not been found in the Philippines) and the form of the fruits present differences:

	Guioa palawanica	*Guioa glauca*
Punctation	absent	present
Form of petals	obovate?	elliptic
Nail of petals	long?	short
Stipe of fruit	slender	(slender to) broadly cuneate
Lobes of fruit	usually longer than high	higher than long

N.B.: The shape of the petals of species, related to *Guioa palawanica* (see note 2) is provided in the table.

2. The differences among *Guioa palawanica, Guioa myriadenia,* and *Guioa parvifoliola* are discussed in the note under the latter.

Specimens studied:
PHILIPPINES. Palawan: *BS (Foxworthy) 562; (Foxworthy) 697; FB (Curran) 3874; Ridsdale 1067; SMHI (Ridsdale) 247.*

Guioa parvifoliola Merr. – Fig. 105 a, b.

Guioa parvifoliola Merr., Philip. J. Sc. 14 (1919) 417; En. Philip. 2 (1923) 508; Radlk. in Engl., Pflanzenr. 98 (1933) 1170; Salvosa, Lex. Philip. Pl. (1963) 105. — Type: *BS (Ramos) 33187* (PNH, holo, †; iso in A, K, P), Philippines, Luzon, Ilocos Norte Prov., Mt. Nagapatan.

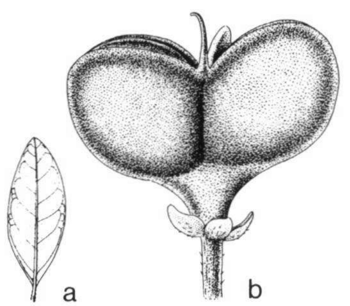


Fig. 105. *Guioa parvifoliola* Merr. a. Leaflet, × 0.5; b. fruit, × 3 (*BS (Ramos) 33187*, K).

Tree? *Branchlets* terete, smooth, golden sericeous when young; flowering twigs c. 3 mm thick. *Leaves* 2–3-jugate; rhachis 0.7–4.8 cm long, dorsally flattened, not winged, subsericeous, petiole 1.1–1.3 cm long; petiolules up to 0.8 cm long. *Leaflets* not subsessile, opposite, elliptic to obovate, 1.6–3.9 by 0.5–1.2 cm, index c. 3.3, slightly asymmetric, acroscopic side broader, very coriaceous, punctate; base attenuate; margin entire, revolute; apex obtuse, very apex rounded, not mucronulate; upper surface smooth, glabrous except for the puberulous midrib; lower surface different coloured, dull, papillate, shortly subsericeous, domatia a single sac on basiscopic side in axil of ± second nerve; venation raised; nerves 0.2–0.7 cm apart, marginally looped; veins densely reticulate, distinct. *Infructescences* axillary, not branching; rhachis somewhat flattened, 2.3–3.7 cm long, subsericeous. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts c. 2.2 mm long; bracteoles 1.3–1.6 mm long. *Pedicels* c. 4 mm long, sericeous; upper part c. 2 mm long, slightly less sericeous. *Flowers* unknown. *Sepals* 5, ovate, margin and outside sericeous, inside glabrous, glands along margin unknown; 2 outer smaller ones c. 2 by 1.8 mm; 3 inner larger ones c. 2.6 by 2.8 mm, margin petaloid. *Disc* incomplete. *Fruit* with 1–3 well-developed lobes, c. 0.9 cm high by 1.1–1.2 cm broad, smooth, glabrous, stipe c. 1.5 mm high, slender, angle between lobes c. 120°, blackish when dry; lobes c. 7 by 6 mm. *Seed* obovoid, c. 5 by 5 mm; hilum c. 1.2 mm long. *Embryo* c. 4.8 by 4 mm; cotyledons secondarily laterally besides each other, lower larger, apices elongated, that of upper straight, that of lower curved; radicle c. 1.1 mm long.

Distribution. Philippines (Luzon: Ilocos Norte Prov.).

Ecology. Dry slopes. Alt.: c. 700 m. Fruiting: Aug.

Vernacular name. Angset (Iloko).

Note. This species is similar to *Guioa myriadenia,* possibly even a synonym. Some differences still separate these two forms from each other and from *Guioa* *palawanica*. Future collections may eliminate the differences between *Guioa parvifoliola* and *Guioa myriadenia.*

	Guioa myriadenia	*Guioa parvifoliola*	*Guioa palawanica*
Leaflets	2.5–14.5 by 1–4.5 cm	1.6–3.9 by 0.5–1.2 cm	2.5–7.6 by 1–2.5 cm
Thickness of	thin (to thick)	thick	very thick leaflets
Apex of leaflets	(truncate to) acuminate (to cuspidate)	obtuse	obtuse to acuminate
Punctation	present	present	absent
Indumentum	long hairs sericeous to hirsute	short hairs sericeous	short hairs sericeous
Domatia	(1 sac or pocket to) many pockets	1 sac	absent or 1 sac
Inflorescence	densely sericeous to hirsute	subsericeous	sericeous

Specimens studied:
PHILIPPINES. Luzon: *BS (Ramos) 33187*, Ilocos Norte Prov., Mt. Nagapatan.

Guioa patentinervis Radlk. – Fig. 106 a–c.

Guioa patentinervis Radlk., Sapind. Holl.-Ind. (1879) 11, 40; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 610, 618; in Engl., Pflanzenr. 98 (1933) 1163. — Lectotype (here proposed): *De Vriese & Teijsmann s.n.*, s.d. (L, holo, sh. no. 908.269-483; iso in BO, K, L, M), Moluccas, Boeroe.

Guioa spec.: Merr., Philip. J. Sc. 11, Bot. (1916) 286. — *Guioa multipunctata* Radlk., Philip. J. Sc. 12, Bot. (1917) 83; in Engl., Pflanzenr. 98 (1933) 1163. — Type: *Robinson 1602* (M, holo), Moluccas, Ambon.

Treelet. *Branchlets*
mm thick. *Leaves* 2–5-jugate; rhachis 4.4–20 cm long, terete, not winged, glabrous, petiole 2.2–6.6 cm long. *Leaflets* subsessile, opposite to alternate, (ovate to) elliptic, 4.9–13.5 by 1.4–4.6 cm, index 2.4–3.8, slightly asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire (*Robinson 1602* subapically often with a tooth on either side of the margin), flat; apex acuminate to cuspidate, usually not mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous, domatia (absent to) a single (to many) sac(s) in axil of basiscopic ± second nerve (to in axils of all major nerves); venation flat on upper side, raised on lower; nerves 0.3–3 cm apart, marginally looped; veins laxly reticulate, rather distinct, especially below. *Inflorescences* axillary, branching in or near axil and along rhachis; latter terete to flattened, 1.6–8.2 cm long, sericeous; first order branches up to 3.1 cm long; cymules cincinnate, c. 3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.5–0.7 mm long; bracteoles 0.2–0.3 mm long. *Pedicels* 1.2–3.2 mm long, sericeous except for the subglabrous, 0.9–2 mm long upper part. *Flowers* c. 2 mm in diam. *Sepals* 5, ovate, margin pilose, outside and inside glabrous; 2 outer smaller

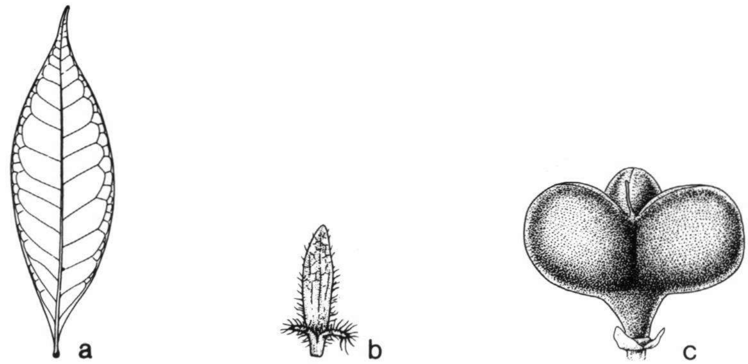


Fig. 106. *Guioa patentinervis* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a: *De Vogel 4210*, L; b: *Kornassi 863*, L; c: *De Vogel 4228*, L).

ones 0.8–1.9 by 0.8–1.3 mm, margin with few glands; 3 inner larger ones 1.3–2.5 by 1.3–1.9 mm, margin petaloid, without glands. *Petals* 5, very reduced, elliptic, 0.8–1.2 by 0.3–0.4 mm, claw 0.2–0.3 mm high, margin pilose, outside and inside glabrous, apex obtuse to acute; scales 0.3–0.4 mm long, free, apex very slender; crest absent. *Disc* complete. *Stamens* 8; filament 1–2.3 mm long, especially basally pilose; anther c. 0.3 mm long, glabrous. *Pistil:* ovary 0.2–0.7 mm high, smooth, subhirsute; style and stigma 0.1–0.7 mm long, elongating in fruit up to 1.5 mm, then upper c. 0.4 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 0.7–0.9 cm high by 0.7–1.3 cm broad, smooth to somewhat rugose-ruminate, glabrous, stipe c. 2 mm high, slender, angle between lobes 115–135°, blackish when dry; lobes 5–7 by 4.5–5.5 mm. *Seed* obovoid, 5–6.4 by 4–4.8 mm; hilum 0.7–1 mm long. *Embryo* 4.3–5.3 by 3.3–4 mm; cotyledons dorsoventrally above each other, usually equal in size, apices usually not elongated, sometimes upper elongated, straight; radicle 1–1.7 mm long.

Field notes. Treelet, 5–8 m high. Fruit red; seed green.

Distribution. Moluccas (Ambon, Buru, Ceram, Obi).

Ecology. Found on porous nickel soil and in transition from coral sand beach to nickel soil in open forest with very little undergrowth. Alt.: sea-level up to 300 m. Flowering: Jan.–April. Fruiting: Sept.–Nov.

Vernacular name. Obi: tofiri (Ternate).

Uses. Wood is used for the construction of houses.

Note. typical for this species are the reduced petals, as in *Guioa acutifolia* (from which it differs by the lack of papillae on the lower side of the leaflets) and the very small fruits. For the differences among *Guioa diplopetala*, *Guioa patentinervis*, and *Guioa hirsuta* see the note under the latter; see also note 2 under *Guioa venusta*.

Specimens studied:

MOLUCCAS. Ambon: *Kornassi 1171; Robinson 1602; Teijsmann s.n.* — Buru: *De Vriese & Teijsmann s.n.* — Ceram: *Kornassi 863.* — Obi: *De Vogel 4210, 4228.*

Guioa pauciflora Radlk. – Fig. 107 a, b.

Guioa pauciflora Radlk., Bot. Jahrb. 56 (1921) 279; Nova Guinea 11 (1926) 183; in Engl., Pflanzenr. 98 (1933) 1160. — T y p e: *Ledermann 9026* (B, holo, †; iso in K, SING), Papua New Guinea, Sepik, Etappe Mt.

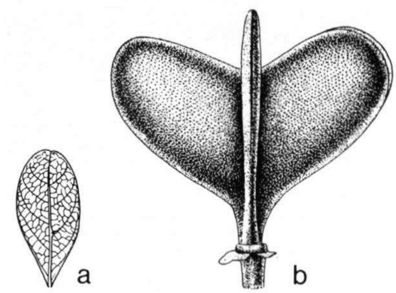


Fig. 107. *Guioa pauciflora* Radlk. a. Leaflet, × 0.5; b. fruit, × 3 (*NGF (Henty et al.) 41517*, L).

Shrub to tree. *Branchlets* terete, rough, sericeous, especially when young; flowering twigs c. 1.7 mm thick. *Leaves* 1-jugate; rhachis 0.2–1.3 cm long, terete, not to slightly winged, sericeous, petiole 0.2–1 cm long. *Leaflets* subsessile, opposite, elliptic to obovate, 1.1–6.3 by 0.5–2.6 cm, index 2.2–3.3, ± symmetric, coriaceous to very coriaceous, usually punctate; base attenuate; margin entire, flat to revolute; apex retuse to acuminate, sometimes mucronulate; upper surface smooth, glabrous, sometimes wax; lower surface differently coloured, dull, papillate, glabrous to very sparsely sericeous, domatia absent or a single small or large sac on basiscopic side in axil of second major nerve; venation raised on both sides; major nerves 0.2–1.1 cm apart, marginally looped; veins densely reticulate, very conspicuous, even the veinlets. *Inflorescences* axillary, not branching to branching in axil; rhachis terete, c. 3.9 cm long, sericeous; cymules cincinnate, 2-flowered. *Bracts* and *bracteoles* immature or caducous. *Pedicels* not yet full-grown. *Flowers* in bud. *Sepals* and *petals* 5, immature. *Disc* complete. *Stamens* 8, immature. *Pistil* not measured. *Fruit* with 2 or 3 well-developed lobes, 1.1–1.2 cm high by 1.1–1.2 cm broad, rugose, glabrous, stipe c. 3.5 mm high, rather broadly cuneate, edge of margin rounded, angle between lobes 75–90°, blackish when dry; dissepiments complete; lobes c. 8 by 5 mm. *Seeds* unknown.

F i e l d n o t e s. Shrub to tree, 3–25 m high; crown bushy, densely branched. Flowers whitish. Fruit dark brown when old and open.

D i s t r i b u t i o n. Irian Jaya (Snow Mts.); Papua New Guinea (W & E Sepik Prov.). A seemingly slightly disjunct distribution. However, the central area of New Guinea is very poorly collected.

E c o l o g y. Once recorded from limestone rocks on the crest of a steep slope. Presumably also found in cloud forest with many epiphytic mosses as the dried specimens are moss-covered. Alt.: 500–2500 m. Buds and young fruits: Oct.

N o t e. The three specimens studied are rather diverse: *Ledermann 9026* has acutely tipped leaflets, the others retuse ones; *Pulle 937* lacks a domatium, while the domatium is far larger in *NGF 41517* than in *Ledermann 9026*. Characters in common are the possession of 1-jugate leaves, papillate leaflets with a very typical venation pattern, and a complete disc. The fruits also look typical (rather small, broadly cuneate stipe, slender lobes). The diversity is presumably only apparent and due to the few collection trips ever made to high areas in central New Guinea.

S p e c i m e n s   s t u d i e d:

NEW GUINEA. Irian Jaya, Snow Mts. Dist.: *Pulle 937*, Mt. Hellwig. — Papua New Guinea: W Sepik Prov.: *NGF (Henty et al.) 41517*, Oksapmin. — E Sepik Prov.: *Ledermann 9026*, Kaiserin Augusta Fluss = Sepik River.

Guioa pectinata Radlk. – Fig. 108a–d.

Guioa pectinata Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 614; Guillaumin, Bull. Soc. Bot. Fr. 79 (1932) 337; Radlk. in Engl., Pflanzenr. 98 (1933) 1172; Guillaumin, Fl. Nouv.-Caléd. (1948) 199; Mém. Mus. Nat. Hist. Nat. B, 15 (1967) 111; Morat et al., Bull. Mus. Nat. Hist. Nat. 4e sér., 8, B (1986) 174. — L e c t o - t y p e (here proposed): *Balansa 3306* (P), New Caledonia, Mt. Poume.

Shrub to treelet. *Branchlets* terete, smooth, sericeous when young; flowering twigs 1.5–3 mm thick. *Leaves* 1–3-jugate; rhachis 0.4–5.6 cm long, slightly flattened, especially upwards, not winged, glabrous, petiole 0.4–3.3 cm long. *Leaflets* opposite to subopposite, (ovate to) elliptic, 2–8.6 by 0.7–3.1 cm, index 2.4–3.9, ± symmetric, very coriaceous, punctate, usually finely wrinkeled when dry; base attenuate; margin entire, (flat to) revolute; apex (rounded to) obtuse, not mucronulate; upper surface smooth, glabrous, often with wax; lower surface differently coloured, more dull, smooth, wrinkled when dry, glabrous, domatia (absent or) single sac on basiscopic side in axil of second nerve; venation on upper surface flat to raised, raised on lower surface; nerves 0.2–1.3 cm apart, marginally looped; veins laxly reticu-

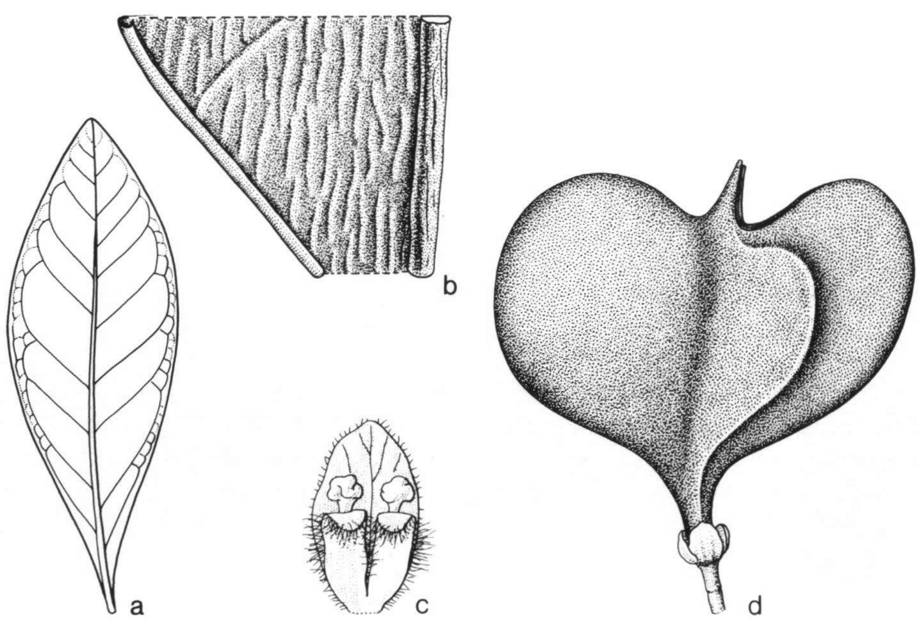


Fig. 108. *Guioa pectinata* Radlk. a. Leaflet, × 1; b. lower surface of leaflet, finely wrinkled when dry, × 12.5; c. petal, × 12.5; d. fruit, × 3 (a–c: *Thibaut s.n.*, VIII-1869, P; d: *Vieillard 2408*, K).

late, rather inconspicuous. *Inflorescences* axillary, branching in or near axil and racemosely along rhachis too; rhachis flattened, 0.7–9 cm long, subsericeous; first order branches up to 2.3 cm long; cymules cincinnate (to seldom dichasial), 2- or 3(–5)-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.8–1.2 mm long; bracteoles 0.3–1 mm long. *Pedicels* 3–6.3 mm long, (subsericeous to) sericeous, also the 1.5–2.8 mm long upper part. *Flowers* 4–4.5 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside subsericeous; 2 outer smaller ones 1.2–2.2 by 1.6–2.2 mm; 3 inner larger ones 2.2–3.3 by 2.2–3.2 mm, margin petaloid. *Petals* (4 or) 5, elliptic, 2.4–3.5 by 1.2–2.1 mm, claw 0.1–0.3 mm high, margin pilose, outside and inside subglabrous, apex retuse to obtuse; scales 1.2–1.9 mm long, free, basally not auricled; crest clavate, lobed, shortly stiped. *Disc* incomplete. *Stamens* 8; filament 1.9–3.5 mm long, especially basically pilose; anther 0.5–0.8 mm long, pilose. *Pistil:* ovary 0.3–3 mm high, smooth, sparsely hirsute; stigma 0.3–2 mm high, both elongating up to 5 mm in fruit, then upper c. 0.5 mm stigmatic. *Fruit* with 1 or 2 well-developed lobes, c. 1.6 cm high by 1.6–1.9 cm broad, smooth, glabrous, stipe c. 3.5 mm high, slender, wall c. 1 mm thick, edge of margin rounded, upper margin more or less flat, parallel to lower, angle between lobes c. 135°, blackish when dry; dissepiments complete; lobes c. 12 by 11 mm. *Seed* and *embryo* immature.

Field notes. Shrub to treelet, 0.5–2 m high. Leaflets shiny dark green above, light green below. Buds light green. Flowers white.

Distribution. NW New Caledonia.

Ecology. In dense forest, gallery forest, secondary forest, and on savannah. Indifferent to substrates: found on ultrabasic (serpentine), vulcanic soil, alluvial, schist. Alt.: 20–450 m. (Partly after Morat et al., 1986.) Flowering: May–Sept.

Note. For the differences among *Guioa pectinata, Guioa fusca,* and *Guioa gracilis* see note under *Guioa fusca.*

Specimens studied:
New Caledonia: 20 specimens.

Guioa pleuropteris (Blume) Radlk. – Fig. 109a–c, 110a–f.

Guioa pleuropteris (Blume) Radlk., Sapind. Holl.-Ind. (1879) 10; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 520, 610; Stapf, Trans. Linn. Soc. Bot. 4 (1894) 119, 142; King, J. As. Soc. Beng. 65, II (1896) 444; Ridley, J. Str. Br. R. As. Soc. 33 (1900) 66; Radlk. in Perk., Fragm. Fl. Philip. 1 (1904) 63; de Clercq, Nieuw Plantk. Woordenb. (1909) 251; Lec., Fl. Gén. I.-C. 1 (1912) 1024, fig. 127: 1–6; Radlk., Philip. J. Sc. 8, Bot. (1913) 446; Bot. Jahrb. 49 (1913) 370; Merr., En. Born. (1921) 361; Ridley, Fl. Mal. Pen. 1 (1922) 505; Merr., En. Philip. 2 (1923) 508; Craib, Fl. Siam. En. 1 (1926) 332; Heyne, Nutt. Pl. ed. 2, 1 (1927) 1000; Steen., Bull. Jard. Bot. Btzg. III, 12 (1931) 172, 187, 189; Radlk. in Engl., Pflanzenr. 98 (1933) 1164; Corner, Gard. Bull. Str. Settl. 10 (1939) 45; Ways. Trees (1940) 588, fig. 211, 212; Masamune, En. Phan. Born. (1942) 426; Gagnep., Fl. Gén. I.-C. Suppl. 1 (1950) 981, fig. 124: 17–26; Salvosa, Lex. Philip. Pl. (1963) 105; Burk., Dict. ed. 2, 1 (1966) 1134; W. Meijer, Bot. News Bull. 9 (1967) 74; Brünig, Heidewald Sarawak Brunei (1968) 373; Martin, Introd. Ethnobot. Cambodge (1971) 90; Corner, Gard. Bull. Suppl. 1 (1978) 153; Gard. Bull. Sing. 38 (1985) 19. — *Cupania pleuropteris* Blume, Rumphia 3 (1847) 158; Walp., Ann. 2 (1851/2) 214; Hiern in Hook. f., Fl. Br. Ind. 1 (1875) 677;

F.-Vill., Nov. App. (1880) 51, p.p.; (1883) 349; Filet, Plantk. Woordenb. ed. 2 (1888) 135, nr. 3354; Ridley, Trans. Linn. Soc. Bot. 3 (1893) 289. — Lectotype (here proposed): *Korthals s.n.*, s.d. (L, holo, sh. no. 908.269-765; iso in L, W), Borneo, Banger, Maping.

Cupania pleuropteris var. *apiculata* Hiern in Hook. f., Fl. Br. Ind. 1 (1875) 677. — *Cupania griffithiana* Kurz, J. As. Soc. Beng. 44, II (1876) 188. — *Guioa pleuropteris* f. *apiculata* Radlk. in Schmidt, Bot. Tidsskr. 32 (1915) 315. — Lectotype (here proposed): *Maingay 442* (BM, holo; iso in A, K, L), Malaya. See note 2.

Guioa aptera Radlk. in Perk., Fragm. Fl. Philip. 1 (1904) 62; Merr., Philip. J. Sc. 1, Suppl. (1906) 87; Radlk., Philip. J. Sc. 8, Bot. (1913) 446; Merr., En. Philip. 2 (1923) 506; Radlk. in Engl., Pflanzenr. 98 (1933) 1166; Salvosa, Lex. Philip. Pl. (1963) 104. — Syntypes: Philippines: *Warburg 11504* (n.v.), Cagayan Prov., Lailo; *Warburg 13108* (n.v.), Luzon, Tayabas Prov., Sampaloc.

Guioa lasiothyrsa Radlk. in Perk., Fragm. Fl. Philip. 1 (1904) 63; Merr., Philip. J. Sc. 1, Suppl. (1906) 87; Radlk., Philip. J. Sc. 8, Bot. (1913) 446; Merr., En. Philip. 2 (1923) 508; Sasaki, Cat. Gov. Herb. (1930) 327; Radlk. in Engl., Pflanzenr. 98 (1933) 1166; Salvosa, Lex. Philip. Pl. (1963) 105. — Type: *Merrill 852* (PNH, holo, †; iso in A, K, NY, SING), Philippines, Paragua I. (= Palawan), San Antonio Bay.

Guioa subapiculata Radlk. in Perk., Fragm. Fl. Philip. 1 (1904) 64; Philip. J. Sc. 8, Bot. (1913) 446; Merr., En. Philip. 2 (1923) 506; Radlk. in Engl., Pflanzenr. 98 (1933) 1166; Salvosa, Lex. Philip. Pl. (1963) 105. — Type: *Merrill 513* (PNH, holo, †; iso in A, K, NY), Philippines, Culion I.

Guioa lasiothyrsa Radlk. f. *elmeri* Radlk., Elmer Leafl. Philip. Bot. 5 (1913) 1609. — Syntypes: Philippines, Luzon: *Elmer 9315* (BM, F, FI, L, K, M, W), Tayabas Prov., Lubcan; *Elmer 9342* (A, BM, BO, FI, M, NY, W), Laguna Prov., Los Baños.

