Taxonomy, Phylogeny, and Biogeography of *Baccaurea*, *Distichirhops*, and *Nothobaccaurea* (Euphorbiaceae)

PROEFSCHRIFT

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RAOUL MARTIN ANNE PETER HAEGENS
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Promotor:	Prof. dr. P. Baas
Co-promotor:	Dr. P.C. van Welzen
Referent:	Dr. P. Hoffmann (Royal Botanic Gardens, Kew, United Kingdom)
Overige leden:	Prof. dr. E. Gittenberger Prof. dr. P.J.M. Maas (Utrecht University, The Netherlands) Prof. dr. F. Schram (University of Amsterdam, The Netherlands) Dr. M. Zandee

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SUMMARY

This study comprises a taxonomic revision and phylogenetic and biogeographic analyses of the genera *Baccaurea*, *Distichirhops*, and *Nothobaccaurea* (Euphorbiaceae). *Baccaurea* was chosen as a model genus for study in the framework of the research program 'Pathways from Asia to new Guinea' of the Dutch Science Foundation because of interesting problems in the areas of phylogeny (Chapter 1), biogeography (Chapter 2), and species delimitation (Chapter 3). Moreover, *Baccaurea* species are also of economic and ecological importance. During the study of *Baccaurea* it became obvious that two species from Pacific islands, formerly recognised as *Baccaurea* species, constitute in fact a new genus: *Nothobaccaurea*. Furthermore, it became obvious that three unidentified species do not belong to any known genus; they are placed in an also newly described genus, called *Distichirhops*.

Chapter 1 contains the phylogenetic analyses of *Baccaurea* and *Nothobaccaurea*. The aim was to find the best hypothesis for the genealogical relationships of the species in *Baccaurea*, *Distichirhops*, and *Nothobaccaurea*. The phylogenies of these genera are a necessary prerequisite for the biogeographic analyses. The morphological species concept is used. Hybridisation is not thought to be a major speciation mechanism in *Baccaurea*. A study of the subtribe Scepinae showed the monophyletic status of *Baccaurea*, *Distichirhops*, and *Nothobaccaurea*. *Aporosa* is chosen as outgroup, because it is the sistergroup of the clade containing the three revised genera. *Distichirhops* and *B. microcarpa* are excluded from further analyses, because of our incomplete knowledge of these taxa. A total of 102 characters have been defined and scored, most of which have distinct states. Fifteen characters were later omitted for several reasons. The final analyses are, therefore, based on 87 characters, of which 23 concern vegetative, 22 staminate, 23 pistillate, 7 fruit, 2 ecological and 10 leaf anatomical characters. For most of the parsimony analyses the computer program PAUP 3.1.1. is used. A parsimony analysis with equally weighted characters resulted in 12 Most Parsimonious Cladograms (MPCs), with a fairly well resolved Strict Consensus Cladogram (SCC). The confidence indices for cladistic analyses like Consistency Index and Retention Index are within the expected range for a data matrix of this size. Even though the SCC is well resolved most internal branches of the 12 MPCs are not corroborated, because they have no Bremer support. A new method of analysis, called Iterative Taxon Reduction (ITR), is applied to find the relatively stable parts of the MPCs, and to make a possible selection among the 12 MPCs. This new method reduces the number of taxa by replacing stable clades (= those with Bremer support) in the data matrix by the character states of their common internal node. A new analysis is then performed with the reduced data matrix. The procedure is repeated till no further reduction of the data matrix is possible or till all clades have obtained Bremer support. The result is a SCC-like cladogram with relative Bremer support per clade. Other methods suitable for selecting cladograms are weighted character analyses. The weighted cladograms are dismissed, because they did not select among the 12 MPCs and preferred other, less homoplasious equal weight cladograms. Therefore, all 12 MPCs are chosen as equally good hypothesis for the phylogenetic relationships in *Baccaurea* and *Notho-*

baccaurea. Important conclusions drawn from the Most Parsimonious Cladograms are that the New Guinean species of *Baccaurea* are not closely related to each other except for *B. papuana* and *B. carinata*. Till recently the phylogenetic connections of several species were unclear, like the close relationships among *B. angulata*, *B. lanceolata*, *B. dulcis*, and the newly described *B. purpurea*. Other relationships, already expected by former taxonomists, like those of the Pacific species *B. nesophila* and *B. taitensis* could be confirmed. The consequences of the phylogenetic analyses for formal classification are limited to the confirmation of *Baccaurea* and *Nothobaccaurea* as monophyletic entities.

Chapter 2 contains the biogeographic analyses. The most important question is how, in time and space *Baccaurea* did reach New Guinea. *Baccaurea* occurs on both sides of Wallace's line (a division through the central part of the Malay Archipelago), which means that *Baccaurea* can only have reached one of the sides through dispersal. Taxon biogeography is based on the phylogenetic relationships of the taxa and the knowledge of the geology of the areas where the taxa occur. The geological framework is derived from the literature. The areas used in the analyses are rather large. The first method used is substituting the species in the 12 MPCs by their distribution areas. The split up of the genera *Baccaurea*, *Maesobotrya*, and *Nothobaccaurea* corresponds with the geological split up of Asia, Africa, and the Pacific. Three or even four dispersal moments between the Sunda Shelf and New Guinea can explain the occurrence of *Baccaurea* in New Guinea. Brooks Parsimony Analysis (BPA) leads to a single scenario with one unexpected feature: *Baccaurea* first arrived in the Pacific from the mainland of South East Asia, and only later dispersed from the Pacific to New Guinea, the Philippines and the Sunda Shelf. Because of this unexpected result the method was adjusted to the situation in *Baccaurea*. Ancestral areas in BPA are simply defined as the combined distributions of the descendant taxa. This is implausible in *Baccaurea*, because geological history shows that the genus largely occurs in areas, which were only reached by dispersal. It is, therefore, assumed that the ancestral distribution areas roughly correspond to the distribution areas of the modern species. An analysis based on this idea showed only little resolution. One of the possible interpretations of this result could be that *Baccaurea* reached most areas at roughly the same time. Hovenkamp Analysis (HA) defines the borders where certain vicariance events occurred, and also the time frame in which the events took place. HA also indicates a dispersal route for *Baccaurea* from India, via the Southeast Asian mainland and the Sunda Shelf to New Guinea. Finally, the distribution patterns in *Baccaurea* are compared with a general area cladogram based on the analysis of many zoological and botanical taxa. This also strongly indicates that the most basal branch in *Baccaurea* occurred in India. The combined information of all above mentioned methods are combined in one dispersal/vicariance scenario (Fig. 2.12) for *Baccaurea* and allied genera. Conclusions drawn from this scenario are that *Baccaurea*, *Maesobotrya*, and *Nothobaccaurea* are of Gondwanan origin. The common ancestor of the clade containing these three genera speciated as reaction on the vicariance event coursed by the split off of Africa, India, and Australia from Gondwana. *Nothobaccaurea* went extinct or was primitively absent on Australia, but survived on Fiji. *Baccaurea* dispersed

from greater India via the Southeast Asian mainland into the Sunda Shelf. From the Sunda Shelf dispersal back to India and the Southeast Asian mainland took place as well as dispersal to the Philippines, New Guinea and the Pacific.

Chapter 3 contains the revisions of the three genera. *Baccaurea*, *Nothobaccaurea* and *Distichirhops* all belonging to subtribe Scepinae of subfamily Phyllanthoideae. A key to the genera of this subtribe is presented. The taxonomic revision of *Baccaurea* Lour (1790) comprises a brief history of the genus, a genus description, a general and several regional identification keys to the species, and descriptions of all 43 species. In comparison with the studies by Airy Shaw, who published most recently about *Baccaurea*, my treatment differs in the following perspectives. The subspecies *B. nesophila* var. *microcarpa* is raised to the species level. Thirteen names are synonymised. Four species are newly described, viz. *B. carinata*, *B. mollis*, *B. purpurea*, and *B. simaloerensis*. Two species, formerly belonging to *Baccaurea*, are transferred to *Nothobaccaurea*, viz. *B. stylaris* and *B. pulvinata*. Finally, *B. dolichobotrys*, which was formerly interpreted as a synonym of *Baccaurea polyneura*, received the species status again. Four names could not be interpreted and they are enumerated as species dubiae. Three names are excluded, because they do not belong to *Baccaurea*.

SAMENVATTING

Dit onderzoek bevat een taxonomische revisie, verwantschaps- en biogeografische analyses van de plantengeslachten *Baccaurea*, *Distichirhops* en *Nothobaccaurea*, alle behorend tot de wolfsmelkfamilie (Euphorbiaceae). *Baccaurea* is gekozen als modelgeslacht in het kader van het onderzoekprogramma 'Wegen van Azië naar Nieuw Guinea' van de Stichting Aard- en Levenswetenschappen vanwege interessante problemen op het gebied van verwantschapsonderzoek (Hoofdstuk 1), biogeografie (Hoofdstuk 2), en het onderscheiden van soorten (Hoofdstuk 3). Bovendien zijn vele soorten in *Baccaurea* economisch en ecologisch belangrijk. Tijdens deze studie werd het duidelijk dat twee soorten van de Pacifische eilanden, voorheen geplaatst binnen het geslacht *Baccaurea*, in feite een nieuw geslacht, *Nothobaccaurea,* vormen. Verder werd het duidelijk dat drie voorheen niet herkende soorten niet tot enig bekend geslacht behoren. Deze soorten zijn daarom in het nieuw beschreven geslacht *Distichirhops* geplaatst.

Hoofdstuk 1 bevat de verwantschapsanalyses van *Baccaurea* en *Nothobaccaurea*. Het doel was om een zo goed mogelijke hypothese voor de stamboom van de soorten in *Baccaurea*, *Distichirhops*, en *Nothobaccaurea* op te stellen. *Distichirhops* en *B. microcarpa*, echter zijn van de analyses uitgesloten, vanwege gebrek aan voldoende kennis van deze taxa. Voor de biogeografische studie van deze geslachten is een stamboom noodzakelijk. Er is gebruik gemaakt van het morfologisch soortconcept en het is niet waarschijnlijk dat hybridisatie een belangrijk mechanisme is in het ontstaan van soorten in *Baccaurea*. Een analyse van de geslachten van het subtribus Scepinae heeft aangetoond dat *Baccaurea* en *Nothobaccaurea* monofyletisch zijn. *Aporosa* is verkozen als buitengroep omdat het de zustergroep is van de tak met de drie gereviseerde geslachten. In totaal zijn er 102 kenmerken gedefinieerd en gescoord, waarvan de meeste met niet overlappende toestanden. Vanwege verschillende redenen zijn vijftien kenmerken later weggelaten. In de uiteindelijke analyses is daarom gebruik gemaakt van 87 kenmerken, waarvan 23 vegetatieve-, 22 mannelijke bloei-, 23 vrouwelijke bloei-, 7 vrucht-, 2 ecologische- en 10 bladanatomische kenmerken. Het computer programma PAUP 3.1.1. is voor de meeste analyses benut. Een parsimonie analyse (d.w.z. een analyse die leidt tot een stamboom waarin zo min mogelijk veranderingen van kenmerktoestanden plaatsvinden) waarin alle kenmerken even zwaar meegewogen zijn, geeft 12 Meest Parsimone Cladogrammen (= stambomen) (MPCs). Deze cladogrammen lijken op elkaar en worden samengevat in het Strikte Consensus Cladogram (SCC). De indicatoren voor de betrouwbaarheid van een verwantschapsanalyse, zoals de 'Consistentie Index' en de 'Retentie Index', vallen binnen het verwachte bereik. Hoewel het SCC goed opgelost is, zijn de meeste interne takken van de 12 MPCs wegens afwezigheid van 'Bremer ondersteuning' niet erg robuust (Bremer ondersteuning is een indicator voor stabiliteit voor interne takken van een stamboom). Om toch de relatief stabiele delen binnen de MPCs te kunnen vinden en een keuze te kunnen maken tussen de 12 MPCs, is er een nieuwe methode 'Iteratieve Taxon Reductie' (ITR) uitgeprobeerd. Het aantal taxa wordt in deze methode gereduceerd, doordat takken met Bremer ondersteuning worden vervangen door de

kenmerktoestanden van hun gezamenlijke interne knoop. Met deze gereduceerde matrix wordt dan een nieuwe analyse gedraaid. Vervolgens wordt de methode herhaald totdat er geen verdere reductie meer mogelijk is, of alle takken Bremer ondersteuning hebben. Het resultaat lijkt op een SCC met relatieve Bremer ondersteuning per tak. Een andere methode om tussen stambomen te kunnen kiezen is gewogen kenmerk analyse. De 'gewogen' stambomen worden hier verworpen omdat zij geen selectie vormen van de 12 MPCs. Omdat er geen keuze tussen de 12 MPCs gemaakt kon worden, zijn alle 12 MPCs gekozen als even goede hypothese voor de verwantschappen in *Baccaurea* and *Nothobaccaurea*. Enkele belangrijke conclusies die uit de 12 MPCs afgeleid kunnen worden zijn dat de soorten van *Baccaurea* uit Nieuw Guinea niet nauw met elkaar verwant zijn, met uitzondering van *B. papuana* and *B. carinata*. Verder zijn nu verwantschappen bekend die voorheen niet gekend waren, zoals die tussen *B. angulata*, *B. lanceolata*, *B. dulcis* en de nieuw beschreven soort *B. purpurea*. Andere relaties, reeds verwacht door voorgaande taxonomen, zoals die tussen de Pacifische soorten *B. nesophila* en *B. taitensis* worden hier bevestigd. De consequenties voor formele classificatie blijven beperkt tot de bevestiging dat *Baccaurea* en *Nothobaccaurea* monofyletische eenheden zijn.

Hoofdstuk 2 bevat de biogeografische analyses. De belangrijkste vraag hierbij is hoe en wanneer *Baccaurea* New Guinea bereikt heeft. *Baccaurea* komt namelijk voor aan beide zijden van 'Wallace's line' (een scheidslijn dwars door het centrale deel van het Indonesisch eilandenrijk). Dit houdt in dat *Baccaurea* een van beide kanten van deze lijn d.m.v. verspreiding bereikt moet hebben. Taxon biogeografie is gebaseerd op de stamboom van die taxa en op de kennis van de geologie van de gebieden waar deze taxa voorkomen. Het geologisch raamwerk is uit de literatuur afgeleid. Er zijn redelijk grote gebieden gebruikt voor deze analyses. De eerste methode die gebruikt is, is het vervangen van de soorten in de 12 MPCs door hun verspreidingsgebied. De opsplitsing van de geslachten *Baccaurea*, *Maesobotrya* en *Nothobaccaurea* komt overeen met de geologische opsplitsing van Azië, Afrika en het Pacifische gebied. Drie of vier verspreidingsmomenten tussen het Sunda Plateau en Nieuw Guinea zijn nodig om het voorkomen van *Baccaurea* in Nieuw Guinea te verklaren. Brooks Parsimonie Analyse (BPA) leidt tot één scenario. Dit scenario heeft een onverwacht kenmerk. *Baccaurea* zou op de Pacifische eilanden gearriveerd zijn vanaf het vasteland van Zuidoost Azië en vervolgens vanaf de Pacifische eilanden naar Nieuw Guinea, de Filippijnen, en het Sunda Plateau verspreid zijn. Vanwege dit onverwachte resultaat, is de methode aangepast om hem beter geschikt te maken voor de situatie in *Baccaurea*. Verspreidingsgebieden van vooroudersoorten worden in BPA gedefinieerd als de gecombineerde verspreidingsgebieden van alle dochter taxa. Voor *Baccaurea* is dit niet erg waarschijnlijk, omdat de geologische geschiedenis van de gebieden laat zien dat *Baccaurea* in veel gebieden voorkomt die alleen d.m.v. verspreiding bereikt kunnen zijn. Daarom is aangenomen dat verspreidingsgebieden van de vooroudersoorten in *Baccaurea* in grootte overeenkomen met de verspreidingsgebieden van de huidige soorten. Een analyse gebaseerd op deze aanname toonde slechts weinig resolutie. Eén van de mogelijke verklaringen van dit resultaat is dat *Baccaurea* de meeste gebieden ongeveer tegelijkertijd bereikt heeft. Hovenkamp Analyse (HA) definieert de grenzen van vicariantie gebeurtenissen (dit zijn gebeurtenissen waarop een natuurlijke barrière ontstaat,

waarop soortvorming plaatsvindt) en bovendien de volgorde in tijd waarin deze vicariantie gebeurtenissen plaatsvinden. Ook HA geeft voor *Baccaurea* een verspreidingsroute aan van India, via het vasteland van Zuidoost Azië en het Sunda Plateau naar New Guinea. Tot slot zijn de verspreidingspatronen van *Baccaurea* vergeleken met een algemeen geldend gebiedencladogram (i.p.v. op het geologisch raamwerk) gebaseerd op de analyses van vele zoölogische and botanische taxa. Ook deze analyse suggereert dat de meest basale tak van de stamboom van *Baccaurea* in India voorkwam. De informatie uit alle hierboven genoemde methodes zijn gecombineerd tot één verspreiding/vicariantie scenario (Fig. 2.12) voor *Baccaurea* en verwante geslachten. De volgende conclusies zijn op dit scenario gebaseerd. *Baccaurea*, *Maesobotrya* en *Nothobaccaurea* hebben hun oorsprong in Gondwana. De gemeenschappelijke voorouder van deze drie geslachten heeft op de vicariantie gebeurtenis die Afrika, India en Australië van Gondwana heeft gescheiden, gereageerd d.m.v. soortsvorming. *Nothobaccaurea* is of uitgestorven in Australië of is daar nooit aanwezig geweest, maar is op Fiji overleefd. *Baccaurea* is via India en het vaste land van Zuidoost Azië naar het Sunda Plateau verspreid. Vanuit het Sunda Plateau heeft er zowel weer migratie terug naar India en het vaste land van Zuidoost Azië plaatsgevonden, als migratie naar de Filippijnen, Nieuw Guinea en de Pacifische eilanden.

Hoofdstuk 3 bevat de revisies van de geslachten *Baccaurea*, *Nothobaccaurea* en *Distichirhops*, alle behorend tot het subtribus Scepinae in de onderfamilie Phyllanthoideae. Een determinatiesleutel voor de geslachten in dit subtribus wordt gepresenteerd. De taxonomische revisie van *Baccaurea* Lour. (1790) bevat een korte geschiedenis en beschrijving van het geslacht, een algemene determinatiesleutel en verschillende sleutels van deelgebieden, alle tot op soortniveau en beschrijvingen van de 43 soorten. In vergelijking met het onderzoek van Airy Shaw, diegene die het kortst geleden over *Baccaurea* gepubliceerd heeft, wijkt mijn studie op de volgende punten af. De ondersoort *Baccaurea nesophila* var. *microcarpa* is tot soort verheven. Dertien namen zijn gesynonimizeerd. Er worden vier nieuwe soorten beschreven, nl. *B. carinata*, *B. mollis*, *B. purpurea* en *B. simaloerensis*. *Baccaurea stylaris* and *B. pulvinata*, twee soorten die voorheen tot *Baccaurea* behoorden, zijn verplaatst naar *Nothobaccaurea*. Tot slot is *B. dolichobotrys*, dat als een synoniem van *B. polyneura* werd beschouwd, opnieuw tot soort verheven. Van vier namen was de interpretatie niet duidelijk. Deze zijn opgesomd als 'species dubiae'. Drie namen zijn uitgesloten omdat zij niet tot *Baccaurea* behoren.

INTRODUCTION

The Malesian region has been divided into two major areas based on the biota's inhabiting them. Since Wallace (1876), the exact location of the demarcation line (Wallace's line, Fig. 1.1) between the two areas has been subject of an ongoing debate (Michaux, 1991). The separation itself is, however, broadly accepted. It is obvious that several groups of organisms do not fit this division. Such groups contain members on both sides of Wallace's line. This study is part of a programme called: 'Pathways from Asia to New Guinea: the origin of non-Australian elements of the Papuan flora and fauna'. This programme is supported by Dutch Science Foundation (NWO/ALW). The aim of the programme is to identify pathways used by floral and faunal elements of Asia and Western Malesia to reach New Guinea and the Western Pacific Islands. The genus *Baccaurea* was selected as floral component, firstly because this genus is found on both sides of Wallace's line (in India, Southeast Asia, Malesia, and the Pacific), and secondly because of the high proportion of endemics (half of the species in this genus is endemic to one of the major islands in Malesia or the Pacific). The ultimate objective of this study is to discover the pathways for *Baccaurea* to New Guinea. The study of *Baccaurea* led to the conclusion that two other genera, formerly not described, had to be recognised. These two genera, viz. *Distichirhops* and *Nothobaccaurea*, are utilised next to *Baccaurea*. This research has resulted in a historical dispersal/vicariance scenario for *Baccaurea* and *Nothobaccaurea*. A generalised area cladogram based on several groups of organisms will be established when all projects within this programme have been finished.

Historical biogeographic analyses (Chapter 2) as discussed in the preceding paragraph are based on the distribution areas and phylogenetic relationships (Chapter 1) of the taxa under study. A sound base for species information is a modern taxonomic revision of all taxa involved. Therefore, a revision (Chapter 3) has been made of the genera *Baccaurea* (43 species), *Distichirhops* gen. nov. (3 species), and *Nothobaccaurea* gen. nov. (2 species). All three genera belong to the subtribe Scepinae (Euphorbiaceae). This research fits well in the research aims of the National Herbarium of the Netherlands (NHN). One of the research projects at the Leiden branch of the NHN (NHN/L), is Flora Malesiana (FM). This is a long-term, multinational flora project. The ultimate goal of FM is to describe and classify the flora of Malesia. One of the major families presently under study is the spurge family (Euphorbiaceae). The revisions for FM provide ample information on the distribution areas of all species, as required for the biogeographic analyses. Another condition is a reliable reconstruction of the phylogenetic relationships of the taxa involved. Cladistic analyses have been carried out in order to hypothesise these relationships. The phylogenetic relationships of taxa are also an important starting point for classifications, because the latter are intended to reflect the natural order of the taxonomic diversity, i.e. the geneological relationships. Additional important considerations to choose *Baccaurea* as study object are more social-economically determined. Many species are locally grown for their fruits. In most species only the arillode is eaten, but in *B. lanceolata* the fruitwall is eaten as well. The fruits are very sour, but in several species sweet varieties are known.

Presently, three species are commonly cultivated and sold on markets (Uji, 1991; Van Valkenburg, 1997), viz.: *B. motleyana* (common name: rambai) in Peninsular Malaysia, Sumatra, Java, Bali, and Borneo; *B. dulcis* (common name: Cupa) in Sumatra; *B. ramiflora* [common name: Latka (India, China), Kanaso (Burma)] in the Southeast Asian mainland. Species less commonly cultivated are: *B. angulata*, *B. bracteata*, *B. edulis*, *B. macrocarpa*, *B. lanceolata*, *B. polyneura*, *B. pubera*, *B. racemosa*, and *B. reticulata*. This enumeration shows that nearly all species in *Baccaurea* with relatively large fruits are cultivated. However, most species have only low economic potential because the edible part is only the arillode; cultivation is often difficult to establish (Wong & Lamb, 1993); only female trees will produce a fruit harvest; the taste of many varieties is rather sour, whereas the sweet varieties are of course preferred (Uji, 1991; Van Valkenburg, 1997); and most species do only produce seeds when a male tree is present to enable pollination. Pollination is necessary, because no arillode will be produced when seeds are absent. The present low economic potential can be substantially increased when promising genotypes of wild species would be exploited (Salma et al., 1997).

Several species of *Baccaurea* are harvested for their wood. *Baccaurea sumatrana* is the tallest species with durable wood and the best-known species in this genus for timber. Other timber trees are: *B. bracteata*, *B. dulcis*, *B. javanica*, *B. lanceolata*, *B. macrocarpa*, *B. macrophylla*, *B. minor*, *B. motleyana*, *B. nanihua*, *B. parviflora*, *B. polyneura*, *B. racemosa*, *B. ramiflora*, and *B. reticulata* (Chapter 3; Salma, 1998). Except for *B. motleyana*, all the species mentioned have rather hard and durable timber. Moreover, the wood *B. trigonocarpa* is used as firewood (Chapter 3). Last but not least, the bark and leaves of several species are used for medicine (Chapter 3; Soejarto, 1965): against painful eyes (*B. motleyana*); for the regulation of menstruation (*B. brevipes*); against stomach-ache (*B. lanceolata*); and used in mixtures against general illnesses.

The species of *Baccaurea* may contribute only marginally to the local economics, but their ecological values are more obvious. The fruits are eaten by many bird species, but also by rodents, deer, and monkeys, including the Orang utan (Rijksen, 1978). The fruit season is in many species year-round and they therefore constitute an important nutrient source during the periods that seasonal fruits are not available. In addition, the population density of most species in *Baccaurea* is relatively high, especially on the Sunda Shelf (Salma et al., 1997), which raises the chance of discovering a fruiting tree. I observed that the understorey in some forests in Peninsular Malaysia and Borneo is dominated by *B. lanceolata*, *B. odoratissima*, *B. parviflora* or *B. tetrandra*.

Local extinctions of species in *Baccaurea* occur all the time due to the very fast declining area of tropical lowland rain forests. However, in *Baccaurea* the situation for most species is quite favourable due to e.g.: the distribution areas for most species are large (i.e. at least one of the major islands in Malesia, like Borneo, or the Pacific, like Fiji); most species are not limited to primary forests (Chapter 3); several species are grown in cultivation; the population densities are high. This combination of characters provides reasonable survival chances for most species. However, some species are seriously threatened or the knowledge about their conservation status is

lacking: *B. annamensis* has not been found recently (1921 is the most recent collection). This may be due to the fact that it is a very rare species. The fact that I could obtain only very few collections from Vietnam and Laos may be due to undercollecting; *B. carinata* is only known from a few specimens in the Sepik area in New Guinea, and may be very rare as well; the relatively few collections of *B. dolichobotrys* are in my opinion due to the fact that this species was not recognised for a long period. However, it cannot be excluded that it is a rare species indeed; *B. microcarpa* is only known from one collection from Ferguson Island, and certainly threatened; *B. nesophila* is known from more collections, but is only found in the Louisiade Archipelago; *B. purpurea* is a very rare species only known from Peninsular New Guinea; *B. seemannii* is known from relatively few collections from Fiji; *B. simaloerensis* also has a restricted distribution area, which makes this species vulnerable to extinction. In the genus *Nothobaccaurea*, the distribution area of *N. pulvinata* is restricted to Fiji. All three species of *Distichirhops* are very infrequent. *Distichirhops megale* is the least known, because only one specimen from the Peninsular of New Guinea has been found. The other two species, *D. minor* and *D. mitsemosik* are extremely rare as well, but known from at least two very different locations.

With this study I hope to contribute to the knowledge of plants and plant diversity of one of the richest areas in plant species on earth, but at the same time one of the most threatened areas as well.

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Chapter 1

PHYLOGENETIC ANALYSES

1.1 – Introduction

The purpose of this study is to find the best hypothesis for the genealogical relationships of the species in the clade constituted by *Baccaurea*, *Distichirhops*, and *Nothobaccaurea*. The phylogenies of these genera will be used, and are a necessary prerequisite, for the biogeographic analyses (Chapter 2).

The results of a preliminary analysis (Chapter 1.4) of the major genera of the subtribe Scepinae show that *Aporosa* is in a basal position, compared with *Baccaurea*, *Nothobaccaurea*, and the allied genus *Maesobotrya*. This is in agreement with the conclusions of Levin (1986). Therefore, two species of *Aporosa* were used as outgroup in this study.

The analysis at the species level produced twelve Most Parsimonious Cladograms (MPCs). In order to make a choice between these cladograms and to obtain better support for the internal nodes, different weighting methods were tested. Because the available methods did not resolve the problem satisfactorily, a new method of cladogram support, viz. Iterative Taxon Reduction (ITR), is presented (Chapter 1.6.3).

The accepted cladograms and the consequences for the classification of *Baccaurea* will be discussed.

1.2 – Species concept

Species have been delimited using a morphological species concept. Theoretically, it would be better to use the phylogenetic (Mayden, 1997, and references therein) or the composite species concept (Kornet, 1993), but these and other concepts require information currently not available for *Baccaurea*.

The choice for using the morphological species concept in order to recognise the different entities is a purely practical one. Even advocates of other species concepts recognise their species on the basis of morphological characters, especially when using herbarium specimens as the main source of information. Nixon & Wheeler (1990) for example stated that phylogenetic species are diagnosed by a unique combination of character states in comparable individuals. In the reality of herbarium or museum taxonomy, most if not all species concepts rely on morphology.

1.3 – Hybridisation

Hybridisation is a problem for phylogenetic analysis, because it causes a reticulate pattern of relationships among species. In a phylogenetic analysis a search for a divergent pattern is carried out. Due to the methods used, a divergent pattern will always be found, even when hybridisation is present.

Do hybrids really cause problems for phylogenetic analyses, resulting in incorrect tree topologies, and if so, are species of hybrid origin recognisable before or during the phylogenetic analysis? McDade (1992) has studied the first problem. Hybrids of closely related parents (Fig. 1.1) usually behave like normal, closely related species. The topological changes are small and the Consistency Index (CI) is higher when this type of hybrid(s) is included in the analysis. Hybrids between distantly related parents (Fig. 1.1) on the other hand cause incongruence. The CI decreases and major topological changes may occur. Even taxa that have no connection with the taxon of hybrid origin may change position. For ancestral hybrids (i.e. hybrids ancestral to a whole clade) no data are available. Thus, if species of hybrid origin are present, except for hybrids of closely related species, this will render the results of the phylogenetic analysis worthless or at least unreliable, when interpreted as directly reflecting evolution.

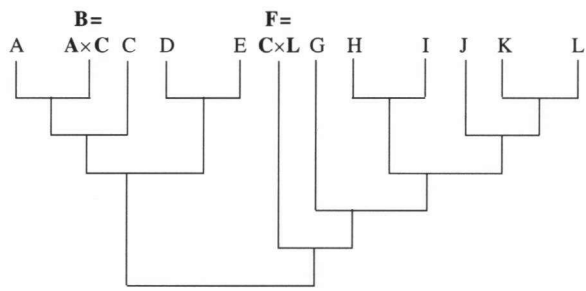


Fig. 1.1. Type of hybrids. **B** is a hybrid of closely related parents (A & C), both parents are members of the same main lineage. **F** is a hybrid of distantly related parents (C & L), both parents are members of different main lineages.

Knowing that species of hybrid origin can confound phylogenetic analysis, recognition of hybrids prior to the analyses is preferable. It is usually possible to recognise recent hybrids of distantly related parents on the basis of morphology. Species with numerous intermediate character states are suspect (Wagner, 1983). It is, however, impossible to distinguish between closely related species and hybrids of closely related parents. This problem can be ignored, because this type of hybrids does not cause real problems for phylogenetic analyses. Variation in chromosome numbers is also an indication of ongoing hybridisation (Haufler, 1987) just as imperfect pollen (Wagner, 1983). If living material is available, it is possible to study chromosome behaviour (Stace, 1989) and the success of F1/F2 generations (Stace, 1989; Sosef, 1994). In *Baccaurea* it is difficult to recognise characters with intermediate states because most characters show gradual variation. However, intermediates from apparently distantly related species (species which do not resemble each other) which would be recognisable, were not found. The chromosome numbers of *Baccaurea* are virtually unknown. In *B. pubera* n = 13 was counted (Moore, 1971; Goldblatt, 1981). It is also the basic number for *Antidesma*, *Aporosa*, *Hymenocardia*, *Maesobotrya*, and *Uapaca* (Moore, 1972; Hans, 1973). The pollen quality was good in the c. 25 species of *Baccaurea* studied by Bojo (1988). The morphological features of *Baccaurea* give no indication for the presence of recent hybrids.

The recognition of hybrids (of distantly related parents) from the phylogenetic analyses itself is more problematic. A low CI (McDade, 1992), branches supported by a high number of homoplasious characters (Hillis et al., 1996, and references therein), and a high number of MPCs are all indicative, but never conclusive. Thus phylogenetic analyses, based on macromorphological characters are poor indicators, as the CI is often low, homoplasy high, and usually several to many MPCs are present. *Baccaurea* is no exception, but for the number of MPCs, which is only 12 in the final analysis.

Recognition of hybrids by means of molecular data is beyond the scope of this research and will, therefore, not be discussed.

Hybridisation has mostly been studied in taxa of temperate areas. In some families hybrids are common (Funk, 1981; McDade, 1992). For the Euphorbiaceae little information is available, as is the case for all mainly tropical plant families, and there is no information at all about the occurrence of hybrids in *Baccaurea*.

In the absence of any morphological indications for the presence of hybrids, it was therefore assumed that hybridisation did play no significant role in the speciation processes of *Baccaurea*.

1.4 – Monophyly and rooting of *Baccaurea*

In a phylogenetic analysis the ingroup should be monophyletic, i.e. derived from a common ancestor and comprising all its descendants. Within the subfamily Phyllanthoideae, *Baccaurea* is placed in the subtribe Scepinae (Webster, 1994). In order to explore the monophyletic, paraphyletic or polyphyletic nature of *Baccaurea*, an analysis was performed with a selection of the genera of the Scepinae as ingroup. The subtribe consists of ten genera (two of which are newly described in this study as segregates of *Baccaurea*) from Asia, Africa and South America. *Baccaurea* is one of the three major genera in the subtribe. The two other important genera are *Aporosa* from Southeast Asia, and *Maesobotrya* from Africa, both resembling *Baccaurea*. The seven remaining genera, viz. *Apodiscus*, *Ashtonia*, *Distichirhops*, *Jablonskia*, *Nothobaccaurea*, *Protomegabaria*, and *Richeria* are monotypic or contain 2 or 3 species only. The generic delimitation in this group has not yet been studied critically. The distinctive characters for the three major genera are listed in Table 1.1. Besides *Baccaurea*, *Aporosa*, and *Maesobotrya*, five more genera are included in the table. *Uapaca* and *Hymenocardia* are both used as outgroups. The new genus *Nothobaccaurea* (Table 1.1) comprises the species *N. stylaris* and *N. pulvinata*, formerly belonging to *Baccaurea*. This genus from the Pacific has characters intermediate between *Baccaurea* and *Maesobotrya*. The new genus *Distichirhops* (Table 1.1) comprises three formerly undescribed species. These species are only known from pistillate and fruiting specimens and show some characters in accordance with *Baccaurea*, but more so with *Aporosa*. The leaf arrangement for example is distichous (Fig. 3.1a), common in *Aporosa*, and a Terminalia branching pattern is absent. Moreover, the pedicel has no abscission zone, which is also congruent with *Aporosa*. The number of locules in the ovaries, however, is 2–4 like in *Baccaurea* and *Maesobotrya* (the ovary consists of 3–5 locules in *Aporosa*). Examination of staminate material, now still lacking, will probably clarify the status of this new genus.

Table 1.1. Distinctive characters for *Baccaurea, Aporosa, Maesobotrya,* and allied genera (see text for explanation). Characters in parentheses (left hand column) have not been used in the phylogenetic analysis.

character phylogeny		*Baccaurea*	*Aporosa*	*Maesobotrya*	*Nothobaccaurea*	*Distichirhops*	*Uapaca*	*Hymenocardia*
1	Stamens shorter than sepals (+) or absent (–)	+	–(+)*	–	–	?	–	+
(2)	Pistillate flower disc present (+) or absent (–)	–	–	+	–	–	–	–
(3)	Pistillode grabrous (+) or pubescent (–)	–	–	–	+	?	–	+
4	Pedicel: abscission zone present (+) or absent(–)	+	–	+	+	–	?	–
5	Glomerules (cluster of sessile flowers) present (+) or absent (–)	–	+	–	–	?	+	+
6	Staminodes present (+) or absent (–)	+/–	–	+	–	?	–	–
7	Leaf arrangement disticous (+) or spiral (–)	–	+/–	–	–	+	–	–
8	Terminalia branching pattern present (+) or absent (–)	+	–	+	+	–	–	–
9	Staminate flower sepals fused (+) or free (–)	–	–	+	+	?	+	+
(10)	Stamen number	4–10	2–4	5	5–7	?	4–5	4–8
(11)	Ovary: number of locules	2–4	3–5	2–4	2	2–4	2–3	2
12	Inflorescences rami- or cauliflorous (+) or only axillary (–)	+	+	+	+	–	–	–

* In the phylogenetically basal species of *Aporosa* the stamens are longer than the sepals, in a number of species with more derived characters the stamens are shorter than the sepals (Schot, in prep.).

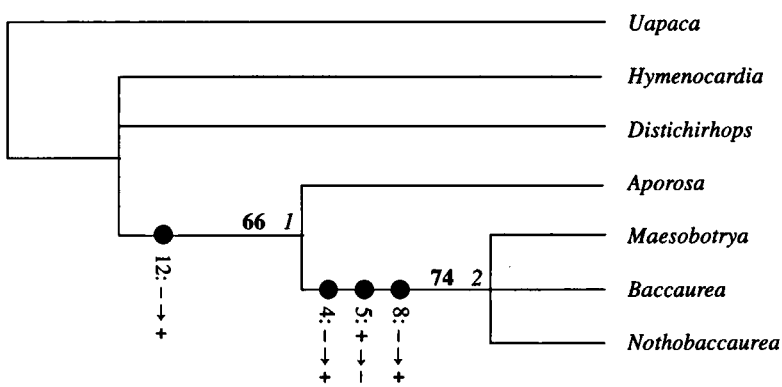


Fig. 1.2. Rooting of *Baccaurea*. Single most parsimonious cladogram obtained by parsimony analysis in PAUP 3.1.1. Length = 11; CI = 0.818; RI = 0.800; RC = 0.655; HI = 0.364; ● = apomorphy; decay index in *italics*; bootstrap values in **bold**. The genera *Upaca* (subtribe Uapacinae) and *Hymenocardia* (tribe Hymenocardieae) are used as outgroups. The numbers of the apomorphies refer to Table 1.1.

Characters in parentheses of Table 1.1 lead to the phylogenetic hypothesis presented in Fig. 1.2. The phylogenetic analysis was performed using PAUP 3.1.1 (Swofford, 1993). The moderate size of the data matrix allowed an exhaustive search with all characters unordered. In this analysis, the monophyletic status of the seven genera is

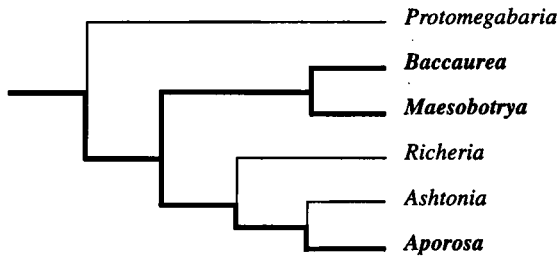


Fig. 1.3. Cladogram of Scepinae (= Aporuseae), after Levin (1986). In **bold**, the taxa treated in the present study.

assumed, which is, to a certain extent, supported by Table 1.1 because all genera show a unique set of characters. Other support was found in the fact that when more species of each of the 5 ingroup taxa (that is, belonging to the subtribe Scepinae) were used in the analysis, the species of each genus were always united in one clade. The analysis was carried out in order to find an appropriate outgroup for *Baccaurea*. *Aporosa* and *Distichirhops* are placed at a basal position relative to *Baccaurea*, *Nothobaccaurea*, and *Maesobotrya*. The relationships between the latter three are not certain from this analysis, mainly due to the intermediate morphology of the genus *Nothobaccaurea*. *Aporosa*, on the other hand, has a stable position (bootstrap value 74%, significant according to Hillis & Bull, 1993; Decay index 2, Bremer, 1988; Källersjö et al., 1992) as sister group of the three other genera together, and is regarded as the most suitable outgroup for *Baccaurea*. The results obtained in this analysis are in agreement with the results obtained by Levin (1986), who performed a cladistic analysis based on foliar morphology of the Phyllanthoideae. The results for the Scepinae (Aporuseae) are shown in Fig. 1.3.

Distichirhops will be omitted from further analyses, because of lack of suitable characters and insufficient knowledge of this genus (i.e. staminate flowers missing). Its placement remains speculative. In order to resolve the clade including *Baccaurea*, *Maesobotrya*, and *Nothobaccaurea* further analyses will be performed with the following ingroup: all species of *Baccaurea* (except *B. microcarpa*, because too much data are lacking for this species) and a selected number of species of *Maesobotrya*.

1.5 – Methods

1.5.1 – *Character choice*

Characters with clearly distinct states were without hesitation used for the phylogenetic analyses. A major concern in *Baccaurea* is the occurrence of many polymorphic taxa for a rather high number of characters. These polymorphies are largely due to quantitative characters, like the leaf shape. Quantitative characters can nevertheless be useful for phylogenetic analysis, because they can indicate evolutionary independence as stated by Swiderski et al. (1998). Turner (1995) studied the problem of coding polymorphies and concluded that, at least theoretically, polymorphic characters should be assigned the local ancestral plesiomorphic character state. In this study it is impossible

to determine a priori which of the character states present is plesiomorphic. Therefore, polymorphic characters were coded as unknown or polymorphic, which is in concordance with Turner's recommendations (Turner, 1995). For multistate characters, coding as polymorphism (only possible in computer program PAUP, Swofford, 1993, 1998) is to be preferred, because polymorphic characters will always be placed in the clade characterised by at least one character state which they possess, at the cost of an extra step for the other state(s). This is the only possible way of coding without a priori assumptions about character transformation, and simultaneously creates no artificial characters or states, as is the case with other ways of coding.

Recent studies show that another type of quantitative characters, namely continuous characters, may also contain phylogenetic information (Wiens, 1995; Rae, 1998). The best way to divide this type of character into character states is to make use of the mean value in combination with the extreme values of the character (Swiderski et al., 1998). Because no mean values for the continuous characters were recorded in this study (only the extreme values), ranges were used to distinguish between character states. Wieringa (1999) used 10% intervals of ranges to separate character states, but this type character subdivision leads to many, artificial states. In order to find dividing lines in continuous characters, for each character a diagram was produced (Fig. 1.4B), in which the species are indicated on the X-axis and the range of values for a character on the Y-axis. In these diagrams horizontal lines were drawn where the fewest ranges are crossed by the horizontal lines, under the condition that the species are split up in at least two groups both with more than 1 member (Fig. 1.4A). These are the values defining the character states. In Fig. 1.4A the lines drawn at 1 and 10 show no crossing

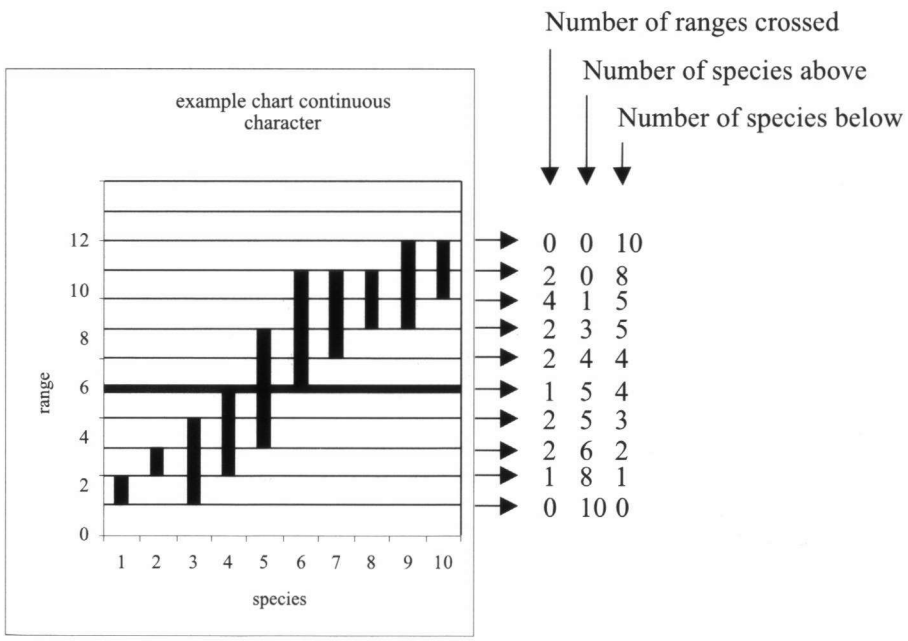


Fig. 1.4A. Way of selecting character states in continuous characters. Selected separation line thickened. For explanation see Chapter 1.5.1.

with any of the species ranges, but the species do not form two (or three) groups based on these lines. At level 2 and 5 there is only one crossing present. The line at level 2 cannot be selected because there is only one species with its range totally below it. The line at level 5 divides the species in two groups and is therefore suitable as dividing line for this character. Four of the quantitative characters used in the analyses are thus presented in Fig. 1.4B. Character 16, maximum leaf length of the lamina, and character 88, maximum petiole length (not used in the final analysis), are an exception as the minimum values of all species are almost identical, only the maximum values are used for the analysis. The dividing lines in this character are drawn at the levels that show a discontinuity (Fig. 1.4B).

