

**LEPIDOPETALUM BLUME (SAPINDACEAE):
TAXONOMY, PHYLOGENY, AND HISTORICAL BIOGEOGRAPHY**

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SUMMARY

The genus *Lepidopetalum* Blume (Sapindaceae) contains 6 species, of which one, *L. fructoglabrum*, is newly described. Four species are found on New Guinea of which one also occurs in Australia, one on the Nicobar Islands and Sumatra and one on the Philippines. Specimens from Java, Sulawesi, the Moluccas, and the Lesser Sunda Islands could not be identified due to the lack of mature fruits.

The genus is characterized by typical domatia (hair tufts), petals (small, triangular with much larger, usually united scales), and fruits (flat, usually 2-locular, sarcotesta present). Important specific characters are the pilosity of the upper part of the pedicel, the shape of the disc, the type of hairs inside the fruit, and the type of sarcotesta.

A putative phylogeny of the genus is selected together with an areagram for the distributions of the species and their ancestral species.

HISTORY AND INTRODUCTION

The genus *Lepidopetalum* was described by Blume in 1847. He based the genus on a species described by Cambessèdes in 1829 (*Cupania perrottetii*). The genus can be distinguished by the typical hair tuft domatia, and the petals, of which the triangular blade is much smaller than the (usually) united scales; as a result at first sight the petal seems to be peltate. Furthermore, the fruits are typical, 2-locular (exceptionally 3-locular), inside usually pilose, with a basal to almost complete sarcotesta around the seed.

Turczaninow (1848) described the genus *Lachnometalum*, based on the species *Lachnometalum glabrum* which appeared to be congeneric with *Lepidopetalum* and conspecific with *Lepidopetalum perrottetii*. He later incorrectly synonymized his genus with *Ratonia*.

Radlkofer (1933) revised *Lepidopetalum* and described most species. He placed several names, described by various authors under different genera, into the synonymy of *L. jackianum* and *L. perrottetii*. He kept *L. jackianum* and *L. montanum* separate because the fruits of the latter were still unknown. During the present revision they appeared to be conspecific, with *L. montanum* as the accepted name.

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Fig. 1. *Lepidopetalum subdichotomum* Radlk. a. Habit with male inflorescences, $\times 0.5$; b. hairtuft domatia on the lower side of the leaflets in the axils of midrib and nerves, $\times 6$; c. male flower, first flowering one on a cymule, with an aberrant number of stamens, $\times 6$; d. petal (small triangle) with large, pilose scale, $\times 12.5$; e. pistil of female flower after pollination showing triangular stigma, disc as high as broad, $\times 6$ [a-d: Schodde (& Craven) 4092, L; e: BSIP (Gafui & collectors) 14557, L].

The genus is readily recognizable at any stage, sterile (hair tufts as domatia, thin leaflets), in flower (petals), and in fruit (2-locular, sarcotesta). However, at the species level all species look alike except when they fruit. Fruiting specimens are easy to identify. Flowering ones are sometimes only identifiable on minor details; the best method to identify those is to use geography. A special problem is created by the specimens from Java, Sulawesi, the Moluccas, and the Lesser Sunda Islands. Except for one specimen they are all either sterile, or flowering, or they possess very young fruits. Mature fruits are only present in *Dommers* 120 and 257 from Java which appear to be the Philippine *L. perrottetii*, but the pedicel is glabrous instead of pilose. In the West (Java, Philippines) the specimens tend to look like *L. perrottetii*, while in the East (Timor, Moluccas, Key Islands) they resemble *L. subdichotomum* or *L. xylocarpum* (both known from New Guinea and the Solomons) because of the irregular numbers of sepals, petals, and stamens in the terminal flowers. For the time being the material from the islands between the Philippines and New Guinea is only identified as *Lepidopetalum* spec.:

Java (Kangean I.): *Dommers* 120, 257.

Sulawesi: *Teijsmann* HB 11745, HB 11760 (Pangadjine), HB 12820 (Maros).

Moluccas: *Pleyte* 68 (Tanimbar); *Taylor* 2612a (Dodaga); *Treub* s.n., 1893 (Babar & Sera); *de Vogel* 3216 (Halmahera); *Whitmore*, *Whitmore & Sidiyasa* TCW 3557 (Bacan).

Lesser Sunda Islands: *Riedel* s.n. (Timor).

Key Islands: *Moseley* s.n., IX-1874; *Warburg* 20545.

CHARACTERS

Several characters interesting for species delimitation in *Lepidopetalum* will be briefly discussed.

Leaflets

The leaflets look very similar in all species. They are always very thin, papery, slightly asymmetric except for the asymmetric base; the lower leaflets of a leaf are ovate, the upper ones elliptic to even obovate. Punctuation is absent. The base is usually cuneate; the margin entire and flat; the apex acute to caudate with a usually emarginate to rounded very apex. The many domatia on the lower surface of the leaflets, which consist of tufts of (seldom caducous) hairs (fig. 1b), are typical for the genus. The length of the leaflets, as given in the descriptions, includes the length of the pulvinus-like petiolule.

Inflorescences and flowers

The inflorescences are ramiflorous to axillary to usually pseudoterminal. They are thyrses, with—due to reduction—usually three cymules branching off per node. The long-peduncled cymules basally repeat this pattern with three instead of the expected two dichasial branches; apically the cymules usually become cincinnate (fig. 1a). There appear to be specimens with male or female inflorescences, indicating that the genus *Lepidopetalum* is either dioecious or shows duodichogamy (see Van Welzen,

1989, chapter 8.2). The female flowers (fig. 1e, after pollination) are small with a well-developed protruding pistil, the stamens are small, and the anthers do not dehisce. The inflorescences with male flowers usually show a well-developed open flower, usually the first developed flower of a cymule, while the other flowers on the cymule are smaller and appear to be developing (fig. 1a). The fully developed male flowers (fig. 1c) show small pistils, long filaments, and dehiscent anthers. The first male flowers of the cymules in *L. subdichotomum* and *L. xylocarpum* often show aberrant numbers of sepals (more than 5), petals (more than 5), and stamens (less or more than 8).

Bracts

The bracts are usually very small and triangular. Only *L. subdichotomum* shows in at least one or two of the inflorescences per specimen large, leaflet-like ovate to obovate bracts.

Peduncle

The peduncle shows two types of hairs, simple ones and glandular ones. In some species the simple hairs are absent in the upper part (above the abscission zone) of the peduncle, then only some glandular hairs remain.

Sepals

The usually five sepals are basally united into a disc-shaped tube. The small lobes are more or less equal in size. The margin and less so the outside are pilose.

Petals

The petals (fig. 1d) are small, triangular. The Sapindaceae petals usually possess two scales; these are united into one large scale in *Lepidopetalum*, although the united scale may still be deeply bifid. The scale is much larger than the petal. Crests in the shape of central ribs on the scales or as flat scales are present in most New Guinea specimens. The scales are usually very hairy, the petal blades usually far less so, quite often only the margin is pilose.

Disc

The disc is circular and usually complete, only in *L. xylocarpum* slits may be present. Depending on the species, the height/width ratio of the disc varies between higher than broad (*L. montanum*) to broader than high (*L. xylocarpum*), most species show a disc which is about as high as broad (fig. 1e). The disc is glabrous.

Pistil

The ovary is 2-locular (except for an occasional 3-locular ovary) and flattened. The pilosity differs per species. The style and stigma are united, triangular, and flattened perpendicular to the ovary. In male flowers the style shows an apical slit with the stigmatic tissue remaining covered on the inside. In female flowers (fig. 1e) the slit folds outwards and the stigmatic tissue is shown; the stigma then looks like an overhanging roof.

Fruits

The fruits swell during boiling, consequently the measurements are taken after boiling. The size differs per species or even within a species (see Biogeography). Shape of the fruit and possession of a stipe are sometimes typical for a species or for

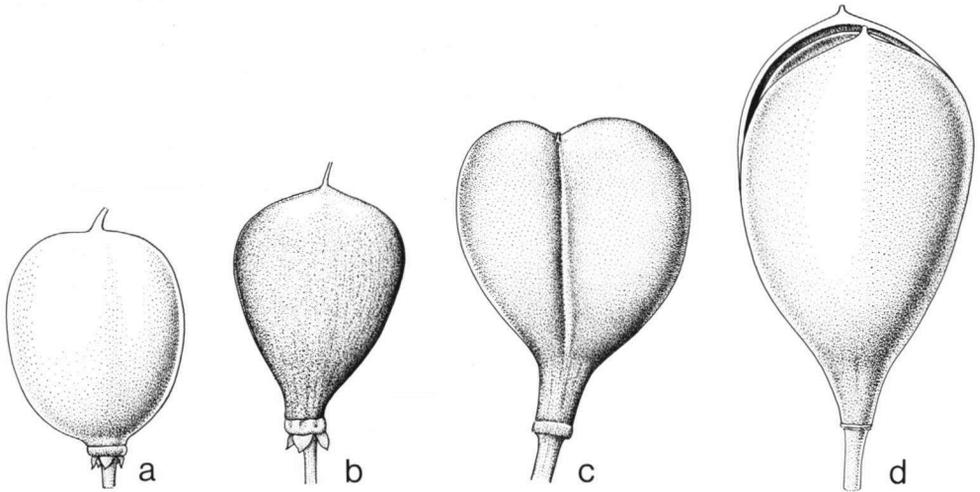


Fig. 2. Fruits of *Lepidopetalum*. a. *L. micans* Lauterb. & Schumann: fruit without stipe, small, $\times 1.5$ [LAE (Wiakabu et al.) 50083, L]; b. *L. montanum* (Blume) Radlk.: fruit with stipe, large, $\times 1.5$ [Kunstler or King's collector 7, M]; c. *L. perrottetii* (Cambess.) Blume: fruit without stipe, small, $\times 1.5$ [FB (Miranda) 20524, US]; d. *L. subdichotomum* Radlk.: fruit with stipe, large, $\times 1.65$ [BSIP (Gafui & collectors) 10242, L].

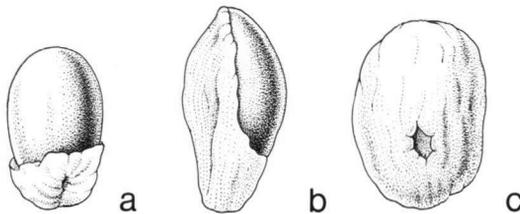


Fig. 3. Seeds of *Lepidopetalum*. a. *L. perrottetii* (Cambess.) Blume: sarcotesta covering basal part of seed, ventral view, $\times 1.65$ [FB (Miranda) 20524, US]; b. *L. xylocarpum* Radlk.: sarcotesta covering seed except for dorsal side, lateral view, $\times 2$ [NGF (Streimann) 27507, L]; c. *L. micans* Lauterb. & Schumann: sarcotesta covering seed completely except for a small dorsal triangle, dorsal view, $\times 2$ [LAE (Wiakabu et al.) 50083, L].

part of the distribution of a species (fig. 2). Important is the presence of hairs inside the fruit; these are absent in *L. fructoglabrum*, present in all other species, and vary from short (*L. xylocarpum*) to long (*L. micans*).