Guioa forbesii Bak. f., J. Bot. 62, Suppl. (1924) 26. — Type: *Forbes 2617* (BM, holo; iso in FI, L, P), Sumatra, R. Goerga, Lampar, Palembang.

Shrub (or woody vine) or tree(let). *Branchlets* terete, smooth (to somewhat ribbed to rough), especially hirsute (to sericeous) when young; flowering twigs 1–6 mm thick. *Leaves* (1–)2–5(–7)-jugate; rhachis 0.8–25.3 cm long, (terete to) upwards flattened, usually (slightly) winged, wing up to 3 mm broad, sericeous to hirsute, petiole 0.6–9.3 cm long. *Leaflets* usually subsessile, opposite to alternate, lower often ovate, upper (elliptic to) obovate, 0.9–18.7 by 0.5–8.3 cm, index 0.5–4.3, asymmetric, especially the base and the apex, acroscopic side broader, (sub)coriaceous, usually punctate; base (acute to cuneate to) attenuate; margin entire (except juvenile leaflets with a few teeth), flat (to revolute); apex (obtuse to) usually abruptly acuminate (to cuspidate), often mucronulate; upper surface smooth, (glabrous to) sparsely sericeous to hirsute; lower surface differently coloured, dull, papillate, (sub)sericeous to usually hirsute (see note 5), domatia many pockets (or sometimes sacs) in axils of nerves, raised; venation on upper surface (slightly sunken to) flat to raised, usually not differently coloured from lamina, below raised; midrib below raised, convex; nerves 0.2–4.9 cm apart, marginally looped, but less distinctly so in lower half of leaflets; veins laxly reticulate, usually distinct. *Inflorescences* axillary to seldom pseudoterminal, (not branching to) branching in or near axil and especially along the rhachis; latter terete, 0.5–21.6 cm long, usually brown hirsute; first order branches up to 13.8 cm long; cymules cincinnate, 2–5-flowered. *Bracts* and *bracteoles* (deltoid to) triangular, outside sericeous, inside (sub)glabrous; bracts 0.7–3.8 mm long; bracteoles 0.2–1.5 mm long. *Pedicels* 1.1–7 mm long, completely hirsute, upper part 0.3–3.4 mm long. *Flowers* 3–4.2 mm in diam.

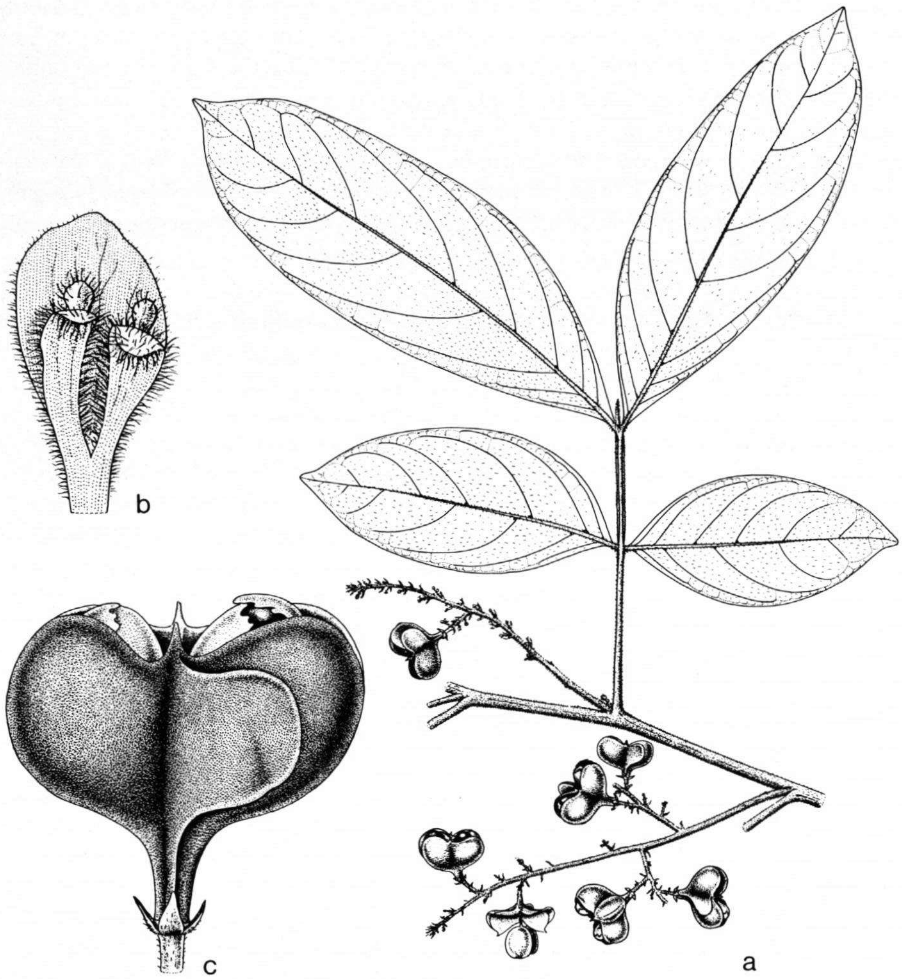


Fig. 109. *Guioa pleuropteris* (Blume) Radlk. a. Habit, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *Davidson 1525*, L; b: *Maxwell 81-34*, L).

Sepals 5, ovate, margin and less so outside pilose, margin with glands, inside (sub)-glabrous; 2 outer smaller ones 0.7–2.8 by 0.6–2 mm; 3 inner larger ones 1.5–3.5 by 0.9–3.3 mm, margin petaloid. *Petals* 5, (elliptic to) obovate, 1.3–3.5 by 0.7–2.2 mm, blade obovate, gradually decurrent into the claw, latter 0.2–1 mm high, margin and sometimes outside pilose, inside glabrous, apex rounded (to acute); scales 0.8–2.2 mm long, free, apex not to hardly broadened; crest usually developed, present as a pilose flat part of the bifid scale apex. *Disc* usually incomplete (gap often small), sometimes complete. *Stamens* 8; filament 1.3–5.1 mm long, especially basally pilose; anther 0.2–0.7 mm long, glabrous. *Pistil:* ovary 0.3–2.8 mm long, smooth, subhirsute; style and stigma 0.1–2.2 mm long, elongating in fruit up to 4 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1–1.9 cm high by 1–2.5 cm broad, smooth to somewhat ribbed to somewhat rugose-ruminate, glabrous, stipe 2–5 mm high, slender, angle between lobes 95–180°, reddish (to blackish) when dry; lobes 7.5–13 by 6.5–13 mm. *Seed* globose to obovoid, 5.5–9.7 by 5–8 mm; hilum 1–3 mm long. *Embryo* 3.3–9 by 3.3–7 mm; cotyledons secondarily laterally besides each other, upper larger, apices usually elongated, that of upper straight, that of lower recurved; radicle 1.5–5 mm long.

Field notes. Shrub, woody vine, or usually a tree, 0.3–30 m high, d.b.h. 5–60 cm; no buttresses. Outer bark variable, smooth to sometimes irregularly fluted, usually dark brown, often mottled with white or grey spots, also greenish to reddish to blackish, soft to hard, c. 0.15 cm thick; inner bark white to yellow to pink to red to dark brown to grey, finely fibrous, c. 0.5 cm thick. Cambium yellow to brown. Sapwood finely grained, soft to hard, white to yellow, without odour or sap. Leaves dark glossy green above, pale glaucous to greyish beneath. Inflorescence green. Buds greyish. Flowers fragrant. Sepals green with red outer surface to white. Petals white to yellow. Filaments white; anthers pink. Pistil green. Fruit red to bluish red. Aril yellow to orange, edible, sour. Seed dark brown, pendulous, edible.

Distribution. Burma, Cambodia (Kampot), Vietnam (Poulo-Condor, Hatien), Thailand, E coast of Malaya, Sumatra, Borneo, Philippines.

Ecology. (Rare to) very common, scattered in lower to middle storey of primary forest, on flat to hilly to mountainous land, on dry to periodically flooded soils (e.g. swamps). Found in primary and especially secondary forest; edge of forests, of plantations; in open landscapes like cultivated land and belukar; in mossy forest; along riverbanks, roads, sea. Vegetation types on Pulau Sekindan (Corner, 1985): *Terminalia–Barringtonia* and *Eugenia grandis* formations. Soil: sandstone, brown stony soil, yellow sandy loam, black sand, ultrabasic alluvial deposits. Alt.: sea-level up to 1800 m. Flowering: Aug.–March(–May); Philippines: Dec.–May. Fruiting: throughout the whole year, with an emphasis on Febr.–April.

Vernacular names. Cambodia: phnum, pongro phnum. Thai: mai som ling, têt ling, tob tab. Malay Peninsula: kelenti nyamok (in common with *Decaspermum*), kelenti nyamok laut, medang puteh (white laurel), pena-pena, penyamok, pokok serawan burang, sugi damar (Kelantan) (Malay); sempayan ular (in common with *Ostodes*; Malay, Selatar) (After Corner, 1940; Burkill, 1966). Sumatra: djelamajam, kadjumpi (Malay); kaju lulup, kaju lentadah (Malay, Palembang). Borneo: Sabah: piri manok, saasa, tingir manok (Bajau); munggulan/gulambir ayam, tanking manok, tarik kakang (Brunei); andipatan, tanggianuk (Dusun); mata pait (Dusun Banggi); gurujod, kanawit, pengkul (D. Kinabatangan); tanggianuk, tanjianuk, tongianuk (D. Kinarut: chicken flesh); kejangan (G. Kundasan); kangi ranok (D. Tambunan); kaju wey, rutan berangat (Kelabit); pelir kambing; Kalimantan Selatan: tapanggang gunung. Philippines: mandidag (Agta); dayendingan (Bisaya); iwah (Ifugao); imug, pamatuten, panagisen (Ikabanag); malasanto (Palawan); hamog-hamog (P.W.S.); salisi (Subanun); tibau (Samal); bunsikag, salab (Sulu, Tagbanua); bunsikag-buhukan (Filipino); malasikag (Spanish-Tagbanua) (Salvosa, 1963).

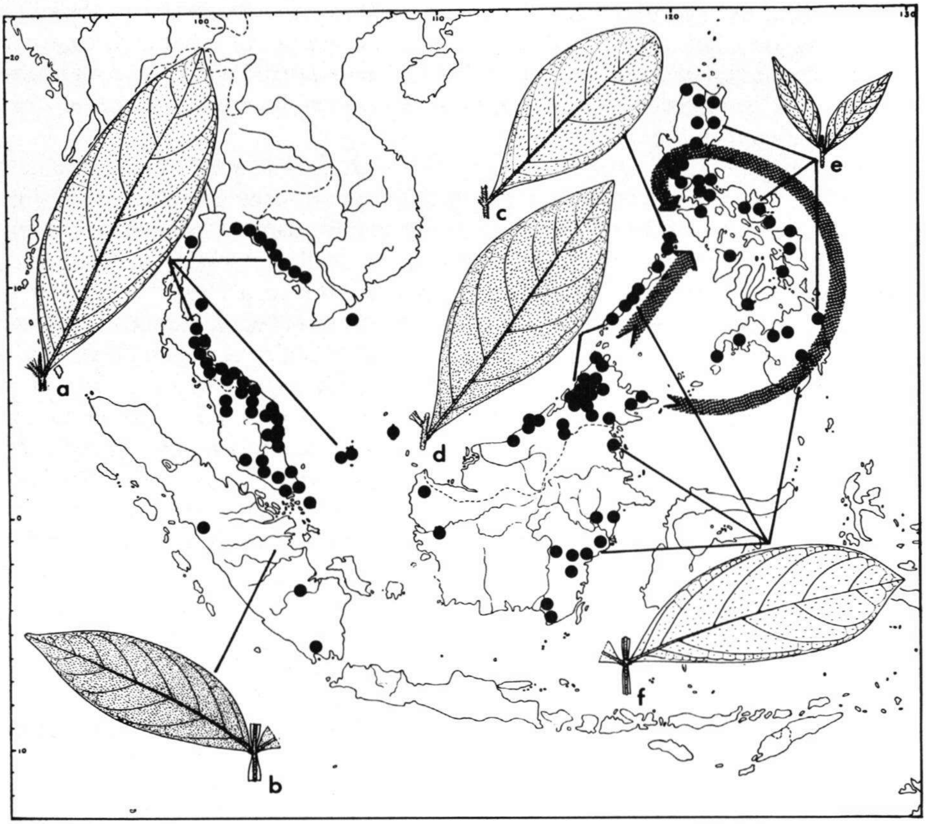


Fig. 110. Distribution of *Guioa pleuropteris* (Blume) Radlk.; two transformation series of leaflets are shown (all leaflets × 0.5). – a. *Guioa pleuropteris* form (*Davidson 1325*, L); b. *'Guioa forbesii'* form (*Forbes 2617*, L); c. *'Guioa subapiculata'* form (*Merrill 513*, K); d. *'Guioa lasiothyrsa'* form (*Elmer 10880*, L); e. *'Guioa aptera'* form (*Elmer 9315*, L); f. *Guioa pleuropteris* form (*Van Niel 4263*, L).

U s e s. Wood is used for torches (Radlkofer, 1913); wood is durable and elastic, but thin, therefore used in Indonesia as handles for axes and shafts of wagons and plows (Heyne, 1927). Medically the roots are used in NE Pahang (Malaysia) in the form of a decoction against fever and stomach ache. The name pokok serawan burang probably refers to a medical use as 'serawan' = sprue (Burkill, 1966). Also used to exterminate intestinal worms.

N o t e s. 1. *Guioa pleuropteris* is a rather variable species. The character to which it owns its name can be absent. The leaflets usually are obovate with a sharply decurrent short apex (see leaflet a and f on fig. 110), but if the latter elongates the shape becomes more elliptic, as is found in forms from Sumatra, N Borneo and the Philippines. The indumentum on the lower surface of the leaflets is usually dense, seldom sparse, it varies from usually velutinous to occasionally sericeous; the hairs are usually long, but can be short too. The domatia are pockets, but an occasional pocket-like sac is found too. The normal form of leaflet, found on the SE Asia mainland, most of Borneo and SE Philippines, is represented by the leaflets a and f on the distribution map (fig. 110).

The Philippines have several distinct forms which unfortunately are not separable as species. Two clines can be found in the Philippines (see arrows on map, fig. 110). One cline ranges from Palawan to Culion and Busuanga I. (Calamian group). On Palawan the leaflets can be rather large and are usually densely velutinous on the lower surface. On the other two islands the size of the leaflets decreases dramatically, but they still remain very velutinous. The latter form has been described as *Guioa subapiculata* (leaflet c). The forms on Palawan are described as *Guioa pleuropteris* (leaflet a, f) and the wingless specimens as *Guioa lasiothyrsa* (leaflet d). The other cline is found from Borneo over Mindanao to Panay, Negros, Leyte, Samar to Luzon and in the end to Mindoro. On Mindanao the situation is rather complex, the rather large-leaved form of Palawan is found, together with a somewhat smaller form of the 'typical' *Guioa pleuropteris* (leaflet a and f) and a third form which was described as *Guioa aptera* or *Guioa lasiothyrsa* f. *elmeri* (leaflet e). This latter form is mainly found on Luzon, it has very asymmetric, small leaflets, with on the lower surface often (few) sericeous hairs and sometimes (partly) sacs instead of pockets. All intermediates among these forms are found. Morley & Flenley (in T.C. Whitmore: Biogeograpical evolution of the Malay Archipelago, 1987, 50–59, Oxford) show in a palaeogeographical reconstruction of the Sunda-Sahul region during the middle Pleistocene that a continuous landmass existed from N Borneo to Palawan and the Calamian group; this land mass is covered by one of the two clines, and they show that a landmass existed from NE Borneo over Mindanao up to Luzon and Mindoro, occupied by the other cline. Probably the clines display dispersal accompanied by phenological change.

In Kalimantan Timur (Borneo) some specimens rather look like *Guioa pterorhachis*, see note under the latter.

Sumatra has very uniform specimens; all leaflets are elliptic (instead of obovate), rather small, and densely velutinous below. They were described as *Guioa forbesii* (leaflet b).

2. Kurz newly named *Cupania griffithiana*; he mentioned the specimen *Helfer 983* (here attributed to *Guioa diplopetala*). However, a description is not provided, only a reference to a description of *Cupania pleuropteris* by Hiern is given. Article 7.16 of the I.C.B.N. obliges one to typify *Cupania griffithiana* with a specimen mentioned by Hiern, irrespective of the fact that Hiern described a fully different species than Kurz had in mind. Consequently *Cupania griffithiana* is now lectotypified with *Maingay 442*, and has become a synonym of *Guioa pleuropteris* instead of *Guioa diplopetala*. Hiern mentioned two varieties, the a variety *bijuga* and the b variety *apiculata*. The most obvious choice for lectotypification would have been *Wallich 8094*, the type of the a variety, instead of *Maingay 442*, the type of the b variety. This choice would have resulted in the rejection of the epithet *bijuga*, which is commonly used, as *griffithiana* is older on the species level. However, both varieties are

based on Malaysian specimens, leaving out the Indonesian ones, on which the species *Cupania pleuropteris* has been based by Blume. The latter specimens should be regarded as a third variety (var. *pleuropteris*), the official 'a' variety. Therefore, it does not matter with which of the two varieties of Hiern *Cupania griffithiana* is lectotypified. Moreover, the choice here presented is in accordance with the meaning of the Code: stability of names, as the epithet *bijuga* remains to be used.

3. Merrill suggested that *Sapindus guisian* Blco is synonymous with *Guioa pleuropteris*. The full synonymy of *Sapindus guisian* is as follows:

Sapindus saponaria auct. non L.: Blco, Fl. Filip. (1837) 288. — *Sapindus guisian* Blco, Fl. Filip. ed. 2 (1845) 201. — *Erioglossum cuneifolium* Blume, Rumphia 3 (1847) 118, nom. illeg. (I.C.B.N. art. 63.1). — *Dittelasma rarak* auct. non Hiern: F.-Vill., Nov. App. (1880) 41. — *Guioa pleuropteris* auct. non Radlk.: Merr., Sp. Blanc. (1918) 241. — *Erioglossum rubiginosum* auct. non Blume: Radlk. in Engl., Pflanzenr. 98 (1932) 695, p.p. — Type: not indicated, lost.

The identification of Blanco's species is notorious, even for himself, as he later on discovered that his *Sapindus saponaria* was a different species from the one Linnaeus had described (resulting in *Sapindus guisian*). Blume was two years too late to rectify Blanco's error.

Merrill suggested that *Sapindus guisian* might be *Guioa pleuropteris*; however, the following points from the original description by Blanco are contrary to *Guioa pleuropteris*: inflorescence terminal; petals 4, occasionally 5, with one scale; filaments on one side within the corolla; disc intrastaminal, 4-lobed; style 2- or 3-lobed, becoming patent (in *Guioa pleuropteris* resp.: inflorescence axillary to seldom pseudoterminal; petals 5, with 2 scales; filaments circular around ovary, free; disc extrastaminal, incomplete, 5-lobed; style entire). The conclusion is that *Sapindus guisian* cannot be interpreted as a synonym of *Guioa pleuropteris*. One remark about the intrastaminal disc: this character is never found in the Sapindaceae, the disc should be extrastaminal. A wrong observation can lead to this error, as it is difficult to see the position of the stamens in very asymmetric flowers (Blanco describes the stamens to be on one side of the flower, with the ovary in the middle of them; the ovary is always in the middle of the disc, so this must be another wrong observation).

Radlkofer's suggestion to place *Sapindus guisian* in *Erioglossum rubiginosum* (now *Lepisanthes rubiginosa*) has already been excluded by Leenhouts (Blumea 17, 1969, 88, under *Erioglossum cuneifolium*).

The synoptic key to the plant families of Hansen & Rahn (Punch Card system; Dansk Bot. Archiv 26, 1969, 1–46) as computerized by Duncan & Meacham (MEKA; Taxon 35, 1986, 492–494) leads directly to Sapindaceae, when the following characters are used: Leaves alternate, pinnately compound, venation pinnate; Inflorescence compound (thyrse); Flowers bisexual, zygomorphic, receptacle small (ovary superior); Disc present; Sepals 5; Petals 4, 5, with scale; Anthers 8; Ovary 3-locular. The identification within the Sapindaceae still is (and hopefully will remain) unsolved.

4. For the difference between the '*Guioa lasiothyrsa*' form of *Guioa pleuropteris* and *Guioa myriadenia* see note 4 under the latter.

5. The character combination disc complete and leaflets with a (sub)sericeous lower surface does not occur.

Specimens studied:
CAMBODIA: 9 specimens. — VIETNAM: 8 specimens. — THAILAND: 31 specimens. — MALAY PENINSULA: 56 specimens. — SUMATRA: 14 specimens. — BORNEO: 140 specimens. — PHILIPPINES: 91 specimens.

Guioa plurinervis Radlk. — Fig. 111a–c.

Guioa plurinervis Radlk. in E. & P., Nat. Pflanzenfam. 3, 5 (1895) 346; Bot. Jahrb. 56 (1921) 280 (typification); in Engl., Pflanzenr. 98 (1933) 1169. — Type: *MacGregor s.n.*, 1890 (M, holo; iso in MEL), E Papua New Guinea, Rossel I.

Treelet. *Branchlets* terete, smooth, sericeous when young; flowering twigs 3.5–5 mm thick. *Leaves* 2–5-jugate; rhachis 4.3–15.2 cm long, somewhat flattened above, not winged, sericeous, petiole 3–6.1 cm long; petiolules up to 1 cm long. *Leaflets* not subsessile, opposite to alternate, ovate, falcate, 5.9–13.2 by 1.5–3.3 cm, index 3.6–4.4, asymmetric, acroscopic side broader, coriaceous to very coriaceous, not punctate; base attenuate; margin entire, flat; apex cuspidate to caudate, mucronulate; upper surface smooth, glabrous except for the puberulous midrib; lower surface differently coloured, dull, papillate, shortly sericeous, domatia absent to a single or two pocket(s), especially on basiscopic side in axil of second major nerve; venation flat above, raised below; nerves 0.2–1.3 cm apart, marginally looped; veins laxly reticulate, indistinct. *Inflorescences* axillary to pseudoterminal, branching along rhachis only; rhachis flattened to terete, 3.1–15 cm long, sericeous; first order branches up to 4.8 cm long; cymules cincinnate, c. 4-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.9–1.1 mm long; bracteoles 0.5–0.6 mm

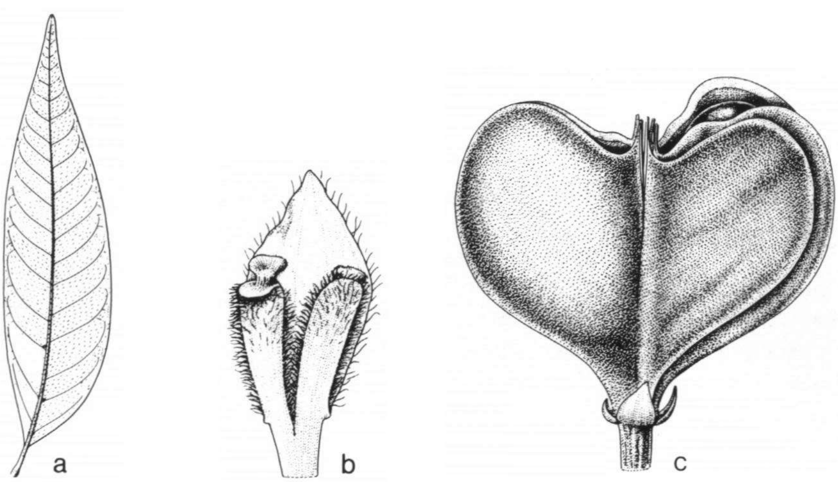


Fig. 111. *Guioa plurinervis* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *Brass 28291*, L; b: *MacGregor MEL 31978*, M).

long. *Pedicels* 2.5–3 mm long, sericeous except for the (sub)glabrous 0.7–2 mm long upper part. *Flowers* c. 3 mm in diam. *Sepals* 5, ovate, margin and sometimes outside pilose, margin with glands, inside glabrous; 2 outer smaller ones 0.9–1.2 by 1–1.3 mm; 3 inner larger ones 1.8–2.7 by 1.5–2.5 mm, margin petaloid. *Petals* 5, elliptic, 3–3.2 by 1.2–1.5 mm, claw c. 0.5 mm high, margin pilose, outside and inside glabrous, apex acute; scales 1.7–1.8 mm long, free; crest clavate, stiped, glabrous. *Disc* incomplete. *Stamens* 8; filament c. 4.2 mm long, completely but especially basally pilose; anther c. 0.7 mm long, pilose. *Pistil:* ovary c. 0.6 mm long, smooth, subhirsute; style and stigma c. 0.4 mm long, elongating in fruit up to 2 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1–1.4 by 1–1.7 cm, slightly ribbed, glabrous, stipe c. 2 mm high, broadly cuneate, indistinct, edge of margin rounded, angle between lobes 90–135°, blackish when dry; dissepiments complete; lobes 8–9 by 7–9 mm. *Seed* obovoid, c. 9 by 6 mm; hilum c. 1.2 mm long. *Embryo* c. 7.2 by 4.5 mm; cotyledons dorsoventrally above each other, upper larger, apex of upper elongated, straight; radicle c. 2.3 mm long.

Field notes. Treelet, 5–12 m high, d.b.h. c. 8 cm; bole c. 2 m high. Outer bark black; middle bark green; inner bark pinkish brown. Sapwood cream; heartwood reddish brown. Leaves greyish green; bluish green below. Fruit red.

Distribution. Papua New Guinea (Milne Bay Prov.: Rossel I.).

Ecology. Hill forest and secondary rain forest. Alt.: 10–50 m. Flowering: July. Fruiting: Oct.