Altogether 102 characters were recorded for the phylogenetic analyses, of which 87 were macromorphological, 3 ecological and 12 leaf anatomical. The leaf anatomical data are based on the study of Ms. Saskia Bodegom et al. (in prep.). For several of the latter characters only 2 specimens per species were examined. Of the 102 characters, 49 characters may cause problems because one or two of the following difficulties are

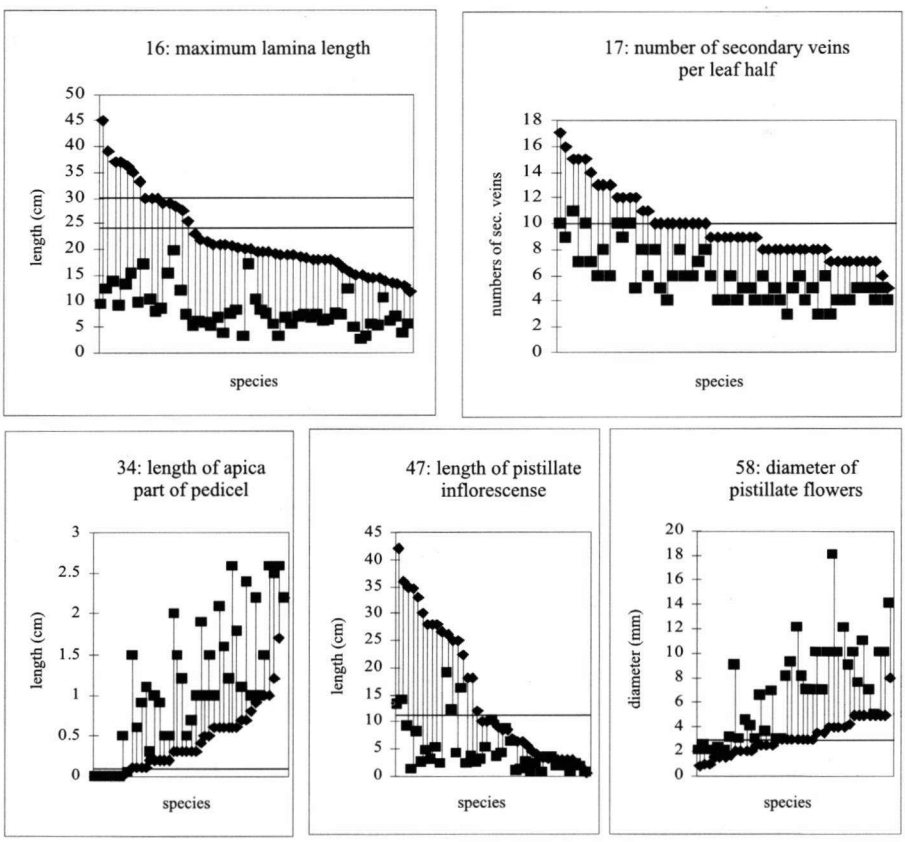


Fig. 1.4B. Continuous characters used for phylogenetic analysis. On the Y-axis the range of variation is given. On the X-axis the species. The horizontal lines indicate were the delimitation between character states was drawn.

present: a. quantitative characters without distinct gaps; b. definition of characters or states is problematic, and therefore difficult to score; c. low sampling number (few measurements per species); d. homology of character states uncertain; e. information obtained from specimen labels and therefore not verifiable. However, an analysis with the 53 remaining characters did not provide enough resolution. An analysis was then performed with all characters. The characters with one or more of the problems mentioned above which scored a ci < 0.1 (characters 88–102) in the analysis, were omitted from further analyses.

Characters used in the phylogenetic analyses are shown below. Letters between brackets indicate ambiguous characters: (a) quantitative characters without distinct gaps; (b) definition of characters or character states is problematic; (c) sampling number low; (d) homology questionable; (e) information from label and therefore not verifiable.

Vegetative:

1. (a, e) Habit: 0 = tree; 1 = tree or shrub.
2. (a, e) Buttresses: 0 = absent; 1 = sometimes present.
   Buttresses or a fluted bole are variably formed in a limited number of taxa. The ability to grow buttresses was chosen as character state for the species as a whole when the species is polymorphic.
3. (e) Colour of fresh outer bark: 0 = grey-brown; 1 = red-brown.
   The colour of the outer bark is usually reddish-brown in the larger species, in most other species greyish.
4. (e) Colour of fresh inner bark: 0 = yellow-brown to white-brown; 1 = red-brown.
   The inner bark is usually inconspicuously coloured, but in several species red.
5. Terminalia branching pattern: 0 = absent; 1 = present (see Fig. 3.1c).
   Terminalia branching pattern is present in all species of *Baccaurea*, *Maesobotrya*, and *Nothobaccaurea*, but absent in *Aporosa*.
6. Terminalia branching pattern: 0 = strong; 1 = weak (see Fig. 3.1b, c).
7. Leaf arrangement: 0 = spiral; 1 = distichous.
   The arrangement of the leaves is spiral, except for the species of *Distichirhops*. This character is uninformative when *Distichirhops* is not used in the analysis.
8. Indumentum of branchlets: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy (Fig. 1.5).
   The hairiness of the plants varies between species in different parts of the plants. The density of the indumentum is used in the following 21 characters: 8, 9, 12, 18, 19, 28, 30, 31, 33, 37, 38, 48, 53, 55, 56, 60, 61, 64, 70, 71, 81. Judging which character state a species shows is sometimes difficult due to intermediates. In those cases both nearest character states were scored.
9. Indumentum of petiole: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
10. Basal pulvinus of petiole: 0 = absent; 1 = present.
    A basal pulvinus is a swelling of the petiole at the place where it connects to the branch, usually accompanied by a bent.
11. (b) Raised glands on petiole: 0 = absent; 1 = present.
    Many species are polymorphic for this character.
12. Indumentum on the outside of stipules: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.

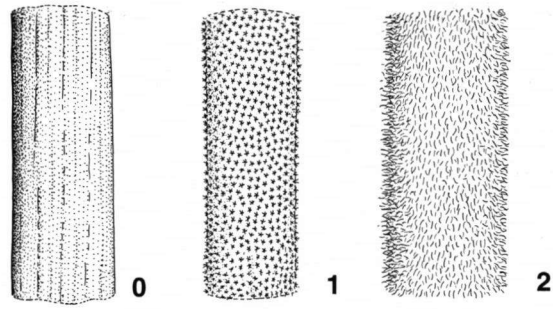


Fig. 1.5. Indumentum of branchlets: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.

13. Stipule margins: 0 = not ciliate; 1 = ciliate.
14. (b) Leaf texture: 0 = papery to slightly leathery; 1 = leathery.
    Judging to which state a species belongs is sometimes difficult due to intermediates.
15. Leaf shape: 0 = ovate; 1 = more or less elliptic; 2 = obovate.
    In most species the range is ovate to elliptic or obovate to elliptic.
16. (a) Maximum lamina length: 0 = < 24 cm; 1 = 24–31 cm; 2 = > 31 cm.
    This is a continuous character, like characters 17, 34, 47, 58. For treatment of continuous characters see Chapter 1.5.1. and Fig. 1.4A, B. In this character the maximum leaf length is used instead of the range, because the minimum leaf length varies only slightly between species.
17. (a) Number of secondary veins: 0 = 3–10; 1 = 10 or more.
    There is overlap in the ranges chosen as character states (Fig. 1.4B).
18. Indumentum on adaxial side of veins: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
19. Indumentum on abaxial side of veins: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
20. Base of leaf: 0 = truncate to attenuate; 1 = cordate.
    The leaf base is usually truncate to attenuate, but cordate in a few species. Truncate to attenuate is abruptly to gradually and concavely tapering to a point. Cordate is heart-shaped.
21. (b) Raised glands on lower leaf surface: 0 = absent; 1 = present (Fig. 1.6).
    Many species are polymorphic for this character.

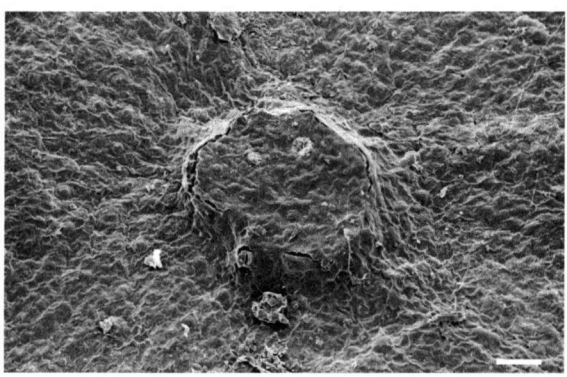


Fig. 1.6. Raised gland on lower leaf surface. – Photo: B.J. van Heuven.

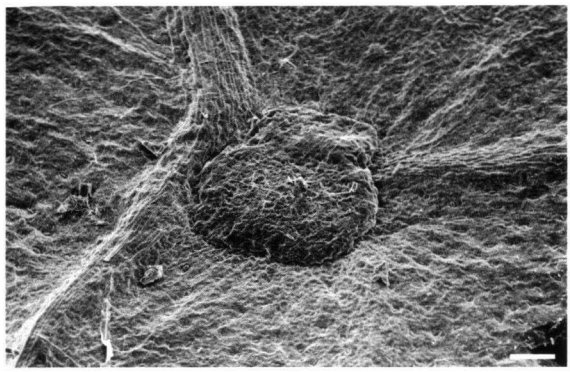


Fig. 1.7. Discoid gland on lower leaf surface. – Photo: B.J. van Heuven.

22. Discoid glands on lower leaf surface: 0 = absent; 1 = present (Fig. 1.7).
    Species are often polymorphic for this character.
23. Tertiary venation: 0 = reticulate; 1 = scalariform (Fig. 1.8).
    In most species a reticulate venation pattern is present, in a few, like *B. polyneura*, the venation pattern is scalariform.

Staminate inflorescences:

24. Position: 0 = axillary; 1 = just below the leaves; 2 = along the branches; 3 = cauline.
    Half the species show one or two states and in seven species all character states are observed. Axillary means growing in a leaf-axil. Cauline is growing on the trunk.
25. Glomerules: 0 = absent; 1 = present.
    Glomerules, here defined as a group of sessile flowers, are only present in *Aporosa*.
26. Branching: 0 = absent; 1 = present.
27. (a) Number of individual inflorescences per cluster: 0 = 1; 1 = 2–10; 2 = > 10.
    The inflorescences are usually single or a few (2–10) clustered together.
28. Indumentum of inflorescence: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
29. Flower placement: 0 = scattered along inflorescence rachis; 1 = clustered at the tip of the rachis (see Fig. 3.4).
30. Abaxial indumentum of bracts: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
31. Adaxial indumentum of bracts: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
    Several parts of the plants show a different density of the indumentum on the abaxial side, compared with the adaxial

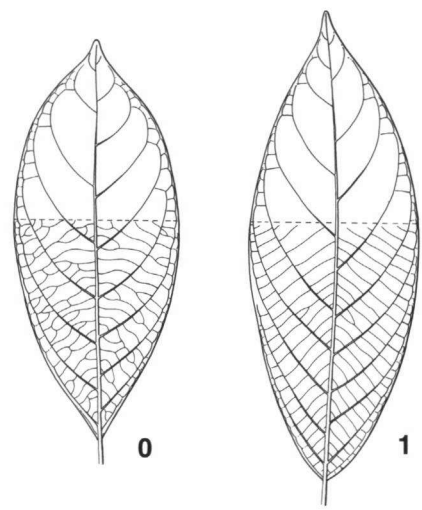


Fig. 1.8. Tertiary venation: 0 = reticulate; 1 = scalariform.

side. The density of indumentum on both sides can therefore be used as independent characters.

32. (b) Bracts: 0 = hyaline; 1 = not hyaline.
    Bracts are in most species not hyaline (transparent) or sometimes hyaline (polymorphic), in several species always hyaline. Due to the indument covering the bracts, and the small size of the bracts, this character is often difficult to interpret.
33. Indumentum of pedicel: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
34. (a) Length of apical part pedicel (part above the abscission zone): 0 = > 0.1 mm; 1 = < 0.1 mm (Fig. 1.4B).
35. Fusion of sepals at their base: 0 = absent to slightly fused; 1 = present.
    In *Maesobotrya* and *Nothobaccaurea* the sepals are fused, in *Baccaurea* and *Aporosa* they are free.
36. (e) Colour of flowers: 0 = green; 1 = white; 2 = red; 3 = yellow; 4 = brown; 5 = pink or purple; 6 = orange.
    The flower colour is quite variable in most species, however, in a few species it is constant.
37. Abaxial indumentum of sepals: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
38. Adaxial indumentum of sepals: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
39. Staminodes: 0 = absent; 1 = present.
    Staminodes are usually present, but absent in several species. A staminode is a rudimentary, sterile stamen.
40. Relative length of stamens: 0 = longer than sepals; 1 = shorter than sepals.
    Stamens are shorter than the sepals in *Baccaurea* and longer than the sepals in the other genera, except for several species in *Aporosa*.
41. Disc: 0 = absent; 1 = present.
    A floral disc is only present in *Maesobotrya*.
42. Number of stamens: 0 = 2 or 3; 1 = 4–10.
    The number of stamens is two or three in most species of *Aporosa*, 4–10 in the other genera.
43. Pistillode: 0 = absent; 1 = present.
    A pistillode is absent in *Aporosa*, present or polymorphic in all other species. A pistillode is a rudimentary, sterile pistil.
44. Indumentum of pistillode: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
    The pistillode is glabrous in *Nothobaccaurea*, hairy in the other genera.
45. Internal structure of pistillode: 0 = hollow; 1 = not hollow.
    The pistillode is sometimes hollow, mostly solid.

Pistillate inflorescences:

46. Position: 0 = axillary; 1 = just below the leaves; 2 = along the branches; 3 = cauline.
    Axillary means growing in a leaf-axil. Cauline is growing on the trunk.
47. (a) Length of inflorescence: 0 = always < 11 cm; 1 = usually > 11 cm.
    There is overlap in the ranges chosen as character states, see Fig. 1.4B.
48. Indumentum of inflorescence: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
49. (a) Number of flowers per inflorescence: 0 = 1; 1 = 2–9; 2 = ≥ 10.
50. (a) Number of individual inflorescences per cluster: 0 = 1–10; 1 = > 10.
51. Abscission zone in pedicel: 0 = present; 1 = absent.
    The abscission zone of the pedicel is absent in *Aporosa*, present in the other genera.

52. Pedicel: 0 = geniculate; 1 = straight.
    Geniculate means bent like a knee and thickened.
53. Indumentum of pedicel: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
54. (b) Number of bracts per flower: 0 = absent; 1 = 1; 2 = 2–6.
    The number of bracts usually is three, but in a few species less than three or polymorphic. This is caused by the reduction of two of the three bracts.
55. Insertion of bracts: 1 = at rachis; 2 = at pedicel.
56. Abaxial indumentum of bracts: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
57. Adaxial indumentum of bracts: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
58. (a) Diameter of flowers: 0 = up to 3 mm; 1 = > 3 mm (Fig. 1.4B).
59. (e) Colour of flowers: 0 = red; 1 = green; 2 = white; 3 = yellow; 4 = brown; 5 = pink or purple.
    The flower colour is quite variable in most species or unknown, only in a few species it is constant.
60. (b) Number of sepals: 0 = 4; 1 = 5; 2 = 6 or more.
    The number of sepals is often polymorphic for states 0 and 1. Because they are often found together in one specimen, it is doubtful whether four and five sepals are different states. However, some species show a constant number (4 or 5) of sepals. Seldom 5 and 6 sepals are found in one species, and therefore each number is taken as a different character state.
61. Abaxial indumentum of sepals: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
62. Adaxial indumentum of sepals: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
63. Number of locules in ovary: 0 = 2; 1 = 3 or 4; 2 = 5.
    This is a constant character, except for 3 or 4 locules. Therefore 3 and 4 locules is interpreted as a single character state.
64. Indumentum of ovary: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
65. (a) Stigma: 0 = not lobed; 1 = usually lobed.
    The stigma branches are two-lobed or united. In case of polymorphism, the lobed state is selected, because this is the most common state.
66. (b) Adaxial indumentum on stigma lobes: 0 = glabrous; 1 = sparsely hairy.
    Indumentum of the upper side of the stigma lobes is absent in most species. This character is, due to the presence of stigmatic papillae, often difficult to score.
67. Stigmatic papillae: 0 = absent to small; 1 = conspicuous (Fig. 1.9).
68. Staminodes: 0 = absent; 1 = present.
    A staminode is a rudimentary, sterile stamen.

Fruits:

69. (b) Dehiscence: 0 = indehiscent; 1 = loculicidally dehiscent; 2 = septicidally dehiscent; 3 = irregularly dehiscent.
    The fruits are usually indehiscent or loculicidally dehiscent. In a few species the dehiscence is septicidal as well as irregular. Sometimes it seems that the state irregularly dehiscent should be referred to indehiscent, because it is found in fruits with a thin testa. These fruits probably dehisce due to drying and pressing. Therefore, the difference between character state 0 and 3 is questionable.
70. Outer indumentum: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
71. Indumentum of septa: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.

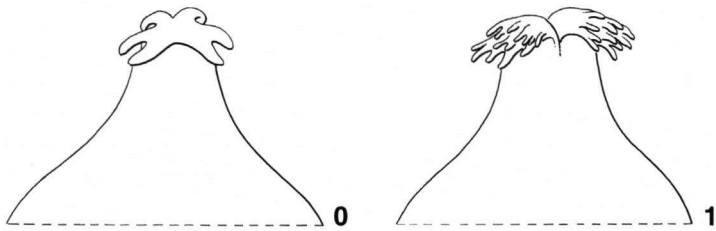


Fig. 1.9. Stigmatic papillae: 0 = absent to small; 1 = conspicuous.

72. Persistence of sepals: 0 = caducous; 1 = persistent.
The sepals are present (persistent) or absent (caducous) at fruit maturity.
73. Persistence of column: 0 = caducous; 1 = persistent.
This character has missing data for numerous species because it can only be recorded when the fruit is of a dehiscing type.
74. Persistence of stigma: 0 = caducous; 1 = persistent.
The stigmas are present (persistent) or absent (caducous) at fruit maturity.
75. (e) Colour of arillode: 0 = white; 1 = blue; 2 = red; 3 = orange; 4 = yellow; 5 = purple; 6 = violet; 7 = translucent.
The colour of the arillode is constant in quite a number of species, but for many others it is unknown.

Ecology:

76. (e) Successional status: 0 = late successional; 1 = early successional.
Most species show no clear preference for primary or secondary forests, and therefore they are polymorphic for this character.
77. (e) Occurrence in swamp forests: 0 = present; 1 = absent.
Only a few species are really confined to swamp forests. Polymorphic species for this character are not exceptional.

Leaf anatomy:

78. (b) Angle of and between two basal pairs of secondary veins: 0 = both angles obtuse; 1 = both angles acute; 2 = most basal more acute; 3 = most basal angle more obtuse (Fig. 1.10).
The distinction between the character states is sometimes ambiguous.
79. Hair type: 0 = simple; 1 = tufts of single hairs; 2 = tufts with partly fused hairs; 3 = stellate tufts.
The indument type of *Baccaurea* consists of only simple hairs in half of the species. In the other species it consists of simple hairs and of tufts of hairs, free or fused at the base (see Fig. 3.3).

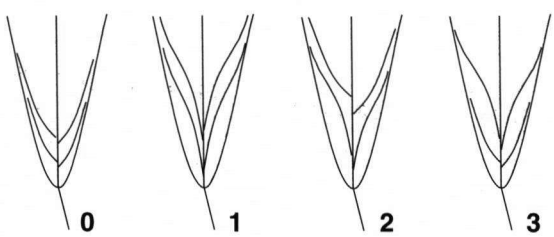


Fig. 1.10. Angle of and between two basal pairs of secondary veins: 0 = both angles obtuse; 1 = both angles acute; 2 = most basal more acute; 3 = most basal angle more obtuse.

80. Position of marginal foliar glands: 0 = marginal only; 1 = alternating marginal and submarginal (between the leaf margin and just in the leaf blade close to the margin); 2 = decurrent and recurrent to margin (marginal at the leaf base, submarginal at the mid-leaf, marginal at the tip of the leaf); 3 = submarginal only (see Fig. 3.2).
The position of the marginal foliar glands is constant in most species.
81. (c) Indumentum of marginal foliar glands: 0 = glabrous; 1 = sparsely hairy; 2 = densely hairy.
82. (c) Number of epidermal layers in upper (adaxial) side of lamina and lower (abaxial) side of lamina: 0 = 1 upper and 1 lower; 1 = 2 upper and 1 lower; 2 = 2 upper and 2 lower.
In most species there is one upper and one lower epidermal layer. In a few species there are two upper and one lower, or two upper and two lower layers of epidermal cells.
83. (c) Secretory cells (idioblasts) in epidermis: 0 = absent; 1 = only in upper epidermis; 2 = in upper and to a much lesser extent lower epidermis; 3 = in equal numbers in upper and lower epidermis.
84. (c) Palisade parenchyma above midrib: 0 = interrupted; 1 = continuous.
The palisade parenchyma is usually interrupted above the midrib.
85. (c) Spongy parenchyma: 0 = not lignified; 1 = lignified.
The lignified, secondary walls are strongly birefringent in polarised light.
86. (c) Druses and fragmented druses in the secretory cells: 0 = both absent; 1 = infrequent and absent; 2 = both abundant; 3 = absent and infrequent.
Druses and fragmented druses in idioblasts are often absent, sometimes either druses or fragmented druses are present, in two species both are present. A druse is a globular compound crystal.
87. (c) Starch in enlarged idioblasts: 0 = absent; 1 = infrequent; 2 = frequent.
Starch is usually absent. The presence of starch is not constant within the species. Therefore, polymorphism abounds.

Vegetative:

88. (a) Maximum length of petiole: 0 = always < 40 mm; 1 = 40–51 mm; 2 = 52–100 mm; 3 = > 101 mm.
89. (b) Transversal cracks on petiole: 0 = absent; 1 = present.
90. (a) Stipule length: 0 = always < 12 mm; 1 = > 12 mm possible.
91. (b) Stipule persistence: 0 = caducous; 1 = late caducous.
92. (b, d) Leaf colour lower surface when dried: 0 = green; 1 = brown; 2 = whitish to grey; 3 = reddish; 4 = yellow.
93. (b) Lower leaf surface with raised glands: 0 = absent; 1 = present.

Pistillate inflorescences:

94. (d) Ovary ribs: 0 = absent; 1 = present.

Fruits:

95. (a) Fruit pedicel length: 0 = always < 10 mm; 1 = always > 8 mm.
96. (b, d) Fruit shape: 0 = globose; 1 = > 2 times as long as wide.
97. (a) Fruit length: 0 = always < 20 mm; 1 = always > 14 mm.

98. (e) Fruit colour: 0 = red; 1 = purple; 2 = yellow; 3 = orange; 4 = blue; 5 = brown; 6 = pink; 7 = green; 8 = white.
99. (b) Fruit with raised glands: 0 = absent; 1 = present.

Ecology:
100. (a, e) Altitude: 0 = up to 250 m; 1 = up to 800 m; 2 = above 800 m possible.

Leaf anatomy:
101. (a, c) Size of marginal glands: 0 = 100–165 µm; 1 = 165–250 µm; 2 = 250–350 µm; 3 = 350–640 µm; 4 = > 640.
102. (a, c) Size of druses: 0 = 12–25 µm; 1 = 25–50 µm.

1.5.2 – *Program choice and adjustments*

The data matrices were analysed using the computer programs PAUP 3.1.1 and 4.0.0 (Swofford, 1993, 1998), Pee-Wee 2.25 (Goloboff, 1993), and MacClade (Maddison & Maddison, 1992). Nearly all analyses were performed with PAUP 3.1.1, whereby the following settings were used. Characters in polymorphic taxa were coded as real polymorphism. Accelerated transformation (ACCTRAN) was chosen as optimisation. With *Aporosa nitida* as first outgroup the shortest cladograms were obtained. All characters were unordered, and had equal weights in all analyses except for the successive weighting analyses. A heuristic search with 10 or 100 random stepwise additions was chosen when searching for MPCs, with TBR as branch swapping option. Using the MPCs as starting trees accelerated Bremer support analysis (Bremer, 1988; Källersjö et al., 1992).

The analyses with Pee-Wee are parsimony analyses using implied weights. These analyses were performed to enforce a choice between MPCs obtained from the analyses with PAUP. The same data matrix was used in PAUP and in Pee-Wee. All characters were coded as non-additive. In Pee-Wee the weight of a character is defined by factor (*f*) (Goloboff, 1993). Factor $f = k/(ES + 1)$ in which ES = number of extra steps observed (see also Turner, 1995), and k = constant of concavity. The k-value has to be added prior to the analysis. This value defines the concavity of the weight factor (*f*). Factor (*f*) weights against homoplasies, and is less steep for high k-values. In these analyses k-values of 1, 3, and 6 were used. The MPCs are now not defined by their length but by their fit (F). If several MPCs were present, a strict consensus was produced.

Apart from successive and implied weighting, a new method was used, namely Iterative Taxon Reduction (ITR). This method is based on the Bremer Index (Bremer, 1988; Källersjö et al., 1992), easily executed with the computer program PAUP (Swofford, 1993, 1998), and presented in Chapter 1.6.3.

1.5.3 – *Data matrix*

The 87 characters used in further analyses are shown in Chapter 1.5.1, together with the 15 excluded characters. In total 102 characters were scored. The data matrix for *Baccaurea* is given in Table 1.2.

Table 1.2. Data matrix. Horizontal: character numbers, see Table 1.3. Vertical: species. *A.* = *Aporosa*; *B.* = *Baccaurea*; *N.* = *Nothobaccaurea*; *M.* = *Maesobothrya*.

character / 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	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
A. nitida	0	?	?	0	0	–	0	0/1	0/1	0	0	2	1	1	1	1	1	0	0	0	0	1	0	0/1	1	?	1	1	?	?	?	?	?	–	0	?	1	0	0	0	0	0	0	–
A. arborea	1	?	0	0	0	–	0	0	0	0	0	1	0	0	1/2	0	0	0	1	0	0	1	0	0	1	0	0/1	2	?	1	0	1	?	–	0	3	1	1	0	0	0	0	0	–
B. angulata	0	0	0/1	0/1	1	1	0	0/1	0	1	0	0/1/2	0/1	1	1/2	2	0	0	0/1	0	1	1	0	3	0	0	1	1	0	2	0	1	2	1	0	?	2	2	1	1	0	1	1	1
B. annamensis	0	0	0	0	1	1	0	2	2	0	0/1	2	1	0	1	1	0	0	2	0	0	1	0	1/2/3	0	0	0/1/2	2	0	2	2	1	2	1	0	2	2	2	0	1	0	1	1	1
B. bracteata	1	1	0/1	0/1	1	1	0	0/1/2	1/2	0	0/1	1/2	1	0	0/1	0	0	0/1	1/2	0	0/1	0	0	0/1	0	1	0/1	1/2	0	2	0	0/1	2	1	0	0/1/2/3/4/5	2	2	0	1	0	1	1	1
B. brevipes	0	0	0	0	1	1	0	0	1/2	0	1	1/2	1	0	1/2	2	1	0	2	0	0	1	0/1	0/1/2	0	0	0/1	2	0	2	0	1	2	1	0	0/3	2	2	0/1	1	0	1	1	1
B. carinata	1	0	0	0	1	1	0	0	0/1	0	0/1	0	1	0	0/1/2	1	1	0	0/1	0	1	1	0	0/1/2/3	0	0	1	2	0	0/1/2	0	1	2	1	0	3	2	2	0	1	0	1	1	1
B. costulata	0	0	0	?	1	0	0	0/1	1/2	0	0	2	1	0	0/1/2	0	0	0	2	0	0/1	0/1	0	0/1	0	1	0	2	0	2	0	1	2	0	0	?	2	2	0	1	0	1	1	2
B. courtallensis	0	0	0	0/1	1	0	0	1	0/1	0	0	0/1	1	0	1/2	0	0	0	1/2	0	1	0/1	0	0/1/2/3	0	0	0/1/2	1/2	0	1/2	0/1	0/1	1/2	1	0	2/5	0/1/2	1/2	0	1	0	1	1	1
B. deflexa	0	1	0/1	1	1	1	0	0	1/2	0	1	2	1	0	0/1/2	0	0	0	2	0	0	0/1	0/1	0/1/2/3	0	1	0/1	2	0	2	0	1	–	0	0	0	2	2	0	1	0	1	1	1
B. dolichobotrys	0	1	1	1	1	1	0	0/1	0/1	0	1	2	0	0	0	1	1	0/1	1	1	0/1	0/1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. dulcis	0	0	0	0	1	1	0	0/1	0	1	0/1	0	0	0	2	1	0	0	0/1	0	1	1	0	0/1	0	0	0/1	1/2	0	0	0	0/1	2	1	0	3	2	2	1	1	0	1	1	1
B. edulis	0	1	0/1	0/1	1	1	0	0	2	0	1	1/2	1	0	1	1	0	2	1/2	0	0	0	0	0/1	0	1	0/1	2	0	2	0/1	1	2	1	0	0/1/3	2	2	0	1	0	1	0/1	1
B. javanica	1	0	0	0	1	0	0	0/1	0/1	0	0/1	0/1	1	0	1/2	0	0	0	0	0	1	0/1	0	0/1	0	0	0/1	1	0	0	0	0	0/1/2	1	0	0/1/3/4	0/1	2	0/1	1	0	1	1	1
B. lanceolata	0	0	0	0	1	1	0	0/1	0	1	0/1	0	0/1	0	0/1/2	2	1	0	0/1	0	1	1	0	3	0	0	2	0/1	0	0	0	0	0/1/2	1	0	1/3/5/6	0	1/2	1	1	0	1	1	1
B. macrocarpa	0	1	0	0/1	1	1	0	0	0/1	0	0/1	1/2	1	0	0/1/2	2	?	0	1	0	0/1	0	0	2/3	0	1	0/1	2	0	1/2	0/1/2	1	2	1	0	0/1/3	2	2	0	1	0	1	1	1
B. macrophylla	0	1	0/1	1	1	1	0	0/1	1	0	0/1	1	1	0	1	2	1	0	1	0	0/1	0	0	0/1/2	0	0	0/1	2	1	1	0/1	1	2	0	0	0/3	2	2	0/1	1	0	1	1	1
B. maingayi	0	1	1	1	1	1	0	2	0/1/2	0	1	2	1	0	0/1	0	1	0/1	2	1	0	0/1	1	0/1	0	0	0/1	2	1	?	?	?	–	0	0	?	2	2	0	1	0	1	0	–
B. microcarpa	1	0	?	?	1	1	0	2	2	0	1	2	1	0	2	0	0	0/1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. minor	0	1	1	1	1	0	0	1	0	0	1	2	0	0	0/1	0	0	0	0	0	0	0	0	0/1	0	0	0/1	2	1	2	?	1	–	0	0	0/3	2	2	0	1	0	1	1	1
B. mollis	0	1	1	1	1	1	0	1/2	2	0	1	2	1	0	0/1	1	1	0/1	2	0	0/1	0	0	2	0	0	1	2	0	2	2	1	2	0	0	0/3	2	2	0/1	1	0	1	1	1
B. motleyana	0	1	1	0	1	1	0	2	2	0	1	0/1	1	0	1/2	2	1	0	2	1	1	0	1	0/1/2/3	0	0	0/1	2	0	2	0	1	2	1	0	0	2	2	0	1	0	1	1	1
B. multiflora	0	0	0	0	1	0	0	0/1	0/1	0	0/1	2	1	1	2	0	0	0	0/1	0	0/1	0/1	0	0/1/2	0	1	0/1	1/2	0	1/2	1/2	1	2	1	0	3	2	2	0	1	0	0/1	1	1
B. nanihua	0	0	0/1	0/1	1	1	0	1	1/2	1	0/1	2	1	0	0/1	0	0	0	1	0	1	0/1	0	0/1	0	1	0/1	2	0	2	1/2	1	2	1	0	1/3	2	2	0	1	0	1	1	1
B. nesophila	?	0	1	?	1	0/1	0	2	0/1	0	1	0	0/1	0	1/2	0	0	0/1	1	0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. odoratissima	0	0	0	0	1	0	0	1	1	0	0	0/1	1	0	1/2	0	0	0	1	0	0/1	1	0	1/2/3	0	0	1/2	2	0	0/1/2	0	0/1	2	1	0	3	2	0/1/2	0	1	0	1	1	1
B. papuana	1	0	0	0	1	0/1	0	1	1/2	0	0/1	0/1	1	0	1/2	0	1	0/1/2	1/2	0	1	0/1	0	0/1/2/3	0	0	0/1	1/2	0	0	2	1	0	0	0	3	2	2	1	1	0	1	1	1
B. parviflora	1	0	0	0	1	0	0	0/1	0	0	0/1	0	1	0	1/2	0	0	0	0/1	0	0	0/1	0	3	0	0	2	2	0	1	0	0/1	1/2	1	0	2	2	0/1/2	0/1	1	0	1	1	1
B. philippinensis	0	0	0	1	1	1	0	1	1/2	1	0/1	2	1	0	0/1	0	0	0	1/2	0	0/1	0	0	0	0	1	0/1	2	0	2	0	1	2	1	0	4	2	2	0	1	0	1	0/1	1
B. polyneura	0	1	0/1	1	1	1	0	2	2	0	0/1	2	1	0	0/1	0	1	1/2	2	1	0/1	0/1	1	0/1	0	0	0/1	2	1	2	0	1	–	0	0	0/1/3	2	2	0	1	0	1	0/1	1
B. ptychopyxis	1	0	?	?	1	0	0	0/1	0/1	0	0	1	1	0	1/2	1	0	0	1	0	1	1	0	0/1	0	0	0	2	0	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?
B. pubera	0	1	0	1	1	1	0	2	2	0	0/1	2	1	0	1	2	1	0	2	0	0	0	0	0/1	0	1	0/1	2	0	2	2	1	2	1	0	0/1/3	2	2	0/1	1	0	1	1	1
B. purpurea	0	0	0	0	1	0/1	0	0	0/1	1	0	0	1	0	1	0	1	0	1	0	1	0/1	0	3	0	0	2	1	0	0/1	0	0	1/2	1	0	5	1/2	2	0/1	1	0	1	1	1
B. pyriformis	0	1	0/1	1	1	1	0	2	2	0	1	2	1	0	1/2	0	0	0	2	0	0	0	0	1/2	0	1	0/1	2	0	2	0	0/1	–	0	0	3/4	2	2	0	1	0	1	1	1
B. racemosa	0	0	0	0	1	0	0	0/1	0/1	0	0/1	0	1	0	1/2	0	0	0	2	0	0/1	1	0	1/2/3	0	0	0/1	2	0	0/1/2	0	0/1	2	1	0	1/3	2	2	0	1	0	1	1	1
B. ramiflora	0	0	0	0	1	0	0	0/1	0/1	0	0	0/1	1	0	1/2	1	0	0	0/1	0	1	1	0	0/1/2/3	0	0	0/1/2	2	0	1/2	0	0/1	2	1	0	3	2	2	0	1	0	1	1	1
B. reticulata	0	0	1	1	1	1	0	1	1/2	0	0/1	2	1	0	1/2	0	0	0	2	0	0/1	0/1	0/1	0/1	0	1	0/1	2	0	2	2	1	2	1	0	0/1/3	2	2	0	1	0	1	0/1	1
B. sarawakensis	1	0	0	0/1	1	0	0	0	0	0	0	1/2	1	1	1/2	0	0	0	1	0	1	0/1	0	0/1	0	0	0/1	2	0	0/1/2	0/1	1	2	1	0	?	0/1/2	0/1/2	0	1	0	1	1	1
B. seemannii	1	0	?	?	1	1	0	2	2	0	0/1	1/2	1	0	0/1/2	0	0	0	1/2	0	0/1	0	0	0/1/2	0	0	0/1	2	0	2	1	1	2	1	0	3/4	2	2	0	1	0	1	1	1
B. simaloerensis	?	0	?	?	1	1	0	1	1/2	0	0/1	1/2	1	0	0/1	0	0	0	1	0	1	0	0	0/1	0	1	0	1/2	0	2	0	1	2	1	0	?	2	2	0	1	0	1	1	1
B. sumatrana	0	1	0	0/1	1	0	0	0	0	0	1	1	0	0	0/1	0	0	0	0	0	0	0	0	0/1	0	0	0	2	1	0	?	1	–	0	0	0/3	0	0	0	1	0	1	1	1
B. taitensis	1	0	?	?	1	1	0	0	1	0	0/1	1/2	1	0	1/2	0	0	0/1	1	0	0/1	0	0	0	0	0	0/1	2	0	2	0	0/1	1/2	1	0	1	0/1	1/2	0	1	0	1	1	1
B. tetrandra	1	0	0	0/1	1	0	0	0/1	0/1	0	0	0/1/2	0/1	0	1/2	0	0	0	0/1	0	1	1	0	0/1	0	0	0/1	1/2	0	0/1/2	0/1	1	2	1	0	1/3	1/2	2	1	1	0	1	1	1
B. trigonocarpa	0	0	0	0	1	1	0	0	1/2	0	0/1	0/1/2	0	0	1/2	0	0	0	0/1/2	0	0	0	0	0/1	0	0	0	2	1	–	–	1	–	0	0	3	2	2	0	1	0	1	1	1
B. velutina	1	0	0/1	1	1	1	0	1/2	2	0	0/1	2	1	0	0/1/2	0	0	0	1/2	0	1	0	0	0	0	1	0	2	0	2	0/1	1	2	1	0	3/4	2	2	0	1	0	1	1	1
N. pulvinata	?	0	?	?	1	1	0	0/1	1	0	0/1	1	1	0	1/2	0	0	0	0/1	0	0/1	0	0	0/1/2	0	0	0/1/2	1	0	0/1	0/1	0/1	0/1	1	1	2	0/1	0	0	0	0	1	1	0
N. stylaris	1	0	0	0	1	1	0	0/1	0/1	0	0/1	1/2	0/1	0	0/1/2	0	0	0	0/1	0	1	0	0	0/1	0	0/1	0/1	1/2	0	1/2	0	1	0/1	0/1	1	1/2/4/5	0	0	0	0	0	1	1	0
M. barteri	1	0	0	?	1	1	0	2	2	0	1	2	1	0	2	0	0	0/1/2	2	0	0	1	0	0/1/2/3	0	0	0/1	2	0	2	0	0	0/1/2	1	1	0/2	0	0	0	0	0	1	1	1
M. pauciflora	1	0	?	?	1	1	0	0/1	0	0	0	1	1	0	1/2	0	0	0	0/1	0	0	0/1	0	0/1	0	0	0	1	0	0	0	?	0/1	1	1	0/1	0	0	0	0	0	1	1	1
M. staudtii	1	0	?	?	1	1	0	1/2	2	0	0/1	2	1	0	1/2	1	0	2	1/2	0	0	0	0	0	0	0	0/1	1/2	0	0	0	?	0	1	1	0/1	0	0	0	0	0	1	1	1