Sarcotesta

The arilloid in *Lepidopetalum* is a sarcotesta (fleshy outgrowth of exotesta). The sarcotesta is basally present around the seed in *L. fructoglabrum*, *L. montanum*, *L. perrottetii*, and *L. subdichotomum* (fig. 3a). In *L. montanum* and *L. perrottetii* this basal sarcotesta produces an obpyramidal outgrowth. The sarcotesta covers the seed almost completely in *L. xylocarpum* (except for the dorsal side = side opposite to central axis of fruit, fig. 3b) and in *L. micans* (except for a small triangular dorsal part, fig. 3c).

Table 1a shows the characters and the character states which were used in the phylogenetic analysis. Table 1b shows the datamatrix for the outgroup and the species of *Lepidopetalum*. The analysis resulted in three cladograms (fig. 4) for all of which the consistency index was 100% (no homoplasy). The three cladograms differ in the position of *L. subdichotomum* and *L. xylocarpum*. The first cladogram (fig. 4a)

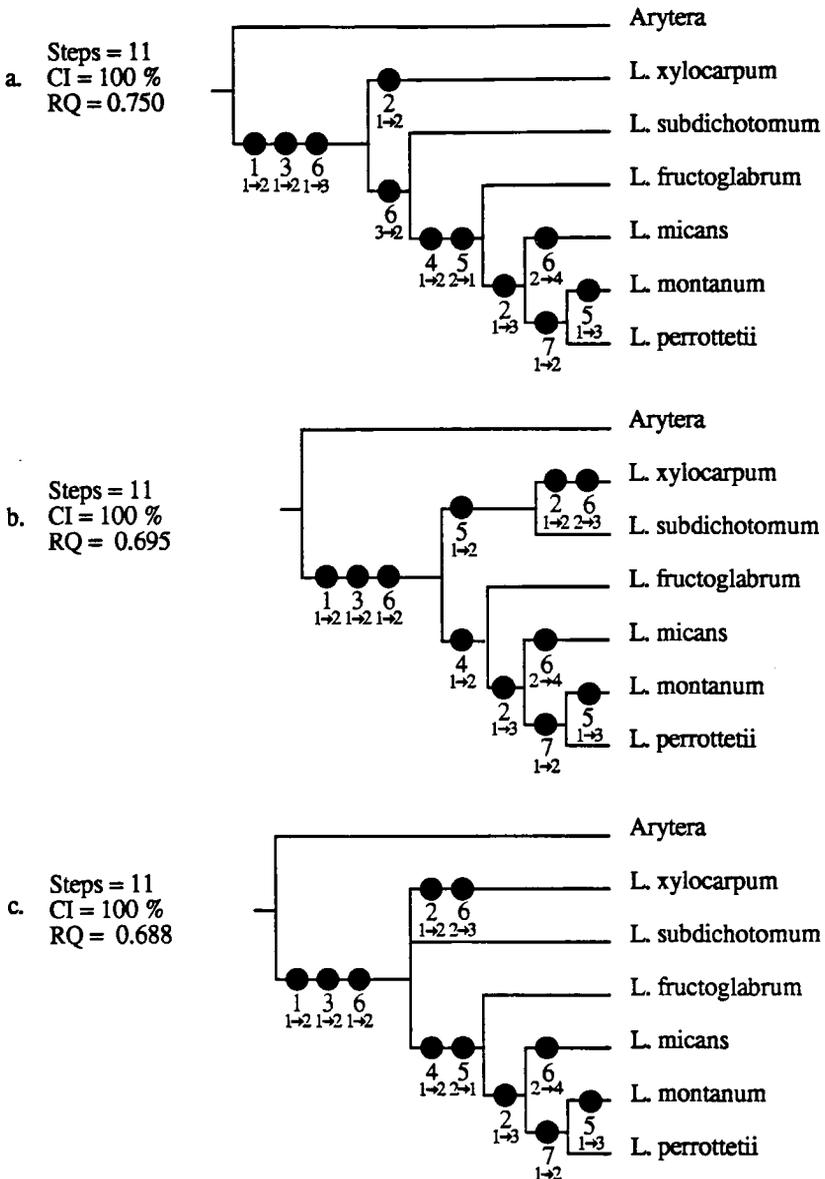


Fig. 4. Resulting cladograms after analysis of the data in table 1 with the program HENNIG86.

Table 2a. Datamatrix for historical biogeographic analysis derived from cladogram a (fig. 4a). Species 1 = *L. fructoglabrum*, 2 = *L. micans*, 3 = *L. montanum*, 4 = *L. perrottetii*, 5 = *L. subdichotomum*, 6 = *L. xylocarpum*, 7 = ancestor of 3 and 4, 8 = ancestor of 2 and 7, 9 = ancestor of 1 and 8, 10 = ancestor of 5 and 9, 11 = ancestor of 6 and 10.

Areas \ Species	1	2	3	4	5	6	7	8	9	10	11
Solomons	0	0	0	0	1	0	0	0	0	1	1
North	0	1	0	0	1	0	0	1	1	1	1
Peninsula/South/Vogelkop	0	0	0	0	0	1	0	0	0	0	1
Morobe	1	0	0	0	0	0	0	0	1	1	1
Philippines	0	0	0	1	0	0	1	1	1	1	1
Sumatra/Andaman-Nicobar Is.	0	0	1	0	0	0	1	1	1	1	1

Table 2b. Datamatrix for historical biogeographic analysis derived from cladogram b (fig. 4b). Species 1 = *L. fructoglabrum*, 2 = *L. micans*, 3 = *L. montanum*, 4 = *L. perrottetii*, 5 = *L. subdichotomum*, 6 = *L. xylocarpum*, 7 = ancestor of 3 and 4, 8 = ancestor of 2 and 7, 9 = ancestor of 1 and 8, 10 = ancestor of 5 and 6, 11 = ancestor of 9 and 10.

Areas \ Species	1	2	3	4	5	6	7	8	9	10	11
Solomons	0	0	0	0	1	0	0	0	0	1	1
North	0	1	0	0	1	0	0	1	1	1	1
Peninsula/South/Vogelkop	0	0	0	0	0	1	0	0	0	1	1
Morobe	1	0	0	0	0	0	0	0	1	0	1
Philippines	0	0	0	1	0	0	1	1	1	0	1
Sumatra/Andaman-Nicobar Is.	0	0	1	0	0	0	1	1	1	0	1

Table 2c. Datamatrix for historical geographic analysis derived from cladogram c (fig. 4c). Species 1 = *L. fructoglabrum*, 2 = *L. micans*, 3 = *L. montanum*, 4 = *L. perrottetii*, 5 = *L. subdichotomum*, 6 = *L. xylocarpum*, 7 = ancestor of 3 and 4, 8 = ancestor of 2 and 7, 9 = ancestor of 1 and 8, 10 = ancestor of 5, 6, and 9.

Areas \ Species	1	2	3	4	5	6	7	8	9	10
Solomons	0	0	0	0	1	0	0	0	0	1
North	0	1	0	0	1	0	0	1	1	1
Peninsula/South/Vogelkop	0	0	0	0	0	1	0	0	0	1
Morobe	1	0	0	0	0	0	0	0	1	1
Philippines	0	0	0	1	0	0	1	1	1	1
Sumatra/Andaman-Nicobar Is.	0	0	1	0	0	0	1	1	1	1

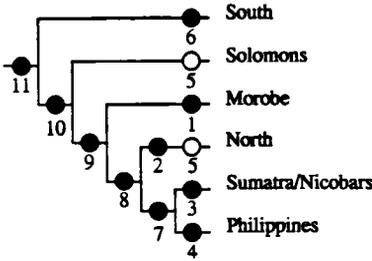
is more or less similar to the third cladogram (fig. 4c), as the latter shows a subbasal trichotomy due to a different interpretation of the character changes in character 6. In the second cladogram (fig. 4b) *L. subdichotomum* and *L. xylocarpum* form a monophyletic group separate from the other species. These three cladograms were evaluated as user trees in the program CAFCA (Zandee, 1988), after which the Redundancy Quotient (also called Redundancy Index; Geesink & Kornet, 1989; Geesink & Zandee, msc.) could be obtained. The RQ is a result of the application of information theory to evolutionary parsimony (see also Brooks & Wiley, 1988). The cladogram with the highest RQ has the highest information content and the lowest amount of chaos that can be drawn from a particular datamatrix. The RQ offers a different selection criterion for cladograms. The first cladogram shows the highest RQ and will therefore be selected as the best. In fact the choice was between the first and the second cladogram, as the third one was not fully resolved.

HISTORICAL BIOGEOGRAPHY AND GEOGRAPHICAL CLINES

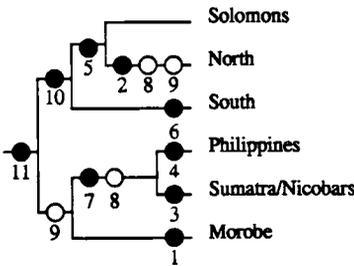
The historical biogeographic analysis was executed with Component Compatibility (CC; Zandee & Roos, 1987) via the program CAFCA and with Brooks' Parsimony Analysis (BPA; Wiley, 1988a & b) via the program HENNIG86 (option ie;) with an additional outgroup area consisting of 0's only. Of these two methods CC is favoured, as BPA can also distinguish components based solely on the absence of species (Van Welzen, 1989). All three cladograms were analyzed by substituting the species of *Lepidopetalum* by their distributions and adding the distributions of the ancestral species based on the assumption that vicariance can explain the historical component of the species distributions (ancestral species inhabited the sum of the areas of the descendant species).

The areas distinguishing represent the smallest distributions. Figure 7 shows the distributions of the *Lepidopetalum* species. In New Guinea s.l. four areas are recognized: Solomon Islands (part of distribution of *L. subdichotomum*), North (distribution of *L. micans* and part of that of *L. subdichotomum*), Morobe (distribution of *L. fructoglabrum*), Peninsula/South/Vogelkop (distribution of *L. xylocarpum*). Furthermore, the Philippines are recognized as area of endemism (see map; *L. perrotetii*) and Sumatra with the Andaman and Nicobar Islands (see map; *L. montanum*). The apparent gap in distribution between the Philippines and New Guinea is only due to the fact that the specimens from the islands in between could not be identified. Consequently, some of the areas recognized may change in the future. Table 2 shows the datamatrices, table 2a corresponds to the cladogram in fig. 4a, table 2b to fig. 4b, and table 2c to fig. 4c.