Notes. 1. *LAE (Patik et al.) 70969* differs somewhat from the other specimens; the leaflets have less major veins, lack domatia, and are not typically greyish brown when dry; however, the field notes indicate that the living material possessed a bluish green lower surface of the leaflets.

2. *Guioa plurinervis* belongs to the *Guioa rigidiuscula*-complex. *Guioa plurinervis*, together with *Guioa misimaensis* and *Guioa novobritannica*, are the only species within the complex with a papillate lower surface of the leaflets. The differences between the species of this complex are discussed in chapter 9.

Guioa	*rigidiuscula*-complex	*misimaensis*	*plurinervis*	*subsericea*
Leaflets				
asymmetric	–	–	+	+
papillate	–	+	+	+
sericeous	–	+	+	+
Inflorescence very pilose	–	–	+	+
Petal type *Guioa rigidiuscula*	+	+	+	–
Disc complete	–(–+)	–	–	+
Stipe fruit broadly cuneate	–	?	+	+

3. *Guioa plurinervis* and *Guioa misimaensis* are intermediate between *Guioa subsericea* and the *Guioa rigidiuscula*-complex. Characters in common with *Guioa subsericea* are the papillate sericeous leaflets and the broadly cuneate stipe of the fruit. More typical for the *Guioa rigidiuscula*-complex are the type of petal and the incom-

plete disc. *Guioa plurinervis* differs from *Guioa misimaensis* in the shape of the leaflets, those of *Guioa plurinervis* are relatively narrower and asymmetric, and *Guioa plurinervis* is more densely pilose, especially the young parts and the inflorescence. See the table on the preceding page.

Specimens studied:
PAPUA NEW GUINEA. Milne Bay Prov., Rossel I.: *Brass 28291; LAE (Patik et al.) 70969; McGregor s.n.*, 10-VII-1890 (M, MEL sh. no. 31978).

Guioa pseudoamabilis Welzen – Fig. 112a–d.

Guioa pseudoamabilis Welzen, Blumea 33 (1988) 419, pl. 13a–d. — Type: *Vinas & Bellamy 261* (L, holo; iso in A, CBG, K, LAE, UPNG, WEI), Papua New Guinea, Morobe Prov., 14 km E of Bulolo, Mt. Missim. N.B.: isotypes can be found under *Rapanea vaccinioides* (Myrsinaceae).
Guioa venusta auct. non Radlk.: Hartley et al., Lloydia 36 (1973) 270; Streimann, Pl. Upper Watut Watershed (1983) 169.

Shrub to tree. *Branchlets* terete, smooth to usually slightly rough, sericeous to somewhat hirsute, especially when young; flowering twigs 1–4 mm thick. *Leaves* (1–)4–6-jugate; rhachis 1.5–12 cm long, terete, winged, wing up to 1 mm broad,

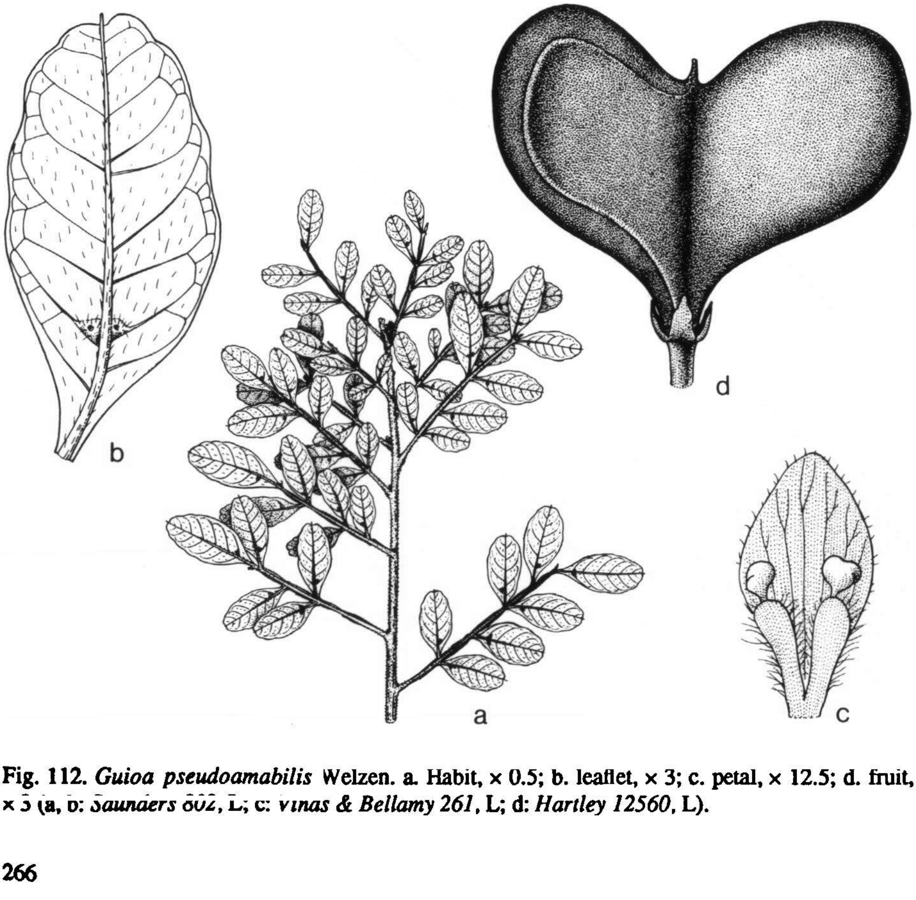


Fig. 112. *Guioa pseudoamabilis* Welzen. a. Habit, × 0.5; b. leaflet, × 3; c. petal, × 12.5; d. fruit, × 3 (a, b: *Saunders 602*, L; c: *Vinas & Bellamy 261*, L; d: *Hartley 12560*, L).

subglabrous to sericeous, petiole 0.6–2.2 cm long. *Leaflets* subsessile, opposite to alternate, ovate to obovate, 0.8–4.3 by 0.5–2 cm, index 1–2.9, asymmetric, acroscopic side broader, subcoriaceous, punctate; base attenuate; margin entire or usually slightly crenate, flat when crenate to revolute when entire; apex retuse to obtuse (to acute), mucronulate; upper surface smooth, sometimes pilose, especially the midrib; lower surface differently coloured, duller, smooth, no papillae, usually sericeous, domatia in at least some leaflets one to several large, hirsute sac(s) in axils of major nerves in especially lower part of leaflets; venation on upper side flat to slightly raised, raised on lower; major nerves 0.1–0.6 cm apart, marginally looped; veins densely reticulate, very inconspicuous. *Inflorescences* axillary to pseudoterminal, not branching to branching along rhachis; latter terete, 2.5–8 cm long, sericeous; first order branches up to 3.1 cm long; cymules cincinnate, c. 2-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.4–1.5 mm long; bracteoles 0.3–0.7 mm long. *Pedicels* 3.3–6 mm long, sericeous; upper part usually less pilose, 1.7–3 mm long. *Flowers* c. 4 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1.1–1.8 by 1–2 mm; 3 inner larger ones 1.9–3.2 by 1.9–2.6 mm. *Petals* 5, elliptic, c. 3.4 by 1.2 mm, claw c. 0.5 mm long, margin pilose, outside and inside glabrous, apex acute; scales c. 0.7 mm long, free; crest stiped, clavate, apex lobed. *Disc* complete. *Stamens* only seen in bud, 8; filament completely but especially basally pilose; anther glabrous. *Pistil* only seen in bud; ovary smooth, subhirsute; style and stigma elongating in fruit up to 2.5 mm long, then upper 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.1–2 cm high by 1.7–1.9 cm broad, smooth (to slightly ribbed), glabrous, stipe 2–3 mm high, rather broadly cuneate, edges of margin rounded, angle between lobes 90–165°, blackish when dry; dissepiments complete; lobes 10–12 by 6–10 mm. *Seed* globose to obovoid, 7–9 by 6–7 mm; hilum 1.8–2.9 mm long. *Embryo* 5.8–6 by c. 5 mm; cotyledons dorsoventrally above each other, inequal, either upper or lower larger, apex of upper slightly elongated, straight; radicle 1.2–2 mm long.

Field notes. Shrub to tree, 2–27 m high, d.b.h. 1–30 cm; bole up to 13 m high, straight, no buttresses. Bark red to brown, smooth; inner bark straw-coloured. Wood white. Leaves dull dark green above; light to midgreen beneath. Sepals pinkish. Petals white to pinkish white. Capsule dull maroon red.

Distribution. Papua New Guinea: Enga, Eastern Highlands, and Morobe Provinces.

Ecology. Occasionally found in submontane, montane, and moss forest with low vegetation (once recorded to be dominated by *Xanthomyrtus*, Myrtaceae). Soil: once found on well-drained latosol in strong shade. Alt.: 1800–3300 m. Flowering: Jan.–April. Fruiting: Oct.–Dec.

Metabolites. Hartley et al. (1973) record an absence of alkaloids in bark and leaflets (*Hartley 12527, 12560*).

Vernacular names. Palya (Enga); kal, katan, kopak, pobuk (Togoba).

Note. This species strongly resembles *Guioa amabilis*, but the latter has papillae, lacks domatia, and the leaflets are only crenate near the apex; the latter species is very locally found in Irian Jaya (Vogelkop), on the other side of New Guinea.

Specimens studied:
PAPUA NEW GUINEA. Enga Prov.: *ANU (Flenley) 2649; Robbins 3061.* — Eastern Highlands Prov.: *NGF (Streimann & Kairo) 45293; Saunders 775, 776, 782, 802.* — Morobe Prov.: *Clemens 5674, 9475; Hartley 12527, 12560; NGF (Ridsdale) 30244; (Womersley & McEwin) 37455; Vinas & Bellamy 261.*

Guioa pteropoda Radlk. – Fig. 113a, b.

Guioa pteropoda Radlk., Sapind. Holl.-Ind. (1879) 11, 41; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 614 (typification); Bot. Jahrb. 56 (1921) 28; in Engl., Pflanzenr. 98 (1933) 1174. — Type: *Beccari it. sec. 16* (Fl, holo), New Guinea, Ansus.
Guioa crenifoliola Merr. & Perry, J. Arn. Arbor. 21 (1940) 514. — Type: *Brass 13082* (A, holo; iso in BM, L), Irian Jaya, Idenburg River, Bernhard Camp. See note 2.

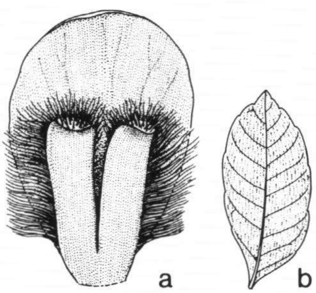


Fig. 113. *Guioa pteropoda* Radlk. a. Leaflet, x. 0.5; b. petal, × 12.5 (*Brass 13702*, L).

Tree. *Branchlets* terete, smooth to ribbed, only sericeous when very young; flowering twigs 3–4 mm thick. *Leaves* 2–7-jugate; rhachis 1.9–17.3 cm long, terete, not to slightly winged, subglabrous, petiole 1.8–4.6 cm long. *Leaflets* subsessile, opposite to alternate, elliptic, 3.5–8.5 by 1.7–3.2 cm, index 2.1–3, asymmetric, the acroscopic side broader, (sub)coriaceous, not punctate; base attenuate; margin laxly crenate, slightly revolute; apex obtusely acuminate to caudate, usually mucronulate; upper surface smooth, glabrous, sometimes wax; lower surface differently coloured, duller, smooth, no papillae, glabrous, domatia absent to a single to several sac(s), mainly on basiscopic side in axils of major nerves; venation on upper side flat, except for the raised midrib, slightly raised below, also the flat midrib; nerves 0.2–1 cm apart, marginally looped; veins laxly reticulate, indistinct. *Inflorescences* axillary, not to at most branching along rhachis; latter terete, 2.4–13 cm long, subsericeous; first order branches up to 5.3 cm long; cymules cincinnate, c. 4-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.8–1 mm long; bracteoles 0.3–0.5 mm long. *Pedicels* 3.8–8 mm long, glabrous or very sparsely pilose, upper part 2.1–4.8 mm long. *Flowers* c. 4 mm in diam. *Sepals* 5, ovate, margin pilose, outside and inside glabrous; 2 outer smaller ones 1.2–2.2 by 1.8–2.3 mm, margin with glands; 3 inner larger ones 3–4 by 3–4.2 mm, margin petaloid, without glands. *Petals* 4, obovate, 2.9–3.1 by 1.5–2.1 mm, claw 0.2–0.3 mm high, margin subglabrous, outside and inside glabrous, apex truncate to rounded; scales 2–2.2 mm long, free; crest usually present as a pilose bifid scale apex. *Disc* incomplete. *Stamens* 8; filament 2.3–4.6 mm long, only basally pilose; anther 0.3–0.4 mm long, glabrous. *Pistil:* ovary 0.4–0.6 mm long, smooth, subhirsute; style and stigma c. 0.3 mm long. *Fruit* with 2 or 3 well-developed lobes, c. 2 cm high by 1.4 cm broad, smooth, glabrous, stipe indistinct, broadly cuneate, edge of margin very sharp, angle between lobes c. 130°, blackish when dry; lobes c. 0.8 by 1.6 cm; dissepiments above attachment of funicle incomplete. *Seed* immature.

F i e l d n o t e s. Tree, 13–20 m high, d.b.h. 20–25 cm; bole c. 8 m high. Flowers white. Fruit red-green when young.

D i s t r i b u t i o n. Irian Jaya (Geelvink Bay, Jayapura Dist.).

E c o l o g y. Common. Found in primary forest along and in flood plains, in *Agathis* forest. Soil: clay, sand. Alt.: sea-level up to 900 m. Fruiting: March.

V e r n a c u l a r n a m e s. Koehiboei (Ambai); mansawoi (Bosnik).

N o t e s. 1. This species is very distinct. *Guioa pteropoda* possesses quite a unique set of characters: not to slightly winged rhachis, crenate margin of leaflets, leaflets show typical wrinkles when dry, broad glabrous petals, apically bifid scales, incomplete disc, filaments which are only basically pilose, and sharply edged fruits. The latter are also found in the genus *Sarcopteryx,* but this genus possesses small sepals which are all equal, while the arilloid has a different appendix; in *Guioa* sepals are dimorphic, and the appendix is much longer.

2. The specimens *Brass 13082,* and *13702* are somewhat different, they have a winged rhachis and a shorter, obtusely acute leaf apex.

3. Reynolds (Austrobaileya 2, 1984, 37, 40, fig. 2; Fl. Austr. 25, 1985, 47, map 56) records the presence of *Guioa pteropoda* (as *Guioa crenifoliola*) for Australia (Queensland). However, she based her opinion on two sterile collections (*Hyland 2311, Webb & Tracey 13314*), which indeed remarkably look like *Guioa pteropoda,* but several differences are present: the two sterile specimens possess more jugae and more acute leaflets with a serrate instead of a crenate margin. Moreover, juvenile specimens of Sapindaceae usually possess a slightly winged rhachis, often have serrate leaflets, and may look quite unlike the adult trees. As the specimens are sterile it is possible that they are still juvenile. Regarding these points and the large gap in distribution (NW New Guinea and NE Australia), it is unlikely that *Guioa pteropoda* occurs in Australia; therefore the two Australian specimens are omitted in this treaty.

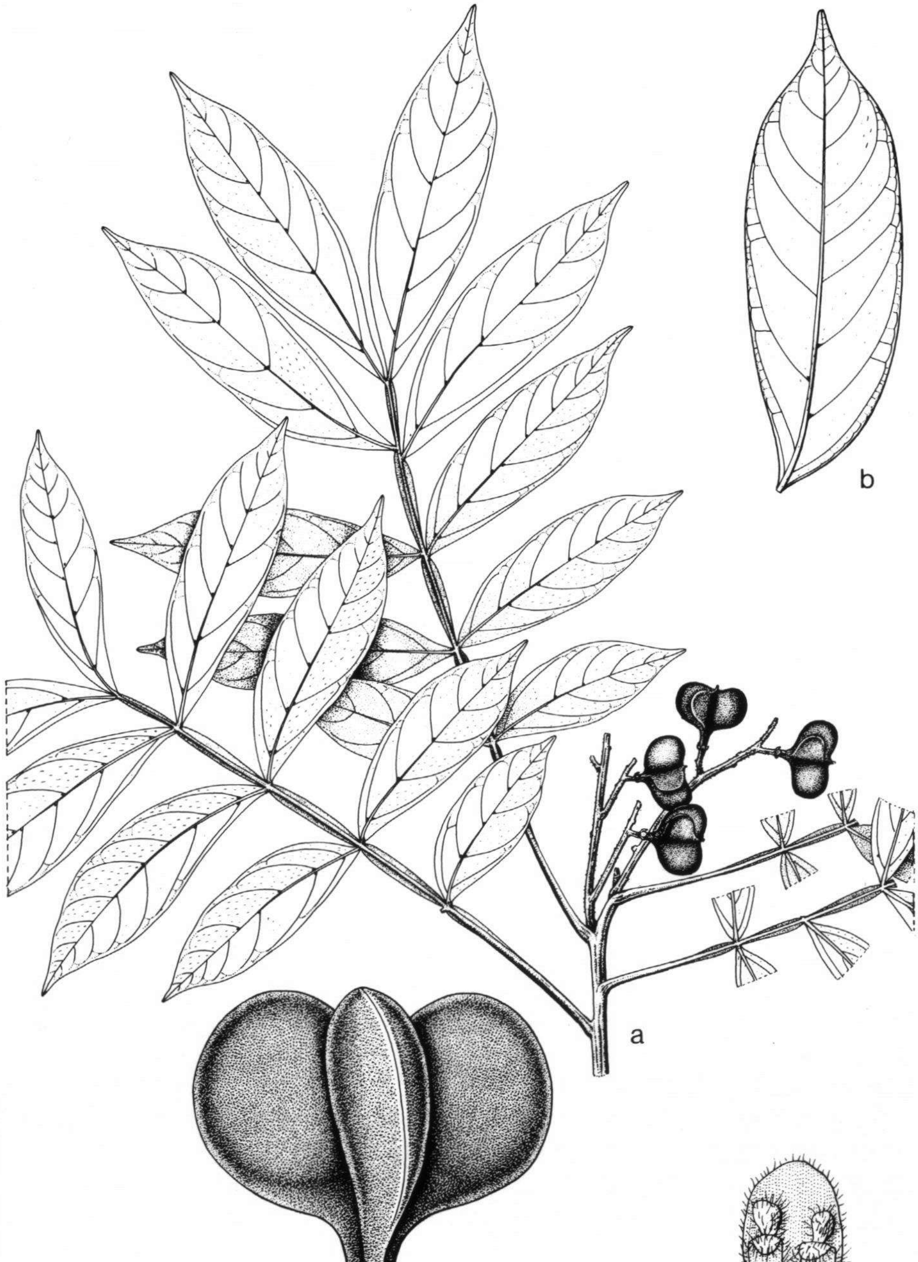
S p e c i m e n s s t u d i e d:

NEW GUINEA. Irian Jaya, Geelvink Bay: *Beccari it. sec. 16,* Ansus; *NIFS bb (Salverda) 21848,* Babo, Kali Oroba; *(van Dijk) 30365,* Japen I. Jayapura: *Brass 13082, 13702,* Idenburg River, Bernhard Camp.

Guioa pterorhachis Welzen – Fig. 114a–d.

Guioa pterorhachis Welzen, Blumea 33 (1988) 419, pl. 12a, b. — T y p e: *Elmer 20268* (L, holo; iso in BM, F, K, M, NSW, P, U), Borneo, Sabah, Myburgh Prov., Sandakan.
Guioa pleuropteris auct. non Radlk.: Merr., Pl. Elm. Born. (1929) 175.

Shrub to tree. *Branchlets* terete, smooth to somewhat ribbed (to rough), usually glabrous, at most sparsely sericeous when young; flowering twigs 2–5 mm thick. *Leaves* 3–7-jugate; rhachis terete, winged, wing up to 4 mm broad, (sub)glabrous, petiole 1.1–12.2 cm long. *Leaflets* subsessile, opposite to subopposite, elliptic (to obovate), 2.4–14.6 by 1–4.6 cm, index 1.9–3.9, often slightly asymmetric, especially basally, then acroscopic side broader, (sub)coriaceous, punctate; base acute to attenuate to cuneate; margin entire (except juvenile leaflets with a few teeth), flat; apex gradually acuminate to cuspidate, sometimes mucronulate; upper surface smooth, glabrous to sometimes puberulous on the midrib (and venation); lower surface


a
b
c
d

differently coloured, dull, papillate, (very) sparsely, usually shortly sericeous, domatia many sacs in axils of major nerves, hardly raised; venation on upper surface (slightly sunken to) flat to raised, slightly raised on lower; midrib below hardly raised, flat; nerves 0.2–3.6 cm apart, marginally looped, arches less developed in lower half of leaflets; nerves laxly reticulate, rather indistinct. *Inflorescences* axillary (to pseudoterminal), (not branching to) branching in or near axil and along rhachis; latter terete, 1–20.8 cm long, subsericeous; first order branches up to 11.5 cm long; cymules cincinnate, 2–5-flowered. *Bracts* and *bracteoles* deltoid to triangular, outside sericeous, inside (sub)glabrous; bracts 0.7–1.2 mm long; bracteoles 0.3–0.8 mm long. *Pedicels* 2–7 mm long, completely sericeous, upper part 1–2.2 mm long. *Flowers* 3.5–4 mm in diam. *Sepals* 5, ovate, margin and sometimes outside pilose, margin with glands, inside (sub)glabrous; 2 outer smaller ones 1–1.9 by 0.8–1.5 mm; 3 inner larger ones 1.7–3 by 1.2–2.7 mm, margin petaloid. *Petals* 5, elliptic (to obovate), 1.1–2.8 by 0.8–1.6 mm, claw 0.2–0.5 mm high, margin pilose, outside and inside glabrous, apex more or less acute; scales 1.1–2 mm long, free; crest present as a pilose flat part of the bifid scale apex. *Disc* incomplete to complete. *Stamens* 8; filament 2–5 mm long, especially basally pilose; anther c. 0.3 mm long, glabrous. *Pistil:* ovary 0.3–1 mm long, smooth, sparsely hirsute; style and stigma 0.1–1 mm long, elongating in fruit up to 3.5 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.4–1.9 cm high by 1.2–2.2 cm broad, (smooth to) somewhat rugose-ruminate, glabrous, stipe 4–7 mm high, slender, angle between lobes 135–190°, blackish when dry; lobes 8.5–11 by 8–12 mm. *Seed* obovoid, 7.5–10.5 by 6–9 mm; hilum 1.7–2 mm long. *Embryo* 6.8–9.2 by 5–7.5 mm; cotyledons secondarily laterally besides each other, upper larger, apices elongated, that of upper straight, that of lower recurved; radicle 3–4.3 mm long.

Field notes. Shrub to tree, 3–16 m high, d.b.h. 10–50 cm. Outer bark smooth, flaked, white to white-brown to brown-green to brown, soft, c. 0.15 cm thick; inner bark fibrous, pink to brownish grey to brown, c. 0.25 cm thick. Cambium yellow. Sapwood white to yellow to brown. Petals white. Fruit yellow to red, edible (presumably arilloid, but seed is also possible), with a yellow exudate.

Distribution. Borneo: E Sabah (Sandakan & Tawau Prov.).

Ecology. Found in understorey of primary and especially secondary forest, along rivers and roadsides, on flat to undulating country. Soil: white, yellow, or black sands. Alt.: sea-level up to 30(–500) m. Flowering season: (July–)Nov.–Jan. Fruiting season: Nov.–May.

Vernacular names. Butang butang; garong, lipang lipang (Sungei); sikip sikip, galid, guruyod (Dusun Kinabatangan), tingir manuk (Bajan); angil manuk (Malay); tanggianggi, tengaranuk (Dusun Kinarut).

Uses. Firewood.

Note. *Guioa pterorhachis* is closely related to *Guioa pleuropteris*. The following set of characteristics separates the two:

Fig. 114. *Guioa pterorhachis* Welzen. a. Habit, × 0.5; b. leaflet, × 0.5; c. petal, × 12.5; d. fruit, × 3 (a: *SAN (Ellen) 55445*, L; b, d: *SAN (Krispinus) 91944*, L; c: *(SAN) A (Kadir) 662*, US).

	Guioa pleuropteris	*Guioa pterorhachis*
Indumentum	hirsute (to sericeous)	sericeous
Indumentum	usually dense	sparse
Rhachis wing	absent to usually narrow to sometimes broad	broad
Leaflets	(elliptic to) obovate	elliptic
Apex	acute to sometimes cuspidate	cuspidate
Colour of lower side when alive	grey-green to glaucous	light green
Domatia	pockets, sometimes sacs	sacs
Domatia	above plain of leaflet	in plain of leaflet to slightly raised
Midrib lower surface	raised, convex	almost in plain of leaflet, flat

Some specimens of *Guioa pleuropteris* from Borneo (NE Kalimantan) are slightly intermediate; especially *Kostermans 4221*, which only lacks the flat hardly raised midrib.

Specimens studied:
BORNEO. E coast of Sabah: 47 specimens.