Table 1.2 (*continued*)

species \ character	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
A. nitida	–	0/1	0	1	0	0	1	1	1	1	0	0	0	?	?	1	0	0	2	?	?	0	0	0	0	0	0	1	1	0	2/3	0/1	0	0/1	0	0	0	0	1	0	0	0	0
A. arborea	–	0/1	0	2	1	0	1	1	2	1	0	0	0	?	?	1	0	0	1	1	0	0	0	0	0	0/1	0	1	1	0	?	0/1	?	1	0	0	1	0	1	1	0	0	0
B. angulata	0	2/3	1	1	1/2	0	0	1	1/2	2	1	1/2	0	1	1/3	1	2	2	1	2	1	0/1	1	0	0	1	0/1	0/1	?	0	0	0/1	0	2	0	3	2	0	1	1	1	0
B. annamensis	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	1	0	?	?	?	?	?	?	1	0	1	2	0	1	0	0	1/3	1
B. bracteata	1	0/1	0	2	1/2	0	0	1	2	1/2	1	2	0	1	1/3/4	0/1	2	2	0/1	2	0	0/1	0	0	1	1/2	1	0/1	1	0/1	3/4	0/1	0	3	1	0	2	1	3	1	0	0/1	0
B. brevipes	1	3	1	2	2	0	0	1	2	2	0	2	0	1	?	0	2	2	0/1	2	1	?	1	0	0	0/1/2	0	0/1	1	0	6	0/1	0/1	3	0	0	1	0	1	1	0	0	0
B. carinata	1	3	?	?	?	0	?	?	?	2	?	?	?	?	?	?	?	?	1	?	?	?	?	?	3	2	0	0	?	0	?	1	0/1	2	0	1	2	1	2	0/1	0	0/1	0
B. costulata	1	0/1/2	?	?	?	0	0	?	?	2	1	?	?	?	?	0/1	?	?	1	?	1	1	1	0	1	0/1	1	1	1	0	0	0/1	1	2	3	0	0	0	2	1	0	0	0
B. courtallensis	1	2/3	1	1/2	2	0	0	1	2	2	0	1	0	1	?	0/1	1	2	1	2	0	0	1	0	0	0/1	0	0	?	1	4	?	0/1	1	0	1	0	0	3	1	0	1	0
B. deflexa	1	0/1/2	0	2	2	0	0	0	2	1/2	1	1/2	0	0	?	1/2	2	2	0	2	0	0	1	0	1/2	1/2	2	0	1	1	?	0	1	0	2	0	2	0	2	0	0	0
B. dolichobotrys	?	2/3	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	1	?	?	?	?	?	1	1	1/2	1	1	0	2/3	?	0/1	0	1	0	0	1	1	0	0	0	0
B. dulcis	0	0/1/2	1	0/1	1/2	0	0	1	1/2	2	0	0/1	0	1	3	0/1	1/2	2	1	0/1	0	0	0/1	0	0	0/1	0	0	?	0	5	0	1	1	0	1	0	0	1	1	0	0	0
B. edulis	1	2/3	1	2	2	0	0	1	2	1	1	1	0	1	1/3	0/1	2	2	0	2	0	0	1	0	0	0	1/2	1	?	1	0/4	0/1	1	1	3	0	2	0	1	0	0	0/3	0
B. javanica	0/1	0/1	1	0	0/1/2	0	0	1	0/1	1	0	0	0	1	1	0	0	2	0	2	1	?	1	0	1	0	0	0	0	0	5/6	0/1	0/1	2	0	1	1	0	2	1	0	3	0
B. lanceolata	1	3	1	0	2	0	0	1	0/1/2	2	0	0/1	0	1	0/2/3/5	0/1	0/1	2	1	1/2	0	0	1	0/1	0	0	0	0	?	0/1	0/7	0/1	0/1	1	0	1	0	0	1	1	0	0	0
B. macrocarpa	0/1	2/3	1	0/1	1/2	0	0	0/1	2	1/2	1	2	1/2	1	?	0/1/2	2	2	1	2	0	0/1	1	0	1	0/1	1/2	1	0	0/1	0	0/1	0	3	1/2/3	0	0	0	3	0	0	0	0/1
B. macrophylla	1	2	1	2	1/2	0	0	0	2	2	1	1/2	?	1	1	0	2	2	1	2	1	0	1	0	0/1	0/1	0/1/2	1	?	1	7	0/1	0/1	0	1/2/3	0	2	0	1	0	0	1	0
B. maingayi	?	2	0	2	1/2	0	0	0	2	2	1	2	2	0	?	2	2	2	1	2	?	?	?	0	1	2	2	1	0/1	0	2	0	0	0	?	0	0	0	0	0	0	0	0
B. microcarpa	?	0/1	?	2	1/2	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	3	1	0	0	?	0	2	?	?	2	0	1	1	0	3	0	1	0	0	0
B. minor	1	2	1	2	1/2	0	0	0	2	2	1	2	2	1	1	0	2	2	1	2	0	0	0	0	1/2	2	2	1	1	0	3/4	0/1	1	0	0	0	0	0	1	0	0	0	0
B. mollis	1	2/3	0	2	1/2	0	0	1	2	2	1	2	2	1	?	0	2	2	0	2	0	1	1	0	0	0/1	1	1	1	0	2	1	?	0	1/2/3	0	2	0	2	0	0	0	0
B. motleyana	0	1/2/3	1	2	2	0	0	1	2	2	1	2	1/2	1	1/3	0/1	2	2	1	2	1	0	1	0	0	0/1/2	0	1	0	0	?	1	1	0	0	0	2	0	1	0	0	0	0
B. multiflora	1	2	0	2	2	0	0	1	2	2	0	2	0/1	1	?	1	2	2	0	2	0	0	1	0	0	2	2	0	1	1	0	0	1	1	0	0	0	0	1	0	1	0	0
B. nanihua	1	0/1/2	0	2	1	0	0	1	2	1	1	2	2	1	?	1	2	2	1	2	?	1	1	0	1	2	2	1	?	0/1	?	0	0/1	0/1	3	0	2	0	2	0	0	3	0
B. nesophila	?	1/2	?	?	0/1/2	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1/2	0/1	0/1	0	1	0	2/3	?	0/1	2	0	0	0	0	2	0	0	2	0
B. odoratissima	1	3	1	0/1	1/2	0	0	1	2	2	1	1/2	0	1	1/3	0	1	2	0	2	1	?	1	0	3	0	0	0	0	1	1	0/1	1	2	0	1	0	0	2	1	0	0/1	1
B. papuana	1	3	1	0/1	1/2	0/1	0	1	2	2	1	1/2	0	1	1/3	1/2	2	2	1	2	?	0	1	0	0	0/1/2	0	0	?	0	4	0/1	0/1	2	0	1	2	0	2	0	0	0	0
B. parviflora	0/1	3	1	2	2	1	0	1	2	2	0	1/2	0	1	0/2/3	0/1	2	1/2	1	2	0	0	1	0	0	1	0	0/1	1	0/1	0/2	0/1	0/1	2	0	0/1	0	0	1/2	1	0	0/1	0/1
B. philippinensis	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	0/1	1/2	2	0	?	0/1	1	0/1	?	0	2	0	1	0	2	0	1	1/3	0
B. polyneura	1	0/1/2	1	2	1/2	0	0	0/1	1/2	0/1/2	1	2	0/1/2	1	?	0/1	2	2	1	2	0	0	0	0	1	1/2	1	1	1	0/1	2	0/1	0	0	2	0	1	1	1	0	0	0	0
B. ptychopyxis	?	3	1	2	2	1	0	0	1	2	2	2	0	1	0	1	2	2	1	2	0	0	1	0	0	0	0	0	?	?	0	?	?	?	2	0	1	0	0	2	1	0	0
B. pubera	1	2/3	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	0/1	2	1	1	1	1	4	0	1	0	2/3	0	2	0	0	0	1	0	0
B. purpurea	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1	?	?	?	?	?	1	1	0	0	1	0	?	?	?	2	0	1	0	0	2	0	0	0	0
B. pyriformis	1	2	0	2	1/2	0	0	?	2	2	1	2	1	?	4	0/1	2	2	1	2	0	0	1	0	0	2	1/2	1	?	0	?	0	1	1	1	0	2	0	2	0/1	0	0	0
B. racemosa	0	0/1/2/3	1	2	1/2	0	0	1	2	2	1	2	0	1	1/3	0	2	2	0/1	2	1	?	1	0	1	0/1	0	0	0	0	0/1/5/6	0/1	0/1	2	0	1	0	0	2	1	1	0	0
B. ramiflora	1	1/2/3	0	2	2	0/1	0	1	2	1	0	1/2	0	1	3	0/1	2	2	1	2	1	0	1	0	0	0/1	0	0	?	1	0	0	1	2	0	1	0	0	2	0	0	0/1	1
B. reticulata	1	2/3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	1	1/2	1	1	?	1	1/4/7	1	1	3	2/3	0	2	0	0	0	1	0	0
B. sarawakensis	1	0/1/2	0	2	1/2	0	0	1	2	2	1	2	0	1	3	0/1	0/1/2	0/1/2	1	2	1	0	1	0	1	1/2	0	0	0	1	1/5	0	?	1	0	1	2	0	1	1	1	0	0
B. seemannii	0/1	0/1/2	0	2	1/2	0	0	0/1	2	2	0	2	1	0	5	0	2	2	0	2	0	0	1	0	1	0	1	0	?	0	?	0	0/1	0	0	0	2	0	3	0	0	0	1	0
B. simaloerensis	1	0	0	2	1	0	0	1	2	2	1	1	0	1	?	1	2	2	1	2	0	0	0	0	1	1/2	1	0/1	?	0	?	?	?	?	0	2	0	0	0	2	0	0	0/1
B. sumatrana	1	0/1/2	0	2	1/2	0	0	0	2	0	?	–	–	0	?	0/1	2	2	0	1/2	1	0	0	0	1	1	1	1	0/1	0/1	2/3	0/1	1	0	0	0	0	2	3	0	0/1	0	0
B. taitensis	?	0/1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1/2	0	?	0	3/4	?	1	2	0	0	1	0	2	0	0	1	0
B. tetrandra	0/1	0/1/2	1	0/1	1/2	0	0	1	1/2	2	1	0/1/2	0	1	1/3	0/1/2	1/2	2	0	1/2	0	0	1	0	1/3	0/1	0	0	0	0/1	1/5	0/1	0	1	0	1	0	0	1	0	1	0/1/3	0/2
B. trigonocarpa	1	2	0	2	1/2	0	0	0	2	2	1	1/2	2	0	3	2	2	2	1	2	?	0	0	0	1	0/1	1	1	0/1	0	2/3/5	0	1	1	?	0	1	2	3	0	0	0	0/1
B. velutina	1	0	0	2	1	0	0	1	2	2	0	2	0	1	3	0	2	2	1	2	0	0	1	0	0/1	2	1	0/1	?	0	3/4	1	0/1	0	1	0	2	0	2	0	1	2	0
N. pulvinata	0	0/1/2	?	?	2	0	?	?	?	?	0	?	?	?	?	0/1/2	?	?	0	?	?	?	?	?	0	0	0	1	?	0	?	?	0	2	0	0	0	0	2	0	0	0	0
N. stylaris	0/1	0/1/2	0	0/1	1/2	0	0	1	1	1/2	1	1/2	0	0	0	1/2	0/1	0	0	0	2	0	1	1	1	0/1	0	1	0/1	0	5	0/1	1	2	0	0	1	0	3	0	0	1/3	0
M. barteri	?	0/1/2/3	0	2	2	1	0	1	1	2	0	1	0	?	1	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	2	1	?	0	0	0	1	0	2	0	0	0	0
M. pauciflora	0/1	0/1	0	?	0/1	0	0	1	0	2	0	1	?	0	1	1	0	0	0	1	0	0	0	0	1	0/1	0	1	1	0	0	?	?	2	2	0	0	0	2	0	0	0	0
M. staudtii	1	2/3	0	2	2	1	0	1	1/2	2	0	0/1	0	0	0	1	0/1	0	1	1	0	0	0	0	3	0	0	1	?	0	0/1	?	?	0	0	0	2	0	2	1	0	0	0

1.6 – **Results**

1.6.1 – ***Results of equal weight phylogenetic analysis***

The equal weight analysis in PAUP resulted in 12 Most Parsimonious Cladograms (MPCs). The well-resolved strict consensus cladogram (SCC) of these 12 MPCs is shown in Fig. 1.11 and 1.16. Only three clades of the SCC show trichotomies.

1.6.2 – ***Discussion of equal weight phylogenetic analysis***

The CI and Retention Index (RI) are often used as indicators of the quality of cladograms. The RI of the MPCs equals 0.545. This value is in the expected range for a data matrix of this size (Archie, 1989a, b; Klassen et al., 1991). The CI equals the rather low value 0.281 when polymorphic characters are coded as uncertainty. The topologies obtained by the uncertainty option are the same as the results obtained by the polymorphy option. However, the treatment of terminal taxa is different, because all character changes due to polymorphism are left out when coded as uncertainty. Therefore numerous autapomorphies are excluded and the CI is much lower. The CI value is kept artificially high in the polymorphism option, in this study as high as 0.729 instead of 0.281 when coded as uncertainty. In a matrix with numerous taxa with polymorphic characters it is preferable to use the uncertainty option, because this is a better indicator for the amount of homoplasy present.

Different indicators of tree stability (as a measure of quality) are bootstrap values (Felsenstein, 1985) and Bremer indices (Bremer, 1988; Källersjö et al., 1992). The bootstrap values were not calculated because studies based only on morphological characters usually do not result in satisfactory bootstrap values (Sanderson, 1995). Bremer support was only found for minor clades (Fig. 1.11). From these data it is evident that the tree stability is weak over the whole cladogram. This is an indication that the hypothesis for most clades is not particularly well-supported, and the internal topology unstable. Furthermore, the tree topology is unbalanced (forming a Hennigian comb) (Mooers et al., 1995).

The conclusion can be drawn that the 12 MPCs are disputable.

1.6.3 – ***New Iterative Taxon Reduction (ITR) method***

Because the 12 MPCs (summarised in the SCC) are disputable (Chapter 1.6.2), weighting analyses were performed. First Successive Weighting (SW), and Implied Weighting (IW) have been applied to find support for one of the 12 MPCs. Secondly, character support was analysed for internal nodes in the cladogram of *Baccaurea*. Because SW and IW both failed in obtaining unequivocal results (Chapter 1.6.4 and Fig. 1.14), a new Iterative Taxon Reduction method was developed in collaboration with Dr. M. Zandee (EEW, Leiden University). This method is based on Bremer support and will from this time on be referred to as 'Iterative Taxon Reduction' (ITR).

Iterative Taxon Reduction explained

ITR is an elaboration of the compartmentalisation approach of Mishler (1994). Besides cutting large data sets to manageable size, ITR was developed to suppress the effect

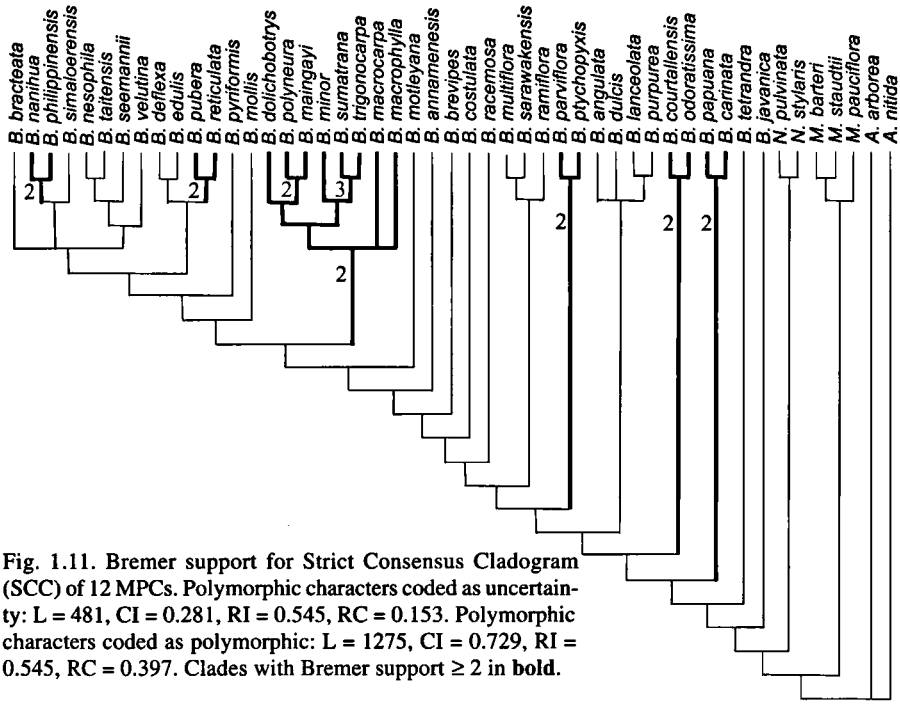


Fig. 1.11. Bremer support for Strict Consensus Cladogram (SCC) of 12 MPCs. Polymorphic characters coded as uncertainty: L = 481, CI = 0.281, RI = 0.545, RC = 0.153. Polymorphic characters coded as polymorphic: L = 1275, CI = 0.729, RI = 0.545, RC = 0.397. Clades with Bremer support ≥ 2 in **bold**.

of spurious homoplasy. In every phase of the analysis this method will only use the SCC of all MPCs (based on equal character weights), contrary to SW and IW (not based on equal weights).

It is expected that the more basal branches of the SCC get a better (Bremer) support using this method, because some clades of the SCC lack Bremer support due to homoplasy in the terminal branches. This method reduces the amount of homoplasy in the terminal taxa, by which the support for the basal branches becomes more evident. This action is repeated until no further reduction is possible.

The SCC of all MPCs is used as starting point. The clades of this cladogram with a Bremer support ≥ 2 are interpreted as stable parts. Their hypothetical ancestor then replaces these clades. This is a formalisation of what Mishler (1994) called archetype. Mishler already stated: "A decay index ... appears to be a sensitive measure of relative support, and is recommended for defining compartments." Thus clades with a high Decay Index (DI) (Bremer, 1988; Källersjö et al., 1992) are reduced to their ancestral states, using the option 'describe trees, states for internal nodes' in PAUP. In this manner the number of taxa in the data matrix will be decreased and possibly also the amount of homoplasy. The latter is partly due to elimination of taxa in these stable clades showing polymorphic characters. All hypothesised character states of ancestral taxa are monomorphic. When homoplasy is reduced, it is expected that more nodes become stable, i.e. get a high DI. Characters in support of these clades (that were only weakly supported in the original cladogram) can then show their full potential. The reduced data matrix is used for a new search for MPC(s). The whole process will be repeated, until further reduction of the data matrix is impossible. It is possible in ITR,

Table 1.3. First reduced data matrix of *Baccaurea* for Iterative Taxon Reduction, consisting of 30 taxa and 87 characters. Ancestors in **bold**.

character / 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	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
B. angulata	0	0	0/1	0/1	1	1	0	0/1	0	1	0	0/1/2	0/1	1	1/2	2	0	0	0/1	0	1	1	0	3	0	0	1	1	0	2	0	1	2	1	0	?	2	2	0	1	1	1	1	1
B. annamensis	0	0	0	0	1	1	0	2	2	0	0/1	2	1	0	1	1	0	0	2	0	0	1	0	1/2/3	0	0	0/1/2	2	0	2	2	1	2	1	0	2	2	2	1	1	1	1	1	1
B. bracteata	1	1	0/1	0/1	1	1	0	0/1/2	1/2	0	0/1	1/2	1	0	0/1	0	0	0/1	1/2	0	0/1	0	0	0/1	0	1	0/1	1/2	0	2	0	0/1	2	1	0	0/1/2/3/4/5	2	2	1	1	1	1	1	1
B. brevipes	0	0	0	0	1	1	0	0	1/2	0	1	1/2	1	0	1/2	2	1	0	2	0	0	1	0/1	0/1/2	0	0	0/1	2	0	2	0	1	2	1	0	0/3	2	2	0/1	1	1	1	1	1
B. costulata	0	0	0	?	1	0	0	0/1	1/2	0	0	2	1	0	0/1/2	0	0	0	2	0	0/1	0/1	0	0/1	0	1	0	2	0	2	0	1	2	0	0	?	2	2	1	1	1	1	2	1
***B. courtallensis* +**																																												
B. odoratissima	0	0	0	0	1	0	0	1	1	0	0	0	1	0	2	0	0	0	1	0	1	1	0	1	0	0	1	2	0	1	0	1	2	1	0	3	2	2	1	1	1	1	1	1
B. deflexa	0	1	0/1	1	1	1	0	0	1/2	0	1	2	1	0	0/1/2	0	0	0	2	0	0	0/1	0/1	0/1/2/3	0	1	0/1	2	0	2	0	1	–	0	0	0	2	2	1	1	1	1	1	1
B. dulcis	0	0	0	0	1	1	0	0/1	0	1	0/1	0	0	0	2	1	0	0	0/1	0	1	1	0	0/1	0	0	0/1	1/2	0	0	0	0/1	2	1	0	3	2	2	0	1	1	1	1	1
B. edulis	0	1	0/1	0/1	1	1	0	0	2	0	1	1/2	1	0	1	1	0	2	1/2	0	0	0	0	0/1	0	1	0/1	2	0	2	0/1	1	2	1	0	0/1/3	2	2	1	1	1	1	1	0/1
B. javanica	1	0	0	0	1	0	0	0/1	0/1	0	0/1	0/1	1	0	1/2	0	0	0	0	0	1	0/1	0	0/1	0	0	0/1	1	0	0	0	0	0/1/2	1	0	0/1/3/4	0/1	2	0/1	1	1	1	1	1
B. lanceolata	0	0	0	0	1	1	0	0/1	0	1	0/1	0	0/1	0	0/1/2	2	1	0	0/1	0	1	1	0	3	0	0	2	0/1	0	0	0	0	0/1/2	1	0	1/3/5/6	0	1/2	0	1	1	1	1	1
***B. macrophylla* ***																																												
B. dolichobotrys	0	1	1	1	1	1	0	0	0	0	1	2	1	0	1	2	1	0	1	0	0	0	0	2	0	0	0	2	1	2	0	1	2	0	0	3	2	2	1	1	1	1	1	1
B. mollis	0	1	1	1	1	1	0	1/2	2	0	1	2	1	0	0/1	1	1	0/1	2	0	0/1	0	0	2	0	0	1	2	0	2	2	1	2	0	0	0/3	2	2	0/1	1	1	1	1	1
B. motleyana	0	1	1	0	1	1	0	2	2	0	1	0/1	1	0	1/2	2	1	0	2	1	1	0	1	0/1/2/3	0	0	0/1	2	0	2	0	1	2	1	0	0	2	2	1	1	1	1	1	1
B. multiflora	0	0	0	0	1	0	0	0/1	0/1	0	0/1	2	1	1	2	0	0	0	0/1	0	0/1	0/1	0	0/1/2	0	1	0/1	1/2	0	1/2	1/2	1	2	1	0	3	2	2	1	1	1	0/1	1	1
B. nesophila	?	0	1	?	1	0/1	0	2	0/1	0	1	0	0/1	0	1/2	0	0	0/1	1	0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***B. papuana* +**																																												
B. carinata	1	0	0	0	1	1	0	0	1	0	0	0	1	0	2	0	1	0	1	0	1	1	0	1	0	0	1	2	0	1	0	1	2	1	0	3	2	2	1	1	1	1	1	1
***B. parviflora* +**																																												
B. ptychopyxis	1	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	1	1	0	1	0	0	0	2	0	1	0	1	2	1	0	2	2	2	1	1	1	1	1	1
***B. philippinensis* +**																																												
B. nanihua	0	0	0	1	1	1	0	1	2	1	1	2	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	2	0	2	0	1	2	1	0	3	2	2	1	1	1	1	1	1
B. purpurea	0	0	0	0	1	0/1	0	0	0/1	1	0	0	1	0	1	0	1	0	1	0	1	0/1	0	3	0	0	2	1	0	0/1	0	0	1/2	1	0	5	1/2	2	0/1	1	1	1	1	1
B. pyriformis	0	1	0/1	1	1	1	0	2	2	0	1	2	1	0	1/2	0	0	0	2	0	0	0	0	1/2	0	1	0/1	2	0	2	0	0/1	–	0	0	3/4	2	2	1	1	1	1	1	1
B. racemosa	0	0	0	0	1	0	0	0/1	0/1	0	0/1	0	1	0	1/2	0	0	0	2	0	0/1	1	0	1/2/3	0	0	0/1	2	0	0/1/2	0	0/1	2	1	0	1/3	2	2	1	1	1	1	1	1
B. ramiflora	0	0	0	0	1	0	0	0/1	0/1	0	0	0/1	1	0	1/2	1	0	0	0/1	0	1	1	0	0/1/2/3	0	0	0/1/2	2	0	1/2	0	0/1	2	1	0	3	2	2	1	1	1	1	1	1
***B. reticulata* +**																																												
B. pubera	0	1	1	1	1	1	0	2	2	0	1	2	1	0	1	0	0	0	2	0	0	0	0	0	0	1	0	2	0	2	2	1	2	1	0	0	2	2	1	1	1	1	1	1
B. sarawakensis	1	0	0	0/1	1	0	0	0	0	0	0	1/2	1	1	1/2	0	0	0	1	0	1	0/1	0	0/1	0	0	0/1	2	0	0/1/2	0/1	1	2	1	0	?	0/1/2	0/1/2	1	1	1	1	1	1
B. seemannii	1	0	?	?	1	1	0	2	2	0	0/1	1/2	1	0	0/1/2	0	0	0	1/2	0	0/1	0	0	0/1/2	0	0	0/1	2	0	2	1	1	2	1	0	3/4	2	2	1	1	1	1	1	1
B. simaloerensis	?	0	?	?	1	1	0	1	1/2	0	0/1	1/2	1	0	0/1	0	0	0	1	0	1	0	0	0/1	0	1	0	1/2	0	2	0	1	2	1	0	?	2	2	1	1	1	1	1	1
B. taitensis	1	0	?	?	1	1	0	0	1	0	0/1	1/2	1	0	1/2	0	0	0/1	1	0	0/1	0	0	0	0	0	0/1	2	0	2	0	0/1	1/2	1	0	1	0/1	1/2	1	1	1	1	1	1
B. tetrandra	1	0	0	0/1	1	0	0	0/1	0/1	0	0	0/1/2	0/1	0	1/2	0	0	0	0/1	0	1	1	0	0/1	0	0	0/1	1/2	0	0/1/2	0/1	1	2	1	0	1/3	1/2	2	0	1	1	1	1	1
B. velutina	1	0	0/1	1	1	1	0	1/2	2	0	0/1	2	1	0	0/1/2	0	0	0	1/2	0	1	0	0	0	0	1	0	2	0	2	0/1	1	2	1	0	3/4	2	2	1	1	1	1	1	1

Table 1.3 (*continued*)

character / species	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
B. angulata	0	2/3	1	1	1/2	1	0	1	1/2	2	1/2	0	1	1/3	1	2	2	1	1	2	1	0/1	1	0	0	1	0/1	0/1	?	1	0	0/1	0	2	0	3	2	0	1	1	1	0	0
B. annamensis	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	1	0	1	2	0	1	0	0	1/3	1
B. bracteata	1	0/1	0	2	1/2	1	0	1	2	1/2	2	0	1	1/3/4	0/1	2	2	0/1	1	2	0	0/1	0	0	1	1/2	1	0/1	1	0/1	3/4	0/1	0	3	1	0	2	1	3	1	0	0/1	0
B. brevipes	1	3	1	2	2	1	0	1	2	2	2	0	1	?	0	2	2	0/1	0	2	1	?	1	0	0	0/1/2	0	0/1	1	1	6	0/1	0/1	3	0	0	1	0	1	1	0	0	0
B. costulata	1	0/1/2	?	?	?	1	0	?	?	2	?	?	?	?	0/1	?	?	1	1	?	1	1	1	0	1	0/1	1	1	1	1	0	0/1	1	2	3	0	0	0	2	1	0	0	0
***B. courtallensis* +**																																											
B. odoratissima	1	3	1	1	2	1	0	1	2	2	1	0	1	3	0	1	2	1	0	2	0	0	1	0	0	0	0	0	0	0	4	0	1	2	0	1	0	0	2	1	0	1	0
B. deflexa	1	0/1/2	0	2	2	1	0	0	2	1/2	1/2	0	0	?	1/2	2	2	0	1	2	0	0	1	0	1/2	1/2	2	0	1	0	?	0	1	0	2	0	2	0	2	0	0	0	0
B. dulcis	0	0/1/2	1	0/1	1/2	1	0	1	1/2	2	0/1	0	1	3	0/1	1/2	2	1	0	0/1	0	0	0/1	0	0	0/1	0	0	?	1	5	0	1	1	0	1	0	0	1	1	0	0	0
B. edulis	1	2/3	1	2	2	1	0	1	2	1	1	0	1	1/3	0/1	2	2	0	1	2	0	0	1	0	0	0	1/2	1	?	0	0/4	0/1	1	1	3	0	2	0	1	0	0	0/3	0
B. javanica	0/1	0/1	1	0	0/1/2	1	0	1	0/1	1	0	0	1	1	0	0	2	0	0	2	1	?	1	0	1	0	0	0	0	1	5/6	0/1	0/1	2	0	1	1	0	2	1	0	3	0
B. lanceolata	1	3	1	0	2	1	0	1	0/1/2	2	0/1	0	1	0/2/3/5	0/1	0/1	2	1	0	1/2	0	0	1	0/1	0	0	0	0	0	?	0/1	0/7	0/1	0/1	1	0	1	0	0	1	1	0	0	0
***B. macrophylla* ***																																											
B. dolichobotrys	1	2	1	2	2	1	0	0	2	2	2	2	1	1	0	2	2	1	1	2	0	0	1	0	1	1	1	1	1	1	2	0	0	0	1	0	0	0	1	0	0	0	0
B. mollis	1	2/3	0	2	1/2	1	0	1	2	2	2	2	1	?	0	2	2	0	1	2	0	1	1	0	0	0/1	1	1	1	1	2	1	?	0	1/2/3	0	2	0	2	0	0	0	0
B. motleyana	0	1/2/3	1	2	2	1	0	1	2	2	2	1/2	1	1/3	0/1	2	2	1	1	2	1	0	1	0	0	0/1/2	0	1	0	1	?	1	1	0	0	0	2	0	1	0	0	0	0
B. multiflora	1	2	0	2	2	1	0	1	2	2	2	0/1	1	?	1	2	2	0	0	2	0	0	1	0	0	2	2	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0
B. nesophila	?	1/2	?	?	0/1/2	1	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1/2	0/1	0/1	0	1	1	2/3	?	0/1	2	0	0	0	0	2	0	0	2	0
***B. papuana* +**																																											
B. carinata	1	3	1	1	2	1	0	1	2	2	1	0	1	3	1	2	2	1	1	2	0	0	1	0	0	2	0	0	0	1	4	1	1	2	0	1	2	0	2	0	0	0	0
***B. parviflora* +**																																											
B. ptychopyxis	1	3	1	2	2	0	0	1	2	2	2	0	1	0	1	2	2	1	0	2	0	0	1	0	0	1	0	0	1	1	0	0	1	2	0	1	0	0	2	1	0	0	0
***B. philippinensis* +**																																											
B. nanihua	1	0	0	2	1	1	0	1	2	1	2	2	1	3	1	2	2	1	1	2	0	1	1	0	1	2	2	0	1	1	1	0	1	0	2	0	2	0	2	0	0	3	0
B. purpurea	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	1	1	0	0	1	1	?	?	?	2	0	1	0	0	2	0	0	0	0
B. pyriformis	1	2	0	2	1/2	1	0	?	2	2	2	1	?	4	0/1	2	2	1	1	2	0	0	1	0	0	2	1/2	1	?	1	?	0	1	1	1	0	2	0	2	0/1	0	0	0
B. racemosa	0	0/1/2/3	1	2	1/2	1	0	1	2	2	2	0	1	1/3	0	2	2	0/1	1	2	1	?	1	0	1	0/1	0	0	0	1	0/1/5/6	0/1	0/1	2	0	1	0	0	2	1	1	0	0
B. ramiflora	1	1/2/3	0	2	2	0/1	0	1	2	1	1/2	0	1	3	0/1	2	2	1	0	2	1	0	1	0	0	0/1	0	0	?	0	0	0	1	2	0	1	0	0	2	0	0	0/1	1
***B. reticulata* +**																																											
B. pubera	1	2	0	2	2	1	0	1	2	1	1	0	1	3	1	2	2	1	1	2	0	0	1	0	1	2	1	1	1	0	4	0	1	0	2	0	2	0	0	0	1	0	0
B. sarawakensis	1	0/1/2	0	2	1/2	1	0	1	2	2	2	0	1	3	0/1	0/1/2	0/1/2	1	1	2	1	0	1	0	1	1/2	0	0	0	0	1/5	0	?	1	0	1	2	0	1	1	1	0	0
B. seemannii	0/1	0/1/2	0	2	1/2	1	0	0/1	2	2	2	1	0	5	0	2	2	0	0	2	0	0	1	0	1	0	1	0	?	1	?	0	0/1	0	0	0	2	0	3	0	0	1	0
B. simaloerensis	1	0	0	2	1	1	0	1	2	2	1	0	1	?	1	2	2	1	1	2	0	0	0	0	1	1/2	1	0/1	?	1	?	?	?	0	2	0	0	0	2	0	0	0/1	0
B. taitensis	?	0/1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	0	1	1/2	0	?	1	3/4	?	1	2	0	0	1	0	2	0	0	1	0
B. tetrandra	0/1	0/1/2	1	0/1	1/2	1	0	1	1/2	2	0/1/2	0	1	1/3	0/1/2	1/2	2	0	1	1/2	0	0	1	0	1/3	0/1	0	0	0	0/1	1/5	0/1	0	1	0	1	0	0	1	0	1	0/1/3	0/2
B. velutina	1	0	0	2	1	1	0	1	2	2	2	0	1	3	0	2	2	1	0	2	0	0	1	0	0/1	2	1	0/1	?	1	3/4	1	0/1	0	1	0	2	0	2	0	1	2	0

that besides an obtained better support for already existing branches in the SCC, other branches will be found (i.e. a new tree topology).

Iterative Taxon Reduction: the example of Baccaurea

In Fig. 1.11 the Bremer support is shown for the SCC. The clades with Bremer support ≥ 2 are replaced with the internal nodes of these clades. *Baccaurea javanica* is in the most basal position within *Baccaurea*. In further analyses this species is used as outgroup, while *Aporosa*, *Maesobotrya* and *Nothobaccaurea* are omitted. This leads to the data matrix shown in Table 1.3. The analysis with this reduced matrix resulted in 62 MPCs of 336 steps long. The strict consensus, CI = 0.376, together with the Bremer support is shown in Fig. 1.12. The support for this cladogram is ambiguous if compared with the original SCC, because the CI equals 0.336 instead of 0.281, but the RI equals 0.435 instead of 0.545. From Fig. 1.12 it is clear that DI ≥ 2 supports many branches, that were not supported in the original SCC.

In order to find better support for the remaining part of the cladogram the method is repeated. The largest clade with Bremer support ≥ 2 (Fig. 1.12) is replaced with the internal node of this clade. This leads to the second reduced data matrix, shown in Table 1.4, containing 15 taxa and 87 characters. The results of the analysis with the second reduced matrix are shown in Fig. 1.13A again with a higher CI and a much lower RI. The results indicate only support for one clade with two taxa. This means that one more branch obtained support, and that one extra reduction is possible.

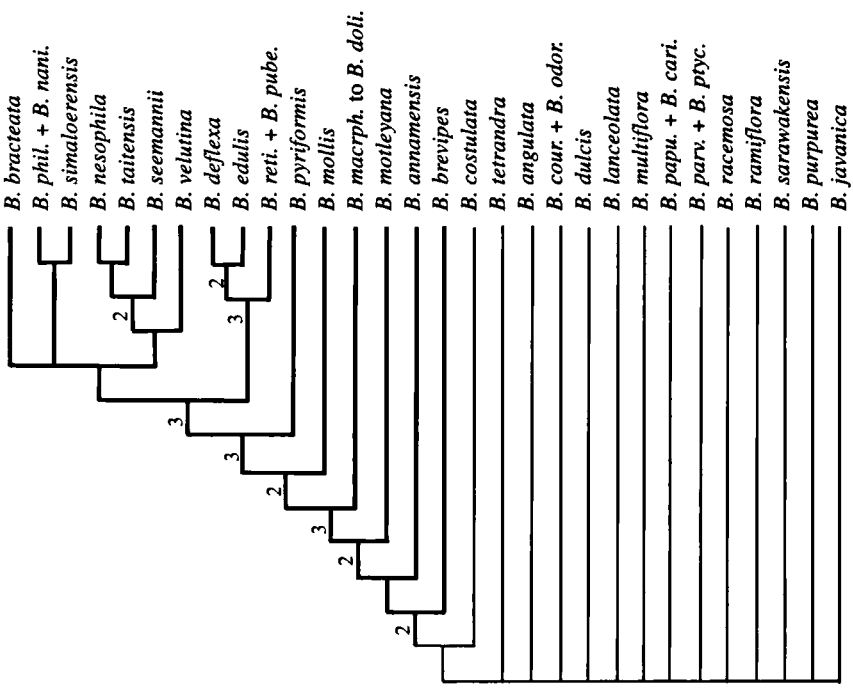
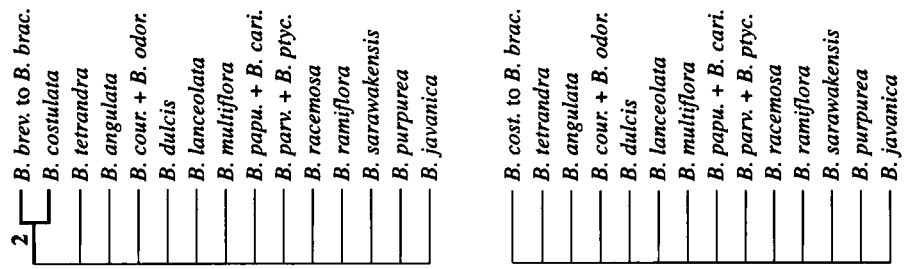


Fig. 1.12. Strict Consensus Cladogram (62 MPCs) of first reduced data matrix of *Baccaurea*. Clade in **bold** supported by Bremer Value ≥ 2. L = 336, CI = 0.376, RI = 0.435, RC = 0.142.

Table 1.4. Second reduced data matrix of *Baccaurea*, 15 taxa and 87 characters. Ancestors in **bold**. The taxon '*B. annamensis* * *B. bracteata*' is the clade *B. annamensis* to *B. bracteata*, containing 15 species.

character / 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	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
B. angulata	0	0	0/1	0/1	1	1	0	0/1	0	1	0	0/1/2	0/1	1	1/2	2	0	0	0/1	0	1	1	0	3	0	0	1	1	0	2	0	1	2	1	0	?	2	2	0	1	1	1	1	1
***B. annamensis* ***																																													
B. bracteata	0	0	0	0	1	1	0	0	2	0	1	2	1	0	1	2	1	0	2	0	0	1	0	2	0	0	0	2	0	2	0	1	2	1	0	3	2	2	1	1	1	1	1	1
B. costulata	0	0	0	?	1	0	0	0/1	1/2	0	0	2	1	0	0/1/2	0	0	0	2	0	0/1	0/1	0	0/1	0	1	0	2	0	2	0	1	2	0	0	?	2	2	1	1	1	1	2	1
***B. courtallensis* +**																																												
B. odoratissima	0	0	0	0	1	0	0	1	1	0	0	0	1	0	2	0	0	0	1	0	1	1	0	1	0	0	1	2	0	1	0	1	2	1	0	3	2	2	1	1	1	1	1	1
B. dulcis	0	0	0	0	1	1	0	0/1	0	1	0/1	0	0	0	2	1	0	0	0/1	0	1	1	0	0/1	0	0	0/1	1/2	0	0	0	0/1	2	1	0	3	2	2	0	1	1	1	1	1
B. javanica	1	0	0	0	1	0	0	0/1	0/1	0	0/1	0/1	1	0	1/2	0	0	0	0	0	1	0/1	0	0/1	0	0	0/1	1	0	0	0	0	0/1/2	1	0	0/1/3/4	0/1	2	0/1	1	1	1	1
B. lanceolata	0	0	0	0	1	1	0	0/1	0	1	0/1	0	0/1	0	0/1/2	2	1	0	0/1	0	1	1	0	3	0	0	2	0/1	0	0	0	0	0/1/2	1	0	1/3/5/6	0	1/2	0	1	1	1	1
B. multiflora	0	0	0	0	1	0	0	0/1	0/1	0	0/1	2	1	1	2	0	0	0	0/1	0	0/1	0/1	0	0/1/2	0	1	0/1	1/2	0	1/2	1/2	1	2	1	0	3	2	2	1	1	1	0/1	1	1
***B. papuana* +**																																												
B. carinata	1	0	0	0	1	1	0	0	1	0	0	0	1	0	2	0	1	0	1	0	1	1	0	1	0	0	1	2	0	1	0	1	2	1	0	3	2	2	1	1	1	1	1	1
***B. parviflora* +**																																												
B. ptychopyxis	1	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	1	1	0	1	0	0	0	2	0	1	0	1	2	1	0	2	2	2	1	1	1	1	1	1
B. purpurea	0	0	0	0	1	0/1	0	0	0/1	1	0	0	1	0	1	0	1	0	1	0	1	0/1	0	3	0	0	2	1	0	0/1	0	0	1/2	1	0	5	1/2	2	0/1	1	1	1	1	1
B. racemosa	0	0	0	0	1	0	0	0/1	0/1	0	0/1	0	1	0	1/2	0	0	0	2	0	0/1	1	0	1/2/3	0	0	0/1	2	0	0/1/2	0	0/1	2	1	0	1/3	2	2	1	1	1	1	1	1
B. ramiflora	0	0	0	0	1	0	0	0/1	0/1	0	0	0/1	1	0	1/2	1	0	0	0/1	0	1	1	0	0/1/2/3	0	0	0/1/2	2	0	1/2	0	0/1	2	1	0	3	2	2	1	1	1	1	1	1
B. sarawakensis	1	0	0	0/1	1	0	0	0	0	0	0	1/2	1	1	1/2	0	0	0	1	0	1	0/1	0	0/1	0	0	0/1	2	0	0/1/2	0/1	1	2	1	0	?	0/1/2	0/1/2	1	1	1	1	1	1
B. tetrandra	1	0	0	0/1	1	0	0	0/1	0/1	0	0	0/1/2	0/1	0	1/2	0	0	0	0/1	0	1	1	0	0/1	0	0	0/1	1/2	0	0/1/2	0/1	1	2	1	0	1/3	1/2	2	0	1	1	1	1	1

character / species	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
B. angulata	0	2/3	1	1	1/2	1	0	1	1/2	2	1/2	0	1	1/3	1	2	2	1	1	2	1	0/1	1	0	0	1	0/1	0/1	?	1	0	0/1	0	2	0	3	2	0	1	1	1	0	0
***B. annamensis* ***																																											
B. bracteata	1	2	1	2	2	1	0	1	2	2	2	0	1	3	0	2	2	1	1	2	1	0	1	0	0	1	0	1	1	1	2	0	1	0	0	0	1	0	1	1	0	0	0
B. costulata	1	0/1/2	?	?	?	1	0	?	?	2	?	?	?	?	0/1	?	?	1	1	?	1	1	1	0	1	0/1	1	1	1	1	0	0/1	1	2	3	0	0	0	2	1	0	0	0
***B. courtallensis* +**																																										
B. odoratissima	1	3	1	1	2	1	0	1	2	2	1	0	1	3	0	1	2	1	0	2	0	0	1	0	0	0	0	0	0	0	4	0	1	2	0	1	0	0	2	1	0	1	0
B. dulcis	0	0/1/2	1	0/1	1/2	1	0	1	1/2	2	0/1	0	1	3	0/1	1/2	2	1	0	0/1	0	0	0/1	0	0	0/1	0	0	?	1	5	0	1	1	0	1	0	0	1	1	0	0	0
B. javanica	0/1	0/1	1	0	0/1/2	1	0	1	0/1	1	0	0	1	1	0	0	2	0	0	2	1	?	1	0	1	0	0	0	0	1	5/6	0/1	0/1	2	0	1	1	0	2	1	0	3	0
B. lanceolata	1	3	1	0	2	1	0	1	0/1/2	2	0/1	0	1	0/2/3/5	0/1	0/1	2	1	0	1/2	0	0	1	0/1	0	0	0	0	?	0/1	0/7	0/1	0/1	1	0	1	0	0	1	1	0	0	0
B. multiflora	1	2	0	2	2	1	0	1	2	2	2	0/1	1	?	1	2	2	0	0	2	0	0	1	0	0	2	2	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0
***B. papuana* +**																																										
B. carinata	1	3	1	1	2	1	0	1	2	2	1	0	1	3	1	2	2	1	1	2	0	0	1	0	0	2	0	0	0	1	4	1	1	2	0	1	2	0	2	0	0	0	0
***B. parviflora* +**																																										
B. ptychopyxis	1	3	1	2	2	0	0	1	2	2	2	0	1	0	1	2	2	1	0	2	0	0	1	0	0	1	0	0	1	1	0	0	1	2	0	1	0	0	2	1	0	0	0
B. purpurea	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	1	1	0	0	1	1	?	?	?	2	0	1	0	0	2	0	0	0	0
B. racemosa	0	0/1/2/3	1	2	1/2	1	0	1	2	2	2	0	1	1/3	0	2	2	0/1	1	2	1	?	1	0	1	0/1	0	0	0	1	0/1/5/6	0/1	0/1	2	0	1	0	0	2	1	1	0	0
B. ramiflora	1	1/2/3	0	2	2	0/1	0	1	2	1	1/2	0	1	3	0/1	2	2	1	0	2	1	0	1	0	0	0/1	0	0	?	0	0	0	1	2	0	1	0	0	2	0	0	0/1	1
B. sarawakensis	1	0/1/2	0	2	1/2	1	0	1	2	2	2	0	1	3	0/1	0/1/2	0/1/2	1	1	2	1	0	1	0	1	1/2	0	0	0	0	1/5	0	?	1	0	1	2	0	1	1	1	0	0
B. tetrandra	0/1	0/1/2	1	0/1	1/2	1	0	1	1/2	2	0/1/2	0	1	1/3	0/1/2	1/2	2	0	1	1/2	0	0	1	0	1/3	0/1	0	0	0	0/1	1/5	0/1	0	1	0	1	0	0	1	0	1	0/1/3	0/2



A. results of second reduced matrix **B.** results of third reduced matrix

Fig. 1.13. **A.** Cladogram (strict consensus of 31 trees) obtained by second reduced matrix: length 194, CI = 0.412, RI = 0.081, RC = 0.033, clade with Bremer support 2 indicated in **bold**. **B.** Cladogram (strict consensus of 31 trees) obtained by third reduced matrix: length 182, CI = 0401, RI = 0.0, RC = 0.0.