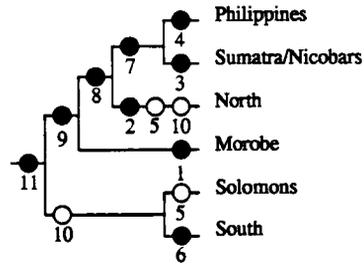
Four areagrams (fig. 5) were found with both CC and BPA. Areagrams a (fig. 5a) and d (fig. 5d) are almost the same except for the basal trichotomy in d, therefore areagram a is preferred over d for its completely dichotomous solution. In both areagrams *L. subdichotomum* (species 5) shows a parallellism. A parallellism in non-adjacent clades indicates dispersal (for the various explanations of homoplasy see Wiley, 1988a & b, and Van Welzen, 1989). Areagrams b (fig. 5b) and c (fig. 5c) were both derived, as the most parsimonious areagrams, from cladogram b. Both show two parallellisms in non-adjacent clades, i.e. two dispersal events. Due to the



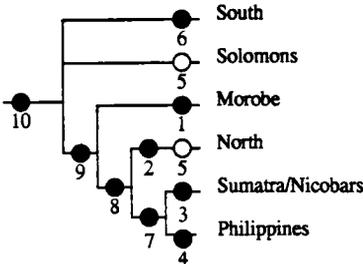
a. Areagram derived from cladogram a; steps = 12.



b. Areagram derived from cladogram b; steps = 13.



c. Areagram derived from cladogram b; steps = 13.



d. Areagram derived from cladogram c; steps = 11.

● = Apomorphy
○ = Homoplasy

Fig. 5. Areagrams found after analysis via Component Compatibility and Brooks' Parsimony Analysis. Areagram a was derived from data from cladogram a (fig. 5a), areagrams b and c are derived from cladogram b (fig. 5b), and areagram d is derived from cladogram c (fig. 5c).

assumption of vicariance, both the ancestor and its descendant show dispersal (species 9 is the ancestor of 8 in areagram b; species 10 is the ancestor of species 5 in areagram c), but only either the ancestor or the descendant has dispersed, so in effect there is also only one homoplasy as in the areagrams a and d. On the other hand, the sequence in which the areas split off is not as logical as in areagram a. In areagram b the Philippines and Sumatra/Nicobars have formed one area together with Morobe Province in E New Guinea. In areagram c the Solomons feature together with the Peninsula/South/Vogelkop, while the Morobe Province, which lies in between, is related to the other areas, moreover, the Solomons are geologically related to the North (see later). In conclusion, areagram a is the preferred areagram as the suggest-

ed relationships between the areas can readily be explained in geological terms (see scenario below), this in contrast with areagram c. The historical geography is another criterion, independent of the RQ, to select cladogram a as the best cladogram.

A generalized areagram was not made. For two reasons it seems more sensible to wait till more cladograms for the New Guinea region become available. 1) Genera like the Sapindaceae *Guioa* (Van Welzen, 1989) and *Cupaniopsis* (Adema, 1991), indicate different areas of endemism, while both are related to each other and somewhat less to *Lepidopetalum*. The certainly non-related cicadas (insects; Duffels & De Boer, 1990) also show different areas of endemism. 2) Compared to these groups *Lepidopetalum* shows many missing areas and is as such not very indicative for geographical patterns. First a consensus about the areas of endemism has to be reached; after that generalized areagrams can be built. One might reason that the distributional data of *Lepidopetalum* cannot be used for a generalized areagram as the cladogram selection is based on geography. However, the cladogram can also be selected on the basis of the highest RQ and then the geographical data are still usable in a historical biogeographic analysis.

A scenario can be built (fig. 6), based on areagram a and the complicated geological history of N New Guinea, an area which consists of at least 32 terranes (Pigram & Davies, 1987). These terranes, partly island arcs, partly continental fragments, partly ocean floor, docked with the South and Central part of New Guinea (Peninsula and the Vogelkop also absent). The South and (nowadays) Central Mountain range have always formed a unity with Australia. Four docking phases are distinguished by Pigram & Davies (1987): a) formation of the 'southern' Northern part, b) formation of the Peninsula, c) formation of the Vogelkop and the 'northern' part of the North, and d) the outer rim of the North together with the docking of some terranes around the Vogelkop. The ancestral species of *Lepidopetalum* already existed 25 million years ago, presumably together with other ancestral Sapindaceae like the ancestral species of *Guioa* (Van Welzen, 1989) and *Cupaniopsis* (Adema, 1991), on the New Guinea-Australian shelf (shown in fig. 6a). Then New Guinea consisted of the South and the (nowadays) Mountain range; the North, Vogelkop, and Peninsula were still absent. Twenty-five million years ago the ancestral species diffused (term introduced by De Jong, 1987) over at least the main part of the present North of New Guinea (fig. 6b1) when this collided with the rest of New Guinea. Another possible scenario is a further dispersal of the ancestral species over the other islands which presently form the rest of N New Guinea, together with the Bismarck Archipelago and the Solomons (fig. 6b2); the island arcs acted as stepping stones, facilitating dispersal. Due to the collision with the northern part the resulting orogeny (presently the mountain range over mid New Guinea) split the genus into two species, *L. xylocarpum* in the South and the ancestral species to all other species in the North (fig. 6c1 & c2). This is a vicariance event. Fifteen million years ago the Peninsula, consisting of several united terranes, collided with New Guinea and *L. xylocarpum* could diffuse along this new part; followed by another diffusion event to the Vogelkop when the main part of this area was formed 10 million years ago. The next species to be split off is *L. subdichotomum*. After the *Lepidopetalum* ancestor diffused to the North, Northern Islands, Bismarck Archipelago, and Solomons, *L. sub-*

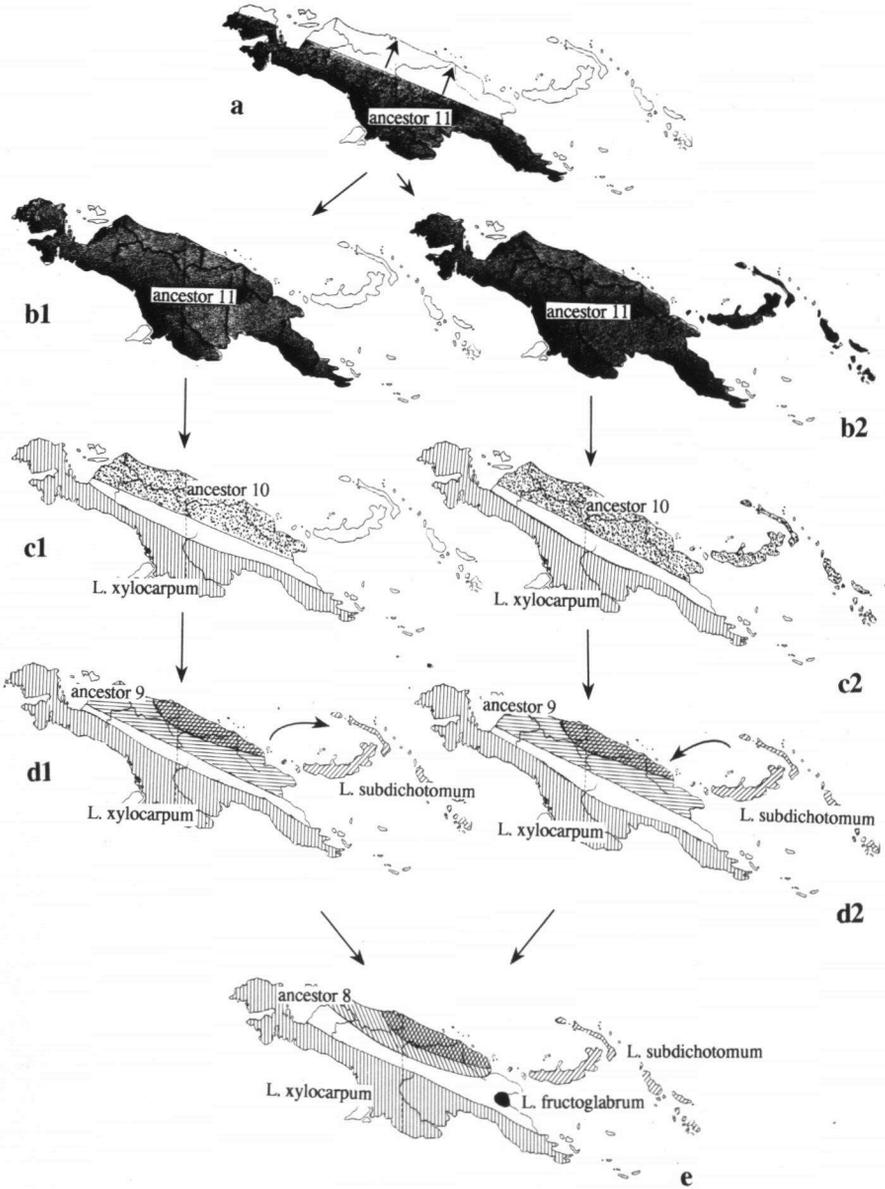


Fig. 6. Historical geographic scenario for *Lepidopetalum*. The outline of New Guinea is for reference only. a. Ancestral species of the genus migrates north after collision between New Guinea and several terranes, 15 million years ago; b. diffusion was either to the North only (1) or also to the Bismarcks and Solomons (2); c. the ancestral species speciated into *L. xylocarpum* in the South and ancestral species 10 in the North, a vicariance event; d. *L. subdichotomum* speciated together with ancestor 9 from ancestor 10, either sympatrically followed by dispersal (1) or allopatrically in the Bismarcks and Solomons followed by dispersal to the North due to docking of several terranes (2); e. the next vicariance event resulted in *L. fructoglabrum* and ancestor 8.

dichotomum either speciated allopatrically on the Northern Islands, Bismarck Archipelago, and the Solomons and migrated back to the North when the Northern Islands docked and more or less formed the present shoreline of New Guinea (vicariance followed by diffusion, 10 million years ago; fig. 6d2); the ancestral species of the remaining species was formed in the North and diffused to the rest of the North when the Northern Islands docked and became partly sympatric with *L. subdichotomum*. The alternative scenario is sympatric speciation into *L. subdichotomum* and the ancestral species of the remaining species followed by dispersal to the Bismarck Archipelago and the Solomons of *L. subdichotomum* (only dispersal, no vicariance; fig. 6d1). The split-off of *L. fructoglabrum* is another vicariance event, probably caused by the docking of the Finisterre terrane and subsequent orogenesis of the mountain ranges (Finisterre Mts, Sarawaket Mts) in the Huon Peninsula, north of Morobe Province (fig. 6e; also c. 10 million years ago). The next speciation event is the split-off of *L. micans* from the ancestral species of *L. montanum* and *L. perrottetii*, a split between N New Guinea and W Malesia. Perhaps the ancestor of *Lepidopetalum* was present on the W Malesian microcontinents as these all (except the Philippines) originated from the New Guinea-Australian plate; if so, this is a vicariance event. Alternatively and more likely, *Lepidopetalum*, just like *Guioa* (Van Welzen, 1989), dispersed to W Malesia when E Malesia collided with W Malesia, less than 10 million years ago. The last event, the speciation of *L. montanum* and *L. perrottetii*, has to be due to dispersal accompanied by speciation, as the Philippine islands, unlike Sumatra, were never part of the New Guinea-Australian plate (see second part of this chapter).