Guioa pubescens (Zoll. & Mor.) Radlk. – **Fig. 115 a–c, 116.**

Guioa pubescens (Zoll. & Mor.) Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8 (1878) 302; Sapind. Holl.-Ind. (1879) 10, 41 (lectotypification); Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 543, 612; Maingay, Kew Bull. (1890) 119; King, J. As. Soc. Beng. 65, II (1896) 445; Ridley, J. Str. Br. R. As. Soc. 33 (1900) 66; Koord. & Val., Bijdr. Boomsoort. Java 9 (1903) 210; Backer, Schoolfl. (1911) 268; Koord., Exk. Fl. Java 2 (1912) 541; Radlk., Philip. J. Sc. 8, Bot. (1913) 446; Elmer Leafl. Philip. Bot. 5 (1913) 1616; Merr., En. Born. (1921) 361; Ridley, Fl. Mal. Pen. 1 (1922) 506; Merr., En. Philip. 2 (1923) 509; Heyne, Nutt. Pl., ed. 2 (1927) 1001; Radlk. in Engl., Pflanzenr. 98 (1933) 1169; Corner, Gard. Bull. Str. Settl. 10 (1939) 45; Ways. Trees (1940) 588, pl. 178; Masamune, En. Phan. Born. (1942) 427; Desch, Mal. For. Rec. 15 (1954) 526; Salvosa, Lex. Philip. Pl. (1963) 105; Backer & Bakh. f., Fl Java 2 (1965) 140; Burk., Dict., ed. 2 (1966) 1134; Keng, Gard. Bull. Sing. 35 (1982) 90. — *Sapindus pubescens* Zoll. & Mor. in Mor., Syst. Verz. (1846) 22, p.p. (*Zollinger 1105*). — Lectotype (Radlkofer, 1879a): *Zollinger 1105* (L, holo; iso in A, BM, FI, P), Java, Tjikoya.

Arytera silaka Miq., Sum. (1861) 199, 510; Filet, Plantk. Woordenb. ed. 2 (1888) 271, nr. 7895. — Type: *Teijsmann HB 610* (U, holo; iso in BO), Sumatra, Singkara.

Cupania pallidula Hiern in Hook. f., Fl. Br. Ind. 1 (1875) 676; Ridley, Trans. Linn. Soc. Bot. 3 (1893) 289; Merr., En. Philip. 2 (1923) 509. — Syntypes: Malaya: *Griffith s.n.* (K); *Maingay s.n.* (K).

Guioa diplopetala (Hassk.) Radlk. f. *dentata* Radlk., Sapind. Holl.-Ind. (1879) 88; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 610; in Engl., Pflanzenr. 98 (1933) 1162. — Type: *Teijsmann HB 3741* (BO, holo), Sumatra, Palembang, Oganulu.

Guioa perrottetii auct. non Radlk.: Meijer, Bot. News Bull. 9 (1967) 75.

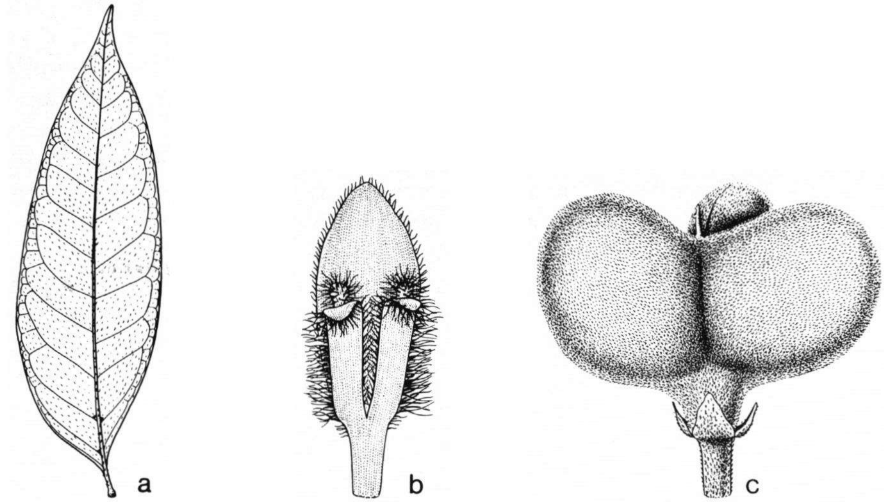


Fig. 115. *Guioa pubescens* (Zoll. & Mor.) Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, b: *Maxwell 82-24*, L; c: *PNH (Sulit) 12461*, L).

Tree(let). *Branchlets* (somewhat flattened to) terete, smooth to somewhat ribbed, sericeous when young; flowering twigs 1.5–6 mm thick. *Leaves* (1–)2–6-jugate; rhachis 2.1–29.5 cm long, terete to sometimes upwards slightly flattened, not winged, subsericeous, petiole 1.4–10.8 cm long; petiolules up to 1 cm long. *Leaflets* usually not subsessile, opposite to alternate, ovate (to elliptic), often slightly falcate, 2.9–19.2 by 0.8–7.2 cm, index 1.3–5.5, especially basally asymmetric, acroscopic side broader, coriaceous, not punctate; base attenuate; margin entire, flat (to revolute); apex gradually acuminate to cuspidate (to caudate), usually mucronulate; upper surface smooth, (glabrous to) sparsely shortly sericeous, sometimes wax; lower surface differently coloured, dull, papillate, (slightly) shortly sericeous, domatia (absent to) a single small sac to many sacs, if single: on basiscopic side in axil of ± second nerve, otherwise in axils of nerves; venation on upper surface (slightly sunken to) flat to raised, below usually raised; nerves 0.3–3.3 cm apart, marginally looped, sometimes less so in lower third of leaflets; veins laxly reticulate, rather indistinct. *Inflorescences* axillary (to pseudoterminal), (not branching to) branching in or near axil to especially along rhachis; latter terete, 1.4–24.2 cm long, brown sericeous; first order branches up to 9.3 cm long; cymules cincinnate, 2–4-flowered. *Bracts* and *bracteoles* deltoid to triangular, outside sericeous, inside (sub)glabrous; bracts 0.6–1.8 mm long; bracteoles 0.2–1.2 mm long. *Pedicels* 1.8–8 mm long, completely sericeous; upper part 0.9–3 mm long. *Flowers* 3.5–4.5 mm in diam. *Sepals* 5, ovate, margin and often outside sericeous, margin with glands, inside (sub)glabrous; 2 outer smaller ones 1–2.8 by 0.8–2.1 mm; 3 inner larger ones 1.4–3.3 by 1.3–3.1 mm, margin petaloid. *Petals* 5, obovate, 1.9–3.4 by 0.7–1.8 mm, blade obovate, gradually decurrent into the claw, latter 0.3–1.2 mm high, margin and sometimes outside pilose, inside glabrous, apex rounded (to acute); scales 1.1–2 mm long, free, apex not to hardly broadened; crest present as a pilose flat part of the bifid scale apex. *Disc* incomplete. *Stamens* 8; filament 1.9–5.2 mm long, especially basally pilose; anther 0.2–0.4 mm long, glabrous. *Pistil:* ovary 0.3–2 mm long, densely hirsute; style and stigma 0.1–2.5 mm long, elongating in fruit up to 3.6 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1–1.5 cm high by 1–1.9 cm broad, smooth (to somewhat ribbed), (very) sparsely sericeous, glabrescent, stipe 1.5–5 mm high, slender, angle between lobes 90–150°, (reddish to) blackish when dry; lobes 7–10 by 6.5–10 mm. *Seed* globose to obovoid, 6.8–10 by 5.8–7.5 mm; hilum 1.1–2 mm long. *Embryo* 5.9–8.3 by 4.9–6 mm; cotyledons secondarily laterally besides each other, upper larger, apices often elongated, upper usually straight, lower (re)curved; radicle 2.5–5.6 mm long.

Field notes. Tree(let), 2–25 m high, d.b.h. 1.3–85 cm; bole straight (to crooked), without buttresses. Outer bark smooth, sometimes deeply fissured, hard, (greenish to) flaky greyish white or greyish brown to dark brown or blackish; inner bark yellowish white to pinkish to reddish brown. Cambium white. Sapwood soft to hard, white to whitish yellow to orange to ochre; heartwood red. Indumentum brown. Leaflets dull dark green above; pale green to whitish below. Inflorescence dull green. Buds green. Calyx green to reddish. Petals white to yellow. Filaments white; anthers pink. Ovary yellowish green. Fruit reddish yellow to red.

Distribution. W Malaysia, Singapore, Sumatra, Bangka, W Java (Djawa barat), Karimun-djawa I., Borneo (above equator), Philippines (Palawan).

Ecology. Rare to rather common. Found in primary and especially secondary forest, in kerangas, in peat swamp forests, in forest along sea. Soil: sand, sandy loam, sandstone, rocky soil, limestone, ultrabasic, dry peat. The trees may be moss-covered. Alt.: sea-level up to 1800 m. Flowering season: Singapore: July–Oct.; Java: Febr., Nov. Borneo: Aug.–Febr. Fruiting: Jan.–April.

Wood. Faint whitish-red, grain coarse, soft and splitting slightly in drying (Maingay, 1890) and/or light brown, heavy and hard (Desch, 1954).

Vernacular names. Malaysia: chenderai kayu, kayu sugil (toothpick), keli layu puteh, nilau, nyamok, senyamok, sugee. Sumatra: kaju digil-digil, k. manari, k. pinggol-pinggol, k. katjang, katjang katjang, sepit, silaka (Sum. W coast). Bangka: pulas/pulis. Borneo: Sabah: angir manuk (Kedayan); geronok (Kedazan Tambunan); saasa, saksah (Bajan); Sarawak: kaju wej, rutan berangat (Kelabit); Kalimantan Timur: marapinang. Philippines: alahan-mabolo (Filipino); bayasi.

Uses. The wood is used as a construction timber, in spite of the fact that it is brittle and the stems too small for large-scale use (Heyne, 1927), although recorded diameters (see field notes) indicate the opposite.

Notes. 1. *Guioa koelreuteria* possesses leaflets with the same shape as those of *Guioa pubescens*, but those of the first are usually smooth and glabrous below and have secretory idioblasts (punctation), while the fruits lack hairs.

2. See note 4 under *Guioa bijuga*.

Specimens studied:

MALAY PENINSULA: 35 specimens. — SUMATRA: 23 specimens. — JAVA: 4 specimens. — BORNEO: 53 specimens. — PHILIPPINES: 4 specimens.

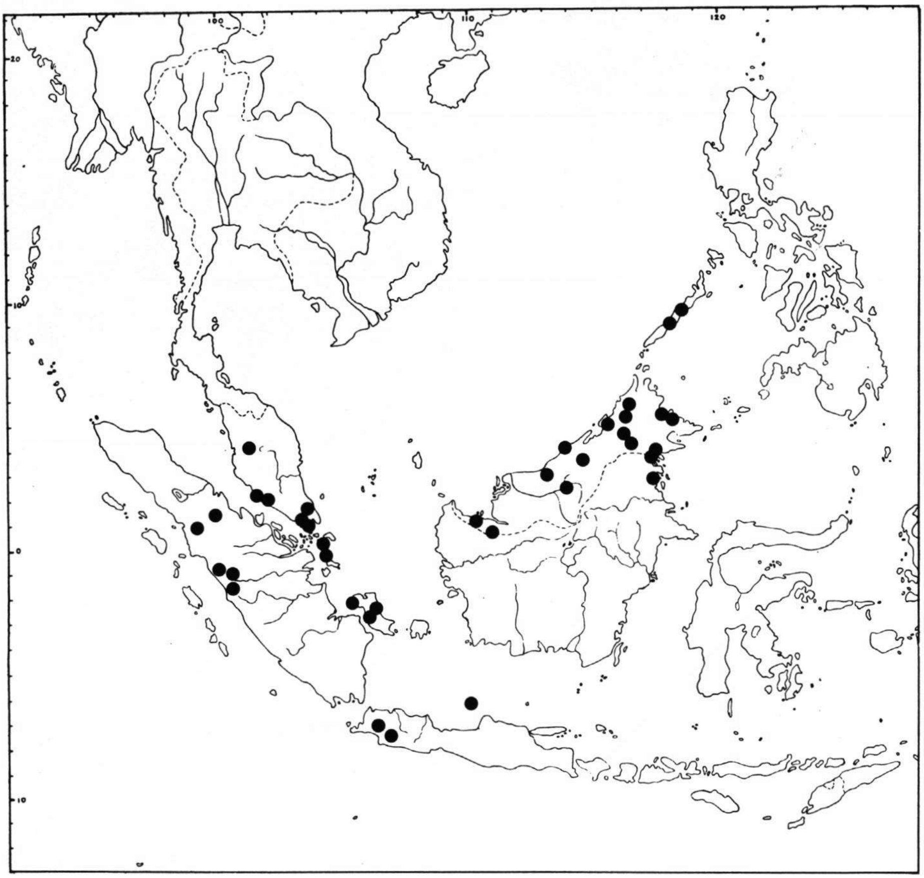


Fig. 116. Distribution of *Guioa pubescens* (Zoll. & Mor.) Radlk.

Guioa punctata Welzen – Fig. 117 a–c.

Guioa punctata Welzen, Blumea 33 (1988) 420, pl. 8a–c. — T y p e: *Greenwood 749* (K, holo), Fiji, Viti Levu, Penang to Ellington.
Guioa rhoifolia auct. non Radlk.: A.C. Smith, Fl. Viti. 3 (1985) 597 (p.p.).

Tree. *Branchlets* terete, smooth (to ribbed to rough), sericeous when young; flowering twigs 1–4 mm thick. *Leaves* 1–5-jugate; rhachis 2.2–13.9 cm long, basally terete to upwards above somewhat flattened, not winged, subsericeous, petiole 0.7–4.3 cm long; petiolules up to 0.6 cm long. *Leaflets* not subsessile, opposite to subopposite, ovate, falcate, 2.1–8.2 by 0.6–3.3 cm, index 2.3–5.1, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire, flat; apex acute to cuspidate, usually gradually tapering, very apex obtuse, sometimes mucronulate; upper surface smooth, (sub)glabrous, midrib basally often puberulous;

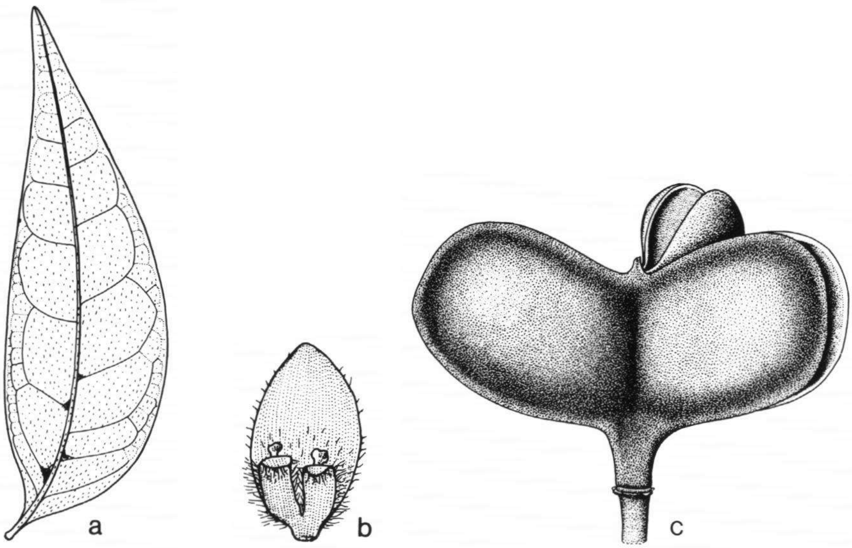


Fig. 117. *Guioa punctata* Welzen. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 2 (a, c: *Bryan 449*, BISH; b: *Parham 5*, K).

lower surface differently coloured, dull, papillate, subsericeous, domatia a single to several large sac(s), with the usually round opening in the top, in axils of veins (see also note 1); venation usually raised, especially on the lower side; nerves 0.2–1.3 cm apart, marginally looped; veins rather laxly reticulate, often inconspicuous. *Inflorescences* axillary, branching along rhachis; latter somewhat flattened or grooved, 0.7–13 cm long, sericeous; first order branches up to 6 cm long; cymules cincinnate to dichasial, 3–8-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.6–1 mm long; bracteoles 0.3–0.8 mm long. *Pedicels* 1.9–6 mm long, sericeous; upper part slightly less sericeous, 0.8–3 mm long. *Flowers* 3.2–3.5 mm in diam. *Sepals* 5, ovate, margin pilose, without glands, outside glabrescent, inside glabrous; 2 outer smaller ones 0.8–2 by 0.8–2.5 mm; 3 inner larger ones 1.3–4 by 1.2–3.8 mm, margin petaloid. *Petals* 5, elliptic, 1.8–2.7 by 0.9–1.8 mm, claw 0.1–0.3 mm high, margin and basally the outside and inside pilose, apex obtusely acute; scales 0.8–1.2 mm long, free (see also note 2); crest usually developed, small, stiped, apex slightly clavate, hardly lobed; petal between two adjacent large sepals not reduced. *Disc* complete. *Stamens* 8; filament 1.3–3 mm long, especially basally pilose; anther 0.3–0.7 mm long, glabrous. *Pistil:* ovary 0.3–0.5 mm high, sparsely hirsute; style and stigma 0.1–0.5 mm high, elongating in fruit up to 2 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.1–2 cm high by 1.1–2.9 cm broad, smooth, glabrous, stipe 1.5–5 mm high, somewhat broadly cuneate, angle between lobes 115–165°, blackish when dry; lobes 8.7–14 by 7–13 mm. *Seed* obovoid, 7.2–11.5 by 6–10.5 mm;

hilum 1–2 mm long. *Embryo* 6.5–9.5 by 5–8.8 mm; cotyledons dorsoventrally above each other, about equal in size, apices not elongated; radicle 1–1.5 mm long.

F i e l d n o t e s. Tree, 3.5–14 m high, d.b.h. up to 60 cm. Bark grey. Buds red. Petals white. Filaments white; anthers red. Arilloid red.

D i s t r i b u t i o n. Fiji: Waya I. (Yasawa Group), Viti Levu, Vanua Levu, Koro I., Vanua Mbalavu, Fulanga I.

E c o l o g y. On bare ground, open spaces, in dense ridge forest, along river banks. Alt.: sea-level up to 2300 m. Flowering: Jan.–March. Fruiting: Febr.–Sept.

V e r n a c u l a r n a m e s. Waya: marasa. Vanua Levu: kauloa. Fulanga, Vanua Mbalavu: masa.

U s e s. Timber for huts, posts, stalks, fire wood.

N o t e s. 1. *A.C. Smith 1477* is somewhat exceptional because several domatia are rather small and have the opening more or less in the front.

2. The petals of *A.C. Smith 1123* lack the scales.

3. See also the note under *Guioa rhoifolia* for the differences between these two species.

4. See the note under *Guioa megacarpa* for the differences between *Guioa punctata, Guioa megacarpa,* and *Guioa novoëbudaënsis*.

5. See note 1 under *Guioa chrysea* for the differences between *Guioa rhoifolia, Guioa punctata,* and *Guioa chrysea.*

S p e c i m e n s s t u d i e d:
FIJI: 19 specimens.

Guioa reticulata Radlk. – Fig. 118 a–c.

Guioa reticulata Radlk., Philip. J. Sc. 8, Bot. (1914) 446, 462; Merr., En. Philip. 2 (1923) 509; Radlk. in Engl., Pflanzenr. 98 (1933) 1168; Salvosa, Lex. Philip. Pl. (1963) 105. — L e c t o t y p e (here proposed): *BS (Ramos) 7055* (M, holo; iso in NSW), Philippines, Luzon, Abra Subprov.

Guioa sulphurea Radlk., Philip. J. Sc. 8, Bot. (1914) 446, 462; Merr., En. Philip. 2 (1923) 509; Radlk. in Engl., Pflanzenr. 98 (1933) 1167; Salvosa, Lex. Philip. Pl. (1963) 105. — T y p e: *FB (Alvarez) 22429* (M, holo; iso in F, L, NSW), Philippines, Luzon, Nueva Ecija Prov.

Tree. *Branchlets* terete, smooth, golden sericeous (to hirsute) when young; flowering twigs 2–4 mm thick. *Leaves* 2–5-jugate; rhachis 2.8–17 cm long, basally terete, upwards flattened above, not winged, subglabrous, petiole 1.5–6.3 cm long; petiolules up to 1 cm long. *Leaflets* not subsessile, opposite to alternate, ovate, falcate, 2.8–12 by 0.7–3 cm, index 3.5–4.5, asymmetric, acroscopic side broader, coriaceous to very coriaceous, not punctate; base attenuate; margin entire, flat to revolute; apex cuspidate to caudate, usually mucronulate; upper surface smooth, glabrous to puberulous on the midrib; lower surface differently coloured, dull, papillate, short (to long) sericeous, domatia a single (to many) sac(s) on basiscopic side in axil of ± second nerve (to in axils of major nerves); venation conspicuously raised, differently coloured from lamina; nerves 0.3–2.1 cm apart, marginally looped; veins densely reticulate, very distinct. *Inflorescences* axillary, branching in or near the axil and along the rhachis; latter usually flattened, 3.4–23.3 cm long, sericeous (to

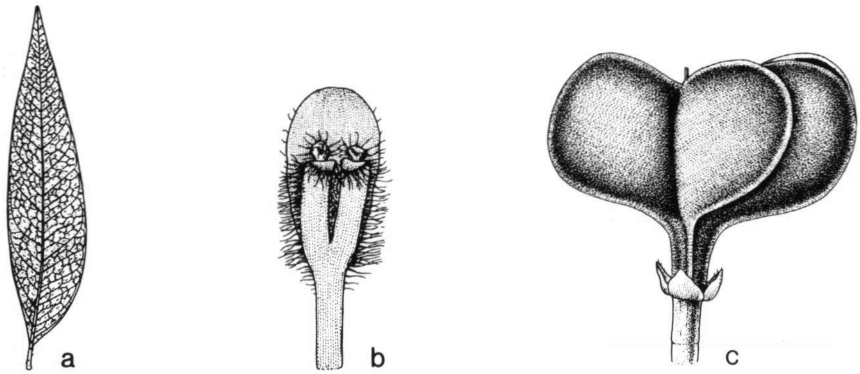


Fig. 118. *Guioa reticulata* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *Santos 5715*, L; b: *FB (Alvarez) 22429*, L).

hirsute); first order branches up to 11.2 cm long; cymules cincinnate (to dichasial), 2–5-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 1–1.8 mm long; bracteoles 0.3–1.1 mm long. *Pedicels* 2.3–5 mm long, sericeous except for the usually subglabrous, 1–2.7 mm long upper part. *Flowers* 3.5–3.8 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside sometimes pilose, inside glabrous; 2 outer smaller ones 1.5–2.2 by 1.1–2.2 mm; 3 inner larger ones 2.2–2.8 by 1.6–2.7 mm, margin petaloid. *Petals* 5, obovate, 2.8–3.1 by 1–1.5 mm, blade obovate, gradually decurrent into the claw, latter 0.8–1.3 mm high, margin pilose, outside and inside (sub)glabrous, apex obtuse; scales 1.2–1.8 mm long, free; crest present as a pilose flat part of the bifid scale apex to clavate and rather glabrous. *Disc* incomplete. *Stamens* 8; filament 1.7–4 mm long, especially basally pilose; anther 0.4–0.6 mm long, glabrous. *Pistil:* ovary 0.4–2 mm long, smooth, subhirsute; style and stigma 0.3–1.2 mm long, elongating in fruit up to c. 1.5 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 1 or 2 well-developed lobes, 1–1.1 cm high by 1.2–1.4 cm broad, smooth, glabrous, stipe c. 2 mm high, slender, angle between lobes c. 130°, blackish when dry; lobes c. 7.5 by 7 mm. *Seed* obovoid, c. 7.2 by 5.8 mm; hilum c. 2 mm long. *Embryo* c. 5.8 by 4.7 mm; cotyledons secondarily laterally besides each other, upper larger, apices elongated, that of upper straight, that of lower recurved; radicle c. 2 mm long.

Field notes. Tree, 7–8 m high, d.b.h. c. 12.5 cm. Fruits red.

Distribution. Philippines (Luzon).

Ecology. Found in secondary forest, on forested slope. Flowering: Jan.–Febr. Fruiting: May.

Vernacular names. Alahan-sinima (Filipino); malaalahan (Spanish-Filipino).

Notes. 1. This species can be distinguished by its leaflets with every (small) vein raised on lower and upper surface, the lower surface has 1 (to many) domatia, dense papillae, and usually a shortly sericeous indumentum.

2. The type of the synonym *Guioa sulphurea* (*FB 22429*) is slightly different, the indumentum is usually patent instead of appressed, a phenomenon also occasionally encountered in other species (e.g. *Guioa chrysea, Guioa subsericea,* etc.). Because of this exceptional feature the name *Guioa reticulata* is preferred (both were published at the same time).

3. See note 3 under *Guioa myriadenia* for the difference between *Guioa reticulata* and the former.

4. *Jacobs 7983* is exceptional because the inflorescence, pedicels, and sepals are very densely sericeous.

Specimens studied:

PHILIPPINES. Luzon: *BS (Ramos) 7055*, Abra Subprov.; (*Ramos & Edaño) 26462*, Mt. Umingan; *FB (Merritt & Darling) 14058*, Ilocos Sur Prov.; *(Curran et al.) 18221*, Benguet Prov., Mt. Pulog; *(Alvarez) 22429*, Nueva Ecija Prov.; *Jacobs 7983*, Sierra Madre Mts., Baher; *Santos 5715*, Ilocos Sur Prov., Conception.

Guioa rhoifolia (A. Gray) Radlk. – **Fig. 119a–c.**

Guioa rhoifolia (A. Gray) Radlk., Sapind. Holl.-Ind. (1879) 38; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 522, 608; in Engl., Pflanzenr. 98 (1933) 1158; Parham, Pl. Fiji Is. (1964) 174; Pl. Fiji Is., rev. ed. (1972) 247; A.C. Smith, Fl. Viti. 3 (1985) 597, fig. 143a, b. — *Cupania rhoifolia* A. Gray, U.S. Expl. Exp. Bot. 1 (1854) 254. — Lectotype (here proposed): *U.S. Expl. Exp. s.n.*, s.d. (US, holo: US sh. no. 17736; iso in A, K, P), Feejee Isl.