The third reduced matrix contained therefore only one taxon less, namely 14 taxa and 87 characters. The analysis of this matrix resulted in one basal polytomy (Fig. 1.13B). No further support for clades can be obtained by this method. There are no more supporting characters present to resolve this part of the cladogram in a stable manner. The RI = 0.

There is only support in ITR for clades that exist in the SCC. The ITR supports the clade *B. costulata* up to *B. bracteata* in the SCC. The reconstructed cladogram, with all taxa no longer reduced to their ancestral nodes, is shown in Fig. 1.14F.

1.6.4 – *Results of weighted phylogenetic analysis*

In Chapter 1.6.3 the reasons for performing weighted analyses are explained. Three methods are used: Successive Weighting, Implied Weighting (IW_k: k = 1, 3, or 6) and Iterative Taxon Reduction. The results of the various methods are shown in Fig. 1.14.

In Table 1.5 the length and fit measures are given for the cladograms shown in Fig. 1.14 and for the original cladograms on which the consensus cladograms are based.

Table 1.5. Length and fit measures of cladograms obtained by the different methods. The values for the Most Parsimonious Cladograms (MPCs) and for the consensus (per method) are given. All characters have equal weights. In **bold** the measures for the cladograms shown in Fig. 1.14. For the constant of concavity (k) three different values are used in Iterative Weighting (IW_k: k = 1, 3, 6). SCC = Strict Consensus Cladogram, ITR = Iterative Taxon Reduction, CI = Consistency Index, RI = Retention Index, RC = Rescaled Consistency Index.

	Original	SCC consensus	IW_1	IW_1 consensus	IW_3	IW_3 consensus	IW_6	SW	ITR
MPCs	12		16		2		1	1	1
Length	481	**484**	530–536	**588**	522–524	**530**	**499**	**485**	**553**
CI	0.281	**0.279**	0.252–0.255	**0.230**	0.258–0.259	**0.255**	**0.271**	**0.278**	**0.244**
RI	0.545	**0.541**	0.473–0.481	**0.405**	0.489–0.491	**0.481**	**0.522**	**0.540**	**0.451**
RC	0.153	**0.151**	0.119–0.123	**0.093**	0.126–0.127	**0.123**	**0.141**	**0.150**	**0.110**

1.6.5 – *Discussion of weighted phylogenetic analysis*

IW and SW were performed to find support for one of the 12 MPCs. None of the trees obtained by IW and SW is congruent with the SCC (Fig. 1.14A–E) and, therefore, all new cladograms are dismissed.

However, the cladogram obtained by SW (Fig. 1.14E) is only one step longer than the SCC (Table 1.5) and quite comparable. The clade composed of *B. ptychopyxis* to *B. bracteata* is identical, except for the taxa *B. macrophylla* and *B. macrocarpa*. These taxa form a polytomy in the SCC, but are resolved in SW. A second difference is that at the basis of the cladogram some taxa have changed position.

At first glance, the trees obtained by IW seem rather different from the SCC. When using a low k value (i.e. selecting strongly for characters with low homoplasy), two important changes in tree topology take place (Fig. 1.14B, D). Firstly, *Nothobaccaurea* and *Maesobotrya* become a monophyletic group. Secondly, the species sequence is largely reversed. Some basal species in the SCC form a monophyletic clade at the tip of the two IW trees with k = 1 and k = 3. However, most of the smaller clades in the SCC are found again in the IW trees. From the viewpoint of species distribution, some strange features are observed in the IW trees. The species present in the Pacific do not have close relationships with each other, in contrast with the results obtained by the initial analysis (resulting in SCC). For this reason, I have no confidence in the IW trees. The IW_6 (Fig. 1.14C) is not very different from the SCC, but I see only few arguments, like the sister relationship of *B. racemosa* and *B. sarawakensis*, in favour of the IW_6 tree.

The cladogram obtained by ITR (Fig. 1.14F) is fully congruent with the SCC. The clade *B. costulata* to *B. bracteata*, as well as some sister relationships at the base of the SCC, are supported by this analysis. These parts of the SCC are therefore well supported. For the basal part of the SCC no support is obtained by ITR.

1.7 – Selected cladograms

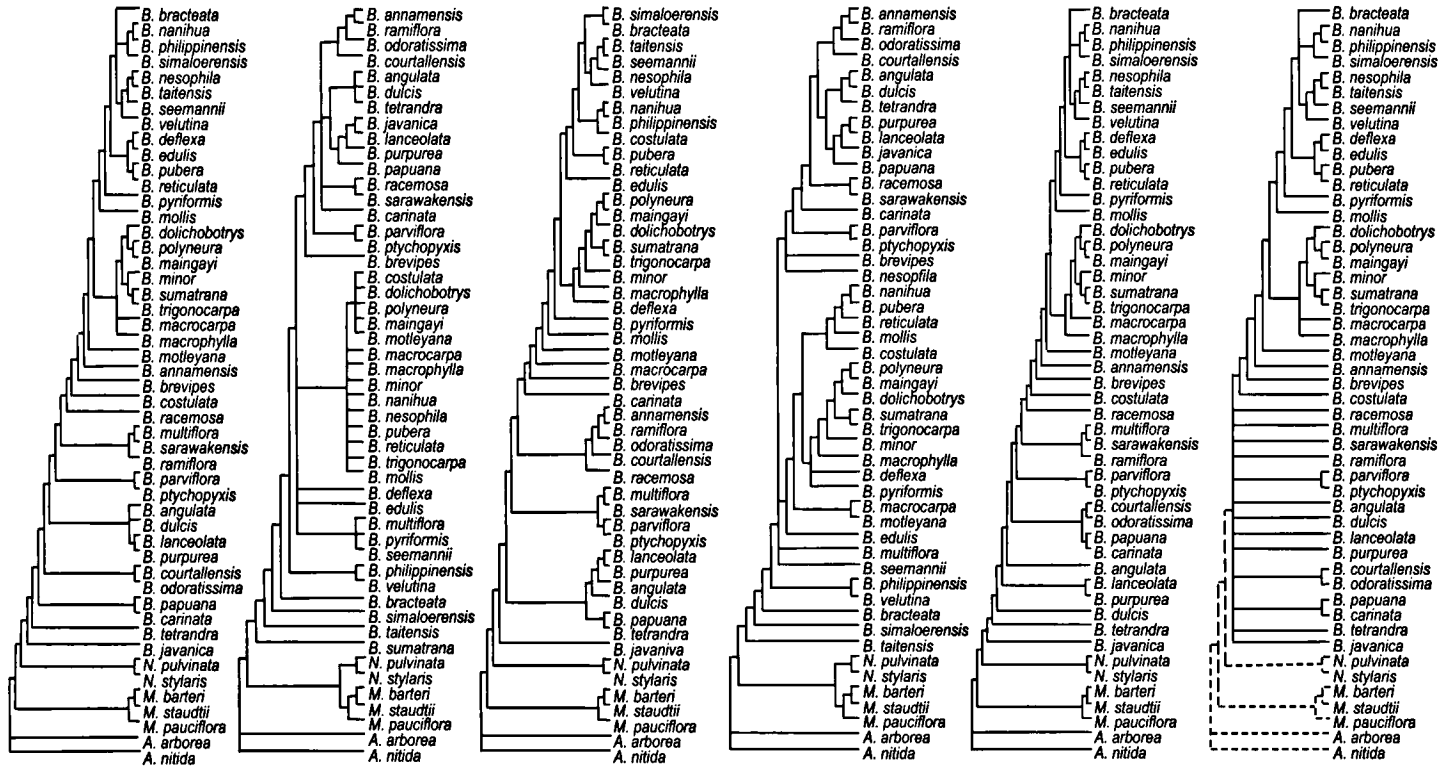
1.7.1 – *Twelve Most Parsimonious Cladograms (MPCs)*

Because it was not possible to choose (Chapter 1.6.5) one cladogram among the 12 MPCs, or to obtain a cladogram with most internal nodes well supported, all 12 MPCs are accepted as the best estimate of the phylogenetic relationships of *Baccaurea* and *Nothobaccaurea*. All following conclusions and discussions (Chapter 1.7 and 1.8) are based on these 12 MPCs. The congruence between the 12 MPCs is substantial and summarised in the Strict Consensus Cladogram (SCC) (Fig. 1.11, 1.14A, 1.16, 1.17).

1.7.2 – *Conclusions drawn from the Most Parsimonious Cladograms*

The representatives of *Maesobotrya* included in the analyses and the genera *Nothobaccaurea* and *Baccaurea* are monophyletic. *Maesobotrya* is in the most basal position, followed by *Nothobaccaurea* and *Baccaurea*. Within *Baccaurea* there is only weak support for infrageneric groupings. Species split off one by one, or in small clusters. However, some conclusions can be drawn.

Fig. 1.14. Original Strict Consensus Cladogram (SCC) and trees obtained by the various (weighting) methods. All cladograms are strict consensus cladograms, except for IW_6, 1 MPC and the ITR (reconstructed cladogram).



Sister species:

- The New Guinean species *B. papuana* and *B. carinata* are sister species, supported by characters 6, 17, 70, 81 (Fig. 1.16), none of which shows a ci ≥ 0.5 (Fig. 1.15).
- *Baccaurea courtallensis* and *B. odoratissima*. Both species belong to the group placed in a basal position in the MPCs, characterised by glabrous leaves and small fruits (supported by the characters 8, 60, 61, 74, 86). Character 61 (abaxial indumentum of the sepals; sparsely hairy instead of densely hairy) gives the strongest support based on ci value (Fig. 1.15). The distribution of the two species is very disjunct, *B. courtallensis* is an Indian species, whereas *B. odoratissima* is Bornean.
- *Baccaurea lanceolata* and *B. purpurea*. The position of *B. lanceolata* was doubtful until recently (Airy Shaw, 1975). Now it shows a sister relationship with the new species *B. purpurea*, which is based on eight characters. Character 61 (abaxial indumentum of the sepals) is the only one with a high ci, but this character is ambiguous for this clade.
- *Baccaurea parviflora* and *B. ptychopyxis* are sister species. *Baccaurea parviflora* is a complex species, with *B. ptychopyxis* as a satellite species north of its distribution area. Four characters support this clade; however, only character 50 (more than 10 pistillate inflorescences clustered together) is strongly supported by ci = 0.5.
- *Baccaurea multiflora* and *B. sarawakensis*. The latter species was postulated by Airy Shaw (1975) to be related to *B. ramiflora*, *B. racemosa*, *B. parviflora*, and *B. odoratissima* (formerly known as *B. trunciflora* and *B. membranacea*), but never with *B. multiflora*. Based on phenetic differences, this relationship was not expected, but seven characters, though all with a low ci, support it.
- *Baccaurea sumatrana* and *B. trigonocarpa*: although this relationship is not mentioned in the literature, it is rather obvious. This clade is supported by ten characters. Two of these have a high ci value: character 4, one of the strong characters is equivocal for this clade; character 82 shows a unique apomorphy for this clade, namely two epidermal layers on both sides of the lamina. *Baccaurea trigonocarpa* has distinctly keeled fruits, which may be the reason why this relationship was not noticed. *Baccaurea sumatrana* has always been mentioned in connection with *B. minor*, and often with *B. maingayi*. These relationships are also shown in this analysis.
- *Baccaurea polyneura* and *B. maingayi*. This relationship was already recognised by Airy Shaw (1975), and is supported by six rather weakly supported characters.
- *Baccaurea pubera* and *B. reticulata*. Three characters in this analysis weakly support the relationship. Airy Shaw (1975) mentioned a relationship between *B. reticulata* and *B. bracteata*, but no evidence for this relationship could be established in the present analysis.
- *Baccaurea deflexa* and *B. edulis*. In this study *B. deflexa* is seen as a distinct species rather than a synonym of *B. costulata*. The sister relationship between these two species is not strongly supported, because it is based on three characters only, all with a low ci.
- *Baccaurea nesophila* and *B. taitensis*. *Baccaurea nesophila* is related with several of the Pacific species. Six characters (all with ci < 0.5) support the sister relationship.
- *Baccaurea nanihua* and *B. philippinensis*. Six characters, of which character 10 (presence of a basal pulvinus) with a high ci support this relationship.

Larger Clades in the cladogram supported by one or more characters with ci > 0.5 are:

- The clade of eight species from *B. bracteata* up to *B. velutina*. The main character is 49 (2–9 flowers per pistillate inflorescence), whereas > 10 flowers is the common state. This clade is geographically very interesting. It comprises the Sundanese species *B. bracteata* and two closely related species with a more restricted geographic distribution, namely *B. simaloerensis* from Simeuluë Island and *B. velutina* from Peninsular Malaysia. Two other species show curious distributions for *Baccaurea*, namely *B. philippinensis* from the Philippines and Halmahera, and *B. nanihua* ranging from Borneo to New Guinea. Furthermore it includes *B. nesophila* from New Guinea and two species from the Pacific, *B. taitensis* and *B. seemannii*. In this small clade nearly the whole distribution range of *Baccaurea* is represented.
- *Baccaurea dolichobotrys*, *B. polyneura*, and *B. maingayi* form a very strong clade, supported by 6 characters of which 3 have a ci > 0.5. The leaf bases are cordate (heart-shaped) in these species (character 20); the tertiary nervation is distinctly scalariform (character 23); the adaxial leaf epidermis is 2-layered (character 82).
- The latter clade, together with the clade containing *B. minor*, *B. sumatrana*, and *B. trigonocarpa*, and the species *B. macrocarpa* and *B. macrophylla* is well supported by 9 characters, two of which have a high ci (character 29, position of flowers in the tip of the staminate inflorescence, and character 52, geniculate pistillate flower pedicel). This clade will be referred to as the *B. minor*-group.
- The clade comprising all the above clades and including the 22 species from *B. macrophylla* up to *B. bracteata* is supported by six characters, including character 4 (inner bark red-brown) with a ci = 0.5.
- Ten characters support the former clade expanded with *B. motleyana*, *B. annamensis*, and *B. brevipes*. The most important character is the presence of raised glands on the petiole (character 11). However, numerous taxa are polymorphic for this character, and it is therefore not a very reliable character.
- Well supported by nine characters is the clade including *B. angulata*, *B. dulcis*, *B. lanceolata*, and *B. purpurea*. Airy Shaw (1975) had no idea about the relationships of these species. From this analysis it appears that they are closely related to each other. The main apomorphy is the pulvinus (swelling in petiole usually accompanied with a bend) at the base of the petiole (character 10).
- Finally the clade comprising the whole genus *Baccaurea* except for *B. javanica*, is well supported. There are eight apomorphies for this clade, one of which with a high ci. Character 61 (abaxial indumentum of the pistillate sepals, is the most important feature. Character 53 (pedicel indumentum) is also important, but this character is polymorphic in *B. tetrandra* and *B. javanica*.

1.7.3 – *Character evolution*

Because of the high number of characters in the analyses only the most important ones are shown. The ci and ri are used as criterion for this purpose. The ci is a measure of homoplasy for a character, higher values mean less homoplasy. The ri is another way of measuring support for a character; contrary to the ci, this measure is sensitive to uninformativeness. A ri of 0 for a character shows that no phylogenetic information is present.

The evolution of characters with a consistency index (ci) ≥ 0.5 combined with a retention index (ri) ≠ 0 is shown in Fig. 1.15. Characters 5, 25, 42, 43, 51 are omitted because they are uninformative for the ingroup. Character 36 and 59 (colour characters), both with ci = 0.5, are excluded because information is lacking for several species and these characters have a high number of steps (character state changes).

Striking character transformations (not confined to ci > 0.5) will now be discussed briefly:

- A number of (unique) apomorphies, mostly characters of the staminate inflorescence, coincide with the origin of *Baccaurea*. The stamens shorter than the sepals, and the sepals not fused at the base are autapomorphies for *Baccaurea* (characters 40 and 35). Several other staminate floral characters show an apomorphy for *Baccaurea*: the pedicels (character 33) are densely hairy, whereas glabrous is the plesiomorphic state, and the sepals are densely hairy at the adaxial side (character 38) except in *B. javanica* and *B. tetrandra*. The pistillate character 62 (densely hairy sepals) coincides also with the origin of *Baccaurea*. The origin of the differences in the staminate flowers of *Baccaurea* compared with its sister genera may have been caused by a change of pollinator. *Aporosa* is usually pollinated by small stingless bees, the pollinators of *Baccaurea* are beetles, flies (Momose et al., 1997), and possibly even thrips (own field observation). In *Baccaurea*, the stamens do not protrude above the sepals, therefore it is possible that bees cannot reach the pollen. Moreover a floral disc is absent in *Baccaurea*, but present in *Maesobotrya*. These features may cause the flowers to be unattractive for bees. The hairiness of the staminate flowers of *Baccaurea* may be useful as a cover for thrips and other small pollinators. It may be possible to reach the anthers of *Baccaurea* from between the sepals, because the sepals are not fused at the base.
- Character 4, the colour of the inner bark, is remarkably stable. Yellow to white-brown is the plesiomorphic state. The red-brown colour has a single origin in the clade from *B. macrophylla* to *B. bracteata*, and only one reversal occurs in the clade *B. sumatrana* and *B. trigonocarpa*. There is a clear correlation with the presence of buttresses (character 2) and also with the colour of the outer bark (character 3). These two characters define the same clade, but with the inclusion of *B. motleyana*. However, the latter two characters show more reversals. In the clade *B. sumatrana* and *B. trigonocarpa* the characters 2, 3, and 4 show a reversal. Seemingly, one character change in the trunk allows other changes. Another correlation with character 4 is found in the density of hairiness of the septa. The septa change from glabrous to sparsely hairy. Parallel occurrences of this apomorphy are found in *B. costulata* and in *M. barteri*.
- In character 10, the absence of a basal pulvinus (swelling in the petiole usually accompanied with a bend) is plesiomorphic. A basal pulvinus has developed twice. Firstly in the clade of *B. nanihua* and *B. philippinensis*, and secondly in *B. purpurea* to *B. angulata*. The ability to drop their leaves or to move the lamina out of the sun may be an evolutionary advantage for these species in drier habitats. Characters correlating with the basal pulvinus are the hairiness of several organs. Usually the plesiomorphic state is glabrous but most organs of *B. nanihua* and *B. philippinensis* are hairy. Apomorphies (developed in parallel) for this clade are densely hairy

Fig. 1.15. Character transformation series for the 20 phylogenetically most important characters for *Baccaurea*. ts = tree steps, i.e. the number of steps of a character on the tree. Taxa or clades which are unknown or undecided (= equivocal) for a character state are deleted from the SCC for that character.

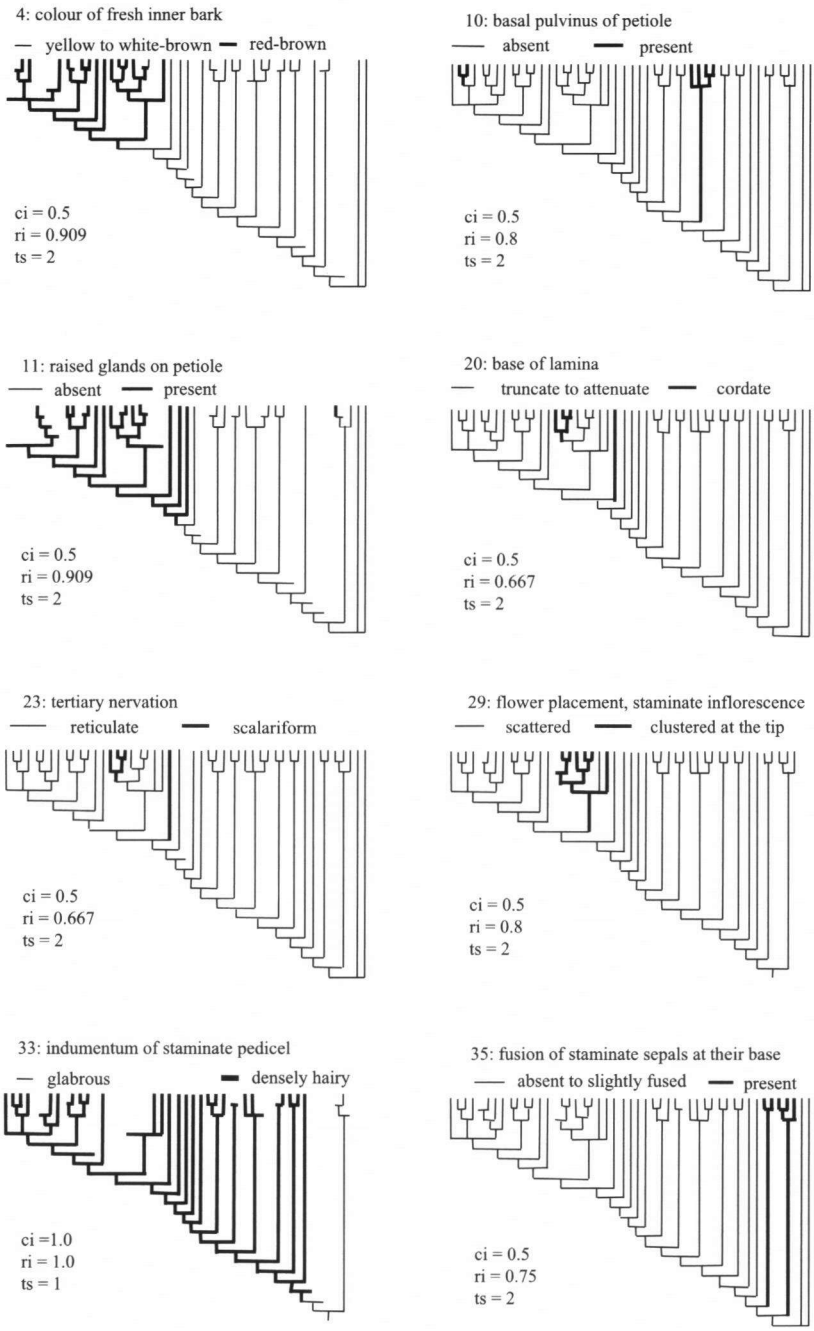
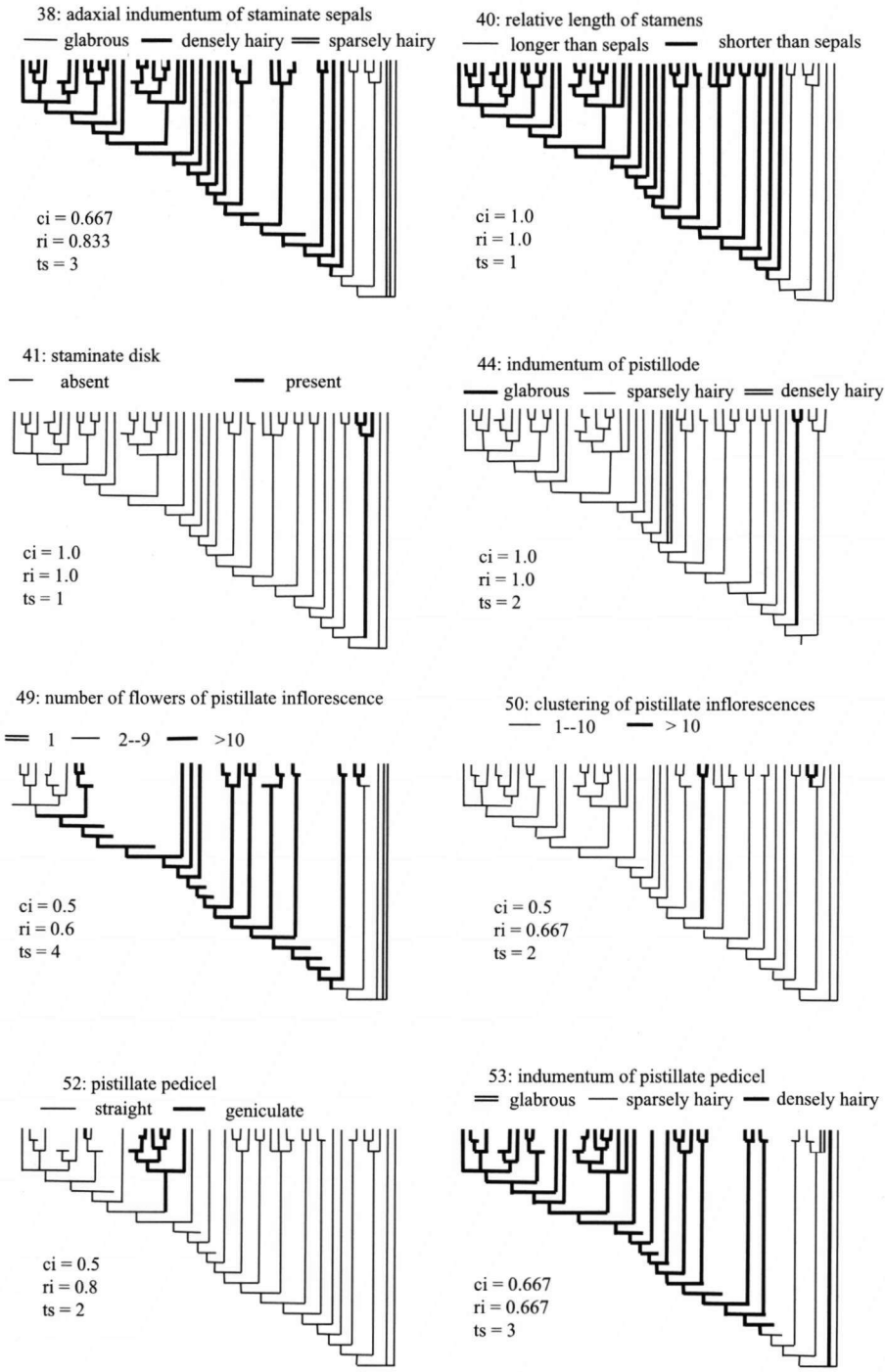


Fig. 1.15 (*continued*)



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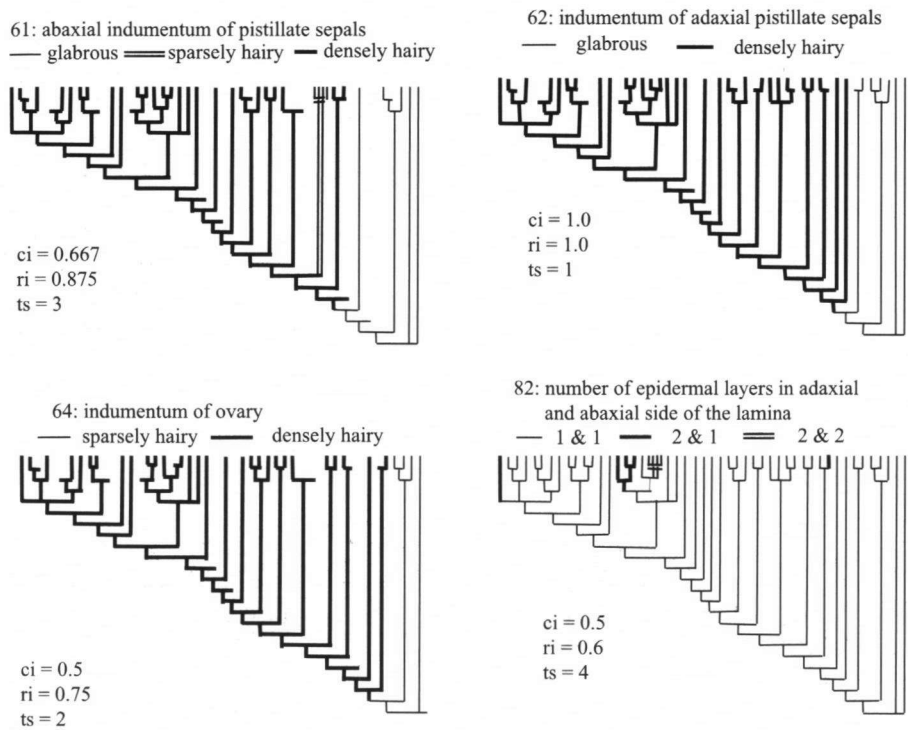


bracts (character 57), stigmatic lobes (character 66), and septa (character 71), and the absence of druses in enlarged cells of the leaf lamina (character 86). The ad hoc explanation, i.e. adaptations to survive drier periods, is certainly not valid for the clade *B. purpurea* to *B. angulata*, because these species occur only on the main, largely everwet, Malesian islands. Several characters coincide with the presence of a basal pulvinus in this clade. These characters are a weak Terminalia branching pattern (Fig. 3.1) (parallel reversal in character 6), the cauline staminate inflorescences (flowering from the trunk, character 24; parallel apomorphy with *B. parviflora*), the sparsely hairy staminate inflorescences (reversal to plesiomorphic state in character 28), and presence of staminodes (rudimentary stamen, character 39; parallel apomorphy amongst others in *B. papuana* and *B. tetrandra*).

- An important transformation occurs in the leaf characters 20, 23 and 82 in the clade *B. dolichobotrys* to *B. maingayi*. A parallel development in the latter clade and in *B. motleyana* is the presence of a cordate leaf base (heart-shaped, character 20), and a scalariform (ladder-like) leaf nervation (character 23). An extra epidermal layer at the upper side of the lamina (character 82) occurs also in the clade *B. dolichobotrys* to *B. maingayi* with parallel developments found in *B. bracteata* and *B. carinata*. There is also a correlation found with the presence of hairs at the upper side of the lamina (character 18). Another character change in this clade is the

regular absence of a pistillode (character 43) in the clade *B. dolichobotrys* to *B. maingayi.*

- Two stable characters show another correlation. In the clade *B. macrophylla* to *B. dolichobotrys* an autapomorphy for the position of the staminate flowers (character 29) is found, i.e. clustered at the tip of the inflorescence. Only *B. macrocarpa* shows a reversal to the plesiomorphic state, i.e. scattered over the rachis. The other apomorphy is the geniculation of the pistillate pedicel (character 52). This character shows a parallel transformation in *B. deflexa.*
- The clustering of more than 10 pistillate inflorescences is the apomorphic state of character 50, whereas clusters of 1–10 is the plesiomorphic state. The clade of *B. parviflora* and *B. ptychopyxis* is characterised by this character. This transformation is seemingly not part of a complex of changes, because no coincidences with other characters are observed.
- Finally some of the more obscure trends in *Baccaurea* will be discussed. A strong Terminalia branching pattern (Fig. 3.1) is plesiomorphic in *Baccaurea* (character 6). Reversals to a weak Terminalia branching pattern are common. The presence of a branched staminate inflorescence (character 26) is apomorphic and a relatively stable character. Less than 10 flowers per pistillate inflorescence is apomorphic (character 49). This feature is mostly present in species occurring on relatively small islands (of the Philippines, Moluccas, and the Pacific). The indument of the fruits (character 70) behaves like several of the other indument characters. Glabrous is plesiomorphic, followed by sparsely hairy; densely hairy is the most apomorphic state. The presence of only simple hairs (character 79) is plesiomorphic, whereas a combination of single hairs and another indumentum type (such as basally fused tufts of hairs) is regarded as apomorphic.

The SCC with all character changes is presented in Fig. 1.16. This shows the character support per branch.

1.8 – Discussion

1.8.1 – *Quality of the twelve Most Parsimonious Cladograms*

The quality of the 12 MPCs (summarised in the SCC) can be expressed in terms of tree stability. Bremer support is only found for minor clades (Fig. 1.11). From these data it is evident that the support for most internal clades is rather weak, as already stated in Chapter 1.6.1. On the other hand, the new method of Iterative Taxon Reduction or Successive Weighting indicates that the clade including *B. costulata* to *B. bracteata* is apparently stable, while the topology of the basal taxa *B. javanica* till *B. racemosa* is not strongly supported by these analyses. The latter group corresponds with the group of species mentioned by Airy Shaw (1975) as the relatively glabrous, small fruited species from the Sunda Shelf, expanded with *B. papuana* and *B. carinata* of New Guinea, and the clade *B. purpurea* up to *B. angulata* of which the relationships were not obvious to Airy Shaw. When Implied Weighting is used, the tree topology is basically reversed in comparison with the SCC. The group from *B. javanica* up to *B. racemosa* then forms a terminal clade, while *B. sumatrana* up to *B. costulata* (corresponding to *B. costulata* up to *B. bracteata*, as mentioned above) is placed in a

Fig. 1.16. Character support for the phylogenetic tree of *Baccaurea*; for characters see Table 1.2; for matrix see Table 1.4. Characters in **bold** have a CI of 1.0.

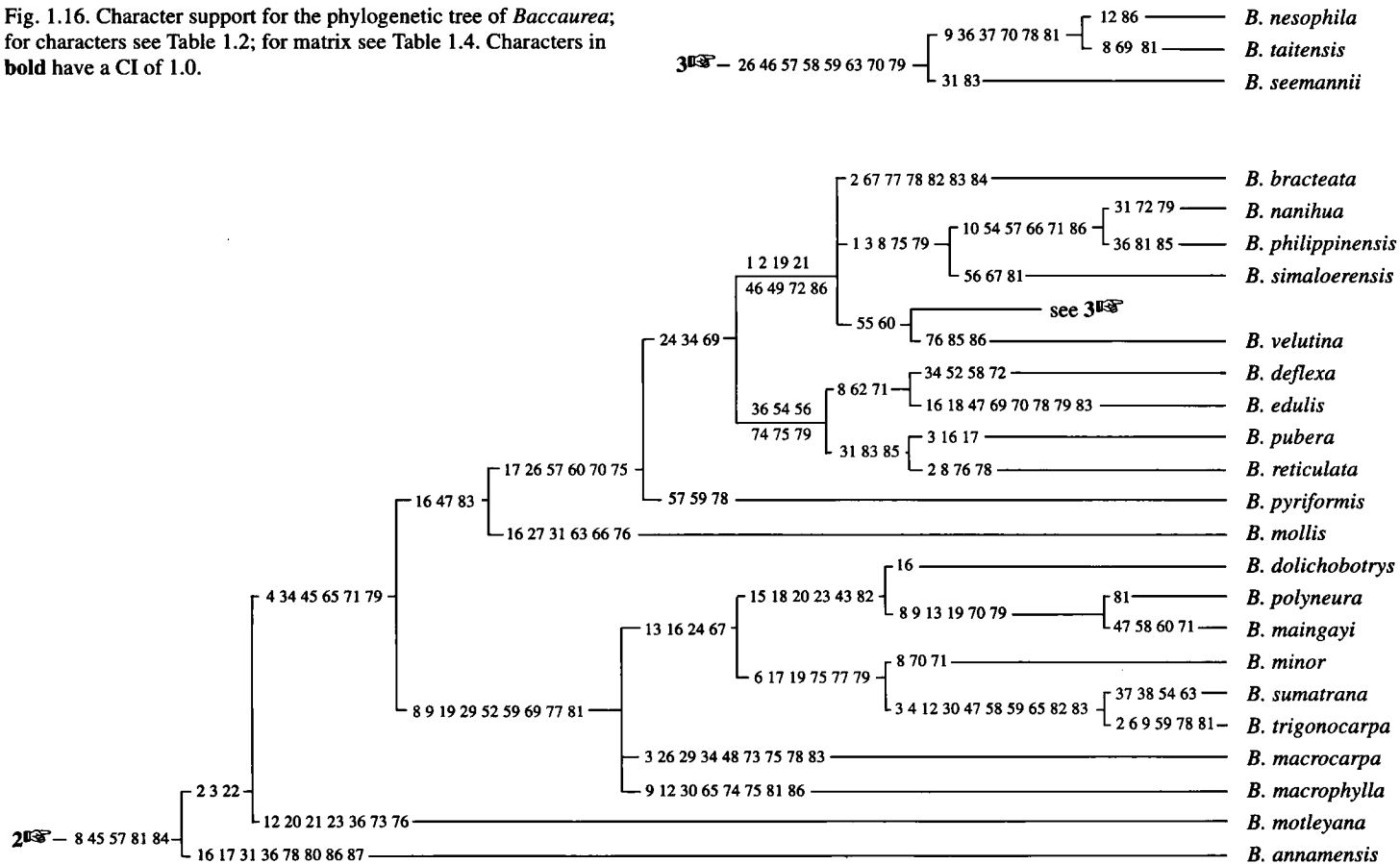
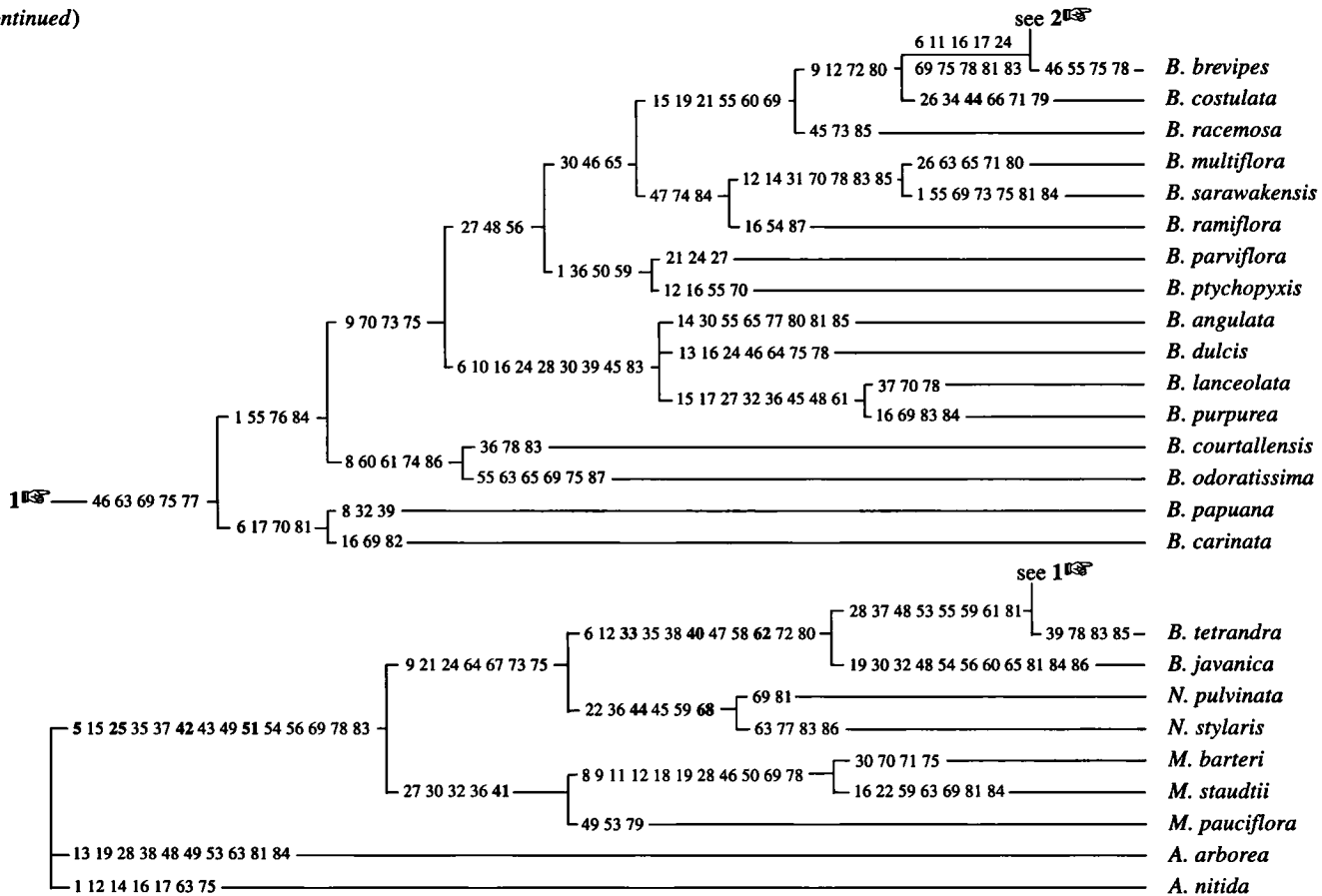


Fig. 1.16 (*continued*)



basal position in the cladogram. *Nothobaccaurea* forms a monophyletic clade in all performed analyses. In the SCC, *Nothobaccaurea* and *Baccaurea* form a monophyletic group, which is in contrast with the results of IW, where *Nothobaccaurea* and *Maesobotrya* are placed together.

Summarising, the conclusion can be drawn that the obtained 12 MPCs are weakly supported by tree statistics. The clade *B. costulata* up to *B. bracteata* is the relatively stable part of the cladograms. The topology in the basal part is rather unstable.

1.8.2 – *Consequences for classification*

Consequences for the taxonomy at the generic level will be examined first. The three newly described species in the new genus *Distichirhops* were excluded from the phylogenetic analysis because of missing data. From the analyses the conclusion can be drawn that *Baccaurea* forms a monophyletic group. However, in a basal position in this clade two species, formerly known as *B. pulvinata* and *B. stylaris* are found. These two species form a monophyletic group, strongly supported by 6 characters (Fig. 1.16). The phylogenetic analysis supports the description of a new genus (i.e. *Nothobaccaurea*). The species of *Maesobotrya* included in this analysis form a monophyletic clade. This is in agreement with the existing taxonomic classification.

Secondly, the consequences for the classification at the infrageneric level will be discussed. In the past, two infrageneric classifications were presented, one by Müller Argoviensis in 1866, and the other one by Pax & Hoffmann in 1922. The circumscription of the sections differed considerably. However, both were based on staminate floral characters, combined with the number of locules in the ovary. Pax & Hoffmann added the type of the indument. The results of both infrageneric classifications are shown in Fig. 1.17. All modern species known by these authors are mentioned and their classifications can be compared with modern views.