In conclusion, the areagram only indicates one instant of dispersal and all other distributions are due to vicariance; the scenario shows that more distributions have to be explained by dispersal. These dispersal patterns were shown as vicariance in the areagram, because the speciation event coincided with the dispersal moment.

The Vogelkop (Bird's head) is a composite area as it features in different patterns. *Lepidopetalum* (*L. xylocarpum*) shows that it is part of a 'southern' pattern (see fig. 7), while the cicadas of the subtribe *Cosmopsaltria* (Duffles & De Boer, 1990) show

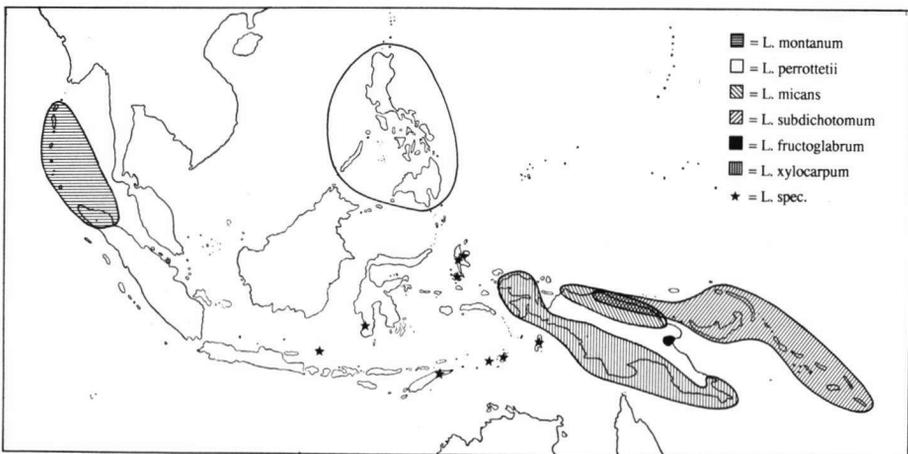


Fig. 7. Distributions of the six species of *Lepidopetalum*.

it to be part of a 'northern' pattern, more or less the distribution of *L. micans* (see fig. 7). This 'northern' pattern is also referred to as an Outer Melanesian Arc distribution (N Moluccas, N New Guinea, Bismarck Archipelago, Solomons, etc.). Michaux (1991) shows the lower part of the Vogelkop to represent the southern distributions and the upper part the northern distributions. The Vogelkop may even show a third pattern as the main part of this peninsula is suspected to have rifted from Australia and after some time of independence was 'scooped up' by New Guinea (Kemum terrane; Pigram & Davies, 1987).

According to Morley & Flenley (1987) the Philippines showed two major land-bridge systems during glacial periods, the western one connecting N Borneo, over Palawan, and the Calamian group and the eastern one stretching from NE Borneo, over Mindanao up to Luzon, and ultimately to Mindoro. Several species of Sapindaceae have probably migrated, diffused from Borneo over the Philippines via these land-bridges as they show geographical clines. A striking example is *Guioa pleuropteris* (Van Welzen, 1989: 262, fig. 110) with two clines, one via the western, the other via the eastern land-bridge. *Gloeocarpus patentivalvis* (Van Welzen, 1991) and *Lepidopetalum perrottetii* only show the eastern cline. All three show a diminishing size of the leaflets from Mindanao to Luzon, *L. perrottetii* also a diminishing fruit size. The view that diffusion is the main historic explanation of the dispersal over the Philippines of these three species is in accordance with the latest geological views (Audley-Charles, 1981, 1987; Michaux, 1991): W Malesia (e.g. Borneo) is of Australian/New Guinea origin, the Philippines were probably partly already present in their present position (island history) and have partly migrated from the Chinese mainland.

On New Guinea two species also show geographical clines. The fruits of *Lepidopetalum subdichotomum* show a geographical cline in size. In the west the fruits have the same size as those of *L. micans* and almost lack a stipe, while in the east the size is about twice as large as in the west and the stipe is well developed. New Britain, New Ireland, and Bougainville show intermediate fruit sizes. The fruits of *L. xylocarpum* are also somewhat smaller in the west; however, the main difference is the absence of a stipe in the west, as the eastern specimens show long stipes. *Guioa subsericea* (Van Welzen, 1989) also shows a geographical cline with smaller leaflets and fruits in the west.

LEPIDOPETALUM

Lepidopetalum Blume, Rumphia 3 (1847) 171, see note 2; Radlk., Bot. Jahrb. 56 (1920) 56; in Engl., Pflanzenr. 98 (1933) 1316; Reynolds, Fl. Austral. 25 (1985) 87. — Type species: *Lepidopetalum perrottetii* (Cambess.) Blume.

Lachnopetalum Turcz., Bull. Soc. Nat. Mosc. 21 (1848) 571. — Type species: *Lachnopetalum glabrum* Turcz. [= *Lepidopetalum perrottetii* (Cambess.) Blume].

Tree. *Branchlets* smooth to slightly rough, sericeous when young. Leaves paripinnate, 2–5-jugate, pulvinate at base; petiolules present as a pulvinus. *Leaflets* subopposite to opposite, basal ones ovate, upper ones elliptic (to obovate), slightly asymmetric, acroscopic side broader, thin, not punctate; base usually cuneate to at-

tenuate, asymmetric; margin entire, flat; apex acuminate to caudate, very apex emarginate to usually rounded to acute; upper surface sometimes glaucous when dry, both surfaces smooth, subglabrous except at least for the subsericeous basal part of the midrib, below (a few) (caducous) hair tufts as domatia; venation raised, especially below, nerves marginally looped, veins reticulate. *Inflorescences* ramiflorous to axillary to pseudoterminal, reduced thyrses with usually 3 cymules per node, not branching to branching in axil or along rhachis; latter (sub)sericeous; cymules basally dichasial to apically cincinnate, sometimes up to more than 10-flowered, cymules with male flowers often with exceptional numbers of sepals, petals, and stamens in first developed flowers. *Bracts* and *bracteoles* triangular to long triangular to at least a few leaf-like in *L. subdichotomum*, mainly margin and outside sericeous. *Pedicels* subglabrous to pilose, glandular hairs present besides simple ones; upper part above abscission zone less pilose to glabrous except for glandular hairs. *Flowers* actinomorphic. *Sepals* 5 (or 6), (sub)equal, basally united; tube disc-shaped, c. 0.3 mm long; blades triangular (to ovate), mainly margin and outside pilose. *Petals* 5 (to 7); nail c. 0.1 mm high; blade triangular, margin only to completely pilose; scales united into one, occasionally still bifid, larger than blade, margin irregularly crenate, pilose; crests usually absent, sometimes present as central ridges or as 2 flat scales. *Disc* circular, complete to with often a few slits in *L. xylocarpum*, flat to high, smooth, glabrous, enveloping base of stamens. *Stamens* (7-)8(-10); filaments especially basally pilose; anthers basifixed, laterally opening with lengthwise slits, pilose. *Pistil*: ovary flat, 2- (or very occasionally 3-)locular, smooth, subglabrous to hirsute; ovule one per locule; style and stigma united, flat, pyramidal, stigmatic part folded outwards like an overhanging roof. *Fruit* an obovoid capsule, regularly dehiscent, with usually one developed seed, flat when 2-locular, coriaceous to woody, smooth to somewhat rough, outside glabrous, inside glabrous to short to long brownish pilose; stipe absent to present; wall thin, at most 2 mm thick. *Seed* ellipsoid, triangular in transverse view, base straight to oblique, smooth, shiny; sarcotesta covering seed only basally to almost completely except for a small triangular dorsal area; testa thin, without radicle pocket on the inside. *Embryo*: cotyledons laterally to secondarily laterally besides each other, equal to unequal, then upper much larger, apices not elongated; radicle present basally to about halfway seed, short; plumule inconspicuous.

Field notes – Bark greyish brown, slightly fissured and/or with lenticels. Flowers yellowish white. Fruit red; sarcotesta orange; seed black.

Distribution – Malesia (Andaman and Nicobar Islands up to the Solomons); NE Australia (NE Queensland).

Ecology – Trees in primary and secondary forest, on waste land, along rivers and roads. Alt.: sea level up to 1200 m. Flowering and fruiting: different per species, variable between seasonal and the whole year through.

Notes – 1. Typical for the genus *Lepidopetalum* are the leaflets with hair tufts as domatia; the small petals with a triangular blade and a much larger scale; the 2-locular ovary; the obovate flattened fruits; and the (partial) sarcotesta around the seed.

2. The date of publication of *Rumphia* 3 is doubtful. The book itself mentions 1847 as year of publication, but Blume is known to have antedated his publications. The first edition of *Taxonomic Literature* (Stafleu, *Regnum Veg.* 52, 1967, 39) mentions 1849, which makes *Lachnometalum* the oldest genus name and would compel

a name change for all species. The last edition of Taxonomic Literature (Stafleu & Cowan, *Regnum Veg.* 94, 1976, 238) mentions 1847 again; this view is followed in the present revision, also because it means stability of names.

KEY TO THE SPECIES OF LEPIDOPETALUM BASED ON FLOWER CHARACTERS

N.B. The differences in floral characters among the species are only slight. Therefore, geography is used as an additional 'character'; however, due to insufficient collecting, the geographical ranges of some species might be larger than described in the key.