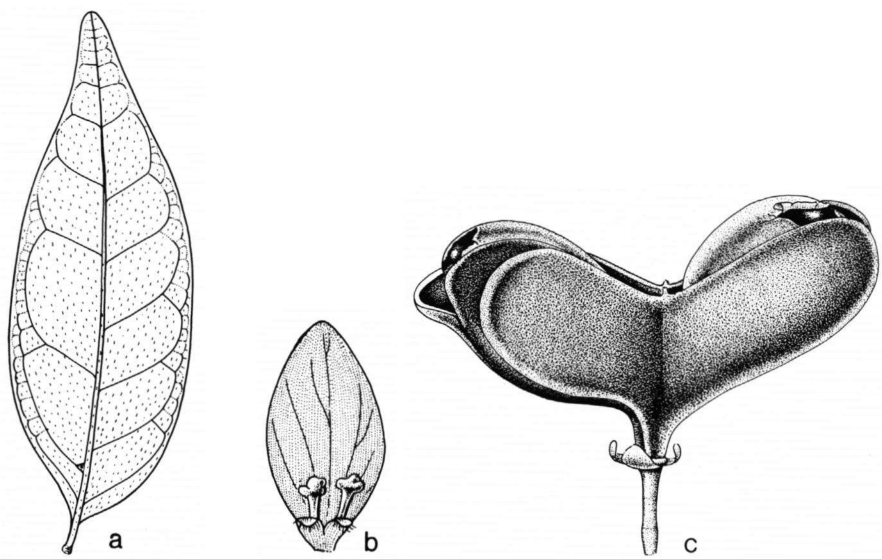


Fig. 119. *Guioa rhoifolia* (A. Gray) Radlk. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, c: *A.C. Smith 4603*, BRI; b: *Koroiveibau et al. 14451*, L).

Shrub to tree. *Branchlets* terete, smooth (to ribbed to rough), glabrous to usually sericeous, especially when young; flowering twigs 1.5–4 mm thick. *Leaves* 2–7-jugate; rhachis 2.3–22.7 cm long, especially upwards slightly flattened, not to slightly winged, glabrous to subsericeous, petiole 0.8–5.8 cm long; petiolules if present up to 0.8 cm long. *Leaflets* usually subsessile, opposite to subopposite (to alternate), ovate (to elliptic), usually falcate, 1.7–11 by 0.4–2.9 cm, index 2.6–5.4, asymmetric, acroscopic side broader, coriaceous, not punctate; base attenuate; margin entire, flat; apex acute to cuspidate, with a sinus, very apex obtuse, usually mucronulate; upper surface smooth, glabrous, midrib basally often puberulous; lower surface differently coloured, dull, papillate, glabrous to sericeous, domatia a single sac on basiscopic side in axil of ± second nerve; venation raised on both sides; nerves 0.2–1.6 cm apart, marginally looped; veins densely reticulate, conspicuous. *Inflorescences* axillary to pseudoterminal, usually only branching along rhachis; the latter somewhat flattened or grooved, 2.4–17.9 cm long, glabrous to sericeous; first order branches up to 10.3 cm long; cymules cincinnate (to occasionally dichasial), 2–4-flowered. *Bracts* and *bracteoles*
bracts 0.4–1 mm long; bracteoles 0.3–0.6 mm long. *Pedicels* 2.5–6.5 mm long, subglabrous to sericeous, except for the less pilose, 1.1–2.8 mm long upper part. *Flowers* c. 4 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 0.9–2 by 1.3–2.2 mm; 3 inner larger ones, 1.5–3.2 by 2.1–3.8 mm, margin petaloid. *Petals* 5, (elliptic to) obovate, 1.2–2.4 by 0.7–1.3 mm, claw c. 0.1 mm high, margin subpilose, outside and inside glabrous, apex obtuse to acute; scales 0.3–0.5 mm long, free; crest very large, on a long stipe, apex broad, clavate, lobed; petal between two adjacent large sepals not reduced. *Disc* complete. *Stamens* 8; filament 1–4 mm long, subglabrous; anther 0.3–0.7 mm long. *Pistil:* ovary 0.2–1.3 mm high, subglabrous; style and stigma 0.1–0.9 mm long, elongating in fruit up to 1.5 mm, then upper c. 0.4 mm stigmatic. *Fruit* with 2 or 3 well-developed lobes, 1.2–1.3 cm high by c. 1.8 cm broad, smooth, glabrous, stipe 3–3.5 mm high, slender, angle between lobes 130–140°, blackish when dry; lobes c. 9 by 6–7 mm. *Seed* obovoid, 6.2–8 by c. 5.5 mm; hilum 1–1.5 mm long. *Embryo* 5–6.5 by c. 4.7 mm; cotyledons dorsoventrally above each other, upper smaller, apices not elongated; radicle 0.7–1 mm long.

Field notes. Shrub to tree, 1–15 m high; d.b.h. up to 10 cm; crown usually spreading. Bark smooth, dark grey; inner bark red brown. Leaves pale green; whitish green underneath. Buds green. Petals white. Filaments white; anthers yellow to red. Gynoecium pale green. Fruits red.

Distribution. Fiji: Serua I., Viti Levu, Ovalau, Vanua Levu, Kadavu I.

Ecology. In open to dense forest, margin of forest, scrubland, thickets. Alt.: sea-level up to 1000 m. Flowering: Sept.–Dec.(–March). Fruiting: June.

Vernacular names. Baka ni Vudi; wive (Kadavu) (Parham, 1964); kailoa (Kauloa).

Note. *Guioa rhoifolia* has always been confused with *Guioa punctata*. The differences are:

	Guioa rhoifolia	*Guioa punctata*
Leaflets	not punctate	punctate
Apex	decurrent with a sinus	tapering or decurrent with a sinus
Venation on upper surface	often flat and indistinct	raised and distinct
Scales	0.3–0.5 mm long	0.8–1.2 mm long
Crest	large	not present to small

For the differences between *Guioa rhoifolia* and *Guioa chrysea* see note 1 under the latter.

Specimens studied:
FIJI: 23 specimens.

Guioa rigidiuscula Radlk. – Fig. 120 a–c.

Guioa rigidiuscula Radlk., Sapind. Holl.-Ind. (1879) 11, 41; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 614 (typification); ibid. 20 (1890) 361; K. Schum. & Lauterb., Fl. Schutzgeb. (1900) 420; Radlk., Bot. Jahrb. 56 (1921) 282; Baker in Rendle, J. Bot. 61, Suppl. (1923) 11; Lauterb., Bot. Jahrb. 62 (1929) 555; Radlk. in Engl., Pflanzenr. 98 (1933) 1173; Rehder, J. Arn. Arbor. 14 (1933) 63; P. van Royen, Man. For. Trees Papua & N.G. 2 (1964) 3, fig. 1g. — Type: *Beccari Fl 2804* (FI, holo, cited by Radlkofer as *Beccari 8*), New Guinea, Humboldt Bay.

Shrub to tree. *Branchlets* terete, smooth (to slightly ribbed), shortly sericeous when young; flowering twigs 2–6 mm thick. *Leaves* 1–4-jugate; rhachis 2.2–17.2 cm long, terete (to somewhat flattened below jugae), not winged, subglabrous, petiole 1.3–8.2 cm long. *Leaflets* subsessile, opposite to alternate, elliptic, 3.6–17.1 by 1.2–6.3 cm, index 2.1–3.8, usually rather symmetric, acroscopic side slightly broader, (sub)coriaceous, usually punctate; base attenuate; margin entire, flat; apex (acute to) acuminate to cuspidate (to caudate), usually mucronulate; upper surface smooth, glabrous, seldom puberulous on the midrib; lower surface differently coloured, duller, smooth, no papillae, subglabrous, domatia in at least some leaflets a single small sac on basiscopic side in axil of ± second major nerve; venation on upper side (slightly sunken to) flat (to raised), raised below; major nerves 0.2–3.8 cm apart, marginally looped, but often less distinctly so in lower part of leaflets; veins laxly reticulate, indistinct. *Inflorescences* ramiflorous (to axillary), not branching to branching in axil and along rhachis; latter terete, 1–13.3 cm long, sericeous; first order branches up to 6.2 cm long; cymules cincinnate to dichasial, (1–)3–4(–5)-flowered. *Bracts* and *bracteoles* triangular, outside hirsute, inside glabrous; bracts 0.4–1 mm long; bracteoles 0.2–0.6 mm long. *Pedicels* 1.9–5.5 mm long, sericeous except for the subsericeous 0.9–3 mm long upper part. *Flowers* 3.5–4 mm in diam. *Sepals* 5, ovate, margin pilose, outside and inside glabrous; 2 outer smaller ones 0.7–2 by 0.8–2.3 mm, margin with glands; 3 inner larger ones 1.8–3.2 by 1.5–3 mm, margin petaloid, at most with few glands. *Petals* 5, ovate to obovate, 1.5–4.2 by 0.7–1.6 mm, claw 0.2–0.5 mm high, margin and usually outside pilose, inside subglabrous, apex acute; scales 1–1.7 mm long, free, basally not

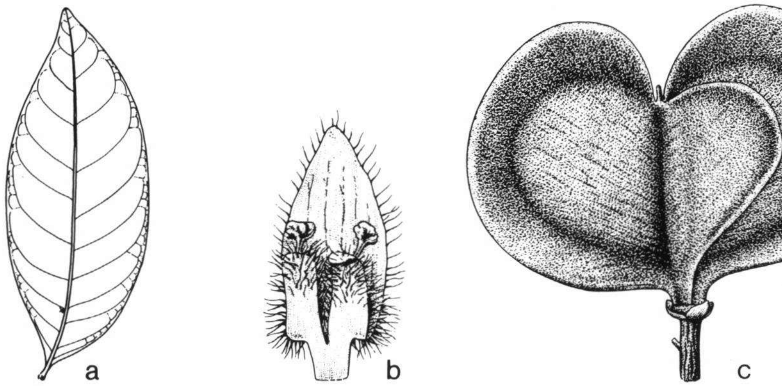


Fig. 120. *Guioa rigidiuscula* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 2 (a, b: *Darbyshire 759*, L; c: *Lauterbach 562*, L).

auricled; crest clavate, stiped, apex lobed. *Disc* incomplete. *Stamens* 8; filament 1.3–3.7 mm long, completely but especially basally pilose; anther 0.6–0.7 mm long, slightly pilose. *Pistil:* ovary 0.3–1.5 mm long, smooth, subhirsute; style and stigma 0.1–1.2 mm long, elongating in fruit up to 3 mm long, then upper c. 0.4 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.1–2.9 cm high by 1.1–3.5 cm broad, smooth to rugose to rugosely ribbed, glabrous, stipe absent to up to 2 mm high, then slender, edge of margin rounded, upper part of margin usually highly convex, lobes almost touching, not parallel to lower margin, angle between lobes 45–135°, blackish when dry; dissepiments complete; lobes 10–18 by 9–22 mm. *Seed* obovoid, c. 8.7 by 5.2 mm; arilloid without or with a small pseudofunicle, but always with a basal rim; hilum c. 1.3 mm long. *Embryo* c. 7.3 by 4.5 mm; cotyledons dorsoventrally above each other, upper larger, apex of upper somewhat elongated, straight; radicle c. 1.6 mm long.

Field notes. Shrub to tree, 2–15 m high, d.b.h. 10–24 cm. Outer bark smooth, blotched variously grey to brown; inner brown; sap red. Wood white to dark cream. Leaves glossy dark green above, paler and duller below. Buds green-white. Flowers faintly fragrant. Sepals, petals, and filaments white. Fruit dull crimson.

Distribution. Irian Jaya (Jayapura); Papua New Guinea (E Sepik, Morobe, Milne Bay, Central, Gulf Prov.).

Ecology. Found in poor lowland rain forest, gallery forest along creek, monsoon forest, garden regrowth, along edge of scrub and eucalypt savannah, road. Alt.: sea-level up to 450(–935) m. Flowering: Aug.–Sept. Fruiting: Jan.

Vernacular names. Ete (Central Prov.); gadzin (Jal: Madang).

Notes. 1. Typical for this species are the elliptic smooth leaflets with a single sac and hardly stiped fruits with highly convex upper margin.

2. *Guioa membranifolia* very much resembles *Guioa rigidiuscula*, but the leaflets are usually thinner and the fruits have a straight upper margin instead of a highly convex one.

3. *Guioa rigidiuscula* is of course part of the *Guioa rigidiuscula*-complex. The differences among the species of this complex are described in chapter 9.

Specimens studied:

IRIAN JAYA. Jayapura: *Beccari Fl 2804*, Humboldt Bay.

PAPUA NEW GUINEA. E Sepik Prov.: *Pullen 1708*, Timbunke. — Morobe Prov.: *Clemens 1746*, *Lauterbach 562*, *Warburg s.n.*, Sattelberg. — Milne Bay Prov.: *LAE (Benjamin) 67935*, Mt. Oiamadawa'a; *(Croft c.s.) 68723*, Gamwabila to Tutubea; *(Croft c.s.) 71089*, Bubuleta Agricultural Station. — Central Prov.: *Anonymous s.n.* (M) Rigo; *Brass 594*, Bisiatabu; *Darbyshire 759*, Kairuku; *Forbes 413*, Sogeri Region; *Goldie s.n.*, Port Moresby; *Heyligers 1380*, Goragatabu Creek; *MacGregor s.n.*, Port Moresby to Kalo; *NGF (Womersley & Simmonds) 5094*, Yule I.; *Pullen 3309*, Goldie River; *3670*, Vanuamai; *Sayer s.n.*, Goberco; *Schodde 2811*, Rigo; *3073*, Laloki River; *UPNG (Pulsford) 227*; *White 707*, Yule I. — Gulf Prov.: *Craven & Schodde 937*, Malalaua.

Guioa scalariformis Welzen – Fig. 121 a–c.

Guioa scalariformis Welzen, Blumea 33 (1988) 420, pl. 20a–c. — Type: *NGF (Sayers) 21576* (L, holo; iso in BM, CANB, U; LAE, n.v.), Papua New Guinea, Morobe Prov., Wagau.

Guioa spec.: Hartley et al., Lloydia 36 (1973) 270 (p.p.: *Hartley 12459*); Streimann, Pl. Upper Watut Watershed (1983) 169 (p.p.: *Hartley 12459*, *NGF 21576*).

Shrub to tree. *Branchlets* terete, smooth, only sericeous when young; flowering twigs 4–5.5 mm thick. *Leaves* 1- or 2-jugate; rhachis 9.3–22.2 cm long, terete, not winged, glabrous, petiole 6–9.5 cm long. *Leaflets* subsessile, subopposite, ovate,

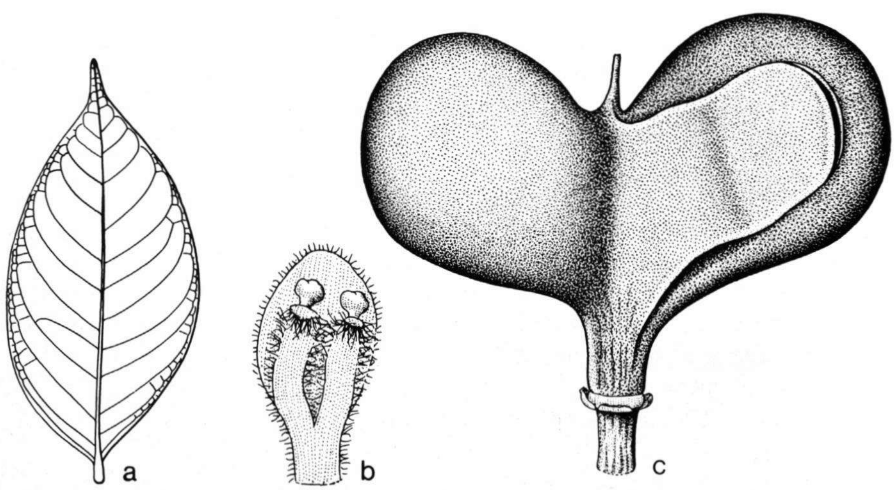


Fig. 121. *Guioa scalariformis* Welzen. a. Leaflet, × 0.25; b. petal, × 12.5; c. fruit, × 3 (a, c: *NGF (Sayers) 21576*, L; b: *Hartley 12459*, L).

11.9–22.7 by 6.1–10.7 cm, index 1.8–2.1, rather symmetric, acroscopic side somewhat broader, subcoriaceous, not punctate; base attenuate; margin entire, flat; apex acuminate to cuspidate, often mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous, domatia absent; venation on upper side flat to raised, raised below; major nerves 0.3–2.9 cm apart, marginally rather looped; veins laxly reticulate to scalariform, very distinct. *Inflorescence* axillary, branching along rhachis; latter flattened to terete when in fruit, 6.1–13.5 cm long, sericeous, glabrescent; first order branches up to 7.8 cm long; cymules cincinnate, c. 3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.7–1 mm long; bracteoles 0.3–0.4 mm long. *Pedicels* 4.2–5.8 mm long, sericeous, except for the glabrous, 1.2–2.5 mm long upper part. *Flowers* c. 4 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1.2–1.9 by 1.8–2.2 mm; 3 larger inner ones 2.4–3.2 by 1.2–2.5 mm, margin petaloid. *Petals* 5, obovate, 2.8–3 by 1.7–2 mm, claw c. 0.5 mm high, margin pilose, outside and inside glabrous, apex obtuse to acute; scales c. 1.8 mm long, free; crest clavate, stiped, apex lobed; petal between two adjacent larger sepals not reduced in size. *Disc* complete. *Stamens* 8: filament 2.5–3.8 mm long, completely but especially basally pilose; anther 0.6–0.7 mm long, glabrous. *Pistil:* ovary c. 0.4 mm long, smooth, subhirsute; style and stigma c. 0.2 mm long, elongating in fruit up to 3.5 mm long, then upper c. 0.5 mm stigmatic. *Fruit* with 2 or 3 well-developed lobes, c. 1.8 cm high by 2.3–2.9 cm broad, slightly ribbed, glabrous, the stipe c. 2.5 mm high, slender, wall less than 1 mm thick at edges, latter rounded, angle between lobes 60–90°, black when dry; dissepiments complete; lobes c. 17 by 12 mm. *Seed* globose, c. 11.2 by 9.8 mm; hilum c. 3 mm long. *Embryo* c. 10.2 by 7.8 mm; cotyledons dorsoventrally above each other, lower larger in size, apex of upper elongated, straight; radicle c. 1.5 mm long.

Field notes. Shrub to tree, 3–10 m high, d.b.h. up to 15 cm. Leaves dark green above, paler below. Sepals greenish white. Petals white. Fruit red.

Distribution. Papua New Guinea (Morobe Prov.: near Wagau).

Ecology. Found in primary midmountain forest. Alt.: 1500–1700 m. Flowering: Dec.

Metabolites. Hartley et al. (1973) record an absence of alkaloids in bark and leaflets (*Hartley 12459*).

Vernacular name. Bacall.

Notes. 1. This species is part of the *Guioa rigidiuscula*-complex. Typical are the large broad leaflets with distinct venation, large petals, and complete disc. The differences with the other species of this complex are discussed in chapter 9.

2. The differences among the species of the *Guioa rigidiuscula*-complex with a complete disc (*Guioa aryterifolia, Guioa molliuscula, Guioa scalariformis,* and *Guioa unguiculata*) are discussed in note 3 under *Guioa aryterifolia.*

Specimens studied:

PAPUA NEW GUINEA. Morobe Prov.: *Hartley 12459,* Mt. Shungol; *NGF (Sayers) 21576,* Wagau.

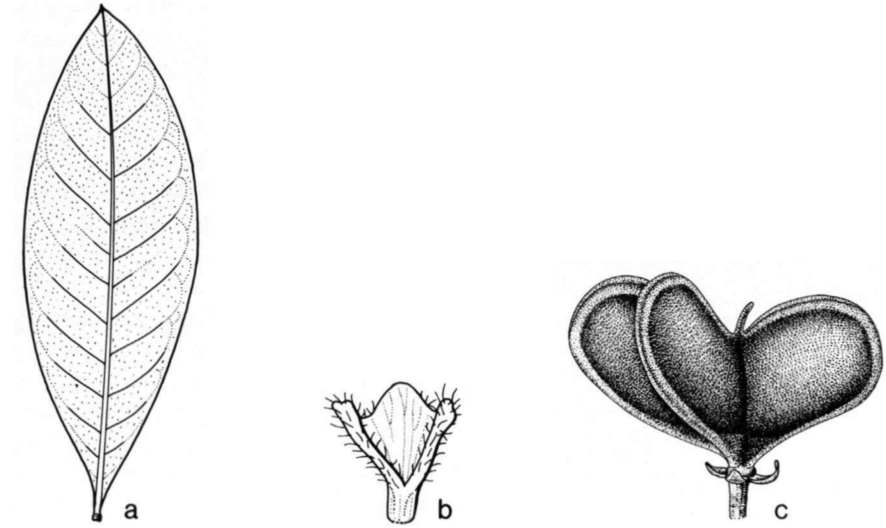


Fig. 122. *Guioa semiglauca* (F. Muell.) Radlk. a. Leaflet, × 1; b. petal, × 12.5; c. fruit, × 3 (a, c: *Everett 324*, BRI; b: *Fraser & Vickery s.n.*, 8-XI-1936, NSW).

Guioa semiglauca (F. Muell.) Radlk. – Fig. 122 a–c.

Guioa semiglauca (F. Muell.) Radlk., Sapind. Holl.-Ind. (1879) 38; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 608; Domin, Bibl. Bot. 22 (1927) 903; Radlk. in Engl., Pflanzenr. 98 (1933) 1160; R.H. Anderson, Trees N.S.W., ed. 2 (1947) 243; Francis, Austr. Rain.-For. Trees, ed. 2 (1951) 21, 249; Beadle et al., Fl. Sydney Reg. (1972) 388; Rotherham et al., Fl. Pl. N.S.W. & S. Queensl. (1975) fig. 298; Beadle, Stud. Fl. NE. N.S.W. 4 (1980) 579, fig. 254c; Veg. Austr. (1981) 147; Reynolds in Stanley & Ross, Fl. S.E. Queensl. 1 (1983) 511, fig. 80a; Austrobaileya 2 (1984) 38, fig. 2d–g; Fl. Austr. 25 (1985) 50, map 59; Fallding & Benson, Cunninghamia 1 (1985) 310. — *Arytera semiglauca* F. Muell., Trans. Philos. Inst. Vict. 3 (1859) 25. — *Cupania semiglauca* F. Muell. in Benth., Fl. Austr. 1 (1863) 457. — *Nephelium semiglaucum* F. Muell., Fragm. 4 (1864) 158; Seem., Fl. Viti. (1865) 46; Bailey, Compr. Cat. Queensl. Pl. (1913) 116. — Type: *Hill & Mueller s.n.* (K, holo), Australia, Moreton Bay.

Tree. *Branchlets* terete, smooth to ribbed to rough, sericeous especially when young; flowering twigs 1–6 mm thick. *Leaves* 1–3-jugate; rhachis 0.8–9.3 cm long, basally terete to dorsoventrally flattened to exceptionally slightly winged especially below the jugae, sericeous, petiole 0.4–4.5 cm long. *Leaflets* subsessile, opposite to alternate, elliptic to obovate, 2.1–11.4 by 0.7–5.8 cm, index 1.6–4.8, usually symmetric, coriaceous, punctate; base attenuate; margin entire (except juvenile leaflets with a few teeth), flat to usually revolute; apex retuse to acute, mucronulate; upper surface smooth, glabrous except for the sometimes puberulous midrib; lower surface differently coloured, dull, papillate, sericeous, domatia absent; venation raised, especially on lower surface; nerves 0.2–2.3 cm apart, marginally looped; veins laxly reticulate, rather indistinct. *Inflorescences* axillary, branching in or near axil and also along rhachis; latter terete, 0.6–8.3(–16.8) cm long, sericeous; first order branches up to 5.4 cm long; cymules cincinnate to usually dichasial, (1–) 3–4(–8)-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.4–1.7 mm long; bracteoles 0.2–1 mm long. *Pedicels* 1–4(–7.2) mm long, sericeous, except for the glabrous, 0.4–1.8 mm long upper part. *Flowers* 2–3 mm in diam. *Sepals* 5 (or 6), broadly ovate to orbicular, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 0.5–1.8 by 0.6–2 mm; 3 (or 4) inner larger ones 1.3–2.5 by 1.2–3 mm, margin petaloid. *Petals* 5, (orbicular to) obovate, 0.5–2 by 0.2–1 mm, claw 0.2–0.7 mm high, margin pilose, outside and inside glabrous, apex obtuse; scales 0.4–1.2 mm long, free; crest absent to slightly developed to clavate on slender stipe, top lobed. *Disc* complete. *Stamens* 8; filament 0.7–3.5 mm long, especially basally pilose; anther 0.3–0.7 mm long, glabrous to sometimes slightly pilose. *Pistil:* ovary 0.3–1 mm high, smooth, sparsely hirsute; style and stigma 0.1–0.2(–1.3) mm high, both elongating up to 2.8 mm in fruit, then upper 0.5–1 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 0.6–1.1 cm high by 0.6–1.4(–1.9) cm broad, smooth to rugose, glabrous, stipe 0–2 mm high, broadly cuneate, angle between lobes 40–135°, blackish when dry; lobes 6–10 by 4–6.5 mm. *Seed* (globose to) obovoid, 4–7.5 by 3–5 mm; hilum 0.8–1.3 mm long. *Embryo* 2–6.4 by 2.7–4.2 mm; cotyledons secondarily laterally besides each other, inequal, upper larger, both apices elongated, apex of lower cotyledon usually recurved over that of upper one; radicle 1.7–2.2 mm long.