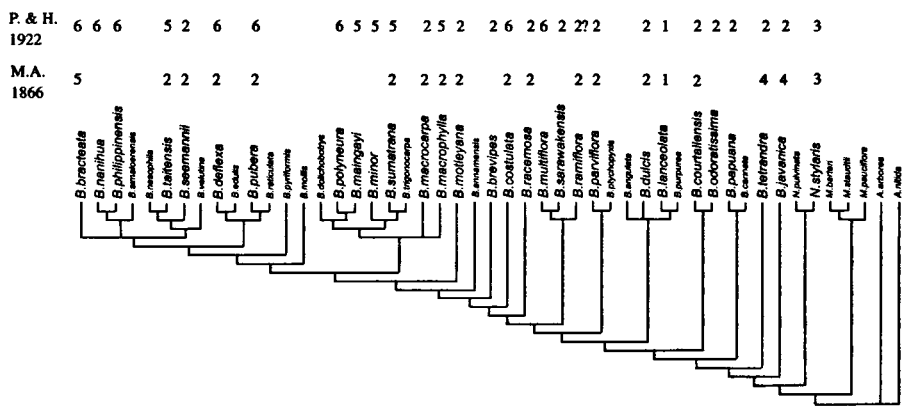


Fig. 1.17. Infrageneric classifications of M.A. = Müll.Arg. and P. & H. = Pax & Hoffm. in numbers, compared with the SCC. The sections are: 1. *Hedycarpus* Miq.; 2. *Pierardia* Roxb.; 3. *Isandrion* Baill.; 4. *Adenocrepis* Bl.; 5. *Calyptroon* Miq.; 6. *Everettiodendron* Merr. Species unknown to both Müll. Arg. and Pax & Hoffm., or not belonging to *Baccaurea* or *Nothobaccaurea* are printed in a smaller letter type.

From Fig. 1.17 it can be seen that the position of *B. lanceolata* (section 1) and *B. stylaris* (section 3) was obscure, because both were placed in a section of their own. Müller Argoviensis also placed the African species of *Baccaurea* (i.e. *Maesobotrya*) in the section *Isandrion*, together with *B. stylaris*. *Baccaurea stylaris* has now been transferred to the new genus *Nothobaccaurea*, together with the former *B. pulvinata*. *Baccaurea lanceolata* is now recognised as part of the clade comprising *B. purpurea* to *B. angulata*. In Pax & Hoffmann there are two other interesting features. Most of the species in the well-supported clade of *B. minor* (SCC, Fig. 1.17) were placed in his section 5. *Baccaurea polyneura* and *B. macrocarpa* were not included, but the position of *B. macrocarpa* in this group is questionable. *Baccaurea taitensis*, in contrast, was part of that section. The second point is that *B. bracteata* together with two clades, *B. simaloerensis* up to *B. nanihua*, and *B. reticulata* up to *B. deflexa*, are all combined in section 6. *Baccaurea polyneura*, *B. costulata*, and *B. multiflora* were also included in this section. This is in sharp contrast with the selected cladograms. Although the classification of Pax & Hoffmann is not fully congruent with modern ideas about phylogenetic relationships within *Baccaurea*, some groups were already partly recognised, but none of them is fully monophyletic. A new, formal infrageneric classification does not seem to be useful, especially if well-recognisable, monophyletic taxa are preferred. If the sequence rule of Nelson (Wiley, 1981, and references therein) is applied, there will be many monophyletic, and often monotypic, groups, which have to be recognised at many different levels. Therefore, no infrageneric classification is presented here, even though some groups are recognisable.

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Chapter 2

BIOGEOGRAPHIC ANALYSES

2.1 – Introduction

Two different types of analysis can be distinguished in historical biogeography. The first is an analysis based on phylogenies of several groups of organisms occurring in the same areas resulting in a general area cladogram that reflects the vicariance events in the history of the areas involved. The second type is an analysis based on only one group of organisms, called taxon biogeography. Here, the result is also an area cladogram, but this type of area cladogram attempts to describe the specific history of distribution of the organisms studied. Depending on the available information about the geological history of the areas involved and the historical changes in climate and sea level, a scenario with explanations for current distributions is formulated. In this chapter only this taxon biogeographical approach will be pursued for the genera *Baccaurea* and *Nothobaccaurea*. Within the framework of the Programme 'Pathways to New Guinea', the data will later be used in combination with information from other taxa to obtain general patterns.

Baccaurea is one out of relatively few plant genera with representatives on both sides of Wallace's Line (Fig. 2.1; Wallace, 1876). Wallace's Line separates the landmasses of different origin and their inhabiting organisms in Southeast Asia. Most of the areas west of this line have a Southeast Asian origin or an early Gondwanan origin, rifted apart from Gondwana more than 120 MaBP. Therefore, Laurasian biotas are found on the west side of Wallace's Line. Most areas east of Wallace's Line, on the other hand, have an Australian origin and are therefore inhabited by Gondwanan

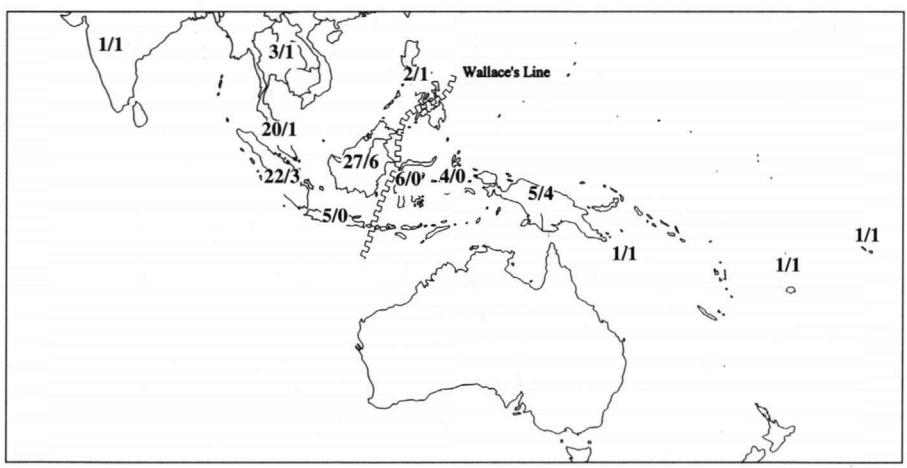


Fig. 2.1. Wallace's Line. Number of *Baccaurea* species (divisor). Number of endemic species (denominator). Areas used as in Fig. 2.3.

biota. Taxa occurring on both sides of Wallace's Line probably reached one of the sides through dispersal. An indication for a Southeast Asian origin of *Baccaurea* (i.e. west of Wallace's Line) is that the most basal branch in the MPCs leads to *B. javanica*, a Sunda Shelf species. The object of this study was to discover the pathways from Asia to New Guinea in time and space for *Baccaurea*. It is also possible that dispersal in the opposite direction would be discovered, i.e. from New Guinea to the Sunda Shelf. This pathway is for example found in several *Sapindaceae* (Van Welzen, 1989; Turner, 1995).

At first it was attempted to obtain historical information about distribution areas directly from the MPCs and the distribution areas of modern species. Subsequently, computer analyses were performed. A dozen computer programs is available for biogeographic analysis. All of them have problems with the interpretation of (lack of) information from widespread species (dispersal), redundant information, the definition of the areas used, and the reticulate nature of areas. Despite these problems a few methods are nowadays accepted as valid methods for historical biogeography. One of the most commonly applied tools, namely Brooks Parsimony Analysis (BPA) (Brooks, 1990), is chosen for this study. In addition, an event-based method, Hovenkamp Analysis (HA) (Hovenkamp, 1997), is used.

2.2 – Methods

2.2.1 – *Geological framework*

The results of the biogeographic analyses are compared with existing geological theories about the history of the Earth. The geological framework is shown in Table 2.1 and in Fig. 2.2. Only very large areas are mentioned, because these areas match the

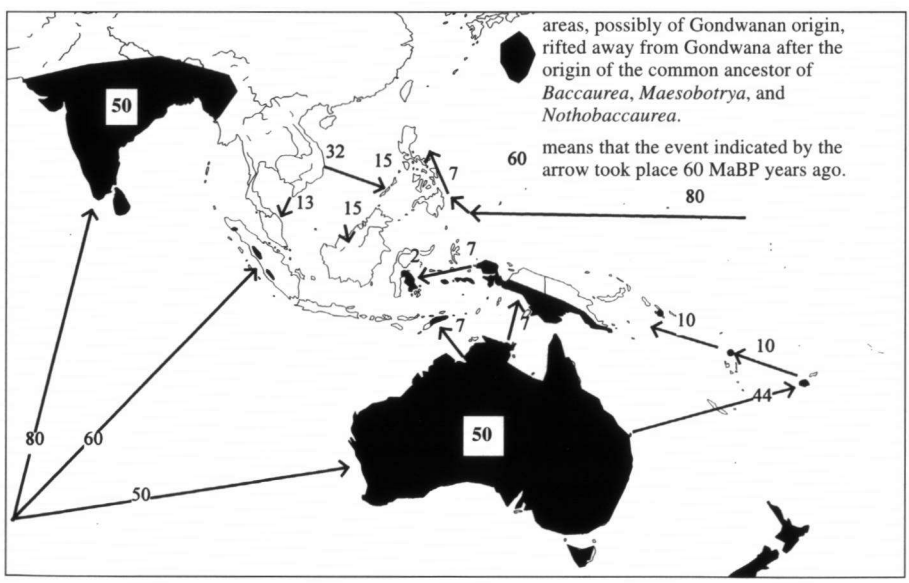


Fig. 2.2. Geological framework.

Table 2.1. Geological history of areas of importance for the biogeographic analysis of *Baccaurea* and *Nothobaccaurea*. Compiled from: Audley-Charles (1988), Barber & Hall (1995), Burret et al. (1991), Hamilton (1979), Kroenke (1996), Metcalfe (1988, 1996), Michaux (1991), Pigram & Davies (1987), Ridder-Numan (1996, 1998), Tarling (1988), Turner (1995).

Late Cretaceous c. 80 MaBP	Major split up of Gondwanaland. Africa and India both drift to the north. Australia and probably South America also still in contact with Antarctica. First Mountains of the pre-Philippines arise far to the east of the modern Philippines.
Paleocene c. 60 MaBP	Part of the Indian Plate grazed terranes of pre-Sumatra (possible floristic contact).
Early Eocene c. 50 MaBP	Collision of India with Burma. Australia splits off from Antarctica and drifts northwards.
Late Eocene c. 44 MaBP	Uplift of Fiji. Parts of Fiji, Vanuatu and the Solomon Islands are of Gondwanan origin and rifted to the east from Australia. Final collision of India with Southeast Asia.
Early Oligocene c. 32 MaBP	Opening of South China Sea. Palawan (Laurasian) and other Laurasian blocks (today part of Borneo) start drifting to the south.
Middle Miocene c. 15 MaBP	Borneo is completed. Palawan stops drifting. Outer Melanesian Arc (OMA), nowadays comprising the Solomon Islands, Vanuatu, Fiji, and Tonga, starts to collide with New Guinea. The Northern and Central Part of New Guinea consist of tens of microterranes rifted from this arc. This process is still continuing.
c. 15 MaBP	Mid-Miocene cooling event.
Late Miocene c. 7 MaBP	Several of the larger Philippine Islands are now uplifted. Timor (of Australian provenance) collides with Sunda Islands.
Middle Pliocene c. 4.5 MaBP	The continuous island chain from Sulawesi to New Guinea is now similar to the present chain.
Late Pliocene c. 2.5 MaBP	Fragments of the Australian continent collide with Sulawesi. The birth of the modern shape and geological position of Sulawesi.
Quaternary 2–0 MaBP	Many glacial periods.

size of the distribution areas of the species. It is, for example, of no use to give all the geological details of Sulawesi (although very interesting) because *Baccaurea* has only a few species in Sulawesi, none of them endemic. Most of these species are widespread on Sulawesi. Therefore, *Baccaurea* will never reflect the complex geological history of Sulawesi.

The cladograms are mapped onto the geological framework and it is assumed that the parts of the cladograms not explained by geological evidence are due to other phenomena like dispersal, extinction, and as yet undiscovered geological species barriers. If vicariance events are an important factor in the speciation and the history of distribution areas of the species, it will be possible to reconstruct the history of distribution of these species. In order to obtain the right time scale for the history of the genera studied, the origin of *Baccaurea*, *Nothobaccaurea* and *Maesobotrya* should be determined. These three genera have a paleotropical distribution. However, the American genus *Richeria* is according to Webster (1994) also closely related to *Maesobotrya*. If this interpretation is correct, the group should be explained starting from an old

pantropical distribution. If a Gondwanan origin is assumed an extinction event should have taken place, or the group has never occurred (primitive absence) in Australia (and Antarctica) because no recent species occur in Australia. Until the late Cretaceous, c. 80 MaBP, exchange of species was still possible between the various fragments previously belonging to Gondwana. Following this hypothesis, the common ancestor of the Scepinae should have been present 80 MaBP. This is in accordance with the idea that most of the Angiosperm families had already originated before 80 MaBP (Magallon et al., 1999).

2.2.2 – *Area choice and programs used*

The first method used for detecting historical biogeographic patterns in *Baccaurea* is to substitute the species in the MPCs by their distribution areas and to map this directly onto the hypothesis of the geological history of the areas involved, and also to map this onto a network of areas obtained by an analysis by Turner et al. (manuscr.). This network is chosen here because it is the most comprehensive biogeographic study of Southeast Asia and the Pacific, and one of the few covering the whole region.

The areas chosen in the biogeographic analysis should not overlap, contain one or more endemic species (Harold & Mooi, 1994), and ideally correspond to non-composite geological areas. In the case of *Baccaurea* the distribution areas are relatively large compared with the small non-composite geological areas present in Southeast Asia. Borneo, for instance, has a composite origin (Barber & Hall, 1995), but most species occur on the whole island. The island as a whole is, therefore, chosen as an area of endemism, although the origin of the sub-areas and, therefore, also of the species present may be different. Another problem is the moderate amount of endemism. On the scale used in *Baccaurea* 20 out of 43 species (46.5%) are endemic for one area. The number of areas used in this study is 11. Six endemic species can be found in Borneo, this means that in most other areas only one endemic species is present (Fig. 2.1). No repeating patterns will be found with these data.

As already mentioned, the areas chosen for biogeographic analysis should not overlap. However, some overlap (Fig. 2.3) is preferred in this analysis. Following the reasoning of Brooks (1990), an area may be represented in the analysis twice if the presence of the different taxa in that area is due to different processes. In this analysis Fiji is represented twice, once as a member of the Pacific (Fig. 2.3, area 9), and once as Fiji on its own (Fig. 2.3, area 10). The reason is that the two genera used in the analysis, viz. *Baccaurea* and *Nothobaccaurea*, probably have a unique history on Fiji. This hypothesis is testable. If the Pacific and Fiji together form a clade in the biogeographic analysis, an obvious explanation is that the same process led to the occurrence of both genera in Fiji. If, on the other hand, Fiji and the Pacific do not form a clade, but show up on different branches in the area cladogram, different origins are expected for *Baccaurea* and *Nothobaccaurea*.

Another problem in *Baccaurea* is that 19 species (42%) have a widespread Sunda Shelf distribution, which may indicate that dispersal (e.g. during glacial periods) after repeated reduction (e.g. during interglacial periods) may well have taken place in *Baccaurea*. This will obscure the initial patterns. Only six species have a widespread distribution with other than Sunda Shelf areas involved.

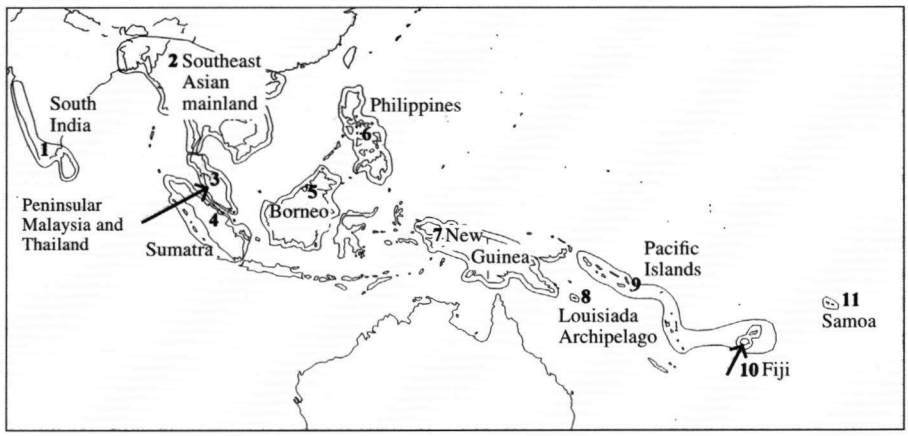
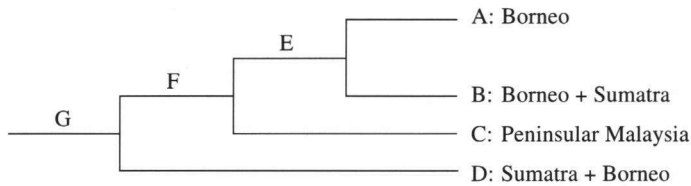


Fig. 2.3. Areas used in the biogeographic analyses (all areas contain at least one endemic species).

The programs used for BPA are PAUP 3.1.1 and 4.0.0 (Swofford, 1993, 1998). For BPA two sets of data are necessary. The first set comprises the phylogenetic relationships between the species studied. It is not appropriate to use a Strict Consensus Cladogram (SCC) as basis for a biogeographic analysis, because due to the collapse of some clades in the SCC some ancestral species and their distributions cannot be defined. Therefore the 12 MPCs found in Chapter 1 are all used for this analysis. The second data set comprises the distribution areas of all species (recent and ancestral) involved. One of the assumptions in BPA is that the distribution area of ancestors is the combined area of its descendants, because vicariance provides the only general explanation. This will only be true when the distribution of modern species can totally be explained by vicariance. Because it is not plausible that the most recent ancestor of *Baccaurea* occupied the whole area presently covered by this genus, analyses are also run with more restricted distribution areas for the ancestral species. Several methods to find the distribution area at the root of a cladogram have been described in recent years (Bremer, 1992; Ronquist, 1994, 1997; Hausdorf, 1998). Bremer's method is the simplest, although Ronquist showed that in certain instances Bremer's method leads to unintentional results. This, however, will usually not cause a problem. In all the methods mentioned, a search for the ancestral distribution of the root of a cladogram is conducted. For the biogeographic analysis, however, all ancestral distribution areas are needed. Therefore, Bremer's method is applied in a slightly different manner, starting with the search for the most common ancestor of a clade. When the distribution area of this ancestor is found, this distribution is used in order to find the area distribution of a more basal ancestor. An example is given in Fig. 2.4. The adjusted method always leads to a lineage of ancestral distribution areas that merge smoothly into each other, in contrast to the above-mentioned methods.

Other methods in historical biogeography are the event-based methods. Ronquist (1997) described a method based on step-matrices, including the computer program DIVA. Due to computational problems this method is only suitable for small problems. Another method (Hovenkamp Analysis, HA) was published by Hovenkamp (1997) and can at the moment only be performed manually. This analysis is also based on



The hypothesised distribution areas for the ancestral taxa E, F, and G using Bremer's method (1992) with a few modifications. The areas with the highest G/L ratio are members of the distribution area of the ancestral species.

E: Borneo: 2 Gains (G), 0 Losses (L), G/L = infinite
Sumatra: 1 G, 1 L, G/L = 1
E occurred in Borneo

F: one descendant occurs in the Peninsular Malaysia (C), the other in Borneo (E)
Borneo: 1 G, 1 L, G/L = 1
Peninsular Malaysia: 1 G, 1 L, G/L = 1
F occurred in Borneo + Peninsular Malaysia

G: one descendant occurs in Sumatra + Borneo (D), the other in Borneo + Peninsular Malaysia (F)
Sumatra: 1 G, 1 L, G/L = 1
Peninsular Malaysia: 1 G, 1 L, G/L = 1
Borneo: 2 G, 0 L, G/L = infinite
G occurred in Borneo

Fig. 2.4. Deduction of reduced ancestral areas.

non-overlapping distribution areas. In order to obtain comparable results from BPA and HA, HA is performed with the same areas as BPA. In HA 'Traceable Vicariance Events' (TVEs) are detected by mutually exclusive areas. The name TVE suggests that vicariance is the only cause of mutually exclusive areas. Other reasons like dispersal and speciation, or extinction can provoke the same distribution patterns. The name (TVE) was chosen because Hovenkamp was explicitly looking for vicariance. Hovenkamp was aware of this problem and defined therefore also Supported Vicariance Events (SVEs). When the same TVE is at least two times present in the investigated cladogram(s), this event is interpreted as a SVE. The order (relative sequence) of TVEs or SVEs is determined by the place in the cladogram where the TVE/SVE occurs. Hovenkamp assumed vicariance as demonstrated when the same TVE is found multiple times. Another explanation could be that the same dispersal event (especially important in island chains) happened over and over again. However, this is in my opinion not a weakness of this method, because the method will detect important geographic separation events for the taxa involved, no matter what the mechanism is. In HA the areas of ancestral species can be deduced from the modern species just by combining all areas in which the descendants occur, as in standard BPA. It is also possible to use restricted ancestral areas corresponding to the adjusted Bremer method (1992) as explained above.

The results of BPA, HA, and direct substitution of species for areas will be compared with the geological information. This is done by hand and by using the computer program Treemap 1.0a (Page, 1995). The results of BPA will also be compared with an unrooted general area cladogram (Turner et al., manuscr.).

2.2.3 – *Data matrix*

The distribution areas from the species are used as characters for the BPA. The species and their distributions are shown in Table 2.2.

Each analysis was repeated 12 times because of small differences in the data matrices based on the 12 MPCs. The 12 data matrices, using standard BPA, are presented in Table 2.3. *Baccaurea* and *Nothobaccaurea* are both used. The matrices based on ITR (Chapter 1.6.3) are also shown in Table 2.3. The matrix produced, utilising the adapted mode of Bremer's ancestral area method, is shown in Table 2.4.

2.3 – Results and discussion

2.3.1 – *Direct conclusions from the 12 MPCs*

The SCC of the 12 MPCs (all 12 are very similar) was taken and the species were substituted for their distribution areas (Fig. 2.5). From this cladogram it is obvious that the first split off within the in-group is between Africa (*Maesobotrya*) and Asia (remaining genera). The second event is the separation of the Pacific (*Nothobaccaurea*) from Asia (*Baccaurea*). This event is confused by the occurrence of *B. seemannii* and *B. taitensis* in the Pacific, but these occurrences are interpreted as secondary introductions.

Table 2.2. Distribution of the species in the areas used for biogeographic analysis. For the area circumscriptions see Fig. 2.3. Abbreviations: Mal: Peninsular Malaysia + Thailand; Sum: Sumatra; Bor: Borneo; NG: New Guinea; LouisIsl: Louisiade Archipelago; SEAsia: Southeast Asian mainland; Phil: the Philippines; PacificIsl: Pacific Islands from the Solomon Islands to Fiji. The numbers in front of the species refer to Table 2.3, 2.4 and Fig. 2.5.

species	areas	species	areas
36 *B. angulata*	2 (SEAsia)	38 *B. odoratissima*	5 (Bor)
24 *B. annamensis*	5 (Bor)	40 *B. papuana*	7 (NG)
08 *B. bracteata*	3,4,5 (Mal, Sum, Bor)	31 *B. parviflora*	3,4,5 (Mal, Sum, Bor)
24 *B. brevipes*	3,4,5 (Mal, Sum, Bor)	06 *B. philippinensis*	6 (Phil)
39 *B. carinata*	7 (NG)	16 *B. polyneura*	3,4,5 (Mal, Sum, Bor)
26 *B. costulata*	4,5 (Sum, Bor)	32 *B. ptychopyxix*	2,3 (SEAsia, Mal)
37 *B. courtallensis*	1 (South India)	11 *B. pubera*	3,4,5 (Mal, Sum, Bor)
09 *B. deflexa*	3,4,5 (Mal, Sum, Bor)	34 *B. purpurea*	7 (NG)
17 *B. dolichobotrys*	5 (Bor)	13 *B. pyriformis*	3,4,5 (Mal, Sum, Bor)
35 *B. dulcis*	4 (Sum)	27 *B. racemosa*	3,4,5 (Mal, Sum, Bor)
10 *B. edulis*	5 (Bor)	30 *B. ramiflora*	2,3 (SEAsia, Mal)
42 *B. javanica*	3,4,5 (Mal, Sum, Bor)	12 *B. reticulata*	3,4,5 (Mal, Sum, Bor)
33 *B. lanceolata*	3,4,5 (Mal, Sum, Bor)	29 *B. sarawakensis*	5 (Bor)
22 *B. macrocarpa*	3,4,5 (Mal, Sum, Bor)	03 *B. seemannii*	10 (Fiji)
21 *B. macrophylla*	3,4,5 (Mal, Sum, Bor)	07 *B. simaloerensis*	4 (Sum)
15 *B. maingayi*	3,4,5 (Mal, Sum, Bor)	18 *B. sumatrana*	3,4,5 (Mal, Sum, Bor)
B. microcarpa	excluded (Chapter 1.4)	02 *B. taitensis*	11 (Samoa)
20 *B. minor*	3,4,5 (Mal, Sum, Bor)	41 *B. tetrandra*	5,6 (Bor, Phil)
14 *B. mollis*	3,4,5 (Mal, Sum, Bor)	19 *B. trigonocarpa*	5 (Bor)
23 *B. motleyana*	3,4,5 (Mal, Sum, Bor)	04 *B. velutina*	3 (Mal)
28 *B. multiflora*	4 (Sum)	43 *N. pulvinata*	10 (PacificIsl)
05 *B. nanihua*	5,7 (Bor, NG)	44 *N. stylaris*	9,10 (PacificIsl)
01 *B. nesophila*	8 (LouisIsl)		

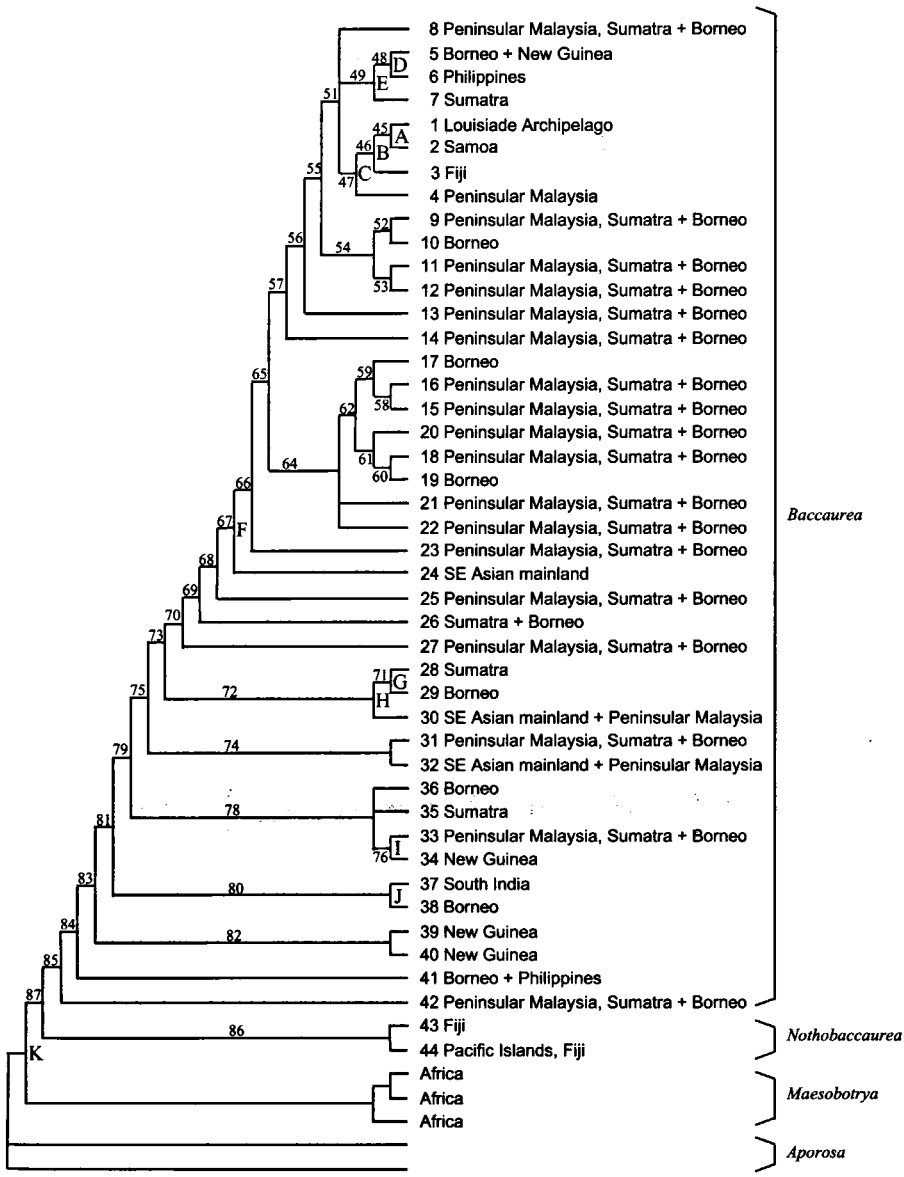


Fig. 2.5. SCC of the 12 MPCs with the species substituted for their distribution areas. Numbers refer to species numbers as used in Table 2.2, 2.3, and 2.4. Letters refer to the TVEs used in Table 2.5. and Fig. 2.10.

From the 12 MPCs it is evident that the most basal species is *B. javanica* from the Sunda Shelf. However, the next three branches lead to the Philippines and Borneo, New Guinea, and to India and Borneo. Bearing in mind that this part of the phylogeny is relatively weakly supported, it is difficult to draw conclusions. One of the possible explanations is that the ancestral species for *Baccaurea* reached the Sunda Shelf and

established itself there while in the meantime dispersal took place into other areas. This is not very plausible if *Baccaurea* reached the region that now forms the Sunda Shelf during the early Eocene via (Greater) India or via parts of Sumatra as judged from the geology. In the early Eocene the distance from the Sunda Shelf to the Philippines and New Guinea was still enormous, which would probably have prevented early escapes to these areas. Another possibility is that the distribution area of *Baccaurea* was for a long period of time restricted, which means that the genus probably hardly speciated. Examples of genera that are not speciose and have restricted distribution areas, are *Nothobaccaurea*, *Richeria*, and less perceptibly *Maesobotrya* (all three are closely related with *Baccaurea*). In this scenario *Baccaurea* behaved in the same way until some event triggered *Baccaurea* into speciation. A possible cause for speciation can be found in glacial periods. Glacial periods create the rise and fall of sea level and major climatic changes. The influence of glacial periods is much bigger in island chains surrounded by shallow water like the Sunda Shelf, compared with continental areas or island chains surrounded by deep-sea. Of the four genera mentioned above, *Baccaurea* is the only genus where the condition of islands surrounded by shallow water is met. If this scenario is true, then *Baccaurea* underwent accelerated speciation roughly between 15 MaBP when the mid-Miocene cooling period started and 4.5 MaBP when the Philippines, Sulawesi and the Moluccas were close to their modern position and a more or less continuous island chain between Borneo and New Guinea was available for dispersal.

After settling on the Sunda Shelf, radiation occurred and several dispersal events took place. Two dispersal events to the Philippines were both ending in isolation and speciation. *Baccaurea philippinensis* is an endemic of the Philippines. The other species occurring in the Philippines, but also in Borneo, is *B. tetrandra*. In this species the first features of isolation are expressed, causing extreme forms in the Philippines compared with Borneo, but overlap in characters is still preserved.

The same interpretation can be given for the three introductions of *Baccaurea* into the Southeast Asian mainland. One occurrence is *B. ptychopyxis*, a species most closely related to *B. parviflora*. Both species occur nowadays sympatrially in Peninsular Thailand, but may have been separated during one of the glacial periods. Another species on the Southeast Asian mainland and very widespread and successful is *B. ramiflora*. A third possible dispersalist is *B. annamensis*. This species has a very local distribution and is only known from a few specimens. The closest relatives are *B. motleyana* and *B. brevipes* who both have a Sunda Shelf distribution.

Only one species of *Baccaurea* is present in India, namely *B. courtallensis*. Its closest relative is a Bornean species. It is therefore extremely difficult to judge what process caused this disjunction. An explanation may be found in the fact that the fruits of *B. courtallensis* are relatively small and probably dispersed by birds. The same character is present in the species of *Baccaurea* occurring in the Pacific. This feature may be a requirement for long-distance dispersal in *Baccaurea*. Based on the fact that modern birds have no migration routes via these areas, and that birds digest the seeds probably in a very short period, dispersal via birds seems not very probable. However, such long distance dispersal happened maybe two times in the history of *Baccaurea* during roughly 15 million years (i.e. chance per day = 3.6×10^{-10}). Therefore, bird dispersal cannot be excluded.

New Guinean species occur in three or maybe even four different clades. It is, therefore, likely that New Guinea, east of Wallace's Line, was reached multiple times by western species of *Baccaurea*. The most common species throughout New Guinea is *B. papuana*. The first arrival of *Baccaurea* in New Guinea may have been the ancestor of this species and its sister species *B. carinata*. The route of this arrival is unclear. A possible second event is the introduction of *B. purpurea* in New Guinea. The sister group of *B. purpurea* is *B. lanceolata*, which has a Sunda Shelf distribution and extended its range into Palawan, showing that this is a species with relatively good dispersal abilities. There is, however, a huge gap between the distribution area of *B. lanceolata* and that of *B. purpurea*, which is only found in the eastern part of Papua New Guinea. The pathway for this species is therefore also uncertain, leaving routes via the Philippines or via Sulawesi and the Moluccas as possibilities. More information is found in the third clade leading into New Guinea. This clade contains two species. The first is *B. philippinensis*, a Philippine endemic. The second is *B. nanihua*, with a distribution range from Borneo via Sulawesi and the Moluccas to New Guinea. The common ancestor was probably widespread over the whole distribution range. The Philippine population probably differentiated from the other populations. If this differentiation was due to isolation, it implies that the populations in New Guinea had more or easier contact with populations of the Moluccas, Sulawesi and Borneo than with the Philippine populations. A pathway between Borneo and New Guinea in this group may lead via Sulawesi and the Moluccas, instead of via the Philippines. The last clade with a possible New Guinean affinity contains *B. seemannii*, *B. taitensis*, and *B. nesophila*. None of these species occur in New Guinea. They all have limited distribution areas in the western Pacific. The pathway followed by the members of this clade remain undetermined. Consequently, only for one event it is possible to indicate the most probable pathway from Asia to New Guinea, viz. from Borneo via Sulawesi and the Moluccas to New Guinea.

Species with large distribution areas are a problem in BPA, because of the presence of redundant areas (Nelson & Platnick, 1981). Still, it was tried to obtain information from widespread species. Areas with 3 or more species in common are: Peninsular Malaysia + Thailand and Sumatra (> 15 species); Peninsular Malaysia + Thailand and Borneo (> 15 species); Sumatra and Borneo (>15 species); Sumatra and Java (5 species); Borneo and Sulawesi (5 species); Borneo and Java (4 species); Borneo and the Moluccas (3 species); Sulawesi and the Moluccas (3 species; the same 3 species as Borneo and the Moluccas). From this it becomes obvious that modern species easily reach all the major islands on the Sunda Shelf. It is also clear that 5 Bornean species occur in Sulawesi, and that three of these species occur in the Moluccas. Moreover, *B. nanihua* even occurs in New Guinea. Thus, although only one modern species, viz. *B. nanihua*, reached New Guinea via Sulawesi and the Moluccas, several other species come close to it. Dispersal in the opposite direction is maybe indicated by the New Guinean species *B. papuana*, because two collections of *B. papuana* are from Sulawesi. Because of the occurrence of species with widespread distribution areas in Sulawesi and the Moluccas with a Bornean connection, it is assumed that a modern pathway for *Baccaurea* between Asia and New Guinea runs through Sulawesi and the Moluccas.

2.3.2 – *Brooks Parsimony Analysis (BPA) based on the twelve MPCs*

The area cladogram (length = 98 steps) based on 11 areas of endemism and the 12 MPCs of *Baccaurea* and *Nothobaccaurea* using standard BPA is shown in Fig. 2.6 (for matrices see Table 2.3). Only one cladogram is shown because all MPCs produce the same area cladogram. In five out of the 12 analyses the area cladogram is 98 steps long. In five other analyses the area cladogram is 99 steps long, and in one of these analyses a second area cladogram is produced. In two analyses, at last, the length of the area cladogram is 100, and one of these analyses produced also a second area cladogram, with the same topology as the above-mentioned one. The topology of the second area cladogram is dismissed, because the length is 99 or 100.

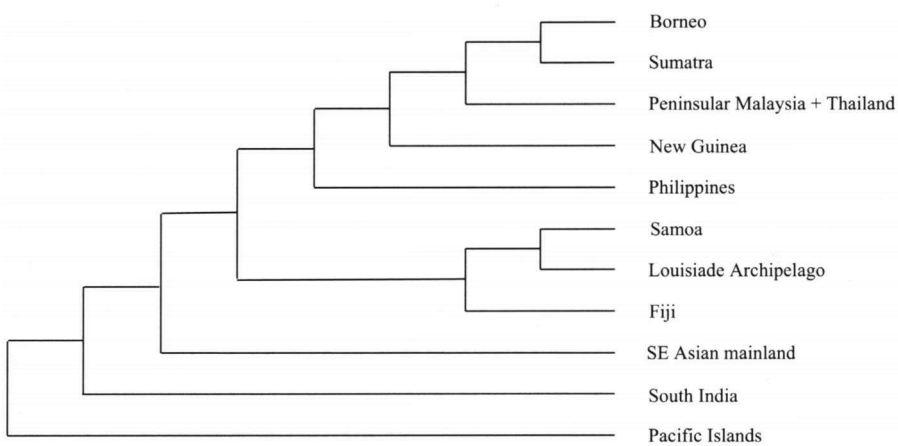


Fig. 2.6. Standard BPA area cladogram, based on the 12 MPCs of *Baccaurea* and *Nothobaccaurea*. L: 98, CI: 0.888, RI: 0.913, RC: 0.811. All 12 MPC's lead to the same area cladogram.

The species cladogram (strict consensus of the 12 MPCs) is compared with the area cladogram. The first split in the area cladogram (Fig. 2.6) is between the Pacific on one side and all other areas on the other side. In the species cladogram the split between *Nothobaccaurea* and *Baccaurea* is in agreement with this. This is an indication that the presence of *Nothobaccaurea* in the Pacific is a very old feature (keeping in mind that the common ancestor of *Baccaurea* and *Nothobaccaurea* probably occurred in Gondwana). If a Gondwanan origin is assumed for *Nothobaccaurea*, it is plausible that this genus went extinct on the Australian continent, but survived on its margin (e.g. Fiji), leading to the present situation with an absence of *Nothobaccaurea* in Australia, but a presence on Fiji. (A primitive absence in Australia, except for the margins, is also possible.)

Table 2.3. Twelve matrices for standard BPA based on the 12 MPCs. The parts of the matrices in *italics* are the stable parts of the 12 MPCs based on Iterative Taxon Reduction (ITR). Abbreviations: S.India = South India; SEAsia = Southeast Asian mainland; M&TP = Peninsular Malaysia + Thailand; Philip = Philippines; NG = New Guinea; L.Isl = Louisiade Archipelago; P.Isl = Pacific Islands.

Table 2.3.