- 1a. Upper part of pedicels pilose 2
- b. Upper part of pedicels glabrous except for glandular hairs 5
- 2a. Disc as high as broad or broader than high (flat). Philippines, New Guinea, Solomons 3
- b. Disc higher than broad. Nicobar Is, Sumatra 3. *L. montanum*
- 3a. Ovary (sub)glabrous (to pilose); if pilose then disc usually with slits. Petals 0.5–2.2 mm high, crests often present as ribs or as flat scales. New Guinea and the Solomons 4
- b. Ovary pilose; disc without slits. Petals 0.4–1 mm high, crests absent. Philippines 4. *L. perrottetii*
- 4a. Disc as high as broad, without slits. Crests usually present on petal scales as ribs or as flat scales. Ovary (sub)glabrous. N coast New Guinea: E Geelvink Bay to Madang Prov 2. *L. micans*
- b. Disc flat to as high as broad, usually with slits. Crests usually absent, at most present as ribs. Ovary subglabrous to pilose. New Guinea: Peninsula to S coast to Vogelkop; NE Australia 6. *L. xylocarpum*
- 5a. Stamens 8, some flowers (of a cymule especially the first flowering male ones) with 9 or more. Solomons and New Guinea (absent in Morobe Prov.) 6
- b. Stamens 8. New Guinea: Morobe Prov. 1. *L. fructoglabrum*
- 6a. Inflorescences up to 17 cm long, axillary to pseudoterminal. Per inflorescence at least a few big bracts; bracts 1–3.3 mm long. Solomons and N New Guinea: Jayapura to Morobe Prov. to Bougainville 5. *L. subdichotomum*
- b. Inflorescences up to 8.5 cm long, usually ramiflorous on thin twigs to axillary to pseudoterminal. Per inflorescence only small bracts; latter 0.7–1.3 mm long. New Guinea: Peninsula to S coast to Vogelkop 6. *L. xylocarpum*

KEY TO THE SPECIES OF LEPIDOPETALUM BASED ON FRUIT CHARACTERS

- 1a. Fruit inside pilose. 2
- b. Fruit inside glabrous 1. *L. fructoglabrum*
- 2a. Sarcotesta only basally present around hilum (fig. 3a). 3
- b. Sarcotesta covering seed except for (part of) dorsal side (fig. 3b & c) 5
- 3a. Upper part pedicels sericeous. Sarcotesta with well-developed basal obpyramidal outgrowth 4
- b. Upper part pedicels glabrous. Sarcotesta with slight basal obpyramidal outgrowth 5. *L. subdichotomum*

- 4a. Fruit 3.2–4.5 cm high by 1.7–2.4 cm broad 3. *L. montanum*
 b. Fruit 1.3–2.5 cm high by 0.8–1.6 cm broad 4. *L. perrottetii*
 5a. Fruit inside long pilose (hairs c. 1.5 mm long). Sarcotesta covering seed except for small dorsal triangular part (fig. 3c) 2. *L. micans*
 b. Fruit inside short pilose (hairs c. 0.5 mm long). Sarcotesta covering seed except for dorsal side (fig. 3b) 6. *L. xylocarpum*

1. *Lepidopetalum fructoglabrum* Welzen, *spec. nov.* – Fig. 7.

Lepidopetalum micante Lauterb. & Schumann similis sed pedicello parte supera sine pilibus simplicibus, fructibus intra glabris, sarcotesta circum hilum cupulata. — Typus: *Hartley 9948* (L, holo; iso in A, BRI, CANB, K), Papua New Guinea, Morobe Prov., Oomis creek, 18 miles W of Lae.

Lepidopetalum hebecladum auct. non Radlk.: Hartley et al., *Lloydia* 36 (1973) 270.

Flowering branchlets 1–4 mm in diam. *Leaves* 3- or 4-jugate; rhachis 2.7–14.5 cm long, terete, subsericeous. *Leaflets* 3.2–17.5 by 1.4–6.1 cm; apex acuminate to usually caudate, very apex emarginate to rounded; upper surface glaucous when dry. *Inflorescences* mainly axillary to pseudoterminal, branching in axil and along rhachis, latter up to 7.5 cm long. *Bracts* and *bracteoles* triangular; bracts 0.6–1 mm long; bracteoles 0.3–0.8 mm long. *Pedicels* subglabrous, upper part up to 5.7 mm long, glabrous except for some glandular hairs. *Flowers* 3.5–4.3 mm in diam. *Sepals* 5; blades 1.3–1.8 by 0.7–1.1 mm, subglabrous. *Petals* 5; blade 0.8–1 by 0.7–1.3 mm, subpilose; scale 0.7–1.3 mm long by 1–1.6 mm broad; crest absent (to well developed central ribs). *Disc* complete, c. 0.6 by 0.5 mm, broader than high. *Stamens* 8; filament in male flowers 2.7–3.3 mm long, in female flowers 0.5–1.5 mm long; anther 0.8–1.1 by 0.5–0.8 mm. *Pistil*: ovary in male flowers c. 0.3 mm high, up to 2.6 mm high in female flowers, 2-locular, subglabrous; style and stigma in male flowers c. 0.1 mm high, in female flowers up to 1.3 mm high. *Fruit* 2–2.2 by 1.2–1.4 cm, inside glabrous; stipe absent. *Seed* 1.1–1.3 by c. 0.9 cm, base straight; sarcotesta covering seed at base, present around hilum, only forming a slight obpyramidal outgrowth below seed; hilum 2–4 mm long. *Embryo* 0.9–1.1 by 0.8–0.9 cm; cotyledons obliquely laterally besides each other; radicle inconspicuous.

Field notes – Tree, 10–17 m high, d.b.h. 7.5–50 cm. Outer bark blotched light and dark grey to dark brown, smooth to finely tessellated to rather warty, c. 6 mm thick; under bark greenish yellow; inner pinkish to reddish brown, hard. Wood cream to dark straw, moderately hard and heavy; heartwood reddish brown. Leaves dark green above, paler below, veins sometimes conspicuous yellow-green. Inflorescence green. Perianth green to white. Filaments white; anthers yellowish. Fruit orange; sarcotesta yellow-orange; seed black.

Distribution – Papua New Guinea: Morobe Prov.

Ecology – Found in second storey of primary and secondary rain forest, periodically flooded forest, and along streams and roads. Alt.: 30–900 m. Flowering: Aug. to Nov. Fruiting: Nov. to Feb.

Vernacular name – Neure (Garaina).

Chemical compounds – Hartley et al. (1973) report *Lepidopetalum fructoglabrum* (as *L. hebecladum*) to be devoid of alkaloids in bark and leaves.

Note — Typical for this species are the glaucous, (sub)glabrous leaflets with very distinct domatia and usually with a caudate apex; the small bracts; the glabrous upper part of the pedicels; the inside glabrous fruits; and the basal, cupular sarcotesta.

2. *Lepidopetalum micans* Lauterb. & Schumann — Figs. 2a, 3c, 7.

Lepidopetalum micans Lauterb. & Schumann in Schumann & Lauterb., Fl. Schutzgeb. (1900) 423. — Type: *Lauterbach 2840* (B, holo, †; iso in BM, K, M), Papua New Guinea, Kaiser Wilhelmsland, Ssigaun-Hochland.

Lepidopetalum hebecladum auct. non Radlk.: Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20 (1890) 269; Schumann & Lauterb., Fl. Schutzgeb. (1900) 422; Radlk., Bot. Jahrb. 56 (1920) 307; Nova Guinea 14 (1926) 184; in Engl., Pflanzenr. 98 (1933) 1319; P. van Royen, Man. For. Trees Papua & N. G. 2 (1964) 30, fig. 13. — In all references *Hollrung 341* excluded; see also note 2.

Flowering branchlets 1.5–2.5(–11) mm in diam. *Leaves* (2–)3–4(–5)-jugate; rhachis 1.7–14 cm long, flat above, especially upper side sericeous. *Leaflets* 2–21 by 1–7 cm; apex acuminate to cuspidate, very apex emarginate to rounded. *Inflorescences* axillary to pseudoterminal, usually not branching, rhachis up to 8 cm long. *Bracts* and *bracteoles* triangular; bracts 1.1–1.6 mm long; bracteoles 0.3–1 mm long. *Pedicels* puberulous, upper part 1.8 (flower)–10 (fruit) mm long. *Flowers* 3.3–6.3 mm in diam. *Sepals* 5; blades 1.2–3.3 by 0.7–2.3 mm, margin pilose. *Petals* 5; blade 0.5–2 by 0.8–2 mm, margin pilose, outside subglabrous; scale sometimes divided into two, 0.5–1.5 mm long by 0.8–2.2 mm broad; crest absent to usually well-developed central ribs to 2 small flat scales. *Disc* complete, c. 0.5 mm high, as high as broad. *Stamens* (7) 8(–10); filament in male flowers 1–3.3 mm, in female flowers 0.8–1.3 mm long; anther 0.8–1.2 by 0.6–1 mm. *Pistil*: ovary in male flowers 0.3–0.4 mm high, up to 2.5 mm high in female flowers, 2- (or occasionally 3-)locular, subglabrous; style and stigma in male flowers c. 0.1 mm high, in female flowers up to 1.2 mm high. *Fruit* 1.6–2.2 by 1–1.6 cm, inside densely hirsute with hairs up to 1.5 mm long; stipe absent to 2.5 mm high. *Seed* 1.2–1.7 by 0.7–1.2 cm, base straight; sarcotesta covering seed almost completely except for small dorsal triangular spot; hilum 1.2–4 mm long. *Embryo* 1–1.3 by 0.5–1 cm; cotyledons laterally besides each other (to obliquely dorsoventrally above each other to almost secondarily laterally besides each other), upper one can be much bigger than lower one; radicle less than 1 mm long.

Field notes — (Shrub to) tree 2–30 m high, d.b.h. 10–85 cm. Outer bark whitish to greyish brown, smooth to somewhat rough with numerous pustular lenticels, thin, hard; under green to straw; inner cream to orange to straw brown, 2.5–6 mm thick. Wood white to brown, sapwood undefined; heartwood reddish brown. Leaves light green above, paler below; young ones reddish. Calyx greenish white. Flower white to yellow. Ovary white. Fruit red; sarcotesta orange.

Distribution — Along north coast of New Guinea from E Geelvink Bay (Irian Jaya) to Madang Prov. (Papua New Guinea).

Ecology — Found in under- to middle-storey of primary forest, secondary forest, swamp forest, and along rivers and roads. Soil: limestone, sandy clay. Alt.: sea level up to 425 m. Flowering: June to Nov. Fruiting: July to April.

Vernacular names – Atah (Kauwera); siritolak (Amele); tuvugen (Madang Prov.).