Field notes. Tree medium-sized, 3–18 m high, d.b.h. 7.5–25(–150) cm; trunk basally often flanged or fluted; boles may be several; crown spreading to dense. Outer bark smooth, grey; inner pink. Sapwood with wrinkled surface, reddish, light. Leaves dark green above; glaucous green below. Petals white. Anthers red.

Distribution. E Australia: Queensland (S Kennedy, Wide Bay, and Moreton Dist.) and NE New South Wales.

Ecology. Common, found in rain forest areas, especially at margins of forest, along coast, creeks, riverbanks, roads, hillsides. Once recorded as associated with *Baloghia lucida* (Euphorbiaceae) and *Derris involuta* (Leguminosae). Vegetation types: Complex and simple notophyll vine forests. Plant alliances: *Argyrodendron, Ceratopetalum–Diploglottis, Ceratopetalum–Schizomeria,* and *Drypetis* communities. Littoral, *Schizomeria–Doryphora–Ackama* community (Beadle, 1981; Fallding & Benson, 1985). Humidity: high. Soil: granite, basalt, alluvial, clay, sand. Alt.: sea-level up to 1000 m. Flowering: Oct.–Nov. Fruiting: Nov.–Febr.

Vernacular names. Wild quince (British).

Notes. 1. Reynolds (1984) doubted whether *Guioa montana* is a distinct species, as it is difficult to separate from *Guioa semiglauca*. The two are vicariant species: several phenetic differences exist (size of flower and fruit, type of petal, shape of leaflets) and the distribution is disjunct. The distribution correlates with the areas of high humidity (Reader's Digest Atlas of Australia, 1977) and rain forests (Beadle, 1981). *Guioa montana* is found in N Queensland (Cairns and surroundings), while *Guioa semiglauca* is found in a pocket in central Queensland (Mt. Dalrymple) and in S Queensland to central New South Wales.

2. Seemann's suggestion to unite *Guioa glauca* and *Guioa semiglauca* must have been made without a thorough investigation of the material as both species are very distinct: *Guioa glauca* often possesses a domatium, has a different type of (larger) petals, and the fruits are much larger.

S p e c i m e n s s t u d i e d:
AUSTRALIA. Queensland: 39 specimens. — New South Wales: 102 specimens.

Guioa subsericea Radlk. – Fig. 123a–d.

Guioa subsericea Radlk., Bot. Jahrb. 56 (1921) 277; in Engl., Pflanzenr. 98 (1933) 1158; Hartley et al., Lloydia 36 (1973) 270; Streimann, Pl. Upper Watut Watershed (1983) 169 (p.p.: *Hartley 11835*). — L e c t o t y p e (here proposed): *Ledermann 10005* (L; iso in K), NE New Guinea, Mt. Lord, 1000 m. See note 1.
Guioa molliuscula auct. non Radlk.: Hartley et al., Lloydia 36 (1973) 270.
Guioa dasyantha auct. non Radlk.: Streimann, Pl. Upper Watut Watershed (1983) 169.

Shrub to tree. *Branchlets* terete (to somewhat flattened), smooth (to somewhat ribbed or rough), shortly sericeous (to hirsute), especially when young; flowering twigs 1.5–7 mm thick. *Leaves* 1–3-jugate; rhachis 1.2–20 cm long, terete to somewhat flattened below the jugae, not winged, subsericeous (to hirsute), petiole 0.9–9 cm long; petiolules up to 0.9 cm long. *Leaflets* usually not subsessile, opposite to subopposite (to alternate), ovate (to elliptic), 3.5–18.3 by 0.9–9.3 cm, index 1.9–4.3, usually very asymmetric, acroscopic side broader, coriaceous to very coriaceous, usually punctate; base attenuate; margin entire, flat (to revolute), apex gradually (acuminate to) cuspidate to caudate, mucronulate; upper surface smooth, densely pilose when young to subsericeous when older, sometimes wax present; lower surface differently coloured, dull, papillate, (sub)sericeous (to hirsute), domatia absent or a single to many small pocket-like sacs in axils of major nerves; venation on upper side (slightly sunken to) flat (to raised), raised on lower; major nerves 0.2–2.8(–4.2) cm apart, marginally looped, but less distinctly so in lower part of leaflets; veins densely to laxly reticulate, usually distinct *Inflorescences* axillary to pseudoterminal, branching in axil and along rhachis; latter terete, 1–26.6 cm long, sericeous (to hirsute); first order branches up to 10.5 cm long; cymules cincinnate (to dichasial), 2–4(–6)-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.5–2.2 mm long; bracteoles 0.2–1.1 mm long. *Pedicels* (1.2–)2.2–3.6(–6) mm long, sericeous except for the (sub)glabrous, 0.7–2.5 mm long upper part. *Flowers* c. 3 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 0.6–1.8 by 0.6–2.3 mm; 3 inner larger ones 0.8–3 by 1–3 mm, margin petaloid. *Petals* 5, rhomboid to elliptic to obovate, 0.9–2.3 by 0.5–1.6 mm, claw 0.2–0.3 mm high, margin and less so outside pilose, inside (sub)glabrous, apex retuse to rounded; scales present as inwardly folded, adnate auricles of the petal, 0.3–1.2 mm high; crest usually absent, sometimes developed, then clavate, shortly stiped. *Disc* complete. *Stamens* 8; filament 1.2–2.8 mm long, completely but especially basally pilose; anther 0.4–0.6 mm long, glabrous to sparsely pilose. *Pistil:* ovary 0.3–1.2 mm long, smooth, subhirsute; style and stigma 0.2–1.3 mm long, elongating in fruit up to 3 mm long, then upper 0.5 mm stigma-

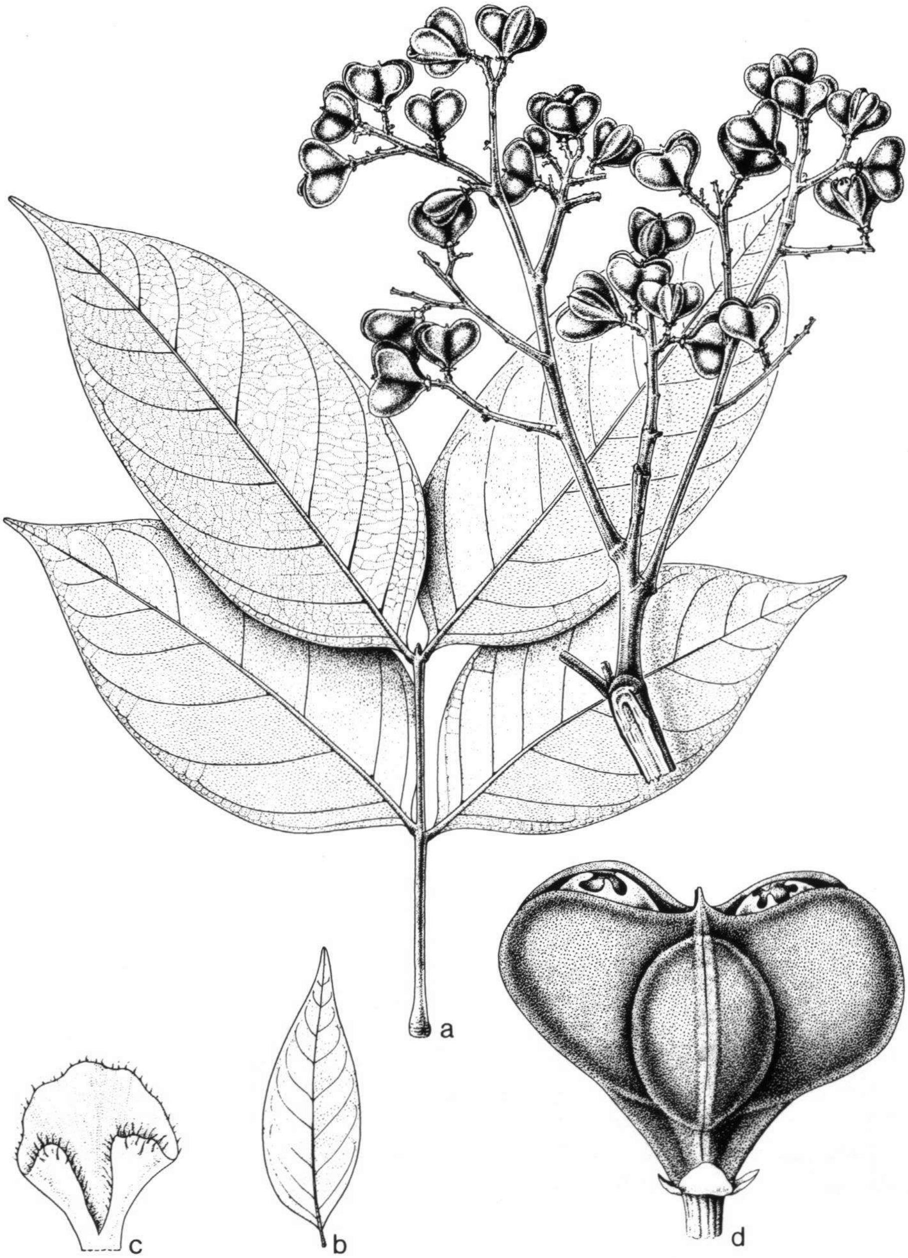


Fig. 123. *Guioa subsericea* Radlk. a. Habit with E New Guinea form of leaflets, × 0.5; b. leaflet of W New Guinea form, × 0.5; c. petal, × 12.5; d. fruit, × 3 (a, d: *ANU (Flenley) 2772*, BRI; b: *BW (Van der Sijde) 4076*, L; c: *NGF (Womersley) 11042*, L).

tic. *Fruit* with 1–3 well-developed lobes, 0.9–1.6 cm high by 0.9–2.4 cm broad, smooth to rugose to slightly ribbed, glabrous, stipe absent to up to 4 mm high, broadly cuneate, indistinct, edge of margin rounded, angle between lobes (55–)90–145(–180)°, usually blackish when dry; dissepiments complete; lobes 7–17 by 5–11 mm. *Seed* (globose to) obovoid, 5.8–7.8 by 3–8 mm; hilum 1–1.2 mm long. *Embryo* 4.2–7 by 3–6.5 mm; cotyledons dorsoventrally above each other, upper larger, apex of upper and sometimes also of lower slightly elongated, straight; radicle 1–3.8 mm long.

Field notes. Shrub to tree, 3–30 m high, d.b.h. 6–50 cm; bole straight. Outer bark usually smooth to longitudinally fissured or finely pustulated, thin, c. 0.5 mm thick, greenish to greyish to reddish brown; underbark c. 8 mm thick, green to yellowish brown; inner bark white to yellowish brown to red-brown, no exudate. Sapwood white, annual rings can be prominent; heartwood brown. Leaves when young light green with reddish rhachis; when old dark glossy green above; paler, dull midgreen to greyish green to glaucous below. Sepals light to midgreen. Petals white to yellow. Filaments white; anthers light pink to purplish red. Ovary midgreen. Fruit pinkish to purplish red when mature; dull brown when old and open. Aril orange.

Distribution. New Guinea: Irian Jaya (Vogelkop, Jayapura); Papua New Guinea (W & E Sepik, Enga, Western Highlands, Chimbu, Southern Highlands, Morobe, Central, Milne Bay Prov.).

Ecology. Occasional to fairly common understorey to sometimes subcanopy tree in lower to midmontane primary forest, in secondary forest and along edges of wood, water and roadsides; often on steep slopes and ridges. Forests often dominated by *Castanopsis, Casuarina, Nothofagus,* and *Pandanus*. Soil: detritus mud, sand, laterite, stony clay or loam; wet. Shade light to medium. Alt.: (70–)1000–3000 m. Flowering: Febr.–July. Fruiting: throughout the whole year.

Metabolites. Hartley et al. (1973) found no alkaloids in the leaflets and bark (*Hartley 11835, 12108*).

Vernacular names. Kombam, palya (W Highlands: Enga); bydie (S Highlands: Tari); milalan.

Notes. 1. *Ledermann 10005* was chosen as lectotype, because all other former syntypes were either not seen (*Ledermann 11456*), had too young buds (*Ledermann 8500*) or were not *Guioa subsericea* (*Ledermann 10365*, type of *Guioa dasyantha*, and *Ledermann 10365a*, both conspecific with *Jagera discolor*).

2. *Guioa subsericea* is distinct by its long-tipped leaflets with on the lower surface a sericeous indumentum and papillae; a complete disc, and the basically broadly cuneate fruits. The species is rather diverse, with some distinct forms which are connected by intermediates. Most obvious is the topocline between W and E New Guinea, with in W as well as in E a reasonably uniform group; mid New Guinea forms the transition zone. Plants in E New Guinea have larger leaflets (3.5–18.3 by 1.4–8.3 cm), usually with longer hairs, and have larger fruits (0.9–1.6 by 1–2.4 cm), while plants in W New Guinea have smaller leaflets (3.6–9.8 by 0.9–3 cm), usually with shorter hairs, and they possess smaller fruits (0.9–1.2 by 0.9–1.4 cm). The overlap already indicates the impossibility to recognize distinct species. Un-

fortunately, mid New Guinea is still very poorly sampled and therefore only a few intermediate specimens are present.

Examples of E New Guinea: *ANU 2031, 2772; Brass 29131; Brass & Versteegh 12505; Carr 13679; Hartley 11835; Hoogland 9265, 9575; Jacobs 8641; Kairo 22; Kostermans 2380; LAE 67755; NGF 11042, 12950, 15683, 17530, 19991, 39707; Schodde 4921.* (*Kanis 1298*, Milne Bay Prov., has short hairs and smaller leaflets. The scales of the petals have a very conspicuous crest.)

Examples of W New Guinea: *BW 1981, 4076; Kostermans & Soegeng 171; LAE 64835; Van Royen & Sleumer 6510.*

Intermediates: *Ledermann 8500* (more or less E New Guinea form), *10005* (± W New Guinea form).

In Morobe and W Highland District (Papua New Guinea) several specimens possess leaflets which are, in a dried condition, very coriaceous and on lower as well as on upper surface of the leaflets very silvery: *ANU 2031, 2772; Brass 29131* (more or less intermediate); *Hartley 11835; Hoogland 9265.*

Guioa subsericea, just like other species of *Guioa*, viz. *Guioa pleuropteris, Guioa chrysea, Guioa villosa*, etc., includes exceptional specimens with a different indumentum. Normally *Guioa subsericea* has a sericeous indumentum, but some specimens are very hirsute and look, at first sight, like a different species. Examples of specimens with a hirsute indumentum: *ANU (Flenley) 2802, Hartley 12108, LAE (Johns et al.) 64835.*

3. *Guioa multijuga* from Irian Jaya remarkably resembles the W New Guinea form of *Guioa subsericea*; however, *Guioa multijuga* always has leaves with more than 3 jugae, the leaflets are almost glabrous below instead of sericeous, and the petals have very different scales, those of *Guioa subsericea* are inwardly folded auricles of the petals, those of *Guioa multijuga* are free scales which are folded outwards.

4. The differences between *Guioa molliuscula* and *Guioa subsericea* are discussed in note 2 under the former; the difference between *Guioa malukuensis* and *Guioa subsericea* are discussed in note 2 under *Guioa malukuensis*; the differentiation between *Guioa comesperma* and *Guioa subsericea* is discussed in note 4 under the first; and note 3 under *Guioa plurinervis* compares *Guioa subsericea* with *Guioa plurinervis, Guioa misimaensis*, and the *Guioa rigidiuscula*-complex.

5. Two specimens of Irian Jaya, *BW 8773* and *(NIFS) bb 30235*, are sterile. The leaflets resemble the velutinous form of *Guioa subsericea*. That latter form, which has long hairs, just like the two sterile ones, is only found in Papua New Guinea. This, together with differences in number of jugae, colour and kind of indumentum, makes it impossible to identify these two specimens as *Guioa subsericea*.

Specimens studied:
NEW GUINEA: 32 specimens.

Guioa sufusana Welzen – Fig. 124a–c.

Guioa sufusana Welzen, Blumea 33 (1988) 420, pl. 16a–c. — Type: *BSIP (Lipaqeto) 3324* (L, holo; iso in K; BSIP, LAE, n.v.), Solomon I., NE Guadalcanal, Rere River, c. 3 miles inland.

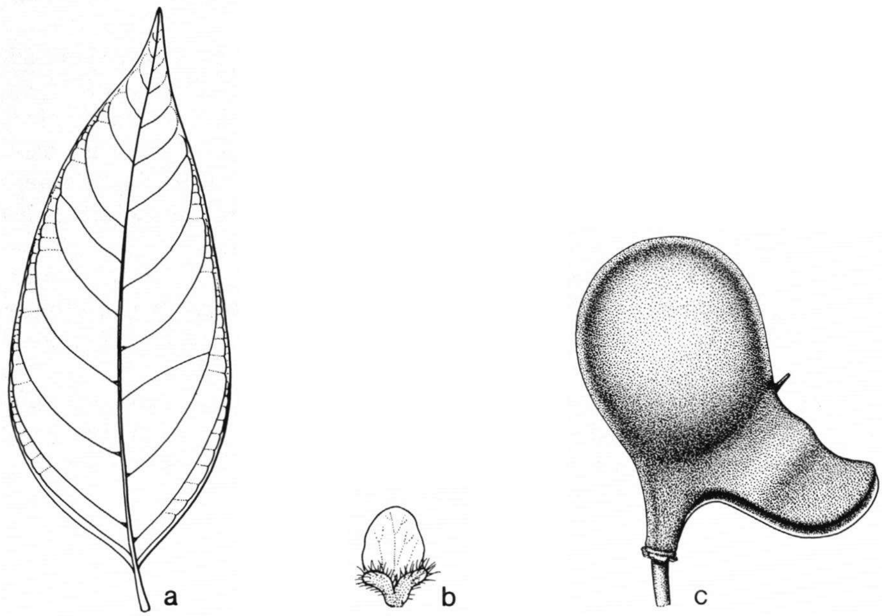


Fig. 124. *Guioa sufusana* Welzen. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 3 (a, c: *BSIP (Gafui et al.) 10975*, L; b: *BSIP (Lipaqeto) 3324*, L).

Tree. *Branchlets* terete, smooth, sericeous especially when young; flowering twigs 2–3.8 mm thick. *Leaves* 1–4-jugate; rhachis 4–22.5 cm long, especially upwards above slightly flattened, not winged, with few appressed hairs, petiole 2.5–10.7 cm long; petiolules up to 1.2 cm long. *Leaflets* usually not subsessile, opposite to subopposite (to alternate), ovate to elliptic, 8.5–18.3 by 2.3–8.4 cm, index 2.1–3.9, ± symmetric to acroscopic side slightly broader, membranaceous to coriaceous, punctate; base attenuate; margin entire, usually flat; apex acuminate (to cuspidate), usually not mucronulate; upper surface smooth, glabrous, midrib basally often puberulous; lower surface differently coloured, dull, papillate, subsericeous, domatia 1 to many small sacs in axils of nerves; venation on upper surface usually flat, on lower raised; nerves 0.6–5 cm apart, marginally looped, but less distinctly so in lower third of leaflets; veins usually laxly reticulate, distinct. *Inflorescences* axillary to pseudoterminal, usually only branching along rhachis; latter somewhat flattened, 2.5–14.4 cm long, subsericeous; first order branches up to 5.8 cm long; cymules cincinnate, 2–4-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.4–1.3 mm long; bracteoles 0.2–0.5 mm long. *Pedicels* 1.5–5 mm long, sericeous except for the glabrous, 0.8–2.7 mm long upper part. *Flowers* c. 3 mm in diam. *Sepals* 5, ovate, margin pilose, outside occasionally with a few hairs, inside glabrous; 2 outer smaller ones 1–1.8 by 0.8–1.8 mm, margin with glands; 3 inner larger ones 1.5–2.4 by 1.3–2.8 mm, margin petaloid, at most with few glands. *Petals* 5, elliptic, 0.7–1.3 by 0.5–0.8 mm, claw c. 0.1 mm high, margin pilose, outside and inside glabrous, apex rounded to obtuse; scales 0.1–0.5 mm long, free, relatively broad, apex not broadened; crest absent; petal between two adjacent larger sepals usually not reduced. *Disc* complete. *Stamens* 8; filament 0.7–2.6 mm long, especially basally pilose; anther 0.3–0.5 mm long, glabrous. *Pistil:* ovary 0.3–0.8 mm high, very sparsely hirsute; style and stigma 0.2–0.8 mm high, elongating in fruit up to 2 mm, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.3–1.5 cm high by 1.6–2.1 cm broad, smooth (to somewhat ribbed), glabrous, stipe 2–4 mm high, slender, angle between lobes 95–125°, blackish when dry; lobes 10–13 by 8–9.5 mm. *Seed* obovoid, 9.5–9.8 by 7.7–8 mm; hilum 1.6–1.8 mm long. *Embryo* 7.2–7.8 by 6.3–6.7 mm; cotyledons dorsoventrally above each other, upper larger, apices elongated, straight; radicle 3.2–3.5 mm long.

Field notes. Tree, 3–17 m high, d.b.h. 15 cm up to 1 m; bole straight to crooked, no buttresses. Bark light to dark green to grey, thin, soft (to hard). Wood white to straw to whitish brown to red, soft to hard. Rhachis yellow-green; leaflets below glaucous to slightly silvery. Buds white. Flowers without smell to scented. Sepals and petals white. Fruits red.

Distribution. W Solomon Islands: Guadalcanal, Kolombangara, Malaita, New Georgia, San Christobal, Santa Ysabel.

Ecology. Common in well drained forest found from along beaches up to ridge tops. Alt.: sea-level up to 1200 m. Flowering: almost throughout the whole year. Fruiting: Sept.–Nov.

Vernacular names. Sufusana, subusane (Kwara'ae: also used for *Guioa elliptica* and *Guioa megacarpa*). Guadalcanal: urukaki.

Note. See also the note under *Guioa elliptica*.

Specimens studied:

SOLOMON ISLANDS. Guadalcanal: *BSIP (Lipaqeto) 3324*, Rere River; *BSIP (Nakisi) 8099*, Tina River; *Kajewski 2570*, Vulolo, Mt. Tutuve. — San Cristobal: *BSIP (Whitmore) 4376*, Wairaha River; *BSIP (Gafui et al.) 10975*, Namunga; *BSIP (Gafui et al.) 11037*, Anganawai; *BSIP (Gafui et al.) 12773*, Maro'u Bay. — Santa Ysabel: *BSIP (Beer et al.) 6704*, Binusa. — New Georgia: *BSIP (Burn-Murdoch et al.) 6994*, Gevala River. — Kolombangara: *BSIP (Mauriasi et al.) 8604*, Kokove; *BSIP (Mauriasi et al.) 11528*, Shoulder Hill. — Small Malaita: *BSIP (Gafui et al.) 16381*, Anihonota'a Area, *BSIP (Gafui et al.) 16993*, Palasu'u Area.

Guioa truncata Radlk. – Fig. 125 a, b.

Guioa truncata Radlk., Elmer Leafl. Philip. Bot. 5 (1913) 1611; Philip. J. Sc. 8, Bot. (1913) 446; Merr., En. Philip. 2 (1923) 509; Radlk. in Engl., Pflanzenr. 98 (1933) 1171; Salvosa, Lex. Philip. Pl. (1963) 105. — Type: *Elmer 11219* (M, holo; iso in A, BM, F, FI, K, L, NY, U, W), Philippines, Mindanao, Davao Dist., Mt. Apo.

Tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 2–3 mm thick. *Leaves* 2–3-jugate; rhachis 2–10 cm long, basally terete to upwards flattened above, slightly winged, glabrous, petiole 1.9–3.8 cm long. *Leaflets* subsessile, opposite to subopposite, elliptic, 3.4–7.6 by 1.3–2.6 cm, index 2.6–3, asymmetric, acroscopic side broader, coriaceous, punctate; base attenuate; margin entire,

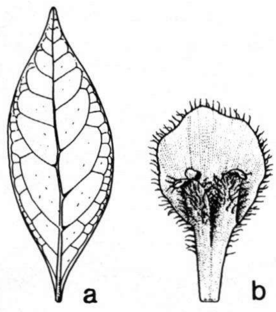


Fig. 125. *Guioa truncata* Radlk. a. Leaflet, × 0.5; b. petal, × 12.5 (*PNH (Sulit) 10053*, L).

flat; apex acuminate, mucronulate; upper surface smooth, glabrous except sometimes for the puberulous midrib; lower surface differently coloured, duller, smooth, no papillae, glabrous to slightly pilose near domatia, latter a single to many sacs in axils of major nerves; venation raised; nerves 0.4–1.6 cm apart, marginally looped; veins laxly reticulate, distinct. *Inflorescences* axillary, branching in or near axil to usually along rhachis; latter flattened, 4.3–15.4 cm long, subsericeous; first order branches up to 4.2 cm long; cymules cincinnate, c. 3-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts c. 0.8 mm long; bracteoles 0.3–0.7 mm long. *Pedicels* c. 3.3 mm long, sericeous except for the subglabrous 1–1.8 mm long upper part. *Flowers* c. 3 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1.4–1.6 by 1–1.3 mm; 3 inner larger ones 2–3.1 by 1.8–2.6 mm, margin petaloid. *Petals* 5, obovate, c. 2.1 by 1.4 mm, blade orbicular, abruptly clawed, latter c. 0.7 mm high, margin pilose, apex rounded; scales c. 0.8 mm long, free; crest present as a flat subglabrous part of the slightly bifid scale apex. *Disc* incomplete. *Stamens* 8; filament 2.9–3.1 mm long, completely but especially basally pilose; anther c. 0.5 mm long, glabrous. *Pistil:* ovary c. 0.7 mm long, smooth, subhirsute; style and stigma c. 0.2 mm long. *Fruit* immature.