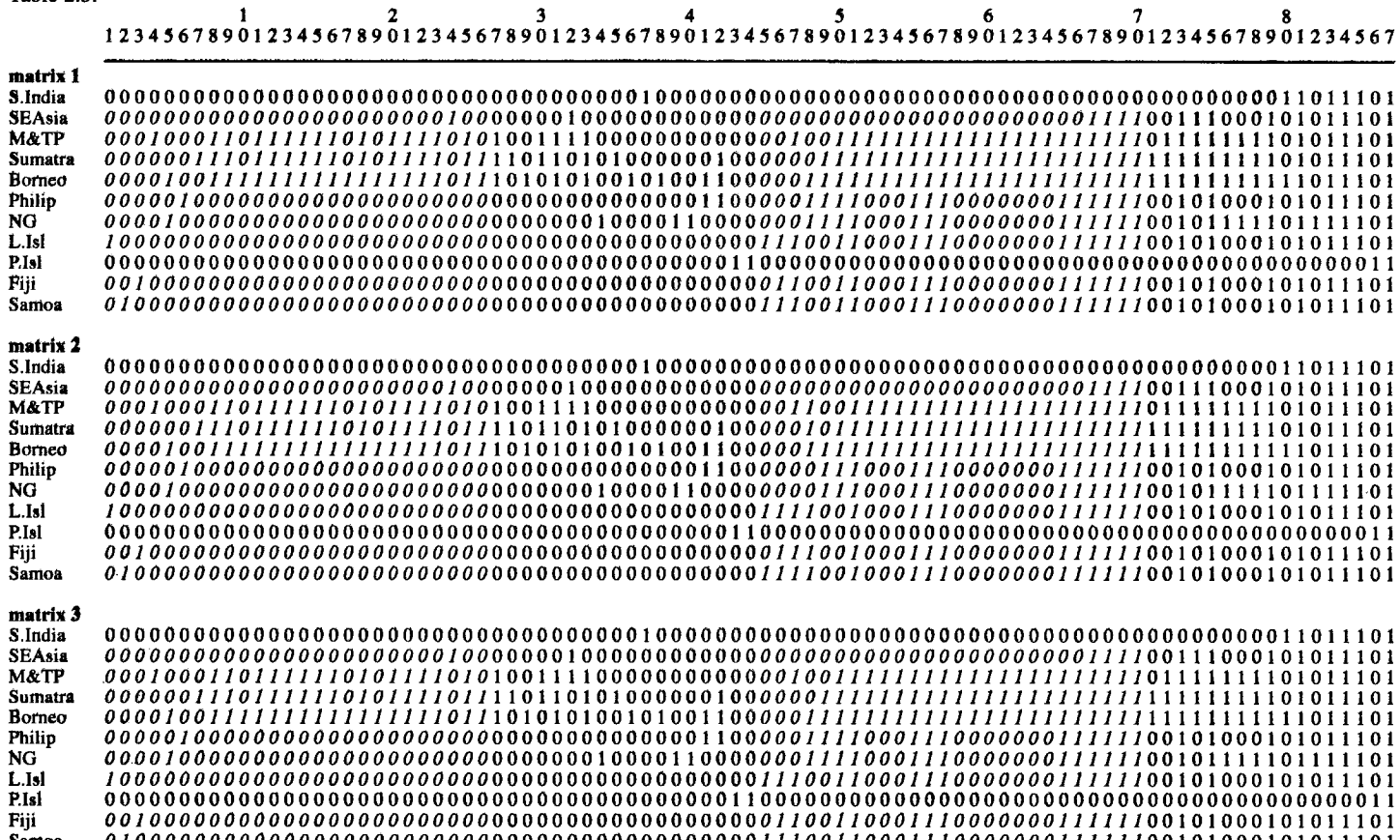

1 2 3 4 5 6 7 8
12345678901234567890123456789012345678901234567890123456789012345678901234567
matrix 1
S.India
SEAsia
M&TP
Sumatra
Borneo
Philip
NG
L.Isl
P.Isl
Fiji
Samoa
matrix 2
S.India
SEAsia
M&TP
Sumatra
Borneo
Philip
NG
L.Isl
P.Isl
Fiji
Samoa
matrix 3
S.India
SEAsia
M&TP
Sumatra
Borneo
Philip
NG
L.Isl
P.Isl
Fiji
Samoa