Notes – 1. Typical for *Lepidopetalum micans* are the triangular bracts, the pilose upper part of the pedicel, the relatively small fruits which are long-hairy inside, and the sarcotesta which envelops the seed nearly completely.

2. The type specimen of *L. hebecladum* (Hollrung 341) has always been incorrectly interpreted. This specimen with its glabrous upper part of the pedicel and occasional large more or less leaf-like bracts is conspecific with *L. subdichotomum*. All other specimens, which were always identified as *L. hebecladum*, have a pilose upper part of the pedicel and always lack the large bracts. The most important difference can be found in the sarcotesta, which nearly envelops the seed in *L. micans*, but is only basally present in *L. subdichotomum*.

3. *Lepidopetalum xylocarpum* strongly resembles *L. micans* in the western part of its distribution. See note 4 under the former.

3. *Lepidopetalum montanum* (Blume) Radlk. – Figs. 2b, 7.

Lepidopetalum montanum Radlk., Sap. Holl.-Ind. (1879) 14; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 510, 535, 623; in Engl., Pflanzenr. 98 (1933) 1320. — *Arytera montana* Blume, Rumphia 3 (June 1847) 171; Filet, Plantk. Woordenb. ed. 2 (1888) 151, nr. 3862. — *Ratonia montana* F.-Vill., Nov. App. (1880) 51, nom. illeg. (see note 2). — Type: *Korthals s.n.* (L, holo, sheet nr. L 908.272-341), Sumatra, '2000 ad 3000 ped. supra maris aequorem' (probably *Junghuhn 41* in L, and *De Vriese 18* in L, are the same specimens).

[*Conarus ? jackianus* Wall., Cat. (after 22 Oct. 1847) 8552, nom. nud.] — *Cupania jackiana* Hiern in Hook. f., Fl. Brit. India 1 (1875) 678; Kurz, J. As. Soc. Beng. 45, 2 (1876) 125. — *Lepidopetalum jackianum* Radlk., Sap. Holl.-Ind. (1879) 45; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 535, 623; Prain, Proc. As. Soc. Beng. (1891) 167; Ann. Roy. Bot. Gard. Calcutta 9, 1 (1901) 17, t. 23; Radlk. in Engl., Pflanzenr. 98 (1933) 1318. — Type: *Jack s.n.* (K, holo; iso in M), Nicobar Islands, Carnicobar.

Flowering branchlets 2–4 mm in diam. *Leaves* 2–4-jugate; rhachis 1.9–14.7 cm long, terete, subsericeous. *Leaflets* 4.5–21 by 1.5–7.5 cm; apex acuminate, very apex rounded (Nicobar I.) to almost acute (Sumatra). *Inflorescences* axillary to pseudoterminal, branching in axil or along rhachis, latter up to 11 cm long. *Bracts* and *bracteoles* triangular to long triangular; bracts 0.8–2 mm long; bracteoles 0.3–1.6 mm long. *Pedicels* sericeous, upper part 1.2–6.3 mm long. *Flowers* 2.8–4.2 mm in diam. *Sepals* 5; blades 1–2.8 by 0.8–1.4 mm, mainly outside sericeous. *Petals* 5; blade triangular, 0.6–1.2 by 0.5–1.1 mm, completely pilose; scale 0.8–1 by 0.8–1.5 mm; crests absent. *Disc* complete, 0.5–0.7 mm high, margin often revolute, higher than broad. *Stamens* 8; filament in male flowers 1.2–3 mm long; anther in male flowers 0.7–1.2 by 0.6–0.8 mm. *Pistil*: ovary in male flowers 0.2–0.5 mm high, 2-locular, subglabrous; style and stigma in male flowers 0.05–0.1 mm high. *Fruit* 3.2–4.5 by 1.7–2.4 cm, inside densely hirsute with hairs 1–1.5 mm long; stipe 3–5 mm high. *Seed* 1.9–2.2 by 1.3–1.7 cm, base oblique; sarcotesta covering seed at base, present around hilum, forming obpyramidal outgrowth below seed; hilum 7–8 mm long. *Embryo* 1.8–1.9 by 1–1.2 cm; cotyledons obliquely dorsoventrally above each other; radicle c. 1.1 mm long.

Field notes — Tree, 5–16 m high. Young leaves reddish, old leaves dark glossy green. Petals and filaments yellow; anthers pink to reddish purple. Fruit reddish; sarcotesta orange; seed black.

Distribution — S Andaman Islands, Nicobar Islands, N Sumatra.

Ecology — Found in primary forest, along rivers and along roads. Alt.: sea level up to 1000 m. Rare to locally common. Flowering and fruiting seemingly the whole year round. The seeds are eaten by *Calenas nicobarica* and other frugivorous pigeons (Prain, 1891).

Vernacular name — Karang karang rimbo (Malay; Filet, 1888).

Notes — 1. *Lepidopetalum jackianum* was only known from the Nicobar Islands, while *L. montanum* was only recorded for Sumatra. Both species are united because they only differ in small details, the Sumatran leaflets tend to be somewhat more slender and have a more acute apex, while the rhachis and petiolules are more hairy than those of the Nicobar Islands. The disc of the Nicobar specimens is usually not revolute as on Sumatra. Typical for *L. jackianum* are the usually few domatia, the small petals, the high and slender disc, the subglabrous pistil, and the large, stiped fruits.

2. Fernandez-Villar (1880) interpreted *Lepidopetalum montanum* incorrectly; he considered it to be identical with the Philippine species *L. perrottetii*. His new combination, *Ratonia montana*, is illegitimate because *Euphoria annularis* is placed into the synonymy of *Ratonia montana* (also an incorrect decision), while the epithet *annularis* is older than *montana*.

3. Williams (Bull. Herb. Boiss. 5, 1905, 222) and Craib (Fl. Siam. En. 1, 1926, 333) record *Lepidopetalum jackianum* (*Arytera montana*) for Thailand. No collections of this species from Thailand are known. It is assumed that this species is absent from Thailand.

4. *Lepidopetalum perrottetii* (Cambess.) Blume — Figs. 2c, 3a, 7.

Lepidopetalum perrottetii (Cambess.) Blume, Rumphia 3 (1847) 172; Miq., Fl. Ned. Ind. 1, 2 (1859) 569; Radlk., Sap. Holl.-Ind. (1879) 15, 46, 92; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 535, 622; Vidal, Revis. (1886) 96; Ceron, Cat. Pl. Herb. Manila (1892) 54; Radlk. in Perkins, Fragm. Fl. Philipp. 1 (1904) 66; Radlk., Bot. Jahrb. 56 (1920) 307; Brown, Minor Prod. Philip. For. 3 (1921) 204; Merr., Enum. Philipp. 2 (1923) 514; Radlk. in Engl., Pflanzenr. 98 (1933) 1317; Brown, Useful Pl. Philipp. 2 (1950) 365. — *Cupania perrottetii* Cambess., Mém. Mus. Hist. Nat. Paris 18 (1829) 45. — Type: *Perrottet s.n.* (P, holo; iso in L, P), Philippines, Samboanga (= Zamboanga), not Manila.

Lachnopetalum glabrum Turcz., Bull. Soc. Nat. Moscou 21 (1848) 572; Miq., Fl. Ind. Bat. 1, 2 (1859) 557. — *Ratonia lachnopetala* Turcz., Bull. Soc. Nat. Moscou 36 (1863, n.v.) 586, nom. illeg. (ICBN art. 63.1); Vidal, Phaner. Cuming. (1885) 38, 105. — Type: *Cuming 1169* (holo unknown; iso in L, M, MEL, NY, P), Philippines, Luzon, S Ilocos Prov.

Cupania ? richii A. Gray, U.S. Expl. Exp. Bot. 1 (1854) 257; Merr., Philipp. J. Sc. 3 (1908) Bot. 79. — Type: *U.S. Expl. Exp.* (A, holo), Philippines, Mindanao, Caldera.

Ratonia montana auct. non. F.-Vill.: F.-Vill., Nov. App. (1880) 52 [only *Lachnopetalum glabrum* Turcz.].

Ratonia littoralis auct. non. Teijsm. & Binnend.: F.-Vill., Nov. App. (1880) 52 [only *Lepidopetalum perrottetii* (Cambess.) Blume], 349 [only *Cuming 1170*].

Flowering branchlets 3–5 mm in diam. *Leaves* 2–4-jugate; rhachis 1.6–17.3 cm long, terete, (sub)sericeous. *Leaflets* 2.5–24 by 1.2–10 cm; apex acuminate, very apex emarginate to usually rounded. *Inflorescences* axillary with a tendency towards ramiflory, branching mainly in axil or along rhachis, latter up to 7 cm long. *Bracts and bracteoles* triangular to long triangular; bracts 1.1–2 mm long; bracteoles 0.6–1 mm long. *Pedicels* sericeous, upper part 2–8 mm long. *Flowers* c. 4 mm in diam. *Sepals* 5 (or 6); blades 0.8–2.3 by 0.6–1.5 mm, mainly outside sericeous. *Petals* 5; blade triangular, 0.4–1 by 1–1.6 mm, completely pilose; scale 0.8–1.7 by 1.2–1.8 mm; crests absent. *Disc* complete, c. 0.4 mm high, broader than high. *Stamens* 8; filament in male flowers 1.2–3.3 mm long, in female flowers 0.4–1.8 mm; anther in male flowers 0.6–0.9 by 0.5–0.8 mm, in female flowers 0.4–0.7 by 0.5–0.8 mm. *Pistil*: ovary in male flowers 0.3–0.4 mm high, in female flowers 1.8–2.5 mm high, 2-locular, hirsute; style and stigma in male flowers 0.05–0.1 mm long, in female flowers 0.9–1.8 mm long. *Fruit* 1.3–2.5 by 0.8–1.6 cm, inside densely hirsute with hairs c. 0.5 mm short; stipe absent (to 2 mm high). *Seed* 6–12 by 5–9.5 mm, base oblique; sarcotesta covering seed at base, present around hilum, forming obpyramidal outgrowth below seed; hilum 0.8–1.1 mm long. *Embryo* 6.5–9.5 by 6.5–8 mm; cotyledons obliquely dorsoventrally above each other; radicle up to 1.3 mm long.

Field notes – Shrub to tree, 2–17 m high, d.b.h. 6–25 cm. Flowers cream. Fruit red; sarcotesta yellow; seed black.

Distribution – Philippines (mainly E and N). See also last paragraph of History and Introduction.

Ecology – Found along roadsides, in secondary forest, on waste land, and along forest edges. Alt.: sea level up to 1200 m. Probably two flowering seasons: Jan. to March (to April) and May to June. Fruiting: (Feb. to) March to June and Sep. to Nov. (to Feb.).