Field notes. Tree, 5–7 m high, d.b.h. 10–15 cm. Bark dull brown, smooth. Sapwood whitish, rather hard, odourless, tasteless; heartwood reddish brown. Twigs moderately short, forming bushes, suberect. Leaflets ascending, slightly recurved, nearly flat, coriaceous, shiny green above, much paler green beneath. Infructescence erect, stalks yellowish green. Flowers white. Fruits green and slightly glaucous when immature.

Distribution. Philippines (Mindanao).

Ecology. In dense moist forests and mossy forests. Alt.: 1300–2300 m. Flowering: March.

Vernacular names. Kaninging (Mangyan); caricir-tababana.

Notes. 1. Typical for this species are the smooth glabrous lower surface of the leaflets, which have one to several large sacs; the petals have a short stipe and an almost orbicular blade. The other Philippine species (except *Guioa myriadenia*) have elliptic to obovate blades.

2. The specimen *PNH 118626 (Guioa koelreuteria)* looks like *Guioa truncata*; however, the venation is not as distinct, the leaflets are narrower and do not possess large sacs. Specimens of *Guioa koelreuteria* have at most 1 large sac, not several as *Guioa truncata* usually has.

Specimens studied:

PHILIPPINES. Mindanao: *Elmer 11219*, Davao Prov., Todaya, Mt. Apo; *PNH (Sulit) 10053*, Bukidnon Prov., Mt. Katanglad.

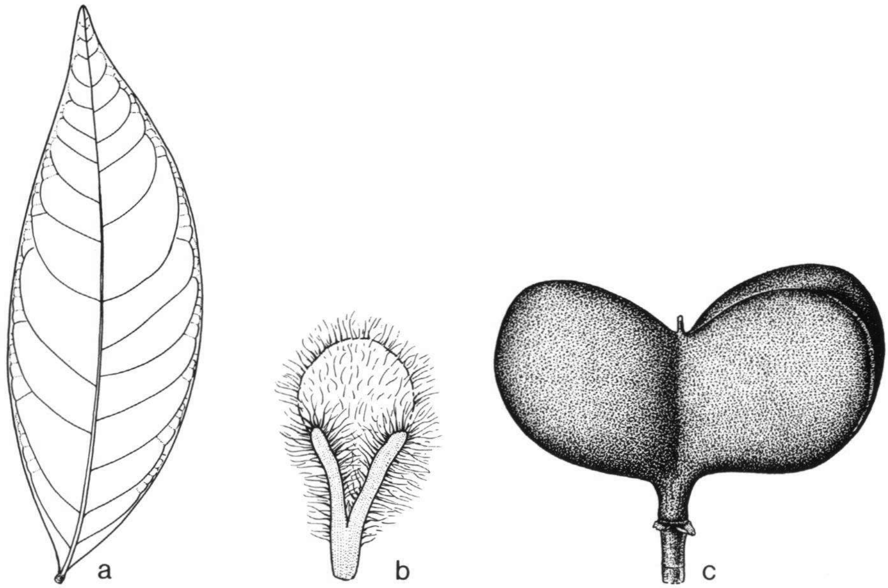


Fig. 126. *Guioa unguiculata* Welzen. a. Leaflet, × 0.5; b. petal, × 12.5; c. fruit, × 1.5 (a, b: *Vink 16407*, L; c: *Hartley 12670*, BRI).

Guioa unguiculata Welzen – Fig. 11, 126 a–c.

Guioa unguiculata Welzen, Blumea 33 (1988) 420, pl. 18a–c. — Type: *Vink 16407* (L, holo; iso in BRI, K, NSW, P; LAE, n.v.), Papua New Guinea, Western Highlands, Uinba.
Guioa membranifolia auct. non Radlk.: Hartley et al., Lloydia 36 (1973) 270.

Tree(let). *Branchlets* terete, smooth (to slightly rough), only sericeous when young; flowering twigs 3–7 mm thick. *Leaves* 1–3-jugate; rhachis 2–15.8 cm long, terete, not winged, glabrous, petiole 1.4–6.9 cm long. *Leaflets* subsessile, subopposite to alternate, elliptic, 6.3–17 by 1.9–6.5 cm, index 2.3–3.7, slightly asymmetric, acroscopic side broader, (sub)coriaceous, usually punctate; base attenuate; margin entire, flat; apex acuminate to caudate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous (to very sparsely sericeous), except sometimes for a few hairs on venation, domatia absent; venation on upper side flat, raised below; major nerves 0.3–2.9 cm apart, marginally looped, but less distinctly so in lower part of leaflets; veins laxly reticulate, rather indistinct. *Inflorescence* axillary to ramiflorous, branching in axil and along rhachis; latter flattened to terete when in fruit, 2.2–8.5 cm long, subsericeous; first order branches up to 2.3 cm long; cymules cincinnate, 2–4-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.5–1 mm long; bracteoles 0.6–0.7 mm long. *Pedicels* 2.8–6.2 mm long, sericeous except for the glabrous 1.8–3.2 mm long upper part. *Flowers* c. 4 mm in diam. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1.2–2 by 1.5–2 mm; 3 larger inner ones 2–2.8 by 1.6–2.9 mm, margin petaloid. *Petals* 5, obovate, 2–3.2 by 1–1.5 mm, claw c. 0.8 mm high, margin pilose, outside and inside subpilose, apex rounded, somewhat fimbriate; scales 1.2–1.5 mm long, resembling folded margins; crest usually absent, sometimes some scales with the crest present as a bifid apex of the scales; petal between two adjacent larger sepals not reduced in size. *Disc* (nearly) complete. *Stamens* 8; filament 2–3 mm long, completely but especially basally pilose; anther 0.4–0.6 mm long, glabrous. *Pistil:* ovary 0.4–1.5 mm long, smooth, subhirsute; style and stigma 0.2–1.5 mm long, elongating in fruit up to 2 mm long, then upper c. 0.4 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 1.5–2.2 cm high by 2–2.7 cm broad, smooth to slightly rugose, stipe 2–3.3 mm high, slender, wall less than 1 mm thick, edge of margin rounded, angle between lobes 95–110°, black when dry; dissepiments complete; lobes 13–18 by 8.5–12 mm. *Seed* not fullgrown.

Field notes. Tree(let), 5–20 m high; d.b.h. up to 15 cm. Outer bark smooth, c. 3 mm thick, greyish green to dark grey; inner bark straw coloured. Wood straw coloured. Leaves dark green on both sides. Calyx light green. Corolla white. Disc ochre-green. Filaments white; anthers very light pink. Pistil green.

Distribution. Papua New Guinea (Western Highlands, Madang, Morobe Prov.).

Ecology. Found in open forest, oak forest, old secondary forest. Alt. 1200–1900 m. Flowering: Aug.–Sept. Fruits eaten by birds.

Metabolites. Hartley et al. (1973) record an absence of metabolites in bark and leaflets (*Hartley 12670*).

Vernacular names. Maakke (Hagen-Chimbu: Yoowi); hatado (Madang Prov.).

Notes. 1. This species is outstanding in the shape of the long-clawed petals with folded, apically bifid scales, in the (nearly) complete disc, and in the leaflets which are, on the lower side, smooth, without papillae or domatia, and which have a strongly raised venation. The differences with the other species of the *Guioa rigidiuscula*-complex are discussed in chapter 9.

2. The differences between the species of the *Guioa rigidiuscula*-complex with a complete disc (*Guioa aryterifolia, Guioa molliuscula, Guioa scalariformis,* and *Guioa unguiculata*) are discussed in note 3 under *Guioa aryterifolia.*

Specimens studied:

PAPUA NEW GUINEA. Western Highlands Prov.: *Hoogland & Pullen 6193,* Upper Wahgi Valley, Komun-Pin Divide E of Korn; *Vink 16407,* Uinba. — Madang Prov.: *Jackson 109,* Yhal, Simbai. — Morobe Prov.: *Hartley 12670,* Bakaia, c. 15 miles SE of Garaina.

Guioa venusta Radlk. – Fig. 127 a, b.

Guioa venusta Radlk., Sapind. Holl.-Ind. (1879) 11, 40; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 609; Bot. Jahrb. 56 (1921) 280; in Engl., Pflanzenr. 98 (1933) 1160. — Type: *Beccari Fl 2813* (FI, holo, cited by Radlkofer as *Beccari 5'*), New Guinea, Tobi I. (= Japen I.), near Surui.

Small tree. *Branchlets* terete, smooth, sericeous when young; flowering twigs 2.5–3 mm thick. *Leaves* 4–9-jugate; rhachis 1.5–12.2 cm long, terete, slightly winged, wing up to at most 0.5 mm broad, subsericeous, petiole 1.3–2.4 cm long. *Leaflets* subsessile, opposite to alternate, elliptic, 1.8–6.5 by 0.6–2 cm, index 2.2–3.3, asymmetric, acroscopic side broader, subcoriaceous, punctate; base attenuate to cuneate; margin entire except for some subapical teeth, flat to slightly revolute; apex acuminate, mucronulate; upper surface smooth, glabrous except for the basally puberulous midrib; lower surface differently coloured, duller, smooth, no papillae, glabrous to slightly sericeous, domatia many pockets to sac-like pockets in axils of major nerves; venation on upper side slightly sunken to flat, raised below; nerves 0.2–1.2 cm apart, marginally looped; veins laxly to densely reticulate, rather distinct. *Inflorescences* axillary, not branching to branching in axil and along rhachis; the latter terete, 1.9–5.4 cm long, pilose; first order branches up to 3.4 cm long; cymules cincinnate, c. 4-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.3–0.6 mm long; bracteoles 0.3–0.4 mm long. *Pedicels* 0.8–3 mm long, sericeous; upper part less pilose, 0.6–1 mm long. *Flowers* in bud. *Sepals* 5, ovate, margin pilose, with glands, outside and inside glabrous; 2 outer smaller ones 1.1–1.5 by 0.7–1.1 mm; 3 inner larger ones 1.4–1.8 by 1.3–1.5 mm, margin petaloid. *Petals* 5, immature, 0.2–1.1 by 0.1–0.2 mm, no distinct claw yet, margin pilose, outside and inside glabrous; scales slightly developed, free; crest (still) absent. *Disc* complete. *Stamens* 8; filament 1.7–2.2 mm long, pilose in lower half; anther c. 0.3 mm long, glabrous. *Pistil:* ovary c. 0.2 mm long, smooth, subhirsute; style and stigma c. 0.1 mm long, elongating in fruit up to 1.5 mm long, then upper c. 0.4 mm stigmatic. *Fruit* with 1 or 2 well-developed lobes, 0.7–0.8 cm high by 0.6–0.9 cm broad, smooth to slightly rugose, glabrous, stipe 2–2.2 mm high, slender, edge of margin rounded, angle between lobes 100–110°, blackish when dry; dissepiments complete; lobes 4–6 by 3.8–4.3 mm. *Seed* immature.

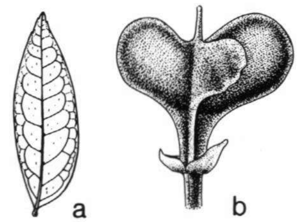


Fig. 127. *Guioa venusta* Radlk. a. Leaflet, × 0.5; b. fruit, × 3 (*Britton 58*, L).

Field notes. Treelet, 2–2.5 m high. Flowers white.

Distribution. Irian Jaya (Schouten I.: Biak and Japen I).

Ecology. On flat terrain, in secondary scrubby vegetation. Alt.: c. 60 m. Flowering: April.

Notes. 1. The type of *Guioa venusta* of Japen I. is somewhat different from the specimens from Biak I.; it has smaller leaflets (1.8–3.9 by 0.6–1.2 cm, against 2.9–6.5 by 0.6–2 cm), more jugae (6–9, against 4 or 5), and the petiole is more densely sericeous.

2. *Guioa venusta* looks like *Guioa patentinervis* of the Moluccas (same shape of leaflets, smoothness, small fruits, reduced petals); however, the rhachis of *Guioa venusta* is slightly winged and the leaflets are subapically serrate.

3. *Guioa venusta* differs in the following characters from *Guioa amabilis*:

	Guioa venusta	*Guioa amabilis*
Margin of leaflets	serrate	crenate
Apex of leaflets	acuminate	emarginate to acute
Papillae	absent	present
Domatia	many	absent
Petals*	0.2–1.1 mm long*	1.8–1.9 mm long
Nail of fruit	slender	broadly cuneate

* Petals only known of young flowers.

Specimens studied:
NEW GUINEA. Irian Jaya, Geelvink Bay Dist.: *Beccari FI 2813*, Japen I.; *Britton 54, 58*, Schouten I., Biak I.

Guioa villosa Radlk. – Fig. 128 a–d.

Guioa villosa Radlk., Sapind. Holl.-Ind. (1879) 39, 40; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 613; Guillaumin & Beauvis, Ann. Soc. Bot. Lyon 38 (1914) 86; Guillaumin, J. Arn. Arbor. 7 (1926) 93; Bull. Soc. Bot. Fr. 79 (1932) 337; Radlk. in Engl., Pflanzenr. 98 (1933) 1171; Guillaumin, Fl. Nouv.-Caléd. (1948) 199; & Virot, Mém. Mus. Nat. Hist. Nat. B, 4 (1953) 18; Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 8 (1959) 135; J. Agr. Trop. Bot. Appl. 11 (1964) 95; Guillaumin et al., Un. Iowa Stud. Nat. Hist. 20, 7 (1965) 36; Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 15 (1967) 111; Morat et al., Bull. Mus. Nat. Hist. Nat. 4e sér., 8, B (1986) 174. — [*Cupania villosa* Panch. & Séb. in Séb., Not. Bois Nouv.-Caléd. (1874) 270, nom. nud.] — *Guioa villosa* Radlk. f. *dasyclados* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 613, nom. illeg. (I.C.B.N. art. 26.1); in Engl., Pflanzenr. 98 (1933) 1171. — *Guioa villosa* Radlk. f. *villosa*: Guillaumin et al., Un. Iowa Stud. Nat. Hist. 20, 7 (1965) 36. — Lectotype (here proposed): *Vieillard 211*, p.p., 1861–67 (M, holo; iso in P), New Caledonia, Wagap. See note 1.

Guioa villosa Radlk. f. *subsericea* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 613; in Engl., Pflanzenr. 98 (1933) 1171; Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 8 (1959) 135; Guillaumin et al., Un. Iowa Stud. Nat. Hist. 20, 7 (1965) 36. — Lectotype (here proposed): *Balansa 159b* (M, holo; iso in K, P), New Caledonia, Prony.

Guioa collina (Panch. & Séb.) auct. non Schltr.: Schltr., Bot. Jahrb. 39 (1907) 175, p.p., *Cupania collina* Panch. & Séb. excluded; Guillaumin, Bot. Syst. 1 (1909) 329, p.p., *Cupania collina* Panch. & Séb. excluded.

Guioa crenulata auct. non Radlk.: Guillaumin et al., Un. Iowa Stud. Nat. Hist. 20, 7 (1965) 36; Guillaumin, Mém. Mus. Nat. Hist. Nat. B, 15 (1967) 110.

Shrub to tree. *Branchlets* terete, smooth, long sericeous to usually loosely appressedly to patently hirsute; flowering twigs 1–4 mm thick. *Leaves* 1–6(–9)-jugate; rhachis 0.3–11.8 cm long, terete to somewhat flattened, not (to slightly) winged, (long sericeous to) hirsute, petiole 0.2–3 cm long. *Leaflets* subsessile, opposite to subopposite (to alternate), ellliptic to obovate, 0.5–7.5 by 0.3–2.8 cm, index 1.1–3.9, usually slightly asymmetric, the acroscopic side broader, (coriaceous to) very coriaceous, usually punctate; base attenuate; margin entire (to crenate to serrate), revolute; apex retuse to acute, exceptionally mucronulate; upper surface smooth, (sericeous to) obliquely to patently hirsute, especially on the venation; lower surface

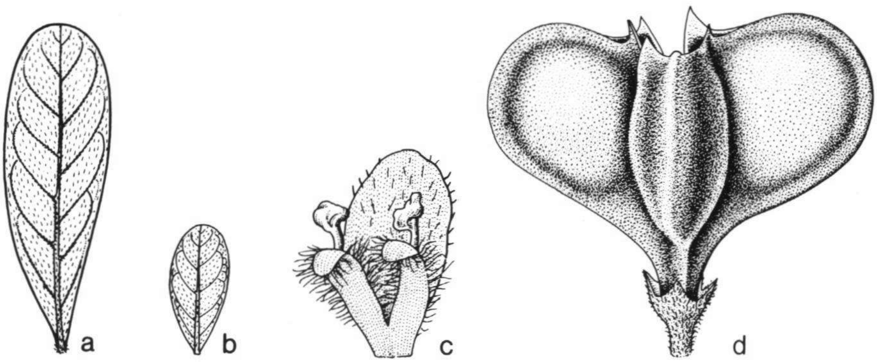


Fig. 128. *Guioa villosa* Radlk. a. Leaflet, × 1; b. leaflet, × 1; c. petal, × 12.5; d. fruit, × 3 (a, d: *MacKee 16248*, L; b: *Grunow s.n.*, IX-1884, M; c: *MacKee 3173*, L).

usually differently coloured, dull, papillate, (exceptionally short to long sericeous to) hirsute, domatia (exceptionally a single sac to) many large to often very shallow pockets; venation on upper surface flat to raised, below raised; nerves 0.1–1.3 cm apart, marginally looped; veins densely reticulate, rather indistinct. *Inflorescences* axillary, mainly branching along rhachis, seldom in or near axil; rhachis terete, 0.7–18 cm long, usually hirsute; first order branches up to 5.2 cm long; cymules cincinnate, (1–)2–3(–5)-flowered. *Bracts* and *bracteoles* triangular, outside sericeous, inside subglabrous; bracts 0.5–2.3 mm long; bracteoles 0.2–1.1 mm long. *Pedicels* 1.3–6 mm long, densely pilose except for the often somewhat less pilose, 0.7–3 mm long upper part. *Flowers* 2–3 mm in diam. *Sepals* 5, dimorph, exceptionally almost equal, completely sericeous, margin with glands; 2 outer smaller ones triangular, 0.7–2.2 by 0.7–1.9 mm; 3 inner usually larger ones more obovate, 1.3–3.2 by 0.9–3 mm, margin petaloid. *Petals* 5, elliptic (to obovate), sometimes reduced in size, 0.8–3 by 0.4–1.5 mm, claw 0.1–0.3 mm high, margin pilose and sometimes outside too, inside subglabrous, apex rounded to obtuse; scales 0.3–1.6 mm long, free, in reduced petals less developed; crest absent to about linear to clavate on a thin stipe, glabrous. *Disc* incomplete, although gap sometimes minute (if gap distinct, then indumentum hirsute in some part). *Stamens* 8; filament 0.8–4 mm long, especially basally pilose; anther 0.2–0.7 mm long, glabrescent. *Pistil:* ovary 0.2–2 mm high, smooth, densely hirsute; style and stigma 0.1–2.3 mm high, both elongating up to 3 mm in fruit, then upper c. 0.5 mm stigmatic. *Fruit* with 1–3 well-developed lobes, 0.8–1.6 cm high by 1–1.8 cm broad, smooth (to rough), glabrescent, stipe 1–5 mm high, relatively slender, angle between lobes 90–150°, blackish when dry; lobes 7–11 by 6.5–10 mm. *Seed* obovoid, 6.2–8.9 by 4.4–5.7 mm; hilum 0.6–1.6 mm long. *Embryo* 5–7.3 by 3–4.8 mm; cotyledons secondarily laterally besides each other, about equal in size, apices elongated, that of lower recurved and sometimes that of upper too; radicle 1.5–2.5 mm long.

F i e l d n o t e s. Shrub to tree, 1–8 m high, d.b.h. up to 30 cm; branches almost vertical. Outer bark slightly rough, brown to grey to blackish. Wood light pink to reddish. Leaflets green above; glaucous, grey-green below. Buds greenish white. Flowers sweet scented. Petals (and sepals?) white to pink, crests or scales yellow. Filaments white; anthers pink. Fruit yellow to brown; arilloid yellow to orange; seed black.

D i s t r i b u t i o n. New Caledonia.

E c o l o g y. Common in scrubs. Found in open to dense (montane) forest, along streams, forest margin. Soil: sediments (schist), ultrabasic (serpentine), lateritic, and vulcanic soils. Alt.: sea-level up to 1300 m. Flowers frequented by bees; nectar of high quality. Flowering: (July–)Sept.–Oct.(–Febr.). Fruiting: Jan.–Aug.

N o t e s. 1. Guillaumin et al. (1965) have chosen the forma *dasyclados* as the form containing the type of the species, therefore the epitheton *dasyclados* is illegitimate and should be *villosa.*

2. The difference between *Guioa glauca* and *Guioa villosa* is very constant. On the lower side of the leaflets *Guioa glauca* always has short appressed hairs and none or one sac-like domatium, while *Guioa villosa* has longer (subappressed to) half-patent to patent hairs and many pocket-like domatia (sometimes a few leaflets per plant with 1 domatium, but there will always be leaflets with 2 or more domatia). Both species are presumably closely related; they occur in the same habitats; both have specimens with more or less reduced petals, and on Mt. Koniambo they very much look alike (see remark below *Guioa glauca*). Both species, together with *Guioa crenata* and *Guioa crenulata,* have leaflets which are below densely papillate (looking greyish). Some specimens of *Guioa villosa* tend to look like the latter two species (see below).

3. *Guioa villosa* is a very variable species. The following forms are all united by transitions, no delimitations were possible.

a) The leaflets can be very small (examples: *MacPherson 5402; Thorne 28050; Vieillard 212*) to relatively large (examples: *Balansa 1452; Boucher 1447; Guillaumin & Baumann-Bodenheim 15534*); with a flat margin (examples: *Balansa 1452; Guillaumin 9829; Vieillard 211*) to completely revolute (examples: *Boucher 1488; Franc 2362; Guillaumin & Baumann-Bodenheim 15534*).

b) Radlkofer distinguished two forms (for examples see types): *subsericea* with smaller leaflets and sericeous indumentum, and *dasyclados* with larger leaflets and hirsute indumentum. These two forms appeared to be extremes of a continuous range of forms. The *dasyclados* type is mainly found in the Southeast of New Caledonia, around Noumea; the *subsericea* type all over New Caledonia.

c) Just like *Guioa glauca* var. *glauca* some plants of *Guioa villosa* also have flowers with more or less reduced petals; these petals are smaller and the scales often lack a crest or the crest is linear instead of clavate. However, contrary to *Guioa glauca,* no delimitation could be made within *Guioa villosa.* The specimens with non-reduced petals are more common on serpentine soils, just as with *Guioa glauca* (var. *vulgaris* 'group 1').

d) On the Tiebaghi Range specimens of *Guioa villosa* are rather peculiar: the leaflets are very small, many-jugate, rather glabrous, the margin is crenate, and the rhachis is slightly winged. Examples are *MacPherson 3304, 6198; Thorne 28050; Virot 1269, 1284*. Comparable specimens from another part of the island (Canala to Thio), only less jugate, are *Grunow s.n.*, IX-1884; *Hodgson 90, MacPherson 5402,* and *Thorne 28401*. The Tiebaghi specimens as well as the Canala specimens rather look like *Guioa crenata,* only the latter species has appressed short hairs on the lower surface of the leaflets, very small flowers, hardly dimorphic sepals without a petaloid margin, and a complete disc (*Guioa villosa* has subappressed to patent long hairs, large flowers, dimorphic sepals with a petaloid margin, and a usually incomplete disc).

e) *MacPherson 2956* looks very much like *Guioa crenulata,* but the leaves lack the winged rhachis, have many domatia instead of none, and are hirsute instead of sericeous. *MacPherson 2956* is also found in the same region as *Guioa crenulata*; perhaps it is a hybrid, although the abundance of flowers may indicate otherwise.

f) *Guioa glauca*-like specimens are known from Mt. Koniambo (see note 1 under *Guioa glauca*; *MacKee 4296; Webster & Jaffré 19263*); from Fort Plate (*Bernardi 10162, 10163*); Col de Vulcain (*Baumann-Bodenheim 15534*); Col de Plum (*Guillaumin & Baumann-Bodenheim 7899*); and from Tontouta (*MacKee 5446; Whaite 3938/4*).

g) *Brousmiche s.n.* (P) has a complete disc, other specimens sometimes have discs with a minute gap.

h) In the two possibly juvenile specimens (*Gaillard s.n.* in P and *Guillaumin & Baumann-Bodenheim 12288*) the leaflets lack papillae below.

Specimens studied:
NEW CALEDONIA: 220 specimens.

Guioa waigeoensis Welzen – Fig. 129a, b.

Guioa waigeoensis Welzen, Blumea 33 (1988) 420, pl. 19a, b. — Type: *P. van Royen 5409* (L, holo), W Irian Jaya, Waigeo I., Kambele hills, SE of Kabare.
Arytera xerocarpa auct. non Adelb.: P. van Royen, Nova Guinea 5 (1960) 60.