Table 2.3 (*continued*)

```
                    1         2         3         4         5         6         7         8
          12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567
matrix 4
S.India   00000000000000000000000000000000000000010000000000000000000000000000000000000000000000000011011101
SEAsia    00000000000000000000000100000001000000000000000000000000000000000000000001111001110001010111101
M&TP      00010001101111111010111110100111110000000000000010011111111111111111111111110111101110101111101
Sumatra   00000011101111111010111110111101101010000001000000011111111111111111111111111111111101011101
Borneo    00001001111111111111111111011010101001010011000001111111111111111111111111111111111111011101
Philip    00000100000000000000000000000000000000000011000001111000111000000011111100101000101011101
NG        00001000000000000000000000000000010000110000000111100011100000001111110010101111011111101
L.Isl     10000000000000000000000000000000000000000111001100011100000001111110010100010101011101
P.Isl     00000000000000000000000000000000000000011000000000000000000000000000000000000000000000011
Fiji      00100000000000000000000000000000000000000011001100011100000001111110010100010101011101
Samoa     01000000000000000000000000000000000000000111001100011100000001111110010100010101011101

matrix 5
S.India   00000000000000000000000000000000000000010000000000000000000000000000000000000000000000011011101
SEAsia    00000000000000000000000100000001000000000000000000000000000000000000000001111001110001010111101
M&TP      00010001101111111010111110100111110000000000000010011111111111111111111111110111101110101111101
Sumatra   00000011101111111010111110111101101010000001000000011111111111111111111111111111111101011101
Borneo    00001001111111111111111111011010101001010011000001111111111111111111111111111111111111011101
Philip    00000100000000000000000000000000000000000011000001111000111000000011111100101000101011101
NG        00001000000000000000000000000000010000110000000111100011100000001111110010111110111111101
L.Isl     10000000000000000000000000000000000000000111001100011100000001111110010100010101011101
P.Isl     00000000000000000000000000000000000000011000000000000000000000000000000000000000000000011
Fiji      00100000000000000000000000000000000000000011001100011100000001111110010100010101011101
Samoa     01000000000000000000000000000000000000000111001100011100000001111110010100010101011101

matrix 6
S.India   00000000000000000000000000000000000000010000000000000000000000000000000000000000000000011011101
SEAsia    00000000000000000000000100000001000000000000000000000000000000000000000001111001110001010111101
M&TP      00010001101111111010111110100111110000000000000010011111111111111111111111110111101110101111101
Sumatra   00000011101111111010111110111101101010000001000000101111111111111111111111111111111101011101
Borneo    00001001111111111111111111011010101001010011000001111111111111111111111111111111111111011101
Philip    00000100000000000000000000000000000000000011000001111000111000000011111100101000101011101
NG        00001000000000000000000000000000010000110000000111100011100000001111110010111110111111101
L.Isl     10000000000000000000000000000000000000000111100100011100000001111110010100010101011101
P.Isl     00000000000000000000000000000000000000011000000000000000000000000000000000000000000000011
Fiji      00100000000000000000000000000000000000000111001000111000000001111110010100010101011101
Samoa     01000000000000000000000000000000000000000111001000111000000001111110010100010101011101
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Table 2.3 (*continued*)

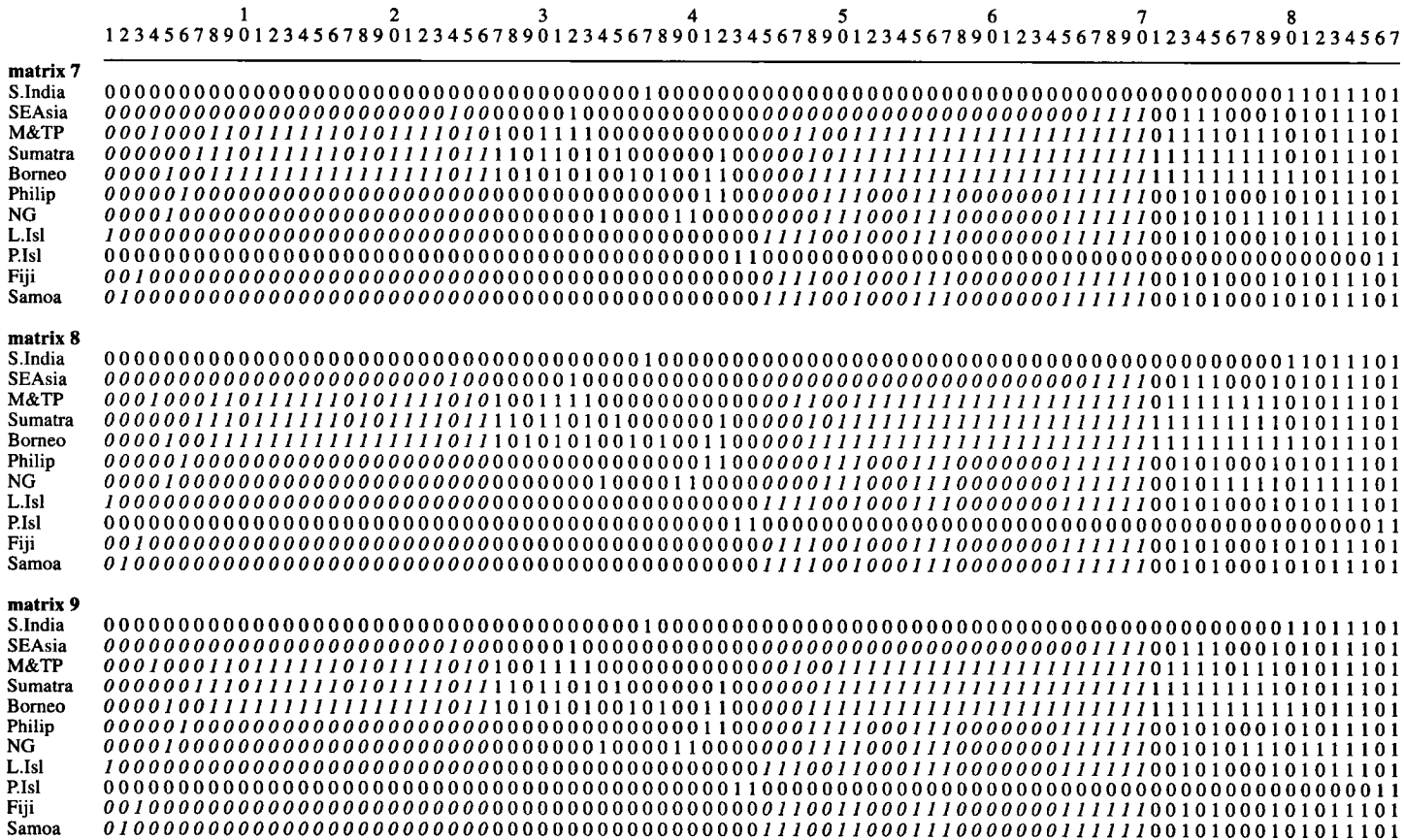
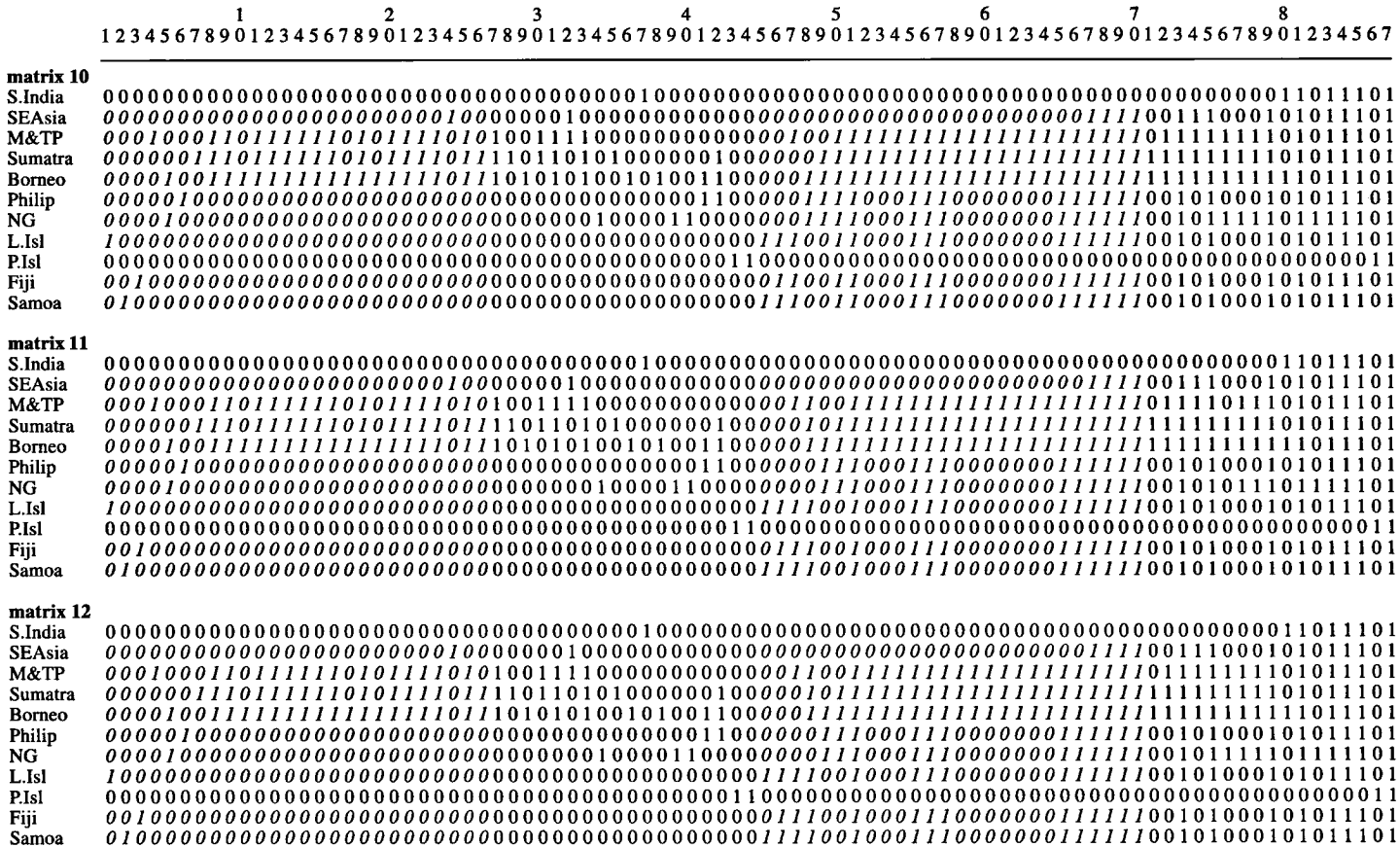


Table 2.3 (*continued*)



Subsequently, a split, between India and the rest of Southeast Asian mainland, Malesia, and the islands in the Pacific, is found (Fig. 2.6). This split is in agreement with the geological framework, but only based on one species (*B. courtallensis*).

The next split between Southeast Asia mainland and Malesia and the Pacific islands is also in agreement with the geological events. The support for this scenario is only found by two species. It is, however, an indication that *Baccaurea* reached Asia via India, followed by radiation into the Malay Archipelago. In this case dispersal is assumed, because the route is through the Southeast Asian mainland, where *Baccaurea* is primitively absent.

The following splits in the area cladogram are in the opposite direction to what would be expected from the geological framework. The area cladogram indicates that first the Pacific islands split off, followed by the Philippines, New Guinea, Peninsular Malaysia, and at last Sumatra and Borneo. From geological evidence, a dispersal direction from the Sunda Shelf towards the Pacific islands is expected. This discrepancy may be due to the limited information about areas beyond the Sunda Shelf present in *Baccaurea*, or due to an unexpected rapid expansion of the distribution area of *Baccaurea*, after which speciation took place.

The cladogram obtained by BPA is also compared with the geological history of the same areas (also moulded in the form of a cladogram) with help of the computer program Treemap 1.0a (Page, 1995). From the geology it is uncertain if the Sunda Shelf was reached through Sumatra or through India. Both possibilities were tried. The cladogram with Sumatra as arrival source for *Baccaurea* on the Sunda Shelf, was optimised in comparison with the BPA cladogram. This comparison showed 4 co-speciations, 7 duplications, and 30 sorting events. The cladogram with South India as arrival source for *Baccaurea* showed 7 co-speciations, 4 duplications, and 18 sorting events. Co-speciations in the analysis correspond to vicariance events (Page, 1994), duplications to dispersal, and sorting events to extinction. The area cladogram with India in a basal position does explain the BPA data much better. The discrepancies between the BPA cladogram and the geological framework (with India in a basal position) are shown in Fig. 2.7.

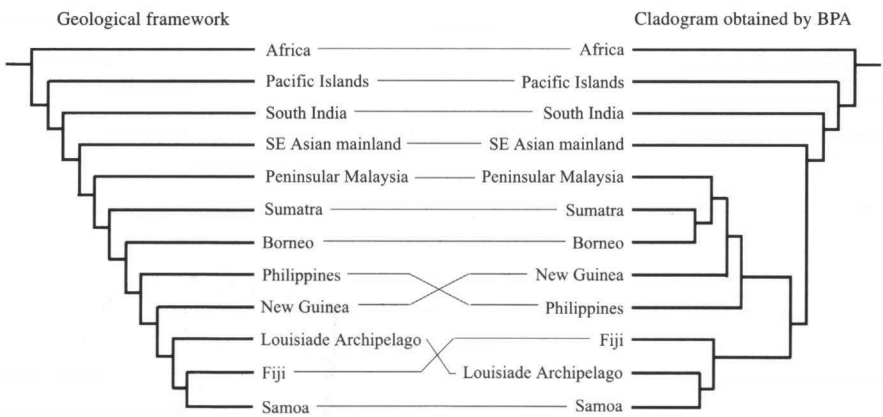


Fig. 2.7. The cladogram obtained by standard BPA optimised in relation to the geological framework. Number of co-speciations: 7; duplications: 4; sorting events: 18.

2.3.3 – *BPA based on the stable parts of the twelve MPCs as indicated by ITR*

The quality of the obtained species cladograms is discussed in Chapter 1. The parts of the cladograms supported by ITR are interpreted as phylogenetically stable. The most reliable information comes from these parts of the MPCs (for matrices see Table 2.3). Therefore BPA analysis was also performed with only the stable parts of the 12 MPCs. The results are shown in Fig. 2.8. Two areas, namely the Pacific islands and India, are now omitted from the analysis, because none of the used species is endemic in these areas. The only difference between this analysis and the former (Chapter 2.3.2) is that New Guinea and the Philippines are now placed in one clade. The placement of this clade is also more basal, but like the first area cladogram, not in agreement with the geological framework.

One of the problems with this type of analysis (BPA) is that only one pattern will be revealed. If more patterns, especially conflicting ones, are present, then these will not be revealed (parsimony analysis tends to search for a single diagram).

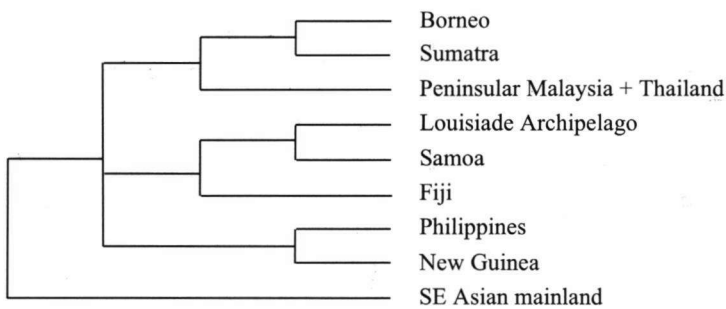


Fig. 2.8. Standard BPA based on the stable parts of the 12 MPCs defined by ITR. Strict consensus of 3 MPCs. L: 56, CI: 0.929, RI: 0.941, RC: 0.874.

2.3.4 – *BPA based on smaller ancestral areas*

Because standard BPA did not produce constant unequivocal results for *Baccaurea*, another approach was tried. In standard BPA the area in which an ancestral species occurs is defined as the combined areas of the descendant species. This is not plausible in *Baccaurea*, as already stated in Chapter 2.2.2. The matrix based on smaller ancestral distribution areas is shown in Table 2.4. At first sight, the resulting BPA (Fig. 2.9) appears to be of limited use. From this analysis it is totally unclear where *Baccaurea* originated and what its vicariance/dispersal pattern could be. However, the interpretation of this analysis is that *Baccaurea* reached all the different areas at roughly the same time in history followed by speciation. Due to the different geological histories of the areas involved the chance that all these areas have been colonised at the same time is unlikely, but this possibility cannot be excluded.

Table 2.4. Matrix for BPA based on one out of twelve MPCs, using restricted size of ancestral areas. Abbreviations: S.India = South India; SEAsia = Southeast Asian mainland; M+TP = Peninsular Malaysia + Thailand; Philip = Philippines; NG = New Guinea; L.Isl = Louisiade Archipelago; P.Isl = Pacific Islands.

	1	2	3	4
	1234567890123456789012345678901234567890123456789012345678901234			
matrix 8				
S.India	0000000000000000000000000000000000000000000010000000			
SEAsia	0000000000000000000000000010000000100000000100000000			
M+TP	0001000110111111101011110101001111000000000000			
Sumatra	0000001110111111101011110111101101010000000100			
Borneo	0000100111111111111111111011101010100101001100			
Philip	0000010000000000000000000000000000000000000001100			
NG	0000100000000000000000000000000000010000110000			
L.Isl	1000000000000000000000000000000000000000000000000			
P.Isl	0000000000000000000000000000000000000000000000011			
Fiji	0010000000000000000000000000000000000000000000000			
Samoa	0100000000000000000000000000000000000000000000000			

	4 5 6 7 8
	5678901234567890123456789012345678901234567
matrix 8 (*continued*)	
S.India	0000000000000000000000000000000000000010000000
SEAsia	0000000000000000000010000100000000000000000000
M+TP	0011001010111100000000000001011100000000000
Sumatra	0000011010111100000000000011000101000000000
Borneo	0000111111111111111111111111111101111111011101
Philip	0000111000000000000000000000000000000000000000
NG	0000100000000000000000000000000010000011000
L.Isl	1110000000000000000000000000000000000000000000
P.Isl	0000000000000000000000000000000000000000000011
Fiji	0110000000000000000000000000000000000000000000
Samoa	1110000000000000000000000000000000000000000000

2.3.5 – *Hovenkamp Analysis (HA) based on the twelve MPCs*

Hovenkamp Analysis (Hovenkamp, 1997) was performed with the ancestral areas defined as in BPA. All TVEs for one of the 12 MPCs (all 12 show the same results in HA) are shown in Table 2.5, and indicated in Fig. 2.5. The series of TVEs as defined by the cladogram are shown in Fig. 2.10A. There is no or hardly any contradiction in the historical order of the obtained TVEs. Therefore, they all fit one scenario.

– **Event A** is between the Louisiade Archipelago and Samoa. This is a clear example of dispersal through the Louisiade Archipelago into the West Pacific.

– **Event B**. Fiji opposed to both the Louisiade Archipelago and Samoa is an odd constellation, because Fiji is geographically placed in between. Event A and B are both based on the clade *B. seemannii*, *B. taitensis*, and *B. nesophila*. All have very restricted non-overlapping distributions. In my opinion it is very well possible that in this particular instance the common ancestor was widespread throughout the West Pacific. In a later period the population exchange between the islands disappeared. As a consequence, speciation took place and the species of the Louisiade Archipelago (*B. nesophila*) and Samoa (*B. taitensis*) remained more similar to each other than to the species of Fiji (*B. seemannii*).

– **Event C** between Peninsular Malaysia + Thailand on one hand, and the Louisiade Archipelago, Fiji and Samoa on the other is not strict. Because of the huge distance

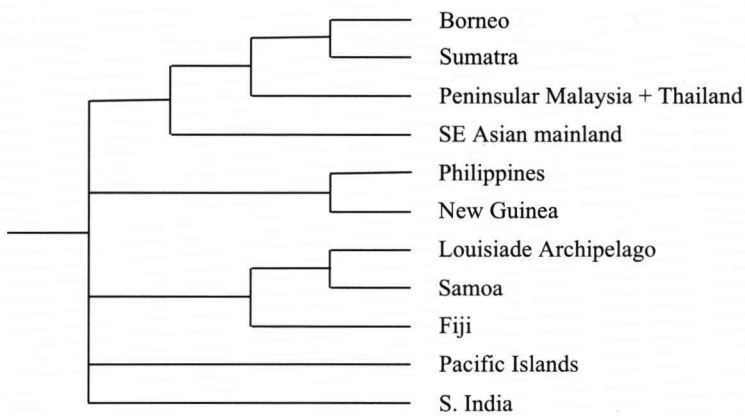


Fig. 2.9. Area cladogram based on one of the 12 MPCs (matrix 8). Ancestral areas restricted in size (see Fig. 2.4). L: 102, CI: 0.853, RI: 0.805, RC: 0.687.

Table 2.5. Hovenkamp Analysis (HA): all Traceable Vicariance Events (TVEs) of the 12 MPCs, areas as in standard BPA.

TVE:			
A:	Louisiade Archipelago	↔	Samoa
B:	Fiji	↔	Louisiade Archipelago + Samoa
C:	Peninsular Malaysia + Thailand	↔	Louisiade Archipelago, Fiji + Samoa
D:	Philippines	↔	Borneo + New Guinea
E:	Sumatra	↔	Philippines, Borneo + New Guinea
F:	Southeast Asia Mainland	↔	Peninsular Malaysia + Thailand, Sumatra, Borneo, Philippines, New Guinea, Louisiade Archipelago, Fiji + Samoa
G:	Sumatra	↔	Borneo
H:	Southeast Asia Mainland + Peninsular Malaysia + Thailand	↔	Sumatra + Borneo
I:	Peninsular Malaysia + Thailand, Sumatra + Borneo	↔	New Guinea
J:	South India	↔	Borneo
K:	Africa	↔	South India, Southeast Asian mainland, Peninsular Malaysia + Thailand, Sumatra, Borneo, Philippines, New Guinea, Louisiade Archipelago, Fiji + Samoa

between these two areas it is not possible to draw an exact line (not even an inaccurate line) where this vicariance/dispersal event took place.

– **Event D** shows an event between the Philippines on the one hand, and Borneo + New Guinea on the other. This is an indication for stronger contact between Borneo and New Guinea than between New Guinea and the Philippines, or between Borneo and the Philippines. In this case, this is only due to the fact that *B. nanihua* is a widespread species with a distribution reaching from Borneo via Sulawesi and the Moluccas into New Guinea, but not into the Philippines.

– **Event E** splits Sumatra from the Philippines, Borneo, and New Guinea. This is an artefact because *B. simaloerensis* only occurs in Simeuluë Island and probably originated due to isolation from an ancestral species (number 51) with a large distribution area.
– **Event F** is the event dividing the Southeast Asian mainland from the rest of Southeast Asia (i.e. Peninsular Malaysia + Thailand, Sumatra, Borneo, the Philippines, New Guinea, the Louisiade Archipelago, Fiji, and Samoa). This split may be due to dispersal of *B. annamensis* into the Southeast Asian mainland. However, it may also be caused by an ancient vicariance event, with *B. annamensis* as the only survivor on the mainland.
– **Event G** is the event separating Borneo from Sumatra. This is probably of relatively recent origin. Numerous sea level changes due to glacial/interglacial cycles resulted in periods when Borneo was connected by land with Sumatra, or, as at present, disconnected from it.
– **Event H** draws a line between the Southeast Asian mainland and the Peninsular Malaysia + Thailand on one side, and Sumatra and Borneo on the other. This event is based on the separation between *B. ramiflora* from its sister species and is slightly in contradiction with event F, where Peninsular Malaysia + Thailand formed an area with the Southeast Asian mainland.
– **Event I** separates the Peninsular Malaysia + Thailand, Sumatra + Borneo, from New Guinea. This is again an indication for direct migration of species from the Sunda Shelf to New Guinea, excluding the Philippines.

A:
series 1: K>F>C>B>A
series 2: K>F>E>D
series 3: K>H>G
series 4: K>I
series 5: K>J

Fig. 2.10A. Series in time of TVEs. TVEs defined in Table 2.5.

B:

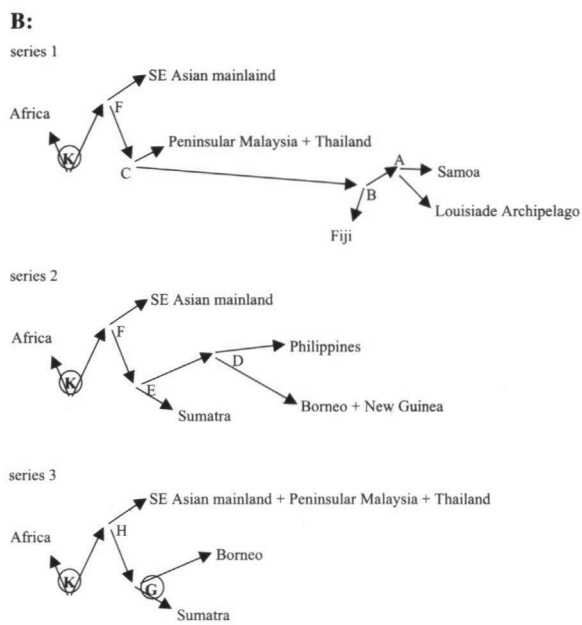


Fig. 2.10B. Series of TVEs from Fig. 2.10A, visualised. Probable vicariance events are encircled.

– **Event J** splits Borneo and India. This is a very unusual event based on the occurrence of *B. courtallensis* in India. This may be due to an unusual case of long distance dispersal. This pattern can also be explained by a vicariance event between Sumatra and India (60 MaBP), followed by dispersal to Borneo and extinction in Sumatra. The latter scenario is at least improbable.
– **Event K** is the event that separated Africa from the rest of Gondwana. If the common ancestor of *Baccaurea*, *Nothobaccaurea* and *Maesobotrya* (and maybe *Richeria*) is as old as assumed in Chapter 2.2.1, this is a clear case of vicariance.

The order of the mentioned TVEs is shown in Fig. 2.10A and the patterns are visualised in Fig. 2.10B. From the patterns it is clear that HA indicates a pathway from Southeast Asia to the Sunda Shelf. Pathways to New Guinea are found through Borneo and not via the Philippines. This is an indication for a pathway that leads from Borneo via Sulawesi and the Moluccas to New Guinea.

2.3.6 – *Distribution patterns in Baccaurea compared with a general area cladogram*

The distribution patterns in *Baccaurea* and *Nothobaccaurea* have in this analysis not been harmonised with a geological history, but with a general area network (Turner et al., manuscr.). This network (Fig. 2.11) is unrooted and based on several plant and animal phylogenies. This network is compared with one of the 12 MPCs of *Baccaurea* and *Nothobaccaurea* with the species substituted for their distribution areas. In this case the general area network defines the areas, and therefore a slightly different area description is used in comparison with elsewhere in this chapter. In this analysis South India has been divided in Kerala and Sri Lanka, Southeast Asia is limited on the west

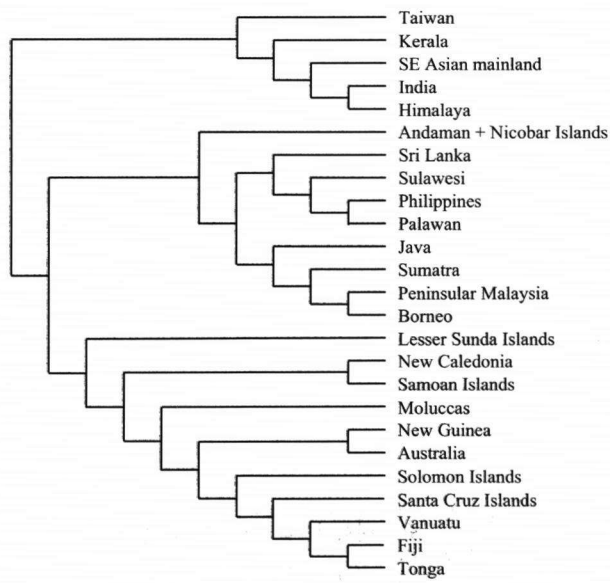


Fig. 2.11. General area network, after Turner et al. (manuscr.). Rooted at the clade Taiwan to Himalaya.

Table 2.6. Fitting *Baccaurea* on the unrooted general area network of Turner et al. (manuscr.) (Host Switches all 0).

	Cospeciations	Duplications	Sorting events
Taiwan	5	38	195
India Kerala Himalaya SEAsia Taiwan	5	38	199
Kerala	5	38	213
India Himalaya	5	38	217
Himalaya	5	38	217
India	5	38	217
India Himalaya SEAsia	5	38	220
SEAsia	5	38	231
Sumatra	4	39	182
AndamanNicobar	4	39	185
Sri-Lanka Sulawasi Philippines Palawan Java Sumatra Peninsular Malaysia Borneo	4	39	189
AndamanNicobar Sri-Lanka Sulawesi Philippines Palawan Java Sumatra Peninsular Malaysia Borneo	4	39	200
Lesser-Sunda-Islands	4	39	202
L.Sunda N.Caledonia Samoa Moluccas N.Guinea Australia Solomons S.Cruz Vanuatu Fiji Tonga	4	39	209
N.Caledonia Samoa Moluccas N.Guinea Australia Solomons S.Cruz Vanuatu Fiji Tonga	4	39	222
Solomons S.Cruz Vanuatu Fiji Tonga	4	39	264
Solomons	4	39	265
S.Cruz Vanuatu Fiji Tonga	4	39	283
S.Cruz	4	39	283
Vanuatu Fiji Tonga	4	39	301
Vanuatu	4	39	301
Fiji Tonga	4	39	319
Tonga	4	39	319
Fiji	4	39	337
Peninsular Malaysia Borneo Sumatra	3	40	176
Peninsular Malaysia Borneo Sumatra Java	3	40	181
Java	3	40	181
Peninsular Malaysia Borneo	3	40	182
Borneo	3	40	186
Peninsular Malaysia	3	40	186
Sri-Lanka	3	40	191
Sri-Lanka Sulawesi Philippines Palawan	3	40	193
Sulawesi Philippines Palawan	3	40	211
Sulawesi	3	40	226
Philippines Palawan	3	40	229
N.Caledonia	3	40	236
N.Caledonia Samoa	3	40	237
Moluccas N.Guinea Australia Solomons S.Cruz Vanuatu Fiji Tonga	3	40	239
Philippines	3	40	247
Moluccas	3	40	251
Palawan	3	40	251
N.Guinea Australia Solomons S.Cruz Vanuatu Fiji Tonga	3	40	253
Samoa	3	40	258
Australia	3	40	267
N.Guinea Australia	3	40	272
N.Guinea	3	40	293

side by Burma (Bangladesh and Assam excluded), the Andaman and Nicobar Islands are an area of their own, like the Lesser Sunda Islands, the Moluccas, Palawan, Santa Cruz, the Solomon Islands, Tonga, and Vanuatu. In order to find the appropriate root of the area network, the substituted MPC was compared with the area network with every single area or clade tried as most basal branch. Again, this search was carried out using the computer program Treemap 1.0a (Page, 1995). The results of the search are shown in Table 2.6. From this analysis it is clear that the MPC (species substituted for areas) fits best on the network if the network is rooted in Southeast Asia. Taiwan is excluded, because none of the studied species occur in this area. The clade from India to Taiwan is the second-best option, optimised with 5 vicariance (= co-speciation in Table 2.6) and 199 extinctions (= sorting events in Table 2.6). If only one area is preferred as most basal branch of the area network, then Kerala is the best option with 5 vicariance and 213 dispersal events. The other possible source area for *Baccaurea* in Southeast Asia is Sumatra. The figures for Sumatra (Table 2.6) are 4 vicariance and 182 dispersal events. The areas are optimised on basis of vicariance, because vicariance is the only general explanation for corresponding plant distributions. Therefore, it is less plausible that Sumatra is the most basal branch of the area network in comparison with Kerala and the Southeast Asian mainland.

2.3.7 – *Dispersal/vicariance scenario for Baccaurea and allied genera*

The historical dispersal/vicariance scenario for *Baccaurea* and allied genera is shown in Fig. 2.12. This scenario is based on the previous paragraphs. A Gondwanan origin is hypothesised for *Baccaurea* and allied genera. The break up of Gondwana in several areas causes the vicariance events that lead to the different genera. For *Baccaurea* a

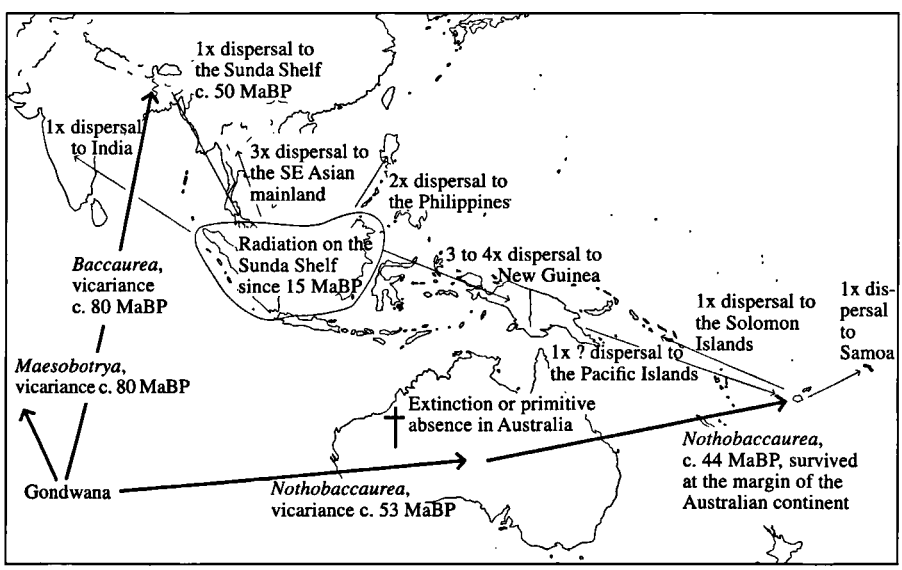


Fig. 2.12. Dispersal/vicariance scenario for *Baccaurea* and alied genera.

pathway from India via the Southeast Asian mainland to the Sunda Shelf is plausible, because this is indicated by BPA, HA and by comparison of distribution areas in *Baccaurea* with the unrooted general area cladogram. The possibility that *Baccaurea* reached the Sunda Shelf directly via a fragment of Gondwana that now belongs to Sumatra is less plausible, albeit the most basal branch of the phylogeny in the Sunda Shelf. An indication for rapid radiation from the Sunda Shelf into several areas during a short time period (15–4.5 MaBP) was found in BPA with restricted areas for ancestral species and in the direct information from the MPCs by substituting species for areas. Evidence for a pathway (at least one time) from the Sunda Shelf into New Guinea through Borneo, Sulawesi and the Moluccas, is indicated by HA and by the direct information from the MPCs by substituting species for areas. *Baccaurea* may have reached New Guinea at least three times in the past, but possibly even four times as was shown by the MPCs by substituting species for areas. The Philippines cannot be excluded as a possible part of the dispersal route from Asia to New Guinea.

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Chapter 3

TAXONOMIC REVISION

3.1 – Key to the genera

Key to the genera of the subtribe Scepinae (Genera in **bold** treated in this study)

1a. Pistillate disc entire (cup-shaped), or absent 2
b. Pistillate disc divided; styles dilated, entire to slightly lobed. — Africa ..... *Protomegabaria*
2a. Staminate disc present (unknown for *Distichirhops*) 3
b. Staminate disc absent (unknown for *Distichirhops*) 7
3a. Pistillate disc absent 4
b. Pistillate disc present 5
4a. Monoecious. Styles not lobed. — Africa ..... *Apodiscus*
b. Dioecious. Styles bifid. — Asia ..... ***Distichirhops***
5a. (3) Dioecious. Inflorescences racemose. Stipules deciduous 6
b. Monoecious. Inflorescences with axillary glomerules. Stipules persistent. — America ..... *Jablonskia*
6a. Capsule loculicidal. Staminate flowers mostly one per bract. — Africa ..... *Maesobotrya*
b. Capsule septicidal. Staminate flowers mostly several per bract. — America .. *Richeria*
7a. (2) Pistillode small. Style with (nearly) sessile stigmas 8
b. Pistillode massive. Stigmas not sessile, style mushroom-shaped. — Asia .... *Ashtonia*
8a. Terminalia branching pattern absent (Fig. 3.1a). Leaf arrangement often distichous 9
b. Terminalia branching pattern present (Fig. 3.1b, c). Leaf arrangement usually spiral 10
9a. One bract per pistillate flower; pistillate disc present (but obscure), pedicel without abscission zone. — Asia, Pacific ..... *Aporosa*
b. Three bracts per pistillate flower, pistillate disc absent, pedicel with abscission zone. — Asia ..... ***Distichirhops***
10a. Stamens shorter than sepals. Staminate inflorescences densely hairy. Sepals slightly fused at base. Leaf arrangement always spiral; glands situated along the margins as well as on the lower surface of the blade (Fig. 3.2a, b). Stipules triangular. — Asia, Pacific ..... ***Baccaurea***
b. Stamens longer than sepals. Staminate inflorescences glabrous to sparsely hairy. Sepals fused at base. Leaf arrangement spiral to opposite; glands exclusively along the margins (Fig. 3.2a). Stipules leaf-like to triangular. — Pacific ..... ***Nothobaccaurea***

3.2 – Revision of *Baccaurea* Lour.

3.2.1 – *Taxonomic history and genus description*

The genus *Baccaurea* was described by Loureiro (1790) to accommodate the species *B. ramiflora* Lour., *B. cauliflora* Lour., and *B. sylvestris* Lour. Merrill (1935) synonymised *B. cauliflora* with the type of the genus, namely *B. ramiflora*. *Baccaurea sylvestris* was later transferred to *Aglaia domestica* (Corrêa) Pellegr. (= *Lancium domesticum* Corrêa) in the Meliaceae.

Baillon (1863) published notes on the genus *Pierardia* Roxb. (a synonym of *Baccaurea*). Furthermore he synonymised the following genera with *Pierardia*: *Hedycarpus* Jack p.p. and *Adenocrepis* Blume. He preserved *Hedycarpus*, *Pierardia*, and *Adenocrepis* as sections. He also created the new section *Isandrion* for the African species. Müller Argoviensis published in 1866 the first revision of *Baccaurea* and allied genera. He also sunk some genera into *Baccaurea*, namely: *Hedycarpus* Miq. p.p., *Pierardia* p.p., *Microsepala* Miq., and *Calyptroon* Miq. He recognised *Hedycarpus*, *Pierardia*, *Isandrion*, *Adenocrepis* and *Calyptroon* as sections within *Baccaurea* based on staminate and pistillate floral characters. Müller Argoviensis distinguished 31 species, although he did not personally study all of them but copied the original descriptions for several names without further comments. Bentham & Hooker (1883) and Pax (1891) published generic descriptions for *Baccaurea*, both following the system of Müller Argoviensis. Hooker (1885), however, published a different classification, namely three series based on staminate inflorescence types. Other authors have never used this classification. Boerlage (1900) for example followed Müller Argoviensis's classification. Hutchinson (1912) transferred all African species of *Baccaurea* to *Maesobotrya* Benth. This means that, except for *B. stylaris* Müll. Arg., the section *Isandrion* became a new section in *Maesobotrya*. Although he did not present arguments for his decision, *Maesobotrya* is nevertheless different from *Baccaurea* (see Chapter 1.4). Pax & Hoffmann (1922) adjusted Müller Argoviensis's system, and combined the genus *Everettiodendron* Merr. with *Baccaurea* and recognised it as a section. Furthermore, they decided to include Müller Argoviensis's section *Adenocrepis* in section *Pierardia*. In addition to floral characters Pax & Hoffmann (1922) also used the trichomes to describe the five sections they distinguished. A number of species was transferred from one section to another, but still they stated that the classification within the genus is unsatisfactory, due to incomplete knowledge of the species and lack of good differences between the species. Their system has been followed by later authors, to begin with Merrill (1929), who described numerous new species within the various sections. However, from Ridley (1924) and Corner (1940) up to today no new infrageneric classification of *Baccaurea* has been proposed. Authors like Backer & Bakhuizen van den Brink (1963), Whitmore (1973), Smith (1978), Fernando (1979) and Airy Shaw (1980, 1981) did not refer to any classification below the genus level. Soejarto (1965) published comprehensive taxonomic descriptions as well as uses of the cultivated species of *Baccaurea*. In 1960 Airy Shaw reduced the monotypic genus *Gatnaia* Gagnep. to *Baccaurea*, and wrote regional treatments for Thailand (Siam) (1972), Borneo (1975), New Guinea (1980), Sumatra (1981), and Central Malesia (1982). He also described several new species in *Baccaurea*, but usually without a reference to generic subdivisions.

Baccaurea Lour., Fl. Cochinch. (1790) 661; Müll. Arg. in DC., Prodr. 15, 2 (1866) 456; Bedd., Fl. Sylv. S. India (1869) 280; Kurz, Forest Fl. Burma 2 (1877) 356; Benth. & Hook.f., Gen. Pl. 3 (1883) 283; Hook.f., Fl. Brit. India 5 (1887) 367; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1891) 30; Brandis, Indian Trees (1906) 562; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 245; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 45; Ridl., Fl. Malay Penins. 3 (1924) 242; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 547; Merr., Trans. Amer. Philos. Soc. New Ser. 24, 2 (1935) 29, 47; Corner, Wayside Trees Mal. 1 (1940) 238; Backer & Bakh.f., Fl. Java 1 (1964) 453; Whitmore, Tree Fl. Malaya 2 (1973) 63; A.C. Sm., Allertonia 1 (1978) 377; Fernando, Philipp. J. Biol. 8 (1979) 301; Airy Shaw, Kew Bull. Add. Ser. 8 (1980) 34; Kew Bull. 36 (1981) 258; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 51. — Type: *Baccaurea ramiflora* Lour. (lecto selected by Merrill, 1935)

Pierardia Roxb. ex Jack, Trans. Linn. Soc. London, Bot. 14 (1823) 119; Blume, Bijdr. Fl. Ned. Ind. (1825) 578; Roxb., Fl. Ind. 2 (1832) 254; Endl., Gen. Pl. 2 (1839) 1124; Walp., Repert. Bot. Syst. 5 (1846) 366; Griff., Ic. Pl. Asiat. (1854) 738; Wight, Icon. Pl. Ind. Orient. (1852) 30; Miq., Fl. Ned. Ind. 1, 2 (1859) 358; Fl. Ned. Ind., Eerste bijv. (1861) 441; Baill., Adansonia 3 (1863) 139. — Type: *Pierardia dulcis* Jack [= *Baccaurea dulcis* (Jack) Müll.Arg.].

Adenocrepis Blume, Bijdr. Fl. Ned. Ind. (1825) 579; Endl., Gen. Pl. 2 (1839) 1123; Baill., Adansonia 3 (1863) 139; Müll. Arg. in DC., Prodr. 15, 2 (1866) 465. — Type: *Adenocrepis javanica* Blume [= *Baccaurea javanica* (Blume) Müll. Arg.].

Microsepala Miq., Fl. Ned. Ind., Eerste bijv. (1861) 444. — Type: *Microsepala accuminata* Miq. [= *Baccaurea javanica* (Blume) Müll. Arg.].

Calyptroon Miq., Fl. Ned. Ind., Eerste bijv. (1861) 471; Müll. Arg. in DC., Prodr. 15, 2 (1866) 466. — Type: *Calyptroon sumatranum* Miq. [= *Baccaurea sumatrana* (Miq.) Müll. Arg.].

Everettiodendron Merr., Philipp. J. Sci., Bot. 4 (1909) 279. — Type: *Everettiodendron philippinense* Merr. [= *Baccaurea philippinensis* (Merr.) Merr.].

Gatnaia Gagnep., Bull. Soc. Bot. France 71 (1924) 870; Airy Shaw, Kew Bull. 14 (1960) 353. — Type: *Gatnaia annamica* Gagnep. [= *Baccaurea ramiflora* Lour.].

Shrub to tree, dioecious, with Terminalia branching pattern. *Indumentum* of simple and often also of stellate hairs. *Bark* finely fissured. *Leaves* simple, alternate, spirally arranged; petiole apically and rarely basally pulvinate, transverse cracks often present; stipules triangular or rarely foliaceous, early to late caducous, often ciliate; blade basally cordate to attenuate; margin entire, marginal glands present; apex usually rounded to cuspidate to rarely retuse; upper surface glabrous, sometimes densely hairy on the veins, raised glands often present, sometimes granulate; lower surface glabrous to densely hairy, raised glands often present, discoid glands sometimes present; nervation raised, secondary veins curved and sometimes closed at margin. *Inflorescences* axillary to cauline, reduced thyrses, solitary to many clustered together; flowers hypogynous, actinomorphic; pedicel with abscission zone. *Staminate inflorescences* not to distinctly branched, 10–many-flowered, flowers scattered along inflorescence to clustered at the tip; bracts triangular to rarely (broadly) ovate; branchlets 1–20 (in *B. bracteata* to 40)-flowered. *Staminate flowers*: sepals (3 or) 4 or 5(–8), free to slightly fused at base; petals absent; disc absent; stamens 3–10, shorter than sepals, glabrous; anthers introrse, basifixed to dorsifixed, opening with a longitudinal apical slit; staminodes (or disc glands) sometimes present, 3–8; pistillode usually present, small. *Pistillate inflorescences* not branched, one- to many-flowered; bracts inserted on rachis to usually along pedicel, 1 or 3 per flower, triangular to ovate. *Pistillate flowers*: sepals 4–6 (or in *B. papuana* up to 9), caducous to persistent; petals absent; staminodes absent; disc absent; ovary cylindrical to globose, 2–4-locular, ovules 2 per locule, attached at apex of column, wings usually absent; stigmas not cleft to completely divided into 2 lobes; protuberances (see Fig. 1.9) often present. *Fruits* berries to late dehiscing

fleshy capsules; raised glands often present; seeds 0–8, 0–2 per locule, ellipsoid but laterally flattened; arillode enclosing seed totally; cotyledons flat, rarely folded.

Distribution — Forty-three species in India, SE Asia and the Pacific.

Habitat & Ecology — Primary to secondary rain forest or freshwater swamp forest. Soil: sand to clay to loam. Altitude: sea level up to 1600(–1800) m, usually in lowland. Flowering and fruiting throughout the year.

Uses — Arillode of all and pericarp of some species edible, sour to sweet.

3.2.2 – *General key to the species of Baccaurea*

Words in *italics* are explained in the glossary (p. 205). Sunda Shelf behind the species name means: species native in Thailand south of the Isthmus of Kra, Peninsular Malaysia, Sumatra, Java, Borneo or Palawan. No regional keys are provided for these areas.

1a. Indumentum consisting of simple hairs only (Fig. 3.3a, or plants *glabrous*, best visible on lower surface of leaves, if possible, use dissecting microscope or strong hand lens); leaf midribs *glabrous* to glabrescent above, never densely hairy . 2
b. Indumentum consisting of *stellate* hair tufts and simple hairs (Fig. 3.3a, b). Leaf midribs *glabrous* to densely hairy above 59
2a. Leaves *glabrous* below 3
b. Leaves sub*glabrous* to densely hairy below 11
3a. Leaves in dense terminal tufts (Fig. 3.1b); pairs of secondary veins 4–10 ... 4
b. Leaves in open terminal tufts (Fig. 3.1c); pairs of secondary veins 5–16 8
4a. Lower leaf surfaces often without *discoid glands*, if present scattered. *Petioles* usually without transverse cracks when dry. Fruits *glabrous* to sub*glabrous* outside and inside 5
b. Lower leaf surfaces with *discoid glands* in a row parallel to midrib, or in a row between secondary veins. *Petioles* usually with transverse cracks when dry. Fruits densely hairy outside and inside. — Sunda Shelf ..... **18. B. minor**
5a. Stipules ciliate. Trees usually less than 15 m high. Leaves *obovate*. *Staminate* flowers scattered along *rachis* (Fig. 3.4b, c). *Pistillate pedicels* straight. Fruits with *glabrous septa* 6
b. Stipules slightly ciliate. Trees usually more than 15 m high. Leaves *ovate*. *Staminate* flowers clustered at the tip of the *rachis* (Fig. 3.4a). *Pistillate pedicels geniculate* (90° bent). Fruits with sub*glabrous septa*. — Sunda Shelf .. **39. B. sumatrana**
6a. Inflorescences (or their scars) *axillary* to just below the leaves to rarely along the branches, solitary to few clustered together. *Staminate* flowers white, yellow or green. Ovaries 2-locular. Fruits globose 7
b. Inflorescences (or their scars) *cauline*, many clustered together. *Staminate* flowers red. Ovaries usually 3-locular. Fruits *fusiform*. — Sunda Shelf **26. B. parviflora**
7a. Branchlets not thickened at the tip. Leaves not whitish when dry. Sepals *glabrous* to sub*glabrous* outside. *Pistillate* inflorescences usually *glabrous*. Infructescences 1–5 cm long. Fruits yellow to orange. — Sunda Shelf ..... **12. B. javanica**
b. Branchlets sometimes thickened at the tip. Leaves sometimes whitish when dry. Sepals sparsely to densely hairy outside. *Pistillate* inflorescences sparsely to densely hairy. Infructescences 3–28 cm long. Fruits red to pink. — Sunda Shelf ... . **41. B. tetrandra**

8a. (3) Leaves papery to sub-leathery, usually (greyish to reddish) brown when dry (*B. lanceolata* green-brown); nervation clearly visible. Fruits globose 9
b. Leaves thick leathery, usually green when dry; nervation hardly visible. Fruits star-shaped in cross section. — Sunda Shelf ..... **1. B. angulata**
9a. Leaves brown to grey to reddish when dry. *Staminate* inflorescences *axillary* to rarely *cauline*, solitary to few clustered together, sub*glabrous* to densely hairy. Sepals densely hairy outside. Infructescences 3.5–13 cm. Fruits 21–35 mm long 10
b. Leaves grey-green to brown-green when dry. *Staminate* inflorescences *cauline*, many clustered together, *glabrous* to sub*glabrous*. Sepals usually *glabrous* outside. Infructescences 8.5–30(–50) cm. Fruits 24–60 mm long. — Sunda Shelf .... **13. B. lanceolata**
10a. Pairs of secondary veins 10–15. Filaments c. 0.3 mm long. *Pistillate* inflorescences *cauline*. Fruits densely hairy. — New Guinea ..... **5. B. carinata**
b. Pairs of secondary veins 5–12. Filaments 0.4–0.7 mm long. *Pistillate* inflorescences usually along the branches to *axillary*. Fruits *glabrous* to sub*glabrous*. — Sunda Shelf, Sumatra, Java ..... **10. B. dulcis**
11a. (2) Branchlets, *petioles* and lower surface leaves densely hairy 12
b. Branchlets, *petioles* and lower surface leaves *glabrous* to sparsely hairy .. 18
12a. Leaves 5–14.5 cm long; pairs of secondary veins 5–8 13
b. Leaves 13.5–37 cm long; pairs of secondary veins 8–17 14
13a. *Staminate* inflorescences with 3 (or 4) *bracts* per branchlet; *staminodes* 4–8. *Pistillate* inflorescences *cauline*; flowers yellow to cream, 4–18 mm diam.; ovaries 2-locular. Fruits 12–14 mm diam. ..... **25. B. papuana**
b. *Staminate* inflorescences with 1 (or 2) *bracts* per branchlet; *staminodes* absent. *Pistillate* inflorescences *axillary* or along the branches; flowers pink, 1.5–2.2 mm diam.; ovaries 3- (or 4-)locular. Fruits 24–40 mm diam. **37. B. seemannii**
14a. (12) Stipules 8–16 mm long 15
b. Stipules 3–6.5 mm long 16
15a. Trees 3–10 m high. Leaf bases *cuneate* to rounded. Ovaries 2- or 3-locular. Fruits 14–20 by 10–18.5 mm; pedicels 1–5 mm long. — Sunda Shelf **4. B. brevipes**
b. Trees 13–20 m high. Leaf bases usually narrowly *cordate*, rarely rounded. Ovaries 3-locular. Fruits 22–45 by 15–25 mm; pedicels 4–10 mm long. — Sunda Shelf ..... **20. B. motleyana**
16a. (14) Leaf bases *cuneate* to *attenuate* 17
b. Leaf bases usually narrowly heart-shaped, rarely rounded. — Sunda Shelf .. .. **20. B. motleyana**
17a. Leaves in open terminal tufts (Fig. 3.1c), 19.5–28.5 cm long, sparsely to densely hairy below along the nervation. *Staminate* inflorescences with 1 *bract* per branchlet, 2–8.5 mm long; flowers reddish ..... **2. B. annamensis**
b. Leaves in dense terminal tufts (Fig. 3.1b), 8–20.5 cm long, sub*glabrous* to sparsely hairy below at nervation. *Staminate* inflorescences with 3 (or 4) *bracts* per branchlet, 0.3–1 mm long; flowers yellow to cream ..... **25. B. papuana**
18a. (11) Leaves in open terminal tufts (Terminalia branching pattern weakly developed, Fig. 3.1c) 19

b. Leaves in dense terminal tufts (Terminalia branching pattern well-developed, Fig. 3.1b) 32
19a. Leaves papery, brown to green when dry. Fruits globose 20
b. Leaves leathery, yellowish green when dry. Fruits star-shaped in cross section. — Sunda Shelf ..... **1. B. angulata**
20a. Stipules 8–16 mm long 21
b. Stipules 2.5–8 mm long 24
21a. Leaves brown to grey when dry. Trunk not gnarled. Wood white to cream. *Petioles* 11–65 mm long. *Staminate* flowers 1–2.2 mm diam., *pedicel* 0.2–1 mm long. Fruits 10–18.5 mm diam. 22
b. Leaves green when dry. Trunk gnarled. Wood yellow to ochre to brown. *Petioles* 16–184 mm long. *Staminate* flowers 2–7 mm diam., *pedicel* 1.8–7 mm long. Fruits (16.5–)24–60 mm diam. — Sunda Shelf ..... **13. B. lanceolata**
22a. *Petioles* only apically *pulvinate*. Leaves 15–35 cm long; pairs of secondary veins 10–15. *Staminate* inflorescences solitary or in clusters of up to 8, densely hairy; flowers yellow (green). Fruits in*dehiscent* 23
b. *Petioles* basally and apically *pulvinate*. Leaves 7.4–17.4 cm long; pairs of secondary veins 6–11. *Staminate* inflorescences many clustered together, sub*glabrous* to sparsely hairy; flowers pink. Fruits *loculicidally dehiscent* ..... **31. B. purpurea**
23a. Lower leaf surfaces sparsely to densely hairy along nervation. Stamens 5. Fruiting *pedicels* above abscission zone 0.1–1 mm long. — Sunda Shelf **4. B. brevipes**
b. Lower leaf surfaces *glabrous* to sub*glabrous* along nervation. Stamens 6–9. Fruiting *pedicels* above abscission zone 1.5–3.5 mm long ..... **5. B. carinata**
24a. (20) *Petioles* basally not to slightly *pulvinate*. *Staminate* flowers white, yellow, orange or pink 25
b. *Petioles* basally strongly *pulvinate*. *Staminate* flowers (purplish) pink ..... **31. B. purpurea**
25a. Lower leaf surfaces with *discoid glands*; leaf apex 0–5 mm long; pairs of secondary veins 4–9. Stipules 2.5–6 mm long 26
b. Lower leaf surfaces without *discoid glands*; leaf apex 0–20 mm long; pairs of secondary veins 5–15. Stipules 3–11.5 mm long 28
26a. *Pistillate* inflorescences along the branches to *axillary*. Fruits 9.5–20 mm diam. *Staminate* inflorescence branchlets 1.5–4.5 mm long (Fig. 3.4c) 27
b. *Pistillate* inflorescences *cauline*. Fruits 24–40 mm diam. *Staminate* inflorescence branchlets 0–0.4 mm long (Fig. 3.4c) ..... **25. B. papuana**
27a. Midrib of stipules often *glabrous* on the outside. Fruits 16–21 mm long; *septa glabrous* to sub*glabrous*; pedicels 2.1–3.6 mm long. — Louisiade Archipelago ..... **23. B. nesophila**
b. Midrib of stipules densely hairy on the outside. Fruits 11–16 mm long; *septa* sparsely to densely hairy; pedicels 3–8 mm long. — Samoan Islands ..... **40. B. taitensis**
28a. (25) Pairs of secondary veins 6–15. Young shoots brown to grey to green when dry. Stipules longer than 3 mm, densely hairy along midrib outside, but *glabrous* to sub*glabrous* on the blade. *Pistillate* inflorescences *cauline*. Fruits 12–60 mm diam. 29

b. Pairs of secondary veins 5–7. Young shoots blackish when dry. Stipules shorter than 3 mm, densely hairy all over outside. *Pistillate* inflorescences *axillary*. Fruits c. 10 mm diam. ..... **17. B. microcarpa**

29a. *Petioles glabrous*. Lower leaf surfaces with *glabrous* nervation. *Staminate* inflorescences many clustered together. *Pistillate* sepals *glabrous* to sub*glabrous* 30

b. *Petioles* sub*glabrous* to densely hairy. Lower leaf surfaces with sub*glabrous* to sparsely hairy nervation. *Staminate* inflorescences solitary in clusters of up to 10. *Pistillate* sepals densely hairy 31

30a. Leaves grey to brown when dry. *Petioles* 21–59 mm long. *Staminate* inflorescences *cauline* to *axillary*, densely hairy; flowers 1.5–1.8 mm diam. Fruits densely hairy ..... **5. B. carinata**

b. Leaves green when dry. *Petioles* 16–184 mm long. *Staminate* inflorescences *cauline*, *glabrous* to sparsely hairy; flowers 2–7 mm diam. Fruits *glabrous*. — Sunda Shelf ..... **13. B. lanceolata**

31a. (29) Stipules 3–6.5 mm long. *Staminate* flowers 1.8–3.5 mm diam.; reduced petals absent. Fruits 24–40 mm diam.; pedicels 5–8(–23) mm long ..... **25. B. papuana**

b. Stipules 5–11.5 mm long. *Staminate* flowers 1.5–1.8 mm diam.; reduced petals present. Fruits c. 12 mm diam.; pedicels 3–5 mm long ..... **5. B. carinata**

32a. (18) Inflorescences or their scars *cauline* and/or along the branches (if only along the branches, both leads are correct) 33

b. Inflorescences or their scars along the branches and/or *axillary* 45

33a. *Petioles* only *pulvinate* apically 34

b. *Petioles pulvinate* basally and apically ..... **31. B. purpurea**

34a. Pairs of secondary veins 3–10. *Staminate* flowers without *staminodes*. *Pistillate rachis* red; sepals 4 or 5. — India, Southeast Asian mainland, Malesia except New Guinea 35

b. Pairs of secondary veins 7–15. *Staminate* flowers with *staminodes*. *Pistillate rachis* yellow; sepals 5–9. — New Guinea ..... **25. B. papuana**

35a. Inflorescences (or their scars) *cauline* and/or along the branches 36

b. Inflorescences (or their scars) *cauline*, but only along the base of the trunk, up to c. 1.5 m high. — Sunda Shelf ..... **26. B. parviflora**

36a. Plants with *staminate* inflorescences 37

b. Plants with *pistillate* inflorescences or fruits 41

37a. Flowers cream to yellow 38

b. Flowers red to pink 40

38a. *Bracts glabrous* at the base inside, 0.2–1.1 mm long 39

b. *Bracts* densely hairy at the base inside, (1.5–)3–4.5 mm long. — Sunda Shelf ..... **34. B. ramiflora**

39a. Inflorescences in clusters of many; not branched (Fig. 3.4a, b); *bracts* only along the *rachis*; filaments c. 0.8 mm long. — Sunda Shelf ... **24. B. odoratissima**

b. Inflorescences solitary or in clusters of up to 10; branched (Fig. 3.4c); *bracts* along the *rachis* and on the branchlets; filaments 0.4–0.6 mm long. — Sunda Shelf ..... **33. B. racemosa**

40a. (37) Inflorescences solitary or in clusters of many; rachis less than 1 mm thick. — S India ..... **7. B. courtallensis**
b. Inflorescences solitary; rachis more than 1 mm thick. — SE Asia ..... **29. B. ptychopyxis**
41a. (36) Flowers yellow to green; ovaries not winged. Fruits globose 42
b. Flowers reddish; ovaries winged. Fruits ellipsoid (*fusiform*) ..... **29. B. ptychopyxis**
42a. Fruits 14–35 mm diam., *loculicidally dehiscing* or in*dehiscent* 43
b. Fruits 6–13.5 mm diam., irregularly dehiscing when dry. — Sunda Shelf ..... **24. B. odoratissima**
43a. Sepals sub*glabrous* outside. Stylar lobes densely hairy below. Seed *arillodes* yellow; cotyledons c. 12 mm long. — Southeast Asian mainland, Malesia 44
b. Sepals densely hairy outside. Stylar lobes sub*glabrous* below. Seed *arillodes* blue to white; cotyledons 5–9 mm long. — S India ..... **7. B. courtallensis**
44a. Fruits *loculicidally dehiscent*, often only partly so. *Pedicels* above abscission zone 1.9(–2.5) mm long. — Sunda Shelf ..... **33. B. racemosa**
b. Fruits in*dehiscent*. *Pedicels* above abscission zone 0.1–1 mm long. — Sunda Shelf ..... **34. B. ramiflora**