Vernacular names – Alahan (also used for *Guioa koelreuteria*), amaya, dapil, hualis, ngisi-ngisi, poas, salab (also used for *Guioa koelreuteria*), ualis (Tagalog); bigas, bugas, tolotigri (P. Bis.); dila-dila (Pampanga); kayascas, oas, uas, uas-na purau (Ilk.); lupangga (Sul.); malakakao (Zamboanga); marinsiano, paga-paga (Mag.); palo negra (Fil.); saanputi (Bik.); sagadan (Mbo.); sala (Bis.); sararu (Bag.); uas (Ting.). Recommended name: Dapil. See Brown (1921, 1950) and Merrill (1923).

Notes – 1. Typical for this species are the usually many domatia, the rather large petals, the broad disc, the hirsute pistil, and the small, usually stipe-less fruits.

2. Clinal variation exists from Mindanao to Luzon (see chapter Biogeography). Therefore, Merrill's observation (1908) that *Cupania richii* (type collected from Mindanao) is probably not distinct from *Lepidopetalum perrottetii* (type collected from Luzon) is correct.

3. Merrill (Spec. Blanc., 1918, 242) interprets Blanco's *Molinaea arborea* (Fl. Filip. ed. 3, 2, 1878, 18) as a synonym of *Lepidopetalum perrottetii*. He even cites two specimens, of which one can easily be regarded as a neotype. However, the description of *Molinaea arborea* is not in accordance with that of *Lepidopetalum perrottetii*; the latter has petals with a very indistinct claw and 2-locular ovaries. For this reason *Molinaea arborea* cannot be regarded as a synonym of *Lepidopetalum perrottetii*.

5. *Lepidopetalum subdichotomum* Radlk. — Figs. 1, 2d, 7.

Lepidopetalum subdichotomum Radlk. in Schumann & Hollr., Fl. Kaiser Wilhelmshand (1889) 67; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20 (1890) 269; Schumann & Lauterb., Fl. Schutzgeb. (1900) 423; Radlk., Bot. Jahrb. 56 (1920) 307; in Engl., Pflanzenz. 98 (1933) 1319; P. van Royen, Man. For. Trees Papua & N. G. 2 (1964) 30; Peekel, Fl. Bismarck Arch. (1984) 339, fig. 549, see note 3. — Type: *Hollrung 387* (B, holo, †; iso in K, L, M, MEL, P), Papua New Guinea, Kaiser Wilhelmshand, Hatzfeldhafen.

Lepidopetalum hebecladum Radlk. in Schumann & Hollr., Fl. Kaiser Wilhelmshand (1889) 67; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20 (1890) 269; Schumann & Lauterb., Fl. Schutzgeb. (1900) 422; Koorders, Nova Guinea 8 (1909) 171; Radlk., Bot. Jahrb. 56 (1920) 307; Nova Guinea 14 (1926) 184; in Engl., Pflanzenz. 98 (1933) 1319; P. van Royen, Man. For. Trees Papua & N. G. 2 (1964) 30, fig. 13; Hartley et al., Lloydia 36 (1973) 270. — All references only include the type: *Hollrung 341* (B, holo, †; iso in K, P), Papua New Guinea, Kaiser Wilhelmshand, Hatzfeldhafen. See note 2.

Flowering branchlets 2–4 mm in diam. *Leaves* 3- or 4-jugate; rhachis 4–15.2 cm long, terete, subsericeous. *Leaflets* 3.6–19 by 1.3–8.5 cm; apex acuminate, very apex rounded. *Inflorescences* axillary to pseudoterminal, mainly branching along rhachis, sometimes also in axil, rhachis up to 17 cm long. *Bracts* and *bracteoles* triangular to at least a few obovate to leaf-like; bracts 1–3.3 mm long; bracteoles 0.4–0.7 mm long. *Pedicels* subglabrous, upper part 1.3 (flower)–12 (fruit) mm long, glabrous except for some glandular hairs. *Flowers* 3–5.5 mm in diam. *Sepals* 5; blades 0.8–2.3 by 0.8–1.6 mm, only margin subpilose. *Petals* 5; blade 0.7–1.6 by 0.8–1.6 mm, mainly margin subpilose; scale 0.5–1.3 mm long by 1.1–2.5 mm broad; crest absent to well developed central ribs to 2 small scales. *Disc* complete, 0.5–0.8 mm high, as high as broad. *Stamens* 8 or at least in some flowers 9; filament in male flowers 2.2–2.7 mm long, in female flowers 0.8–1.7 mm long; anther 0.7–1.2 by 0.6–1 mm. *Pistil*: ovary in male flowers 0.4–0.5 mm high, up to 2.5 mm high in female flowers, 2- (or occasionally 3-)locular, subglabrous; style and stigma in male flowers c. 0.1 mm high, in female flowers up to 1.3 mm high. *Fruit* 1.6–3.1 by 1–2.5 cm, inside densely hirsute with hairs 0.5–0.8 mm short; stipe 1–6 mm high. *Seed* 1.3–1.7 by 0.9–1.1 cm, base straight; sarcotesta covering seed at base, present around hilum, only forming a slight obpyramidal outgrowth below seed; hilum c. 1.5 mm long. *Embryo* 1–1.5 by 0.8–1 cm; cotyledons (obliquely) dorsoventrally above each other with the upper cotyledon much larger than the lower one (to laterally besides each other); radicle c. 1 mm long.

Field notes — Tree, 3–20 m high, girth 15 cm to 1 m. Outer bark light to dark brown to grey, smooth to slightly fissured to scaly, soft; inner pinkish to middle brown. Wood (soft to) hard, white to reddish brown. Flowers white to creamy yellow to yellow-green, fragrant. Anthers green. Stigma yellow. Fruit dark red; sarcotesta yellow; seed black.

Distribution — Irian Jaya: Jayapura (Hollandia) Prov. Papua New Guinea: W Sepik to Morobe Prov., New Britain, New Ireland, Bougainville. Solomon Islands: Big Nggela, Choiseul, Guadalcanal, Malaita, Savo, San Cristoval, Small Nggela. See also last paragraph of History and Introduction.

Ecology — Found mainly in secondary forest, also in primary forest, littoral forest, and grassland. At least found on sandy clay. Occasionally common. Alt.: sea level up to 330 m. Flowering and fruiting the whole year round.

Vernacular names – Onnokow (Sentani; Jayapura Prov.); dahe taka na borek (New Ireland); ipika, piranga (Bougainville); aioko, felofelongwane, sara, sufusane (Kwara'ae; Solomons). Sufusane is also used for the Solomon species of *Guioa* (Sapindaceae; Van Welzen, 1989).

Uses – Wood is used in house construction (Bougainville).

Notes – 1. Typical for this species are the occasional large, leaf-like bracts; the glabrous (except for the glandular hairs) upper part of the pedicel; the flowers occasionally with 9 stamens; the fruits which inside have hairs of usually middle length; and the sarcotesta which surrounds the hilum only basically and which at most only shows a slight basal obpyramidal outgrowth. The leaflets have a peculiar light green shade when dry. The fruits show a geographical cline, see chapter Biogeography.

2. *Lepidopetalum hebecladum* has always been wrongly interpreted. The type specimen appeared to be conspecific with *L. subdichotomum*, while all other '*L. hebecladum*' specimens appeared to be *L. micans*. *Lepidopetalum hebecladum* and *L. subdichotomum* were published simultaneously, but because of the confusion around the interpretation of *L. hebecladum* the name *L. subdichotomum* was preferred as the correct name.

3. Peekel (1984) describes *Lepidopetalum subdichotomum* with both paripinnate and imparipinnate leaves, with 2-lobed and 3-lobed fruits. *Lepidopetalum subdichotomum* has only paripinnate leaves and very occasionally 3-locular fruits which are not or hardly lobed. The original version of Peekel's Flora (in German) shows two plates of which one (Nachträge, 1947, 95) may be *L. subdichotomum*, the other plate (Nachträge, 1947, 94), also depicted in the English version of 1984, is definitely not a *Lepidopetalum*.

6. *Lepidopetalum xylocarpum* Radlk. – Figs. 3b, 7.

Lepidopetalum xylocarpum Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20 (1890) 269; Bot. Jahrb. 56 (1920) 307; in Engl., Pflanzenr. 98 (1933) 1319; P. van Royen, Man. For. Trees Papua & N. G. 2 (1964) 30. — Lectotype (here proposed): *Forbes 379* (M, holo; iso in BM, MEL), Papua New Guinea, Base of Owen Stanley's Ranges, Sogeri region.

Lepidopetalum hebecladum auct. non Radlk.: Koorders, Nova Guinea 8 (1909) 171.

Lepidopetalum subdichotomum auct. non Radlk.: Reynolds, Austrobaileya 2 (1985) 175; Fl. Austral. 25 (1985) 87, fig. 16, 21k, map 111.

Flowering branchlets 1–3 mm in diam. *Leaves* 2–4-jugate; rhachis 1.7–16 cm long, flat above, especially upper side sericeous. *Leaflets* 3–22.5 by 1.5–7.5 cm; apex (slightly) acuminate (to cuspidate), very apex emarginate to rounded (to mucro-qualate); above often glaucous when dry. *Inflorescences* usually ramiflorous on thin twigs to axillary to pseudoterminal, at most branching along rhachis, latter up to 8.5 cm long. *Bracts* and *bracteoles* triangular; bracts 0.7–1.3 mm long, broad; bracteoles 0.4–0.5 mm long. *Pedicels* (sub)glabrous except for glandular hairs to puberulous, upper part 2.3 (flower)–9 (fruit) mm long. *Flowers* 3.5–5 mm in diam. *Sepals* 5 (see note 2); blades 1.2–2.9 by 1–2.2 mm, margin and outside pilose. *Petals* 5 (see note 2); blade 0.5–2.2 by 0.7–2 mm, margin pilose, outside subglabrous; scale sometimes divided into two, 0.4–1.3 mm long by 1–2 mm broad; crest absent to sometimes central ribs. *Disc* often with slits, usually 5-lobed, flat, 0.3–0.5 mm

high, usually broader than high to as broad as high. *Stamens* 8(–10; see note 2); filament in male flowers 1.8–3.3 mm long, in female flowers 0.7–1.6 mm long; anther 0.7–1.3 by 0.4–1.2 mm. *Pistil*: ovary in male flowers c. 0.4 mm high, up to 2.5 mm high in female flowers, 2- (or occasionally 3-)locular, subglabrous to pilose; style and stigma in male flowers up to 0.1 mm high, in female flowers up to 1.5 mm high. *Fruit* 1.7–3.6 by 1.2–2 cm, inside densely hirsute with hairs c. 0.5 mm short; stipe absent to 7 mm high. *Seed* 1–1.9 by 0.7–1.1 cm, base straight; sarcotesta covering seed for greater part, present around hilum, ventral side and apex, absent from dorsal side; hilum 3–5.5 mm long. *Embryo* 0.9–1.6 by 0.6–1 cm; cotyledons laterally besides each other to dorsoventrally above each other to secondarily laterally besides each other; radicle less than 1 mm long.