Small tree. *Branchlets* terete, smooth, sericeous, especially when young; flowering twigs c. 1 mm thick. *Leaves* 3- or 4-jugate; rhachis 0.4–3.7 cm long, flattened above, slightly winged (wing less than 1 mm broad), subsericeous, petiole 0.4–0.8 cm long. *Leaflets* subsessile, opposite to subopposite, elliptic, 1.3–2.4 by 0.4–0.6 cm, index 3.3–4, rather symmetric, coriaceous, punctate; base attenuate; margin at least in some leaflets slightly serrate, revolute; apex acute, mucronulate; upper surface smooth, subsericeous; lower surface differently coloured, dull, papillate, shortly sericeous, domatia in at least some leaflets a single, rather small sac on basiscopic side in axil of second major nerve; venation flat to slightly raised on lower side; nerves 0.2–0.4 cm apart, marginally looped; veins densely reticulate, indistinct. *Infructescences* axillary, not or at most branching along rhachis; latter flattened, 1.2–2 cm long, sericeous; first order branches up to 0.6 cm long. *Bracts* and *bracteoles* triangular, outside sericeous, inside glabrous; bracts 0.6–0.7 mm long; bracteoles c. 0.3 mm long. *Pedicels* c. 5.8 mm long, sericeous, except for the glabrous, 2–2.2 mm long upper part. *Flowers* unknown. *Sepals* 5, ovate, margin pilose, glands unknown, outside and inside glabrous; 2 outer smaller ones c. 1.8 by 1.3–1.9 mm; 3 inner larger ones 2–2.4 by 1.7–2.4 mm, margin petaloid. *Petals* unknown. *Disc* complete. *Stamens* and *pistil* unknown. *Fruit* with 1–3 well-developed lobes (see also note 3), c. 1.2 cm high by 1.2 cm broad, smooth to slightly rugose, glabrous, stipe c. 3 mm high, rather slender, edge of margin rounded, angle between lobes c. 100°, blackish when dry; dissepiments complete; lobes c. 8 by 7 mm. *Seed* immature.

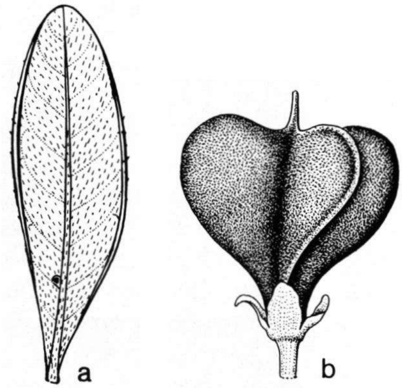


Fig. 129. *Guioa waigeoensis* Welzen. a. Leaflet, × 3; b. Young fruit, × 3 (*Van Royen 5409*, L).

Field notes. Small tree, about 4 m high, d.b.h. 5 cm. Leaves dark green greyish green below. Flower white. Fruit yellowish green when immature, black when mature.

Distribution. W Irian Jaya, Waigeo I.

Ecology. Relatively common tree, found in hilly xerophytic vegetation. Alt.: c. 300 m.

Notes. 1. This species resembles the small-leaved mountanous species, such as *Guioa venusta* and *Guioa pseudoamabilis*, but it differs by the smaller leaflets with a usually entire margin, acute apex, papillate lower surface, and solitary domatium.

2. Although Waigeo I. belongs to the Sahul shelf, its vegetation can be very different from the mainland of New Guinea, due to two factors: the climate is drier (Whitmore, Wallace's line and plate tectonics, 1981, fig. 5.2) and the soil can locally be serpentine (ultrabasic), like south of the Kambele Hills (type locality). This may explain the speciation. Another endemic species on Waigeo is *Maesa rheophytica* Sleumer (Myrsinaceae).

3. One fruit had 4 lobes instead of 3, which is unique in *Guioa*.

Specimens studied:
NEW GUINEA. Waigeo I.: *P. van Royen 5409.*

20. DUBIOUS NAMES

Guioa elegans Radlk., Bot. Jahrb. 56 (1920) 280; in Engl., Pflanzenr. 98 (1933) 1162. — Type: *Schultze Jena 337* (B, holo, †), Papua New Guinea, Sepik River.

Description of 1933: Frutex?; rami teretes thyrsique petiolique pube tenera subflavida induti; folia abrupte pinnata; foliola circ. 8, alterna vel opposita, lanceolata, subaequilatera, longe et acute acuminata, breviter petiolulata, integerrima vel margine revoluto subsinuata, subchartacea, nervis lateralibus sat crebris patulis, utrinque laevia, supra glabra, subtus pilis adpressis laxe adspersa glandulisque microscopicis rubro-fuscis cylindricus (± eruciformibus) e cellulis disciformibus circ. 12 1-seriatis conflatis et cellula ovali saepius longitudinaliter septata terminatis ornata, utrinqe opaca, variegata (secus margines fusca, tertia mediana parte flavo-viridi), impunctata, attamen cellulis secretoriis teneris instructa, efoveolata; thyrsi axillares, vix folia dimidia aequantes; alabastra flavo-sericea; sepala glandulis elongate clavatis longe stipitatis aurantiacis ciliata; discus nondum sat evolutus, ut videtur, completus.

Rami floriferi 2 mm crassi. Folia petiolo circ. 3 cm longo incluso 15–18 cm long; foliola cum petiolulis 2–3 cm lata. Inflorescentiae 4–8 cm longi.

N o t e. Only the lost type specimen is known of this species. Plants identified as *Guioa elegans* by Hartley et al. (Lloydia 36, 1973, 270) appeared to represent *Toechima erythrocarpum* subsp. *papuanum*. The leaflets of *Guioa elegans* should be small (6–8 by 1.5–2 cm), the margin revolute and sinuate, the disc complete. The sinuate margin reminds of *Guioa pteropoda* (a species of Radlkofer, so hardly likely to be identical to *Guioa elegans*), of *Guioa amabilis*, and of *Guioa pseudoamabilis*. The latter two have a revolute margin and a complete disc. However, both are mountain species, and, moreover, *Guioa amabilis* is only found near the Anggi Lakes in the Vogelkop, Irian Jaya.

Guioa subfalcata Radlk., Sapind. Holl.-Ind. (1879) 90; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 609, 617; in Engl., Pflanzenr. 98 (1933) 1161; Christophersen, Bull. Bish. Mus. 128 (1935) 132; A.C. Smith, Bull. Bish. Mus. 141 (1936) 89. — T y p e: *U.S. Expl. Exp. s.n.*, s.d. (US, holo, n.v.; iso presumably in A, NY), Samoa, Upolu.
Cupania lentiscifolia auct. non Pers.: A. Gray, U.S. Expl. Exp. Bot. (1854) 256.

Shrub to treelet. *Branchlets* terete, smooth, sericeous when young; flowering twigs 2–4 mm thick. *Leaves* 2–3-jugate; rhachis 3.2–9 cm long, upwards flattened above, not (to only slightly) winged, subsericeous, petiole 1.3–3.3 cm long; petiolules up to 0.7 cm long. *Leaflets* not subsessile, opposite to subopposite, ovate, falcate, 3.2–11.9 by 1.4–3.6 cm, index 2.3–4.3, asymmetric, acroscopic side broader, coriaceous, not punctate; base attenuate; margin entire, flat; apex acuminate to cuspidate, mucronulate; upper surface smooth, glabrous; lower surface differently coloured, duller, smooth, no papillae, glabrous except for a few hairs around domatia, latter 1 (or 2) small sac(s), in axils of lower nerves, especially on basiscopic side; venation usually raised, especially on the lower side; nerves 0.3–1.6 cm apart, marginally looped; veins rather densely reticulate, conspicuous. *Inflorescences* axillary, only branching along rhachis; latter somewhat flattened, 7.6–11.7 cm long, subsericeous; first order branches up to 5.3 cm long; cymules unknown. *Bracts* and *bracteoles* deltoid to triangular, outside sericeous, inside subglabrous; bracts c. 1.1 mm long; bracteoles c. 0.3 mm long. *Pedicels* c. 3.7 mm long, sericeous, also the c. 2.2 mm long upper part. *Flowers* c. 6 mm in diam. Sepals 5, ovate, margin pilose, glands unknown, outside and inside glabrous; 2 outer smaller ones 2–2.2 by 2.2–2.3 mm; 3 inner larger ones c. 3 by 3.4–4 mm, margin petaloid. *Petals* 5, elliptic, 2.5–3 by c. 1.1 mm, claw c. 0.6 mm high, margin pilose, outside and inside glabrous, apex obtuse; scales absent, margins auriculate and folded inwards, 1.2–1.5 mm high, easily detachable; crest on short stipe, apex clavate, lobed; petal between two adjacent large sepals not reduced. *Disc* complete. *Stamens* 8; filament 2.8–3.5 mm long, especially basally pilose; anther c. 0.4 mm long, glabrous. *Pistil:* ovary c. 0.3 mm high, sparsely hirsute; style and stigma c. 0.1 mm high. *Fruit* unknown.

Field notes. Shrub to treelet, 3–7 m high. Flowers white.

Distribution. Samoa: Upolu I., Tutuila I.

Ecology. In wet forest to scrub forest. Alt. 300–500 m. Flowering: Oct.

Notes. 1. The material identified as *Guioa subfalcata* contained three forms (besides obvious misidentifications). One form appeared to be *Arytera*. Both other forms were very different from each other, but both lacked good flowers and fruits, only sterile material, buds and loose flowers were present. Unfortunately, *Guioa* is especially characterized by its fruits. Both forms are (almost) consistent with the description by Radlkofer (the *Cupaniopsis*-form lacks punctation). One form resembled *Cupaniopsis concolor* (colour and texture of the leaflets); however, the leaflets are falcate, which is rather atypical for *Cupaniopsis*. This form is for the time being regarded as a *Cupaniopsis*. The other form, which includes the presumed isotype, is described above as *Guioa subfalcata*. It is doubtful, however, whether this species belongs to *Guioa*, because one specimen, with loose(!) flowers, had a kind of petals so far hardly encountered within *Guioa* (folded auricles as scales). This type of petal is extremely peculiar for the Pacific, were it shows, transversing from the Solomons to the Tonga I., a reduction of the crest in special, but also of the scales. *Guioa lentiscifolia* of Tonga, closest to Samoa, even lacks scales and crests completely.

2. A.C. Smith records this species (*A.C. Smith 1456*) for Fiji. However, it is very doubtful whether the specimen cited (not seen by me) belongs to this species as *Guioa subfalcata* is only known from Samoa.

Specimens studied:
SAMOA. *Christophersen 560*, Upolu I.; *3483*, Tutuila I.; *U.S. (Wilke's) Expl. Exp. s.n.*, s.d.

21. EXCLUDED TAXA

(alphabetically arranged by epitheton under *Guioa* or under *Hemigyrosa*)

1. *Hemigyrosa canescens* Blume, Rumphia 3 (1847) 166.—*Molinea canescens* Roxb., Pl. Corom. 1 (1796) 43, t. 60. — *Cupania canescens* Pers., Syn. Pl. 1 (1805) 413. — Type: *Roxburgh s.n.* (G, n.v.), India, Madras, Circars = **Lepisanthes tetraphylla** (Vahl) Radlk.
See for more information: Leenhouts, Blumea 17 (1969) 63.

Guioa chrysantha Radlk., Fedde Rep. 20 (1924) 28; in Engl., Pflanzenr. 98 (1933) 1175; Reynolds, Austrobaileya 2 (1984) 39 (doubtfull species); Fl. Austr. 25 (1985) 50 (imperfectly known). — Type: *Moore s.n.*, May 1867 (K, holo), Australia, New South Wales, Richmond River = **Toechima dasyrrhache** Radlk.
Ms. S.T. Reynolds (BRI) is thanked for the identification.

3. *Guioa collina* Schltr., Bot. Jahrb. 39 (1907) 175, p.p.: *Cupania collina*; Guillaumin, Not. Syst. 1 (1909) 329, p.p.: *Cupania collina*. — *Cupania collina* Panch. & Séb. in Séb., Not. Bois. Nouv. Caléd. (1874) 230, 270 (typification). — *Arytera collina* Radlk., Not. Syst. 2 (1911) 10; in Engl., Pflanzenr. 98 (1933) 1282. — Syntypes: New Caledonia: *Fournier & Sébert 3* (P); *Petit (8)3* (P); *Pancher 79* (P) = **Arytera collina** (Panch. & Séb.) Radlk.

Guioa concolor Gillesp., Bull. Bish. Mus. 83 (1931) 83, f. 19. — *Arytera concolor* A.C. Smith, J. Arn. Arbor. 31 (1950) 298; Parham, Plants Fiji Is. (1964) 173. — *Cupaniopsis concolor* Van der Ham, Blumea 23 (1977) 290; A.C. Smith, Fl. Viti. 3 (1985) 604. — Type: *Gillespie 4794* (BISH, holo?, n.v.; iso in A, B, K, NY), Fiji, Taviuni, vicinity of Waiyevo = **Cupaniopsis concolor** (Gillesp.) Van der Ham.

5. *Guioa curvidens* Radlk. ex Dur. & Jacks., Ind. Kew., Suppl. 1 (1906) 190 = **Cupaniopsis curvidens** Radlk.
Durand and Jackson misplaced several combinations, made in *Cupaniopsis* by Radlkofer, under the genus *Guioa*.

6. *Guioa dasyantha* Radlk., Bot. Jahrb. 56 (1921) 277; in Engl., Pflanzenr. 98 (1933) 1159. — Type: *Ledermann 10365* (B, holo, †; iso in L), Papua New Guinea, Sepik area = **Jagera** spec., presumably synonymous with *J. discolor* Reynolds.

7. *Hemigyrosa deficiens* Beddome, Fl. Sylv. (1872) t. 231. — *Sapindus ? deficiens* W. & A., Prod. (1834) 111. — *Anomosanthes deficiens* Blume, Rumphia 3 (1847) 151. — *Lepisanthes deficiens* Radlk., Sitzungsber. Math.-Phys. Cl. Kön. Bayer. Akad. Wiss. München 8 (1878) 276. — Type: *Wight 390* (K, n.v.) = **Lepisanthes tetraphylla** (Vahl) Radlk.
See for more information: Leenhouts, Blumea 17 (1969) 63, 64.

8. *Guioa dictyophylla* Radlk. ex Dur. & Jacks., Ind. Kew., Suppl. 1 (1906) 190. — *Cupaniopsis dictyophylla* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20 (1890) 359. — *Aphania dictyophylla* Radlk., Bot. Jahrb. 56 (1920) 268; in Engl., Pflanzenr. 98 (1932) 713. — *Lepisanthes dictyophylla* Leenh., Blumea 17 (1969) 83. — Type: *W. Sayer s.n.* (M, holo), Papua New Guinea, Mt. Obree = **Lepisanthes dictyophylla** (Radlk.) Leenh.
See note under *Guioa curvidens* in this chapter.

9. *Guioa eriantha* Merr. & Perry, J. Arn. Arbor. 21 (1940) 513. — Type: *Brass 8244* (A, holo; iso in L), Papua New Guinea, Lower Fly River, Sturt I. = **Atalaya papuana** (Radlk.) Leenh.

10. *Guioa geminata* K. Schum. & Lauterb., Fl. Schutzgeb. (1900) 420. — *Arytera geminata* Radlk. in K.Schum. & Lauterb., Nachtr. (1905) 308. — Type: *Lauterbach 2306* (B, holo, †, n.v.), Papua New Guinea = **Arytera litoralis** Blume.

11. *Gioa krempfii* Gagnep., Not. Syst. 12 (1947) 30; Fl. Gén. I.-C., Suppl. 1 (1950) 981. — Type: *Krempf 1595* (P, holo; iso in A, K), Annam, Province Nhatrang, massif du Ton-ha = **Pavieasia annamensis** Pierre.

12. *Hemigyrosa longifolia* Hiern in Hook. f., Fl. Br. Ind. 1 (1875) 671. — *Lepisanthes longifolia* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8 (1878) 276. — *Anomosanthes longifolia* Pierre, Fl. Coch. (1895) t. 327 text. — Syntypes: *Griffith KD 994* (M, n.v.); *Maingay KD 446* (L, n.v.), both Malay Peninsula, foot of Mt. Pangai = **Lepisanthes tetraphylla** (Vahl) Radlk.
See for more information: Leenhouts, Blumea 17 (1969) 64.

13. *Guioa macropetala* Radlk. ex Dur. & Jacks., Ind. Kew., Suppl. 1 (1906) 190 = **Cupaniopsis macropetala** Radlk.
See note under *Guioa curvidens* in this chapter.

14. *Hemigyrosa ? pervillei* Blume, Rumphia 3 (1847) 166. — *Deinbollia pervillei* Radlk., Sapind. Holl.-Ind. (1879) 40; in Engl., Pflanzenr. 98 (1933) 688. — Type: *Pervillé 676* (L, holo), Ambongo = **Deinbollia pervillei** (Blume) Radlk.

15. *Guioa platycarpa* Radlk. ex Dur. & Jacks., Ind. Kew., Suppl. 1 (1906) 190 = **Cupaniopsis platycarpa** (Radlk.) Radlk.
See note under *Guioa curvidens* in this chapter.

16. *Guioa spathulata* C.E.C. Fischer, Kew Bull. (1927) 83; Radlk. in Engl., Pflanzenr. 98 (1933) 1176. — Type: *Parkinson 1618* (K, holo), Burma, S Tenasserim, Ngawun Valley = **Lepisanthes tetraphylla** (Vahl) Radlk.

This specimen certainly is a new, undescribed race within the complex species *Lepisanthes tetraphylla*. Typical are the slender inflorescence and the large sepals of which the outer two are less pilose than the inner three. In the revision of *Lepisanthes* (Leenhouts, Blumea 17, 1969: 42, 43) the following character states can be added to the synoptical key of the races of *Lepisanthes tetraphylla* to key out this new form: 1d, 2a, 3a, 4b, 5a, 6a, 7b, 8b, 9b, 10b, 12c, 13b, 14b, 15b, 16b, 17b, 18b, 19b, 20a?, 21a?, 22a?.

17. *Guioa subserrata* Radlk. ex Dur. & Jacks., Ind. Kew., Suppl. 1 (1906) 190 = **Cupaniopsis subserrata** Radlk.
See note under *Guioa curvidens* in this chapter.

18. *Hemigyrosa trichocarpa* Thw., En. Pl. Zeyl. (1858) 56. — *Hemigyrosa canescens* Blume var. *trichocarpa* Trim., Ceylon Br. J. R. As. Soc. 9 (1885) 20. — *Lepisanthes trichocarpa* Radlk., Fedde Rep. 18 (1922) 335. — Type: *Thwaites CP 607*, p.p. (iso in A, BO, n.v.), Ceylon = **Lepisanthes tetraphylla** (Vahl) Radlk.
See for more information: Leenhouts, Blumea 17 (1969) 64.

22. IDENTIFICATION LIST

The numbers refer to the numbers between brackets behind the accepted species names in the index.

A 662: 50; A 777: 7; A 1032: 50; A 1215: 46; A 1252: 46; A 2196: 50; A 4167: 14; A 4351: 46; A 4751: 50 — Abdullah 54: 46 — Agama 530: 46 — Ahern 100: 23; 212: 23; 267: 23; 433: 23; 613: 23; 765: 23 — Allen, D. 621: 7 — Allen, M.S. 228-81: 46; 259-81: 15 — Amdjah 209: 46; 1059: 14 — Anang 655: 29 — ANU 1652: 23; 2031: 59; 2649: 48; 2772: 59; 2802: 59 — Apostol 7171: 46 — Aranez 15: 23 — Arbain 308: 51 — Atkin NSW 168606: 57 — Atkinson 24: 57 — Aubréville & Heine 126: 40; 283: 18.2.

Backer 23468: 51; 31475: 14 — Bailey 28: 2; 35: 2; 22437: 2 — Bakar 2371: 46 — Baker, C.F. 2425: 46 — Balajadia 2913: 46 — Balansa 146: 19; 152: 17; 154: 18.1; 155: 18.2; 159: 64; 159a: 64; 159b: 64; 1444: 18.2; 1448: 40; 1452: 12; 1452: 64; 1452a: 12; 2265: 30; 2266: 18.1; 2273: 17; 2274: 17; 2275: 64; 2275a: 2275b: 64; 2840: 12; 2842: 30; 2842a: 30; 2843: 18.1; 3305: 18.2; 3306: 45; 3505: 30; 3513: 64 — Balgooy 3658: 21; 3942: 21; 3995: 21; 5087: 2 — Balgooy & Wiriadinata 2828: 14 — Barnard 123: 2 — Batianoff & MacDonald 1171: 2; 1231: 2 — Baudouin 219: 17; 356: 64 — Bauerlen 56: 57; 862: 57 — Baumann-Bodenheim 5413: 30; 5611: 64; 6104: 18.2; 6263: 18.2; 6319: 18.2; 6344: 64; 8064: 64; 12444: 18.2; 14341: 18.2; 14782: 19; 14787: 19; 15343: 30; 15534: 64; 15637: 30; 15933: 64 — Baume 270: 46 — bb 5461: 14; 13606: 14; 21484: 49; 30365: 49; 30953: 2; 34880: 51 — Beaman 6795: 46; 8396: 46; 9459: 46 — Beauchamp 1098: 23 — Beauglehole 5821: 11; 6125: 11 — Beccari PB 3675: 46; PP 807: 29 — Benzeville 673: 57; 1033: 57 — Bernardi 9795: 18.1; 9843: 18.2; 10100: 18.2; 10162: 64; 10163: 64; 10213: 64; 10248: 18.2; 10257: 45; 10421: 64; 12550: 18.2; 13284: 38 — Bernier 64: 17; 113: 64; 177: 64; 658: 17; 1289: 64 — Beumée 765: 14 — Beusekom 2688: 51 — BKF 14593: 7 — Blake, S.T. 18868: 2 — Blanchon 321: 18.1; 440: 64; 497: 18.2; 522: 64; 603: 64; 657: 30; 953: 30; 995: 40; 1127: 18.1; 1300: 64; 1357: 45; 1462: 64; 1463: 18.1 — Boden Kloss 14594: 14 — Boerrigter 60: 14; 410: 14 — Bogle & Bogle 577: 46 — Bogor HB 1443: 14; 1543: 46; 3049: 14; 3654: 46; 6041: 46; 14484: 14; 14521: 14; 14594: 14; III-F-25: 51; III-I-20: 51; III-I-20a: 51; III-I-43: 46; III-J-45: 46; III-J-46: 46; III-J-66: 14; III-J-103a: 46; III-J-103b: 46; III-K-14: 51; III-K-14a: 51; III-K-17: 46; III-K-23: 14; III-K-23a: 14; III-K-43: 46; XII.B.IX.37: 46 — Boorman 11988: 11 — Boucher 1433: 18.1; 1447: 64; 1488: 64 — Bourret 1058: 64 — Branderhorst 183: 2 — Brass 594: 55; 614: 4; 2884: 16; 7513: 2; 7739: 2; 8290: 39; 12783: 28; 13082: 49; 13699: 28; 13702: 49; 25521: 36; 27661: 31; 28291: 47; 29131: 59 — Brass & Versteegh 12505: 59 — Bremer & Bremer 1842: 46 — Brinon 588: 18.1; 869: 64; 920: 64; 924: 64; 962: 18.2; 1139: 19; 1346: 64; 1347: 64; 1348: 64; 1534: 64 — Britton 54: 63; 58: 63 — Brousmiche 494: 64; 1198: 64 — Brown, R. 6353: 57 — BRUN 709: 46; 5038: 7; 5426: 7; 5427: 7 — Bryan 449: 52 — BS 43: 23; 88: 23; 463: 7; 562: 41; 697: 41; 1873: 23; 1874: 23; 2340: 23; 4910: 23; 6759: 23; 6973: 23; 7055: 53; 7079: 23; 7412: 46; 9608: 23; 10916: 1; 11201: 23; 12319: 23; 12746: 23; 13048: 23; 13204: 23; 16585: 1; 17542: 46; 17977: 23; 18089: 23; 19295: 23; 20197: 23; 20611: 46; 20612: 46; 20728: 23; 20745: 23; 20833: 23; 22730: 23; 24554: 46; 25450: 6; 25469: 6; 26462: 53; 26636: 35; 26801: 23; 26873: 23; 26886: 23; 27400: 23; 27905: 23; 28677: 46; 31246: 46; 33187: 42; 33798: 6; 34026: 23; 34487: 6; 34673: 23; 36871: 46; 37235: 46; 39639: 23; 41273: 46; 41412: 23; 41874: 23; 42181: 35; 43160: 23; 43613: 23; 44460: 23; 44526: 23; 44689: 23; 45664: 6; 46830: 46; 48748: 23; 76069: 23; 76739: 23; 77366: 46; 79891: 6 — BSIP 216: 27; 338: 27; 1566: 27; 1670: 27; 1690: 27; 2410: 16; 3324: 60; 4376: 60; 6704: 60; 6994: 60; 7012: 27; 8099: 60; 8604: 60; 10975: 60; 11037: 60; 11528: 60; 12773: 60; 16381: 60; 16776: 16; 16993: 60; 17023: 27 — Buasa-Angian 3927: 46 — Buchholz 1072: 64; 1158: 64; 1314: 64; 1531: 30; 1615: 64 — Bünnemeyer 1437: 51; 1747: 14; 7632: 51; 7645: 51 — Burkill 438: 51; 1324: 46; 4340: 46 — Burkill & Kiah 601: 46 — Burley 187: 23 — Burut 2383: 50; 2774: 50; 2980: 50 — BW 1981: 59; 4061: 34; 4076: 59; 6412: 39; 8295: 2; 14124: 3; 14202: 3.

23. INDEX

References are only made to the species descriptions and to the synonyms. The accepted names are printed in Roman type, the synonyms in *italics*. The number in brackets behind an accepted name refers to the species number as used in the Identification list (chapter 22).