Field notes – Tree, 4–22 m high; d.b.h. 5–25 cm; complexly branching buttress system may be present. Outer bark blotched pale green and greyish to grey-brown to dark brown with many round pustular lenticels, 0.5–2 mm thick; under bark red to purple-brown; inner bark straw to pinkish brown, 3–8 mm thick, shortly fibred. Wood straw, turning pale red-brown to centre, moderately hard and heavy, splits very readily, tendency to rings. Leaves dull green above, below pale green; young ones red. Calyx green. Petals pale green to white. Disk pale green to yellow. Filaments white; anthers brown. Fruits orange-red to bright red; sarcotesta orange-yellow to orange; seed black.

Distribution – Irian Jaya (Vogelkop, Fakfak, Mimika, Digul), Papua New Guinea (Western, Gulf, Central, Milne Bay, and Northern Prov.), and NE Australia (Torres Strait and Cape York Peninsula). See also note 4.

Ecology – Growing in understorey of primary forest, secondary forest, lower montane forest, gallery forest, and along rivers. Soil: alluvial, lava, limestone. Alt.: sea level up to 700 m. Flowering: Sep. to April. Fruiting: Jan. to Aug. (and Nov.).

Vernacular names – Abair (Kiwai); duwiduwi (Koreaf dial., Onjob lang.); ibih (Managalase); igia (Totobu); kivura (Naukwate dial., Onjob lang.); kwairoro (Kabubu and Utukap dial., Minufia lang.); ookojo (Mooi lang.); pikeri (Maipa dial., Mekeo lang.); umbupu (Mumuni dial., Orokaiva lang.).

Uses – In the Vogelkop the wood is used to start a fire [*BW (Moll) 12782*].

Notes – 1. Typical for this species are the hairy leaves, the usually glabrous upper part of the pedicel, the flat disc usually with slits, the usually highly stiped fruit with inside short hairs, and the sarcotesta which covers the seed except for the dorsal side.

2. Flowers, usually male, at the end of an inflorescence often show aberrant numbers of sepals (6), petals (6 or 7), and anthers (9 or 10).

3. Geographical variation exists within this species. See chapter Biogeography.

4. Specimens from the western part of the distribution (*Aet 287, Bauerlen 449, bb 32673, BW 12782, Everill 449, Jacobs 9132, 9200, NGF 35311, and Versteeg 1356*) resemble *Lepidopetalum micans* strongly. The fruits are almost similar, at least in shape, the only differences are the short hairs inside the fruit and the sarcotesta which does not cover the dorsal side of the seeds (in *L. micans* long hairs are present and the sarcotesta almost completely covers the seed except for a small dorsal triangle). Flowering specimens can only be separated when the flower pedicel is glabrous (always pilose in *L. micans*); if the flower pedicel is pilose then the gap in geography has to be used to identify the species.

EXCLUDED SPECIES

Lepidopetalum australe F. Muell. ex Ewart, Proc. Roy. Soc. Victoria 19 (1907) 41, nom. nud. – Cited specimen: *Hill de Mueller s.n.*, s.d. (K), Australia, Moreton Bay. = *Toechima tenax* (Benth.) Radlk.

Note – *Lepidopetalum australe* is a name on a herbarium sheet, it has never been published except as a nomen nudum in the synonymy of *Toechima tenax* by Ewart.

Lepidopetalum triloculare Kanehira, Bot. Mag. Tokyo 47 (1933) 400, nom. nud. – *Mischocarpus guillauminii* Kanehira, Bot. Mag. Tokyo 46 (1932) 672. – *Cupaniopsis guillauminii* Adema, Leiden Bot. Ser. 15 (1991) 121. – Type: *Kanehira 1268* (FU, holo, n.v.; iso in A, P), Caroline I., Truk I. = *Cupaniopsis guillauminii* (Kanehira) Adema.

Note – The herbarium sheet shows the name *Lepidopetalum triloculare* as an initial identification by Kanehira. Guillaumin in Paris identified it as a new species in *Mischocarpus*, after which Kanehira (1932) described this species as *Mischocarpus guillauminii* in honour of Guillaumin. He did not use the intended epithet on the sheet, but cited this name as a synonym (1933). The citation of the type specimen shows an error, it should be *Kanehira 1268* instead of *Kanehira 1368*.

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IDENTIFICATION LIST

The numbers refer to the species: *Lepidopetalum fructoglabrum* Welzen = 1, *L. micans* Lauterb. & Schumann = 2, *L. montanum* (Blume) Radlk. = 3, *L. perrotetii* (Cambess.) Blume = 4, *L. subdichotomum* Radlk. = 5, *L. xylocarpum* Radlk. = 6, *L. spec.* = 7.

- Adduru 12: 4 — Aet 287: 6 — Ahern 542: 4.
- Bauerlen 449: 6 — bb 32673: 6 — BCL 402: 5 — Brass 1371: 6; 3010: 5; 24044: 6; 24294: 6 — Britton 17: 4 — BS 7099: 4; 7293: 4; 8285: 4; 9968: 4; 11382: 4; 17976: 4; 26931: 4; 26932: 4; 27385: 4; 28145: 4; 28236: 4; 38096: 4; 46950: 4; 77065: 4; 83750: 4; 85123: 4 — BSIP 792: 5; 4939: 5; 4962: 5; 5038: 5; 8373: 5; 8382: 5; 9163: 5; 10242: 5; 10388: 5; 12272: 5; 12408: 5; 12468: 5; 14557: 5; 14712: 5; 15124: 5; 15284: 5; 18411: 5; 18536: 5; 18712: 5 — BW 4736: 5; 5371: 2; 12782: 6.
- Carr 11590: 6; 11618: 6; 16148: 6; 16160: 6; 16161: 6; 16201: 6; 16227: 6; 16347: 6 — Chakraborty 2139: 3; 2235: 3; 4637: 3 — Clemens 305: 4; 17901: 4; 18082: 4 — Coode (& Ridsdale) 5306: 4 — Craven (& Schodde) 45: 5 — Cuming 1036: 4; 1169: 4; 1170: 4.
- Darbyshire 1005: 6 — Docters van Leeuwen 9348: 2; 9454: 2; 11224: 2; 11264: 2; 11303: 2; 11376: 2 — Dommers 120: 7; 257: 7.
- Elmer 5721: 4; 8938: 4; 10935: 4 — Enriquez 82: 4 — Everill's Expedition 449: 6.
- FB 419: 4; 2710: 4; 5980: 4; 14832: 4; 16952: 4; 18275: 4; 18590: 4; 20524: 4; 23503: 4; 23813: 4; 24742: 4; 24948: 4; 26101: 4; 28286: 4; 28393: 4 — Forbes 379: 6; 830: 6; 830a: 6.
- Hallier 639: 4; 639b: 4; 4639: 4 — Hartley 9948: 1; 12354: 1 — Herre 277: 5 — Hollrung 341: 5; 387: 5; 707: 2 — Hoogland 4530: 6; 4787: 6 — Hoogland & Taylor 3738: 6.
- Jacobs 9132: 6; 9200: 6 — Junghuhn 41: 3.
- Kajewski 1902: 5; 2302: 5 — Kamphövar 2378: 3 — Katik W 2805: 2 — King's Collector (Kunster) 1: 3; 7: 3.
- LAE 50083: 2; 70240: 6; 70345: 2; 70364: 2; 74234: 5; 75093: 2 — Lam 420: 2 — Lauterbach 2840: 2 — Ledermann 10741: 2; 12265a: 2 — Loher 2074: 4; 2075: 4; 2076: 4 — Lörzing 5596: 3; 8458: 3; 12315: 3; 14580: 3; 17348: 3.
- Maule 850: 4 — Merrill 650: 4; 876: 4; 1404: 4; 1439: 4.
- Nair 912: 3 — NGF 2062: 6; 2915: 1; 3793: 2; 3844: 2; 3892: 2; 4750: 6; 5863: 6; 7145: 6; 7164: 6; 8075: 6; 8251: 6; 10701: 6; 11597: 1; 11649: 1; 12034: 1; 14345: 1; 14839: 1; 17196: 1; 19616: 6; 19628: 6; 20102: 1; 21901: 5; 23589: 6; 27507: 6; 28727: 6; 32833: 2; 35311: 6; 37984: 1; 38601: 6; 41844: 6; 45938: 2; 45981: 2; 46707: 2; 49211: 2.
- Peekel 766: 5 — Pleyte 68: 7 — PNH 11487: 4; 11838: 4; 18000: 4; 36620: 4; 42047: 4; 77983: 4 — Pullen 3459: 6; 6307: 6; 6321: 6; 6729: 6.
- Quadras 241: 4; 246: 4.
- Robbins 1318: 2; 1442: 2; 1445: 2; 1556: 2; 1570: 2; 1620: 2; 1676: 2; 1719: 5; 2456: 2.
- Saunders 172: 6; 947: 2 — Schlechter 14570: 2; 16767: 2; 18358: 2 — Schodde 2514: 6 — Schodde (& Craven) 4092: 5; 4410: 6; 4616: 6.

Takeuchi & Damas 4425: 2 — Tappenbeck 8: 2 — Taylor 2612a: 7 — Teijsmann HB 11745: 7; HB 11760: 7; HB 12820: 7 — Thomson, Th. 635: 2.
UPNG 264: 6; 1034: 6; 1457: 6; 4213: 6; 6577: 6 — Usteri 145: 4.
Versteegh 1356: 6 — Vidal 223: 4; 223b: 4; 1079: 4; 1227: 4; 1229: 4; 1229b: 4; 1231: 4; 1232: 4; 2485: 4; 2486: 4; 2494: 4; 2506: 4 — de Vogel 3216: 7 — de Vriese 18: 3.
Warburg 20545: 7; 20551: 5 — Waterhouse 171: 5; 406b: 5; 471b: 5; Y 171: 5 — Whitmore, Whitmore & Sidiyasa TCW 3557: 7 — Williams 2088: 4; 2160: 4; 2848: 4; 2893: 4; 2993: 4.

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