45a. (32) Branchlets solid. Stipules usually densely hairy along midrib on the outside, 2.5–6.5(–11) mm long 46
b. Branchlets hollow. Stipules usually *glabrous* along midrib on the outside, 6–15 mm long. — Sunda Shelf ..... **10. B. dulcis**
46a. Leaves papery, dull, brown to green to whitish when dry 47
b. Leaves leathery, slightly glossy, grey-brown to green when dry. — Sunda Shelf ..... **36. B. sarawakensis**
47a. Leaves lower surface with *discoid glands* 48
b. Leaves lower surface without *discoid glands* 51
48a. Pairs of secondary veins 4–10. *Staminate* flowers without *staminodes*. *Pistillate* flowers 3–9.2 mm diam.; sepals 4 or 5 49
b. Pairs of secondary veins 7–15. *Staminate* flowers with *staminodes*. *Pistillate* flowers 4–18 mm diam.; sepals 5–9 ..... **25. B. papuana**
49a. Leaf apex (*obtuse* to) *acuminate* to *cuspidate*, 0–25 mm long. Lower leaf surfaces with few *discoid glands*. Seed *arillodes* blue or yellow; pedicels 3–9 mm long. — S India and W Malesia 50
b. Leaf apex (*retuse* to) *obtuse* to slightly *acuminate*, 0–3 mm long. Lower leaf surfaces with many *discoid glands*. Seed *arillodes* red to orange; pedicels 2.1–3.6 mm long, inflorescences unknown. — Louisiade Archipelago ..... **23. B. nesophila**
50a. *Staminate* flowers red to pink. *Pistillate* inflorescences with *bracts* only along *rachis;* sepals sub*glabrous* outside. Fruits c. 35 mm diam., in*dehiscent*; seeds 13–19 mm long, *arillode* yellow ..... **7. B. courtallensis**
b. *Staminate* flowers cream to yellow to white. *Pistillate* inflorescences with *bracts* along *rachis* and *pedicels*; sepals densely hairy outside. Fruits 16–30 mm diam., *loculicidally dehiscent*; seeds 5–11.5 mm long, *arillode* blue. — Sunda Shelf ..... **33. B. racemosa**

51a. (47) Leaves above *glabrous* along midrib; pairs of secondary veins 4–10. *Staminate pedicels* 0.4–3 mm long. *Pistillate* sepals 4–6, 1.5–6 mm long. *Arillode* blue or white or (in S India) yellow 52
b. Leaves above *glabrous* to densely hairy along midrib; pairs of secondary veins 7–15. *Staminate pedicels* 1.2–4.2 mm long. *Pistillate* sepals 5–9, 3–11 mm long. *Arillode* yellow. — Sunda Shelf, New Guinea ..... **25. B. papuana**
52a. Plants with *staminate* inflorescences 53
b. Plants with *pistillate* inflorescences or fruits 56
53a. *Bracts glabrous* at base inside, 0.2–1.3 mm long 54
b. *Bracts* densely hairy at base inside, (1.5–)3–4.5 mm long. — Sunda Shelf .. .. **34. B. ramiflora**
54a. Flowers cream to yellow to white. — Southeast Asian mainland, Malesia . 55
b. Flowers red to pink. — S India ..... **7. B. courtallensis**
55a. Inflorescences *cauline* to just below the leaves; stamens 5–7, 0.5–0.8 mm long; *staminodes* absent. — Sunda Shelf ..... **33. B. racemosa**
b. Inflorescences just below the leaves to *axillary*; stamens (3 or) 4 or 5, 0.6–1.4 mm long; *staminodes* often present. — Sunda Shelf ..... **41. B. tetrandra**
56a. (52) Inflorescences *cauline* to *axillary*. Ovaries (2- or) 3- or 4-locular. Fruits 16–35 mm diam. 57
b. Inflorescences along the branches to usually *axillary*. Ovaries 2-locular. Fruits 6.5–15 mm diam. — Sunda Shelf ..... **41. B. tetrandra**
57a. Sepals sub*glabrous* outside; stylar lobes densely hairy below. Seed *arillodes* yellow; cotyledons c. 12 mm long. — Southeast Asian mainland and Sunda Shelf 58
b. Sepals densely hairy outside; stylar lobes sub*glabrous* below. Seed *arillodes* blue to white; cotyledons 5–9 mm long. — S India ..... **7. B. courtallensis**
58a. Fruits *loculicidally dehiscent*, often only partly so. *Pedicels* above abscission zone 1.9(–2.5) mm long. — Sunda Shelf ..... **33. B. racemosa**
b. Fruits in*dehiscent*. *Pedicels* above abscission zone 0.1–1 mm long. — Sunda Shelf ..... **34. B. ramiflora**
59a. (1) Upper leaf surfaces with densely hairy midrib 60
b. Upper leaf surfaces with *glabrous* to sparsely hairy midrib 62
60a. Fruits sub*glabrous* to densely hairy inside. *Staminate* inflorescences *axillary* to rarely along the branches; *pedicels* 1–1.7 mm long; *staminode*s absent. *Pistillate* flowers 2.5–7 mm diam.; sepals 4 or 5. — W Malesia 61
b. Fruits *glabrous* inside. *Staminate* inflorescences *axillary* to *cauline*; *pedicels* 1.2–4.2 mm long; *staminode*s present. *Pistillate* flowers 4–18 mm diam.; sepals 5–9. — New Guinea ..... **25. B. papuana**
61a. Branchlets *glabrous*. Leaf bases rounded to *cuneate*; nervation *reticulate*. *Staminate* inflorescences branched (Fig. 3.4c), flowers scattered along inflorescences (Fig. 3.4b, c). *Pistillate* inflorescences *cauline* to sometimes along the branches; ovaries 2-locular. Fruits 23–60 mm diam., in*dehiscent*. — Sunda Shelf .... **11. B. edulis**
b. Branchlets densely hairy. Leaf bases usually *cordate* to rounded; nervation *scalariform*. *Staminate* inflorescences not branched (Fig. 3.4a, b); flowers in tip of inflo-

rescences (Fig. 3.4a). *Pistillate* inflorescences *axillary* to along the branches; ovaries 3-locular. Fruits 12–26 mm diam., *loculicidally dehiscent.* — Sunda Shelf ..... **28. B. polyneura**

62a. (59) Stipules *caducous*, 3–11.5 mm long. *Petioles glabrous* to densely hairy 63

b. Stipules late *caducous* or persistent, 10.5–17 mm long. *Petioles* densely hairy. — Sunda Shelf ..... **19. B. mollis**

63a. Lower leaf surfaces without black dots (at base of hairs) 64

b. Lower leaf surfaces with black dots (at base of hairs), dots only c. 0.1 mm diam. but visible with the naked eye. — Sunda Shelf ..... **3. B. bracteata**

64a. Pairs of secondary veins 9–13 65

b. Pairs of secondary veins 3–8 80

65a. Twigs densely hairy 66

b. Twigs *glabrous* to sparsely hairy 69

66a. Leaves *ovate* to *elliptic* (if *elliptic*, both leads are correct) 67

b. Leaves *obovate* to *elliptic* 68

67a. Stipules 3–7.5 mm long. Leaves green to brown when dry; bases *cordate* to *attenuate*; nervation *scalariform. Staminate* inflorescences not branched (Fig. 3.4a, b); flowers usually at tip of inflorescences (Fig. 3.4a). Fruits 13–22 mm diam. — Sunda Shelf ..... **16. B. maingayi**

b. Stipules 5.5–11 mm long. Leaves brown when dry; bases rounded to *attenuate*; nervation *reticulate* to weakly scalariform. *Staminate* inflorescences branched (Fig. 3.4c); flowers scattered along inflorescences (Fig. 3.4b, c). Fruits 29–40 mm diam. — Sunda Shelf ..... **30. B. pubera**

68a. (66) *Petioles* 34–130 mm long. Blades 13–36 cm long; hair tufts on the margins inconspicuous. *Staminate* inflorescences with *bracts* 1.5–4 mm long; *staminodes* absent. *Pistillate* inflorescences *cauline* to along the branches. Fruits 29–40 cm diam. — Sunda Shelf ..... **30. B. pubera**

b. *Petioles* 14–72 mm long. Blades 6.8–18.6 cm long; hair tufts on the margins striking. *Staminate* inflorescences with *bracts* 0.3–1.5 mm long; *staminodes* present. *Pistillate* inflorescences along the branches to rarely *axillary*. Fruits 14–22 cm diam. — Sunda Shelf ..... **32. B. pyriformis**

69a. (65) Lower leaf surfaces without hair tufts in axils of the secondary veins 70

b. Lower leaf surfaces with hair tufts in axils of the secondary veins. — Sunda Shelf ..... **9. B. dolichobotrys**

70a. Plants with *staminate* inflorescences 71

b. Plants with *pistillate* inflorescences 75

71a. Flowers scattered along inflorescences *rachis* (Fig. 3.4b, c) 72

b. Flowers at the tip of inflorescences (Fig. 3.4a) 74

72a. Lateral branches of inflorescences 3–many-flowered; *pedicels* 1–2 mm long. Leaf nervation (weakly) *scalariform* 73

b. Lateral branches of inflorescences 3-flowered; *pedicels* absent. Leaf nervation *reticulate* to weakly *scalariform.* — Sunda Shelf ..... **8. B. deflexa**

73a. *Petioles* 10–145 mm long. Inflorescence branchlets 1–2 mm long; stamens 0.1–0.25 mm long. — Sunda Shelf ..... **14. B. macrocarpa**

b. *Petioles* 16–64 mm long. Inflorescence branchlets 2–35 mm long; stamens 0.3–0.6 mm long. — Sunda Shelf ..... **22. B. nanihua**

74a. (71) Blades 9.6–33 cm long. Inflorescences 2.5–9 mm long; sepals 4 or 5; stamens 4 or 5, 0.2–0.7 mm long; *staminodes* usually present. — Sunda Shelf ..... **15. B. macrophylla**

b. Blades 7–16.5 cm long. Inflorescences 1–3 mm long; sepals (5) or 6; stamens 6, 0.9–1 mm long; *staminodes* absent. — Sunda Shelf .... **42. B. trigonocarpa**

75a. (70) Inflorescences *cauline* to along the branches (if along the branches, both leads are correct) 76

b. Inflorescences *axillary* to along the branches 78

76a. *Pedicels* 2–7.5 mm long. Flowers 2–4.5 mm diam. Fruits globose when dry, usually in*dehiscent* 77

b. *Pedicels* 1–1.5 mm long. Flowers 1–2 mm diam. Fruits angular when dry, *loculicidally dehiscent.* — Sunda Shelf ..... **42. B. trigonocarpa**

77a. Stipules triangular. Stigmas 2-lobed. Fruits 35–73 mm diam., yellow to brown. — Sunda Shelf ..... **14. B. macrocarpa**

b. Stipules triangular to foliaceous. Stigmas not cleft into 2 lobes. Fruits 9–15 mm diam., usually green. — Sunda Shelf ..... **15. B. macrophylla**

78a. (75) Ovaries 3- or 4-locular 79

b. Ovaries 2-locular. — Sunda Shelf ..... **8. B. deflexa**

79a. *Pedicels* c. 4.5 mm long. Flowers 3–7 mm diam. Fruits 25–29 mm diam. — Sunda Shelf ..... **22. B. nanihua**

b. *Pedicels* 1–1.5 mm long. Flowers 1–2 mm diam. Fruits 9–15 mm diam. — Sunda Shelf ..... **42. B. trigonocarpa**

80a. (64) Leaves *ovate* to *elliptic* (if *elliptic*, both leads are correct) 81

b. Leaves *obovate* to *elliptic* 91

81a. Twigs densely hairy 82

b. Twigs *glabrous* to sub*glabrous* 85

82a. Leaf nervation *reticulate* to weakly *scalariform. Staminate* inflorescences branched (Fig. 3.4c); flowers scattered along inflorescences (Fig. 3.4b, c). Fruits 25–40 mm diam. 83

b. Leaf nervation (weakly) *scalariform. Staminate* inflorescences not branched (Fig. 3.4a, b); flowers at the tip of inflorescences (Fig. 3.4a). Fruits 6–22 mm diam. 84

83a. Stipules 5.5–11 mm long. Leaves 13–36 cm long; pairs of secondary veins (5–)8–13. *Staminate bracts* persistent, 1.5–4 mm long; flowers 1.3–2.5 mm diam. *Pistillate* inflorescences *cauline* to along the branches. Fruiting pedicels 11–14 mm long. — Sunda Shelf ..... **30. B. pubera**

b. Stipules 3–7 mm long. Leaves 5–19.5 cm long; pairs of secondary veins 5–7. *Staminate bracts caducous*, 4–7 mm long; flowers 1.8–4 mm diam. *Pistillate* inflorescences *axillary*. Fruiting pedicels 4–5 mm long. — Sunda Shelf .... **43. B. velutina**

84a. (82) *Pistillate* inflorescences along the branches to *axillary*; ovaries 2-locular. Fruits 6–15 mm diam. *Petioles* 17–50 mm long. Leaf bases acute to *attenuate.* — Sunda Shelf ..... **8. B. deflexa**

b. *Pistillate* inflorescences along the branches; ovaries 3-locular. Fruits 14–22 mm diam. *Petioles* 13–120 mm long. Leaf bases *cordate* to *attenuate.* — Sunda Shelf ..... **16. B. maingayi**

85a. (81) *Staminate* inflorescences branched (Fig. 3.4c). *Pistillate pedicels* straight; stigmas usually 2-lobed. Fruits yellow, red, brown or bluish 86
b. *Staminate* inflorescences not branched (Fig. 3.4a, b). *Pistillate pedicels geniculate* (90° bent); stigmas not 2-lobed. Fruits usually green, rarely whitish, brownish, purplish or yellowish. — Sunda Shelf ..... **15. B. macrophylla**
86a. Leaf nervation *reticulate* to weakly *scalariform*. *Staminate bracteoles* present; branchlets 3–20-flowered; flowers *pedicellate*. Ovaries usually 3-locular; styles 0.5–1.5 mm long. Fruits 15–75 mm diam. 87
b. Leaf nervation (weakly) *scalariform*. *Staminate bracteoles* absent; branchlets 3-flowered; flowers sessile. Ovaries 2-locular; styles absent. Fruits 8–15 mm diam. — Sunda Shelf ..... **8. B. deflexa**
87a. *Petioles* 12–75 mm long. Lower leaf surfaces usually with scattered *discoid glands*. *Pistillate* inflorescences *axillary* to along the branches, 1–10-flowered. Fruits 15–38 mm diam. (up to 50 mm when fresh) 88
b. *Petioles* 10–145 mm long. Lower leaf surfaces with *discoid glands* in rows between 2 secondary veins. *Pistillate* inflorescences along the branches to *cauline*, 8–many-flowered. Fruits 35–75 mm diam. — Sunda Shelf **14. B. macrocarpa**
88a. *Staminate bracts* small, not covering lateral axis. *Pistillate* flowers 3–7 mm diam. — Philippines, Borneo, Sulawesi, Moluccas, and New Guinea 89
b. *Staminate bracts* big, covering lateral axis. *Pistillate* flowers 8–14 mm diam. — Simeuluë Island, Sunda Shelf ..... **38. B. simaloerensis**
89a. Fruits *loculicidally dehiscent*, densely hairy inside; seeds 7–11.5 mm long. *Staminate* inflorescence branchlets 1.3–35 mm long, 3–many-flowered 90
b. Fruits in*dehiscent*, sparsely hairy inside; seeds 12–19 mm long. *Staminate* inflorescence branchlets 1.5–3 mm long, 3–6-flowered. — Sunda Shelf ..... **6. B. costulata**
90a. Pairs of secondary veins 6–10. *Staminate bracteoles* 0 or 1 per branchlet; flowers white to pale yellow; sepals 4–6. Fruits 25–29 mm diam.; column 11–14 mm long. — Sunda Shelf ..... **22. B. nanihua**
b. Pairs of secondary veins 4–7. *Staminate bracteoles* 7–12 per branchlet; flowers brownish; sepals 3 or 4. Fruits 26–38 mm diam.; column 16–23 mm long. — Sunda Shelf ..... **27. B. philippinensis**
91a. (80) Twigs densely hairy 92
b. Twigs *glabrous* to sub*glabrous* 94
92a. *Petioles* 14–80 mm long. Leaves 5–20 cm long; pairs of secondary veins 5–9. *Staminate bracts* densely hairy inside; *staminodes* absent. *Pistillate* inflorescences *axillary* to along the branches. Fruits 14–31 mm diam.; column 13–19 mm long; pedicels 3–9 mm long 93
b. *Petioles* 34–130 mm long. Leaves 13–36 cm long; pairs of secondary veins (5–)8–13. *Staminate bracts glabrous* to sub*glabrous* inside; *staminodes* present. *Pistillate* inflorescences *cauline* to along the branches. Fruits 29–40 mm diam.; column 19–24 mm long; *pedicels* 11–14 mm long. — Sunda Shelf ..... **30. B. pubera**
93a. Leaves with raised glands; hair tufts on the margins striking. *Staminate bracts caducous*; *bracteoles* 0 or 1; flowers 1–2 mm diam. *Pistillate* flowers 2.5–3.5 diam. Fruits 14–22 mm diam. — Sunda Shelf ..... **32. B. pyriformis**

b. Leaves without raised glands; hair tufts on the margins inconspicuous. *Staminate bracts* persistent; *bracteoles* 4–8; flowers 2.5–5 mm diam. *Pistillate* flowers 5–10 mm diam. Fruits 25–31 mm diam. — Sunda Shelf .... **43. B. velutina**

94a. (91) Leaves densely hairy below 95

b. Leaves *glabrous* to sub*glabrous* below 98

95a. Leaf nervation (weakly) *scalariform* 96

b. Leaf nervation *reticulate* to weakly *scalariform* 97

96a. Leaves brown to grey when dry. *Staminate* inflorescence branchlets 3-flowered; pedicels absent. Ovaries 2-locular. Fruits 6–15 mm diam. — Sunda Shelf .. .. **8. B. deflexa**

b. Leaves green to yellow to whitish brown when dry. *Staminate* inflorescence branchlets (3–)9–15 flowered; *pedicels* 0.6–1.5 mm long. Ovaries 3- or 4-locular. Fruits 29–51 mm diam. — Sunda Shelf ..... **35. B. reticulata**

97a. (95) Stipules 2.5–5.5 mm long, ciliate. Lower leaf surfaces with *discoid glands* in rows between secondary veins. *Staminate* inflorescences branched (Fig. 3.4c). *Pistillate* sepals 4 or 5. Fruits circular in cross section, 19–30 mm diam. (up to 50 mm when fresh), in*dehiscent*. — Sunda Shelf ..... **6. B. costulata**

b. Stipules 4–9 mm long, usually not ciliate. Lower leaf surfaces with *discoid glands* in a row parallel to midrib. *Staminate* inflorescences not branched (Fig. 3.4a, b). *Pistillate* sepals (5 or) 6. Fruits triangular in cross section, 9–15 mm diam., *loculicidally dehiscent*. — Sunda Shelf ..... **42. B. trigonocarpa**

98a. (94) *Staminate* inflorescences not branched (Fig. 3.4a, b). *Pistillate pedicels geniculate* (90° bent); styles without or with small *protuberances*. Fruits 9–15 mm diam. 99

b. *Staminate* inflorescences branched (Fig. 3.4c). *Pistillate pedicels* straight; styles with *protuberances*. Fruits 3–8 or 19–30 mm diam. (up to 50 mm when fresh) 100

99a. Leaves 9–33 cm long. *Staminate* inflorescences 2.5–9 cm long; *bracts* 1.5–2.5 mm long; stamens 4 or 5; *staminodes* present. *Staminate* and *pistillate* sepals 4 or 5. *Pistillate* inflorescences 12–25 cm long; flowers 2–4 mm diam. Fruits usually green, usually in*dehiscent*. — Sunda Shelf .... **15. B. macrophylla**

b. Leaves 7–17 cm long. *Staminate* inflorescences 1–3 cm long; *bracts* absent; stamens 6; *staminodes* absent. *Staminate* and *pistillate* sepals (5 or) 6. *Pistillate* inflorescences 1–3 cm long; flowers 1–2 mm diam. Fruits yellow, orange or purple, *loculicidally dehiscent*. — Sunda Shelf ..... **42. B. trigonocarpa**

100a. (98) Leaves 3–20 cm long, below with or without *discoid glands*, if present scattered; pairs of secondary veins 4–8. Ovaries 2- or 3-locular. Fruits 19–30 mm diam. (up to 50 mm when fresh), in*dehiscent* 101

b. Leaves (7–)9–37 cm long, below with *discoid glands* in rows between the secondary veins; pairs of secondary veins 6–13. Ovaries 3- (or 4-)locular. Fruits 34–75 mm diam., *loculicidally dehiscent*. — Sunda Shelf .... **14. B. macrocarpa**

101a. Leaves papery. Ovaries 3-locular. Fruits sparsely hairy outside; *pedicels* 2–8 mm long. — Sunda Shelf ..... **6. B. costulata**

b. Leaves (slightly) leathery. Ovaries 2-locular. Fruits densely hairy outside; *pedicels* 8–9 mm long. — Sunda Shelf ..... **21. B. multiflora**

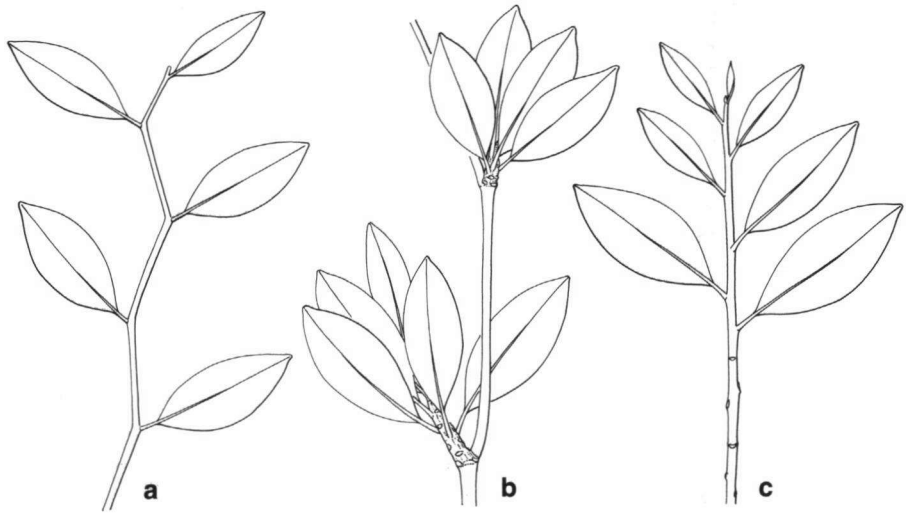


Fig. 3.1. Leaf arrangement. a. Distichous; b. Terminalia branching: dense tufts; c. Terminalia branching: open tufts.

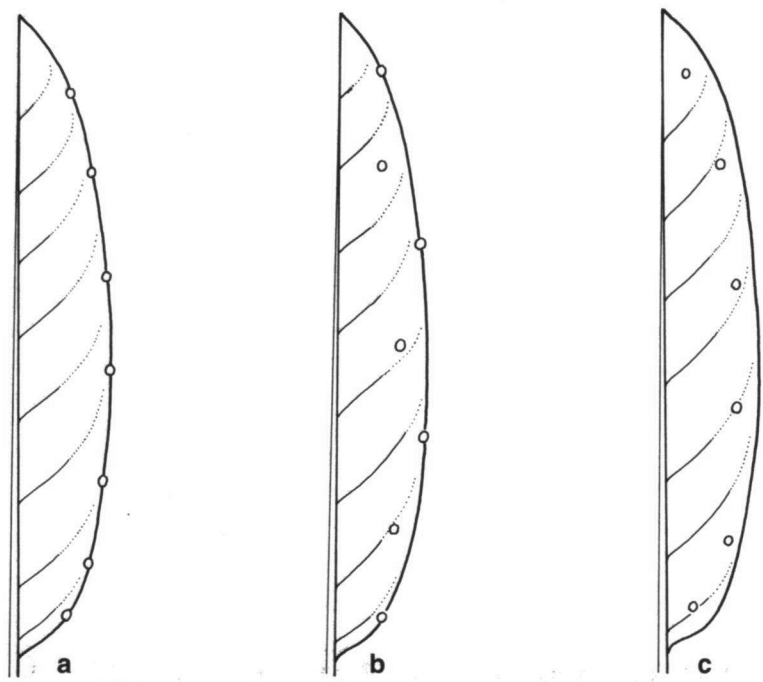


Fig. 3.2. Arrangement of marginal glands (lower leaf surface). a. Marginal only; b. marginal and submarginal; c. submarginal only.

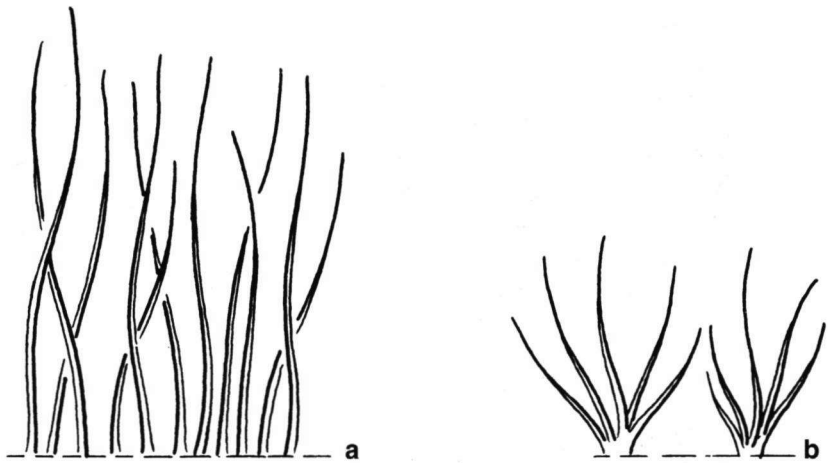


Fig. 3.3. Indumentum types. a. Simple hairs; b. stellate hair tufts.

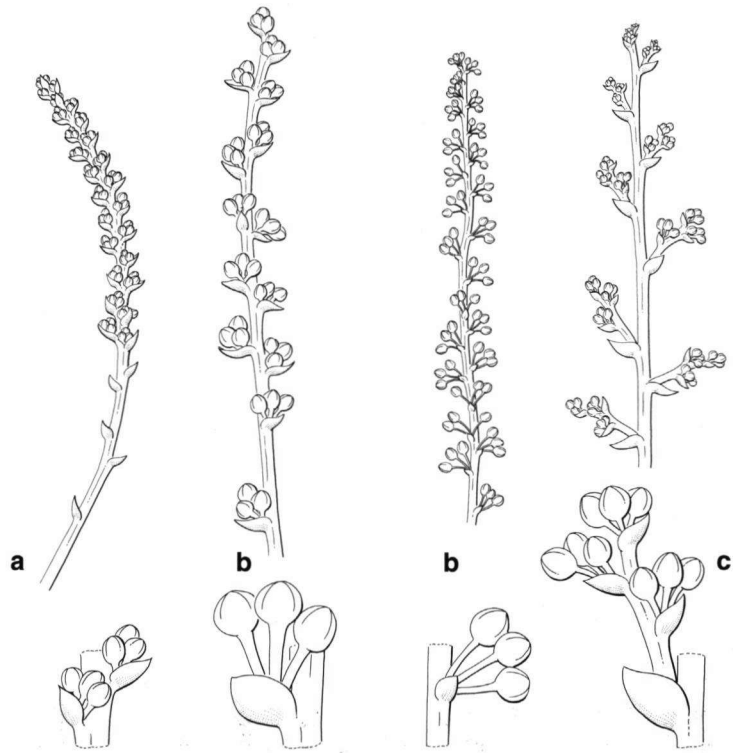


Fig. 3.4. Staminate inflorescences, branching patterns. a. Flowers arranged at the tip of the inflorescences, not branched; b. flowers scattered along inflorescences, not branched; c. flowers scattered along inflorescences, branched.

3.2.3 – *Regional keys*

Key to the species of India and Southeast Asian mainland north of the Isthmus of Kra [Words in *italics* are explained in the glossary (p. 205)]

1a. Twigs *glabrous* to sparsely hairy. Leaves 2.6–8.8 cm wide; lower surface usually sparsely hairy 2
b. Twigs densely hairy. Leaves 9.5–12.1 cm wide; lower surface densely hairy .. .. **2. B. annamensis**
2a. Plants with *staminate* inflorescences 3
b. Plants with *pistillate* inflorescences or fruits 5
3a. Flowers red to pink; *bracts* unknown or 0.4–1.3 mm long 4
b. Flowers cream to yellow; *bracts* (1.5–)3–4.5 mm long ..... **34. B. ramiflora**
4a. Inflorescences solitary or in clusters of many; rachis less than 1 mm thick. — S India ..... **7. B. courtallensis**
b. Inflorescences solitary; rachis more than 1 mm thick. — Burma .... **29. B. ptychopyxis**
5a. (2) Flowers yellow to green; ovaries not winged. Fruits globose 6
b. Flowers reddish; ovaries winged. Fruits ellipsoid (*fusiform*) **29. B. ptychopyxis**
6a. Sepals sub*glabrous* outside; stylar lobes densely hairy below. Seed *arillode* yellow; cotyledons c. 12 mm long. — Southeast Asian mainland .... **34. B. ramiflora**
b. Sepals densely hairy outside; stylar lobes sub*glabrous* below. Seed *arillode* blue to white; cotyledons 5–9 mm long. — S India ..... **7. B. courtallensis**

Key to the species of Sulawesi, the Moluccas and Halmahera [Words in *italics* are explained in the glossary (p. 205)]

1a. Leaves arranged in open tufts (Fig. 3.1c) 2
b. Leaves arranged in dense tufts (Fig. 3.1b) 4
2a. Twigs and nervation on the lower leaf surface sparsely hairy. Stipules 3.5–7.5 mm long. Indumentum consisting of *stellate* hair tufts and simple hairs (Fig. 3.3a, b). Pairs of secondary veins 4–10 3
b. Twigs and nervation on the lower leaf surface densely hairy. Stipules 5–10 mm long. Indumentum consisting of simple hairs only (Fig. 3.3a). Pairs of secondary veins 10–17 ..... **20. B. motleyana**
3a. *Staminate bracteoles* absent or 1 per branchlet; sepals 4–6. *Pistillate* inflorescences along the branches to *axillary*. Fruit columns 11–13.5 mm long; *pedicels* 8.5–15 mm long ..... **22. B. nanihua**
b. *Staminate bracteoles* 7–12 per branchlet; sepals 3 or 4. *Pistillate* inflorescences *axillary*. Fruit columns 16–23 mm long; *pedicels* 4.5–9 mm long .... **27. B. philippinensis**
4a. (1) Inflorescences *axillary* to rarely along the branches. *Staminate* inflorescences with 1 *bract* per branchlet. Ovaries 2-locular. Fruits 6.5–15 mm diam. 5
b. Inflorescences *cauline* to just below the leaves. *Staminate* inflorescences with 3 *bracts* per branchlet. Ovaries 3-locular. Fruits 16–30 mm diam. .... **33. B. racemosa**

5a. Branchlets sometimes thickened at the tips. Leaves sometimes whitish when dry. Sepals sparsely to densely hairy outside. *Pistillate* inflorescences usually sparsely to densely hairy. Infructescences 3–28 cm long. Fruits red to pink, rarely yellow ..... **41. B. tetrandra**

b. Branchlets not thickened at the tips. Leaves not whitish when dry. Sepals *glabrous* to sub*glabrous* outside. *Pistillate* inflorescences usually *glabrous*. Infructescences 1–5 cm long. Fruits yellow to orange ..... **12. B. javanica**

Key to the species of the Philippines (excluding Palawan) [Words in *italics* are explained in the glossary (p. 205)]

1a. Leaves arranged in dense tufts (Fig. 3.1b). Indumentum consisting of simple hairs only. Leaves whitish when dry. *Staminate* inflorescences not branched (Fig. 3.4a, b). Ovaries 2-locular. ..... **41. B. tetrandra**

b. Leaves arranged in open tufts (Fig. 3.1c). Indumentum consisting of *stellate* hair tufts and simple hairs. Leaves brown when dry. *Staminate* inflorescences branched (Fig. 3.4c). Ovaries 3-locular ..... **27. B. philippinensis**

Key to the species of New Guinea and surrounding islands [Words in *italics* are explained in the glossary (p. 205)]

1a. Indumentum consisting of simple hairs only (or *glabrous*, best visible on the lower leaf surface) (Fig. 3.3a; use dissecting microscope or strong hand lens) 2

b. Indumentum consisting of *stellate* hair tufts and simple hairs (best visible on the lower leaf surface) (Fig. 3.3a, b; use dissecting microscope or strong hand lens) ..... **22. B. nanihua**

2a. *Petioles pulvinate* apically only. *Staminate* inflorescences solitary or in clusters of up to 10; *cauline* to *axillary* 3

b. *Petioles pulvinate* basally and apically. *Staminate* inflorescences in clusters of 10 or more; *cauline* ..... **31. B. purpurea**

3a. Pairs of secondary veins 4–9 4

b. Pairs of secondary veins 10–15 5

4a. Stipules 5–11.5 mm long. Leaves 15–29 cm long. *Staminate* flowers 1.5–1.8 mm diam. Fruits c. 12 mm diam. ..... **5. B. carinata**

b. Stipules 3–6.5 mm long. Leaves 8–20.5 cm long. *Staminate* flowers 1.8–3.5 mm diam. Fruits 24–40 mm diam. ..... **25. B. papuana**

5a. (3) *Petioles* 8–31 mm long. Leaves 3.5–12.9 cm long. *Pistillate* inflorescences along the branches to *axillary*; ovaries 2-locular 6

b. *Petioles* 7–60 mm long. Leaves 8–20.5 cm long. *Pistillate* inflorescences *cauline*; ovaries 3- or 4-locular ..... **25. B. papuana**

6a. Lower leaf surfaces without *discoid glands*. Fruits 9–10.5 mm long; irregularly dehiscing ..... **17. B. microcarpa**

b. Lower leaf surfaces with *discoid glands*. Fruits 16–21 mm long; *loculicidally dehiscent* ..... **23. B. nesophila**

Key to the species of the Pacific Islands [Words in *italics* are explained in the glossary (p. 205)]

1a. Twigs and *petioles* densely hairy. *Staminate* inflorescences unbranched or with lateral branches of up to 0.3 mm; *pedicel* 0.5–1.3 mm long. Fruits *loculicidally dehiscent* ..... **37. B. seemannii**

b. Twigs and *petioles glabrous* to sparsely hairy. *Staminate* inflorescences with lateral branches of 1.5–4.5 mm; *pedicel* 0.2–0.5 mm long. Fruits in*dehiscent* or only outer layer *loculicidally dehiscent* ..... **40. B. taitensis**

3.2.4 – *Species descriptions*

1. Baccaurea angulata Merr. — Fig. 3.5, Map 3.1, Photo 1

Baccaurea angulata Merr., Univ. Calif. Publ. Bot. 15 (1929) 148; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 35; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 46. — Type: *Elmer 21842* (holo A; iso B, DS, G, L, U), Borneo, Sabah, Tawau.

Tree 6–21 m high, dbh 9.6–40 cm, buttresses absent; branchlets glabrous; young shoots pale straw when fresh, green-grey to blackish when dry; Terminalia branching pattern weakly developed. *Indumentum* of simple hairs. *Bark* grey-brown to red-brown to green when fresh, grey when dry, smooth to rough, flaky, soft to hard, corky; inner bark yellow to reddish to green, 0.6–4 mm thick. *Heartwood* brown. *Leaves*: petiole 20–125 mm long, glabrous, brown to grey to greenish when dry, raised glands usually present; stipules 4–11 by 2–5 mm, glabrous to densely hairy outside, glabrous inside, margin ciliate, not hyaline; lamina elliptic to obovate, 12–39 by 4–13.6 cm, l/w ratio 2–4.4, thick leathery; base cuneate to attenuate (rounded); apex acuminate to cuspidate to rarely obtuse, (0)3–22 mm long; upper surface glabrous, raised glands absent, usually not granulate, dull to glossy dark green when fresh, grey to green to rarely brown when dry; lower surface glabrous, sometimes subglabrous at midrib, discoid glands absent, pale green with whitish midrib below when fresh, grey to green to rarely brown when dry; secondary veins 9–16 per side, closed at margin; nervation reticulate, not clearly visible. *Staminate inflorescences* cauline, few clustered together, 0.5–23 cm long, c. 1 mm thick, sparsely hairy, branching minute, up to 50-flowered, flowers

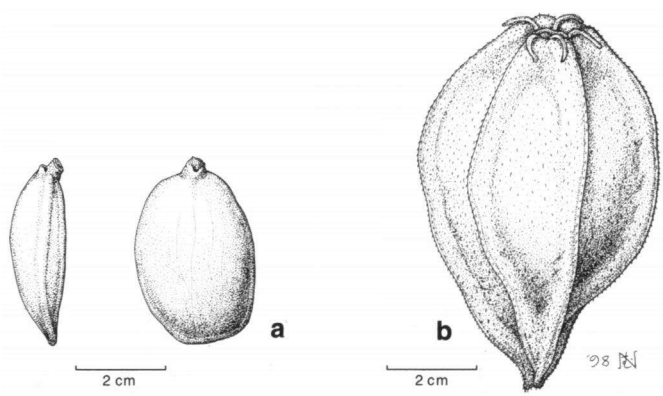
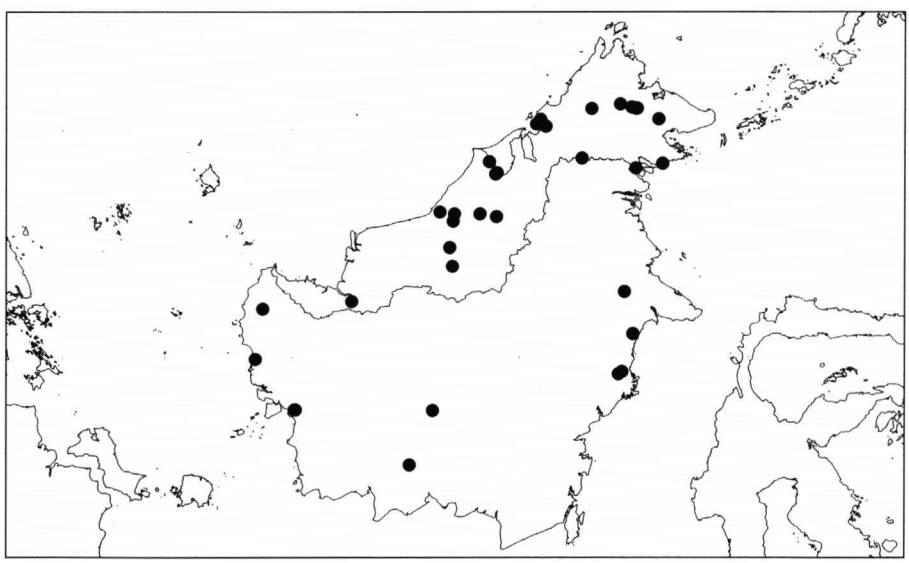


Fig. 3.5. *Baccaurea angulata* Merr. a. Seed; b. fruit (*Jacobs 5349*).

scattered along inflorescence, yellow; bracts 1 per branchlet, 1–1.5 mm long, densely hairy outside, glabrous inside, margin ciliate, not hyaline; bracteoles c. 0.5 mm long, 2 per cymule; cymules cylindrical, c. 0.5 mm long, densely hairy, 3-flowered. *Staminate flowers* 2–2.6 mm diam.; pedicel 2–4 mm long, upper part 1.2–2.5 mm long, densely hairy; sepals 4 or 5, obovate, 1.1–1.4 by 0.6–0.7 mm, apex slightly recurved, outside and inside densely hairy; staminodes 6; stamens 6, 0.6–0.8 mm long, glabrous; filaments 0.5–0.7 mm long, straight; anthers 0.1–0.2 by 0.2–0.25 by c. 0.1 mm; disc absent; pistillode obtriangular, c. 0.3 mm high, densely hairy, hollow. *Pistillate inflorescences* cauline to ramiflorous, solitary or up to 7 clustered together, 4–25 cm long, 1–3 mm thick, subglabrous to densely hairy, 8–many-flowered, red; pedicel 2.5–5.5 mm long, upper part thickened, 0.5–1 mm long, sparsely to densely hairy; bracts 3 per flower, sparsely to densely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 4–10 mm diam., pale yellow to cream yellow to greenish; sepals 5 (or 6), elliptic, (3.5–)8–11 by 1–2 mm, outside and inside densely hairy, persistent to caducous; ovary urn-shaped, 3–6 by 1.5–3 mm, 3-locular, densely hairy, wings 6; style absent; stigmas 0.7–1.5 mm long, cleft for upper 0–20(–50)%, persistent to rarely caducous; lobes 0.7–1.5 by 0.7–1.5 mm, glabrous to subglabrous above, glabrous to densely hairy below, protuberances above and below. *Fruits* obovoid, star-shaped in cross section, 1–3-seeded berries, 30–52 by 10–26 by 10–26 mm when dry, c. 50 by 26 mm when fresh, raised glands present, sparsely hairy outside, glabrous to subglabrous inside, red to purple to pink to red-brown; pericarp 1–2 mm thick, ruminate when dry; column 22–25 mm long, straight; pedicel 4–8 mm long, upper part 0.5–1 mm long. *Seeds* globose to ellipsoid, laterally flattened, 16–23 by 7–16 by 4–9.5 mm; arillode white; testa cream to greenish; cotyledons often folded, 8–12.5 by 6–11 by c. 0.1 mm; radicle 1.2–3 mm long; endosperm c. 1.5 mm thick.

Distribution — Borneo.



Map 3.1. Distribution of *Baccaurea angulata* Merr. in Borneo.

Habitat & Ecology — Primary and secondary rain forest, riverine and non-riverine forest. Soil: sandstone or laterite. Altitude: 0–800 m. Flowering: May, June, Aug., Oct., Nov. Fruiting: throughout the year.

Uses — Pericarp and arillode edible, sour to sweet.

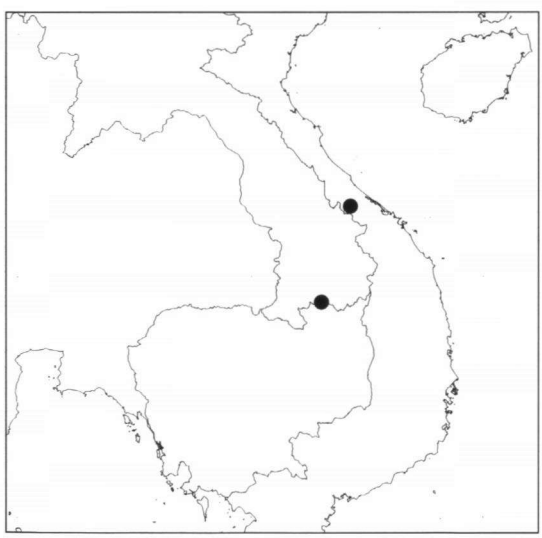
Vernacular names — Borneo (Kalimantan): Asem ketiak, pidau, umbing, umbung. Sarawak: Uchong, ujung (Iban). Brunei: Embaling bobou (Dusun); belimbing hutan. Sabah: Embaling (Dusun), belimbing uchong, pelawak, popotong, tampoi hutan.

2. **Baccaurea annamensis** Gagnep. — Map 3.2

Baccaurea annamensis Gagnep., Bull. Soc. Bot. France 71 (1923) 235; Fl. Gén. Indo-Chine 5 (1927) 550; Merr., Trans. Amer. Philos. Soc. New Ser. 24, 2 (1935) 233; Vu Van Dung, Vietnam For. Tr. (1996) 189. — Type: *Polaine 1269* (holo P; iso A, K), Indo-China, Prov. de Quang-tri, Lang-khoai.

Baccaurea harmandii Gagnep., Bull. Soc. Bot. France 71 (1923) 235; Fl. Gén. Indo-Chine 5 (1927) 550; Vu Van Dung, Vietnam For. Tr. (1996) 190, syn. nov. — Type: *Harmand 1436* (holo P; iso A), Laos, Attopeu Plateau.

Tree c. 6 m high, dbh c. 11 cm, branchlets densely hairy, Terminalia branching pattern weakly developed. *Indumentum* of simple hairs. *Bark* grey when fresh; inner bark brown to white when fresh; branchlets densely hairy. *Leaves*: petiole 24–55 mm long, densely hairy, rarely sparsely hairy, apically and often basally pulvinate, scars big, raised glands usually absent; stipules 5–6 by 2.5–3 mm, velutinous outside, glabrous inside, margin ciliate, not hyaline; lamina elliptic to slightly obovate, 19.5–28.5 by 9.5–12.1 cm, l/w ratio 2–2.4, papery; base cuneate to attenuate; apex cuspidate to acute, 8–20 mm long; upper surface glabrous, raised glands absent, grey to brown when dry; lower surface densely to sparsely hairy, velutinous on the midrib, raised and discoid glands absent, brown when dry; nervation (slightly) sunken above; secondary veins 8–10 per side, ending open; nervation reticulate to weakly scalariform. *Staminate inflorescences* cauline to just below the leaves (to axillary), solitary to



Map 3.2. Distribution of *Baccaurea annamensis* Gagnep. in Laos and Vietnam.

many clustered together, 2–19 cm long, 0.7–1.5 mm thick, velutinous, many-flowered, flowers scattered along inflorescence; bracts 1 per branchlet, prominent, triangular to lanceolate, 2–8.5 mm long, densely hairy outside and inside, margin ciliate, not hyaline; branching minute, cylindrical, 0–2.5 mm long, 3-flowered, densely hairy. *Staminate flowers* 2–3.5 mm diam., reddish; pedicel 1–1.9 mm long, upper part 0.3–0.7 mm long, densely hairy; sepals 4 or 5, obovate, (0.5–)1–2 by (0.4–)0.8–1.4 mm, apex recurved, densely hairy outside and inside; stamens 7 (or 8), 0.5–0.8 mm long, glabrous; filaments 0.2–0.5 mm long, straight; anthers 0.2–0.3 by 0.2–0.3 by c. 0.15 mm; disc present to absent; pistillode obtriangular, 0.8–1.1 mm high, densely hairy, slightly hollow. *Pistillate flowers* mainly unknown; ovary 4-locular. *Fruits* globose, c. 4-seeded, fleshy capsules, c. 30 mm diam., raised glands present, sparsely hairy outside, glabrous inside; pericarp c. 1 mm thick. *Seeds* ellipsoid, laterally flattened, 15–17 by 10–11 by 4.5–5.5 mm; cotyledons sometimes folded, c. 7.5 by 9 by 0.5 mm; radicle c. 0.5 mm long; endosperm c. 1 mm thick.

Distribution — Laos, Vietnam.

Habitat & Ecology — Flowering: Mar., Apr. Fruiting: Apr.

3. **Baccaurea bracteata** Müll.Arg. — Fig. 3.6, Map 3.3

Baccaurea bracteata Müll.Arg. in DC., Prodr. 15, 2 (1866) 466; Hook.f., Fl. Brit. India 5 (1887) 372; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 330; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 65; Ridl., Fl. Malay Penins. 3 (1924) 246; Merr., Univ. Calif. Publ. Bot. 15 (1929) 145; Pax & K. Hoffm., Mitt. Staatsinst. Allg. Bot. Hamburg 7 (1931) 233; Corner, Wayside Trees Mal. 1 (1940) 239; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 36; Airy Shaw, Kew Bull. 26 (1972) 219; Whitmore, Tree Fl. Malaya 2 (1973) 76; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 46; Kew Bull. 36 (1981) 260. — Type: *Wallich 7834* (holo K; iso G), Singapore and Penang (both are mentioned on specimen label).

Baccaurea crassifolia J.J. Sm., Bull. Jard. Bot. Buitenzorg 3, 1 (1920) 394; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 66; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 46; Kew Bull. 36 (1981) 260. — Type: *Hallier 2158* (holo L; iso BO, K), Borneo, Soengei Kenepai.

Treelet or tree 2–25 m high, dbh 4–40 cm, buttresses sometimes present, up to 1 m high, c. 13 cm thick, stilt roots rarely present, bole rarely fluted; branchlets glabrous to densely hairy, Terminalia branching pattern weakly developed. *Indumentum* of simple and stellate hairs. *Bark* brown to grey to pink to red to yellow when fresh, (dark to red-)brown to blackish when dry, 0.25–1 mm thick, usually smooth, hard, flaking in rectangular flakes of c. 10 by 2 mm; inner bark red to pale yellow to (red)-brown to green to pink, 0.25–8 mm thick, hard to soft. *Heartwood* pink to brown. *Leaves*: petiole 8–65(–87) mm long, subglabrous to densely hairy, simple hairs longer than those of the stellate tufts, transverse cracks often present, (pink)brown when fresh, black to red brown when dry, raised glands usually absent; stipules triangular, 2–6 by 1–2.5 mm, subglabrous to velutinous outside, glabrous to subglabrous inside, rarely densely hairy, margin ciliate, not hyaline; lamina ovate to elliptic (to obovate), 3.5–21 by 1.7–9.8 cm, l/w ratio 1.4–3.4, papery to sub-leathery; base truncate to attenuate; marginal glands sometimes slightly visible as small indentations; apex obtuse to cuspidate, up to 20 mm long; upper surface glabrous to subglabrous, small raised glands present, granulate, white green to dark green when fresh, pale to dark green-

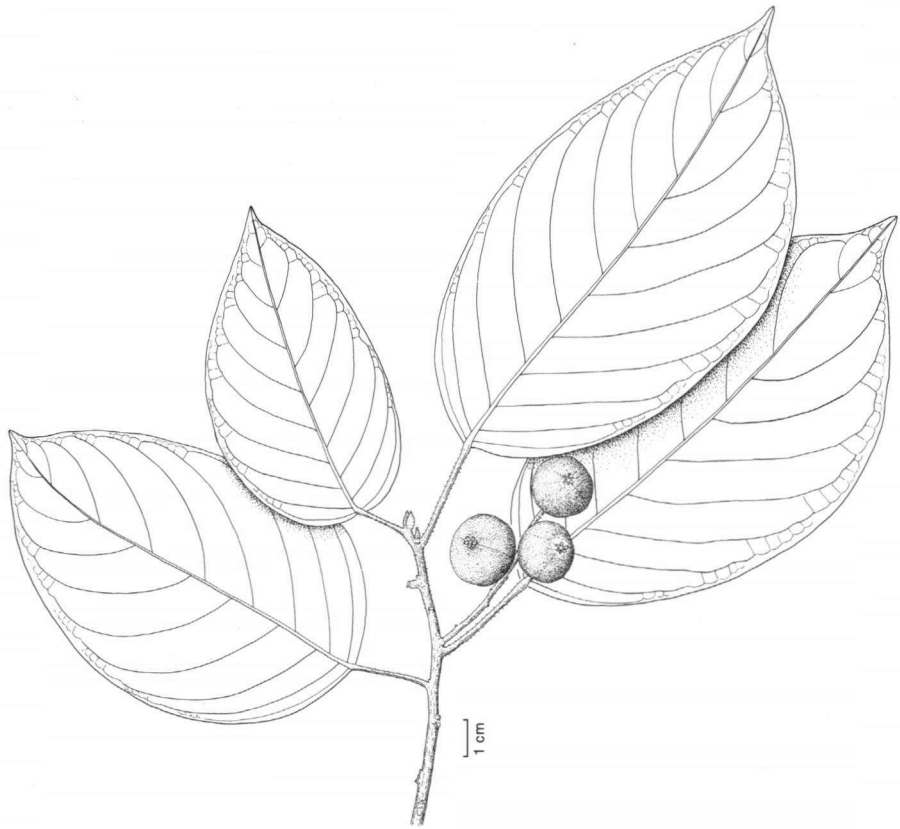
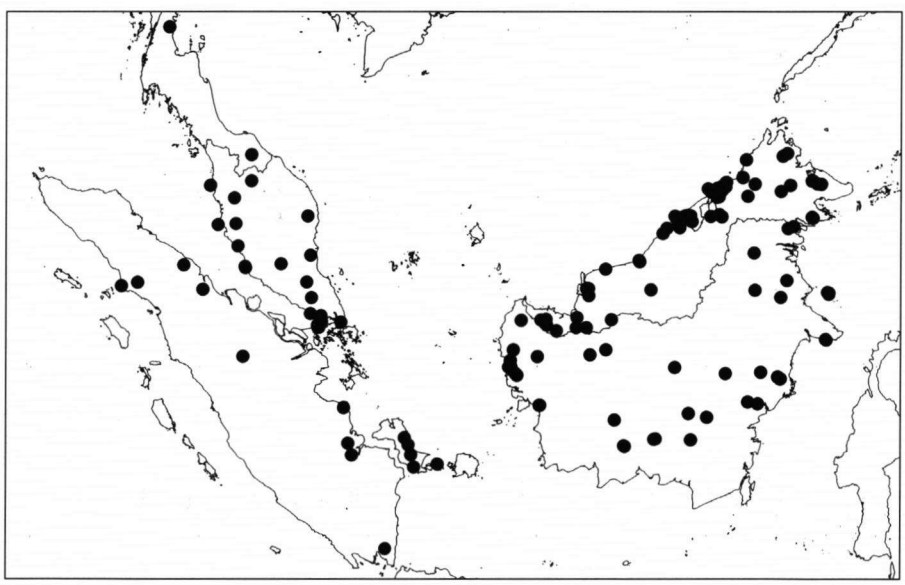


Fig. 3.6. *Baccaurea bracteata* Müll. Arg. Habit with infructescence (*Sidiyasa & Ambriansyah 812*).

brown when dry; lower surface sparsely hairy to rarely densely hairy, sparsely hairy to velutinous on the midrib (to subglabrous), stellate hair-tufts at base with a conspicuous black gland, discoid glands usually present, placed in rows to scattered, raised glands sometimes present, bigger, white to pale green below when fresh, (pale) green-brown below when dry; nervation whitish to black-brown above when dry, blackish brown below, often sunken above; secondary veins 3–8 per side, not to almost closed at margin; nervation reticulate to weakly scalariform. *Staminate inflorescences* axillary to just below the leaves, solitary to 3 clustered together, 0.5–16 cm long, 0.5–1.2 mm thick, sparsely hairy to velutinous, branched, c. 10–100-flowered, flowers scattered along inflorescence, red; sometimes leaf-like bracts present; bracts 1 per branchlet, (broadly) ovate to triangular, conspicuous, 2–6 mm long, caducous to persistent, margin ciliate, sometimes hyaline, densely hairy to rarely subglabrous outside, glabrous inside, red to pale green; bracteoles c. 6, 1–5 mm long; branchlets cylindrical, 2–15 mm long, densely hairy, (3- or) 4–17(–40-)flowered. *Staminate flowers* 1.5–2.9 mm diam., caducous at the moment of opening; pedicel 0.3–1.2 mm long, upper part c. 0.1–1.1 mm long, densely hairy; sepals 4 or 5, ovate, 1–2.2 by 0.6–1.5 mm, apex recurved, densely hairy outside and inside, white to yellow to green to pink to red to brown

when fresh; stamens 4 or 5, 0.25–0.5 mm long, glabrous, yellow; filaments 0.05–0.3 mm long, straight; anthers 0.1–0.25 by 0.15–0.2 by c. 0.1 mm, light yellow to reddish; disc absent; pistillode usually present, cylindrical to globose, up to 1 mm high, densely hairy, solid. *Pistillate inflorescences* axillary to just below the leaves, solitary, 1–6.5 cm long, in Borneo up to 16 cm long, c. 1.5 mm thick, sometimes branched, densely hairy, 5–30-flowered; pedicel 1–5 mm long, upper part 0.5–2 mm long, densely hairy, raised glands often present; bracts 1–6 per branchlet, (broadly) ovate, velutinous outside, glabrous inside, margin ciliate, persistent to caducous; rachis pink to brown-red to yellow-brown-green. *Pistillate flowers* 4–12 mm diam., yellowish to greenish to (red)brown; sepals 4 or 5 (or 6), ovate to elliptic, 3.5–11 by 0.9–3.5 mm, outside and inside densely hairy, caducous to persistent; staminodes rarely present; ovary cylindrical to globose, 2–4 by 1.5–3 mm, 2- or 3-locular, velutinous, wings absent (to 6), brown-yellow; style 0–1.6 by 0.5–1 mm, velutinous, pale yellow green; stigmas 0.9–2.5 mm long, cleft for upper 70–90%, persistent to caducous; lobes 0.8–1.8 by 0.2–0.5 mm, glabrous to subglabrous, protuberances small above, below densely hairy, protuberances strong. *Fruits* globose to triangular, 3–6-seeded, fleshy capsules, 19–25 mm diam. when fresh, 10.5–23 by 14–25 by 14–25 mm when dry, only partly loculicidally dehiscent, raised glands usually present, subglabrous to densely hairy outside, glabrous to sparsely hairy inside, septa subglabrous to sparsely hairy, red to orange-brown-green; pericarp 1–4.5 mm thick, often ruminate when dry; column 8–19.5 mm long, straight, persistent; pedicel 3–9 mm long, upper part 1.5–4.5 mm long, sometimes thickened. *Seeds* ovoid to obovoid, (6.2–)7–10 by (4–)4.5–6.5 by 3–4.8 mm; arillode (orange) yellow; testa white; cotyledons sometimes folded, 3–5 by (3–)4–5.5 by 0.05–0.1 mm; radicle 0.5–1.5 mm long; endosperm 0.5–1 mm thick.

Distribution — Thailand, Peninsular Malaysia, Sumatra, Borneo.



Map 3.3. Distribution of *Baccaurea bracteata* Müll. Arg. in Thailand, Peninsular Malaysia, Sumatra and Borneo.

Habitat & Ecology — Primary or secondary rain forest, freshwater swamp, peat swamp, heath swamp, kerangas, rarely in mangrove forest. Altitude: sea level up to 390(–900) m. Soil: usually white sand. Flowering and fruiting: throughout the year. Fruits eaten by birds.

Uses — Sarawak: Shoots are used in making laminaang (= Dayak Kenya longhouse). Sabah: used for construction; arillode and pericarp edible, sour.

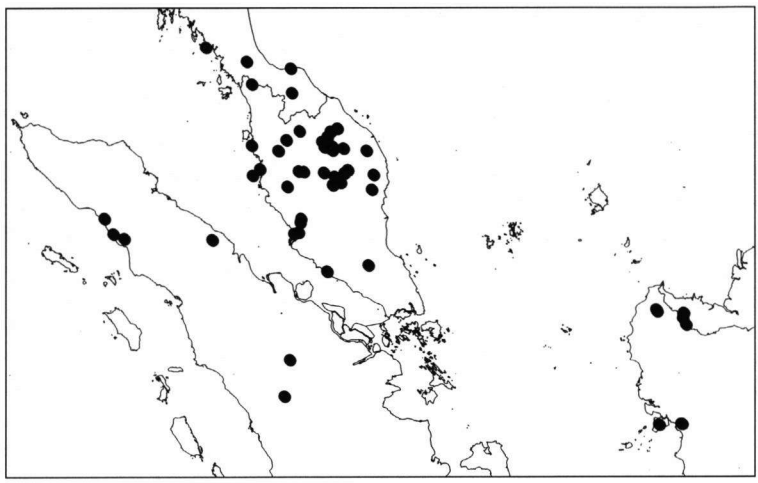
Vernacular names — Thailand: Khao-rang. Sumatra: Berat mata, tampui kaka. Bangka: Kelempa. Borneo: Kapul pugi nentalon, pugi ranau (Dusun); tampoi paya (Brunei, Kedayan); puak, puak burong, pugi barong (Iban); depot kayu masam (Mili); kelibon (Murut); jemating, selantikan, tampoi hutan, tampoi-tampoi hutan, tampoi munyit, terai rapak.

Note — See note *B. simaloerensis*.

4. **Baccaurea brevipes** Hook.f. — Map 3.4

Baccaurea brevipes Hook.f., Fl. Brit. India 5 (1887) 372; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 73; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 58; Ridl., Fl. Malay Penins. 3 (1924) 250; Corner, Wayside Trees Mal. 1 (1940) 239; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 36; Whitmore, Tree Fl. Malaya 2 (1973) 66; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 47; Kew Bull. 36 (1981) 260. — Type: *Maingay KD 1366* (lecto K, selected here; isolecto L), Peninsular Malaysia.

Tree 3–10 m high, dbh 4–15 cm, buttresses absent; branchlets glabrous, densely hairy when young, Terminalia branching pattern weakly developed. *Indumentum* of simple hairs. *Bark* brown to grey to cream to white to green when fresh, brown when dry; inner bark (orange-)brown to white. *Leaves*: petiole 11–50 mm long, sparsely to densely hairy, usually not apically pulvinate, raised glands often absent; stipules 8–16 by 2–5 mm, glabrous on both sides, midrib velutinous outside, margin ciliate, not hyaline, caducous to late caducous; lamina elliptic to obovate, 15–35 by 6.2–14.4 cm, l/w ratio 1.9–3, papery; base cuneate to rounded; apex cuspidate to acute to rarely rounded, (0–)6–20 mm long; upper surface glabrous, raised glands absent, not granulate, brown when dry; lower surface densely to sparsely hairy, discoid glands absent, brown when dry; secondary veins 11–15 per side, sometimes closed at margin; nervation scalariform to somewhat reticulate. *Staminate inflorescences* ramiflorous to just below the leaves (to axillary), solitary to 8 clustered together, 8–17.5 cm long, up to 1.5 mm thick, velutinous, many-flowered, flowers scattered along inflorescence; bracts 1–3 per branchlet, 1.5–6 mm long, densely hairy outside, glabrous inside, margin ciliate, not hyaline, persistent; branchlets present to absent, cylindrical, 0–1 mm long, velutinous, 3-flowered. *Staminate flowers* 1.5–3 mm diam., yellowish green; pedicel 1.7–2.2 mm long, upper part 0.7–1.1 mm long, densely hairy; sepals 3–6, obovate or different in shape, 0.5–2 by 0.5–1.4 mm, apex recurved, densely hairy outside and inside; stamens 5, 0.5–1 mm long, glabrous; filaments 0.3–0.9 mm long, geniculate; anthers 0.1–0.2 by 0.1–0.2 by 0.1–0.3 mm; disc present to absent; pistillode obtriangular to globose, 0.4–1.1 mm high, densely hairy to velutinous, solid. *Pistillate inflorescences* cauline (to ramiflorous to axillary), solitary to 3-clustered together, 12–22.5 cm long, 0.7–3 mm thick, densely hairy, many-flowered; rachis pink; pedicel 0–4.5 mm long, upper part 0–1.2 mm long, velutinous; bracts 3 per branchlet, densely hairy outside, glabrous



Map 3.4. Distribution of *Baccaurea brevipes* Hook. f. in Thailand, Peninsular Malaysia, Sumatra and NW Borneo.

inside, ciliate, persistent. *Pistillate flowers* 5–7 mm diam.; sepals 4, obovate to elliptic, 5.6–6.5 by 1.5–3.5 mm, densely hairy, caducous to persistent; ovary globose, 2.2–2.6 by 2.2–3 mm, 2- or 3-locular, velutinous; style c. 0.2 by 1 mm wide, velutinous; stigmas c. 1 mm long, persistent. *Fruits* globose, 1–3-seeded, fleshy capsules to berries, 14–20 by 10–18.5 by 10–17 mm, not dehiscing to rarely splitting, raised glands present, glabrous to densely hairy outside, glabrous inside, white to red to pink; pericarp 0.5–1.5 mm thick; column 15–17 mm long, straight, persistent; pedicel 1–5 mm long, upper part 0.1–1 mm long. *Seeds* ellipsoid, laterally flattened, 8–13 by 6–8 by 3.1–5 mm; arillode blue to violet to rarely red; testa brown; cotyledons 5–7 by 6–7 by < 0.1 mm; radicle c. 1 mm long.

Distribution — Thailand, Peninsular Malaysia, Sumatra, NW Borneo.

Habitat & Ecology — Primary and secondary rain forest, and seasonal swamp forest. Altitude: 20–700 m. Soil: sand, clay or granite. Flowering: Dec. to Apr. Fruiting: May, July to Nov.

Uses — Locally grown for fruits.

Vernacular names — Peninsular Malaysia: Rambai, rambai hutan.

5. **Baccaurea carinata** Haegens, *spec. nov.* — Map 3.5

> Ab omnibus congeneribus malesianis praeter combinationem charactorum sequentium truncus non nodosus, folia in caespitibus terminalibus laxis papyracea brunnea i.s., supra costa glabra, indumento simplici, infra subglabra, costa nervisque glabris ad dense pubescentibus, stamina 6–9, fructus inalati indehiscentes differt. — Typus: *Hoogland & Craven 10350* (holo L), Papua New Guinea, East Sepik Province, Ambunti subdistrict, near Melawei.

Shrub to tree 7.5–10.5 m high; branchlets glabrous, densely hairy when young, Terminalia branching pattern weakly developed. *Indumentum* of simple hairs. *Bark* grey-brown when fresh, flaky; inner bark white, c. 2.5 mm thick. *Leaves*: petiole 21–59

mm long, glabrous to sparsely (to densely) hairy, transverse cracks usually absent, (dark to red-)brown when dry, raised glands absent to present; stipules 5–11.5 by 2–4.5 mm, glabrous outside, midrib glabrous to densely hairy, margin ciliate, hyaline or not; lamina ovate to obovate, 15–29 by 9.3–15.3 cm, l/w ratio 1.8–2.0, papery to slightly leathery; base attenuate to cuneate; apex rounded to acute, up to 10 mm long; upper surface glabrous, raised glands sometimes present, dark brown to greyish when dry; lower surface glabrous to subglabrous, midrib and secondary veins glabrous to densely hairy, raised glands present, discoid glands absent, (dark) brown when dry; nervation whitish to (light to dark) brown above when dry, (light to red) brown below when dry; secondary veins 10–15 per side, not completely parallel, closed at margin; nervation reticulate to weakly scalariform. *Staminate inflorescences* axillary to cauline, few clustered together, (4–)7–17 cm long, c. 1 mm thick, densely hairy, subglabrous at base, many-flowered, flowers scattered along inflorescence; bracts 3 per branchlet, 0.5(–2) mm long, glabrous to densely hairy outside, glabrous inside, margin ciliate, not hyaline; branchlets minute, 3-flowered. *Staminate flowers* 1.5–1.8 mm diam., yellow; pedicel 1.5–1.8 mm long, upper part 0.8–1 mm long, densely hairy; sepals 4, ovate, c. 1 mm long, apex straight, densely hairy outside and inside; stamens 6–9, c. 0.5 mm long, glabrous; filaments c. 0.3 mm long, straight; anthers c. 0.2 by 0.25 by 0.1 mm; disc absent; pistillode obtriangular, c. 0.5 mm high, densely hairy, solid. *Pistillate inflorescences* cauline, many clustered together; bracts 3 per branchlet. *Pistillate flowers*: sepals caducous; ovary 3-locular; stigmas persistent. *Infructescences* 8–13 cm long, 1.5–2.5 mm thick. *Fruits* ellipsoid, usually 5-seeded berries, c. 21 by 12 by 12 mm, slightly ruminate when dry, raised glands present, densely hairy outside, glabrous inside, green with pink tinges; pericarp c. 1 mm thick; column c. 17 mm long, straight; pedicel 3–5 mm long, upper part 1.5–3.5 mm long.

Distribution — Papua New Guinea (Prov.: E and W Sepik, Madang).

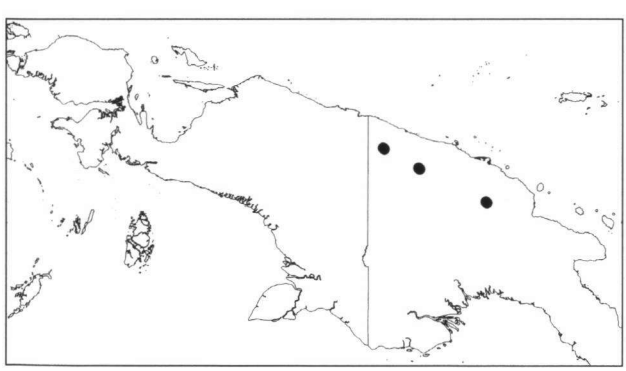
Habitat & Ecology — Secondary rain forest, swamp forest. Altitude: 50–100 m. Fruiting: Aug. to Sept.

Uses — Arillode edible.

Vernacular names — New Guinea: Mapiok (Waskuk).

Note — The species is named for its strongly and sharply raised midvein at the lower side of the lamina, which resembles a keel.

Specimens studied: *Hoogland & Craven 10350*; *Ledermann 6933*; *NGF 3861*; *Pullen 996*; *De Vriese s.n.* (L 994.355-118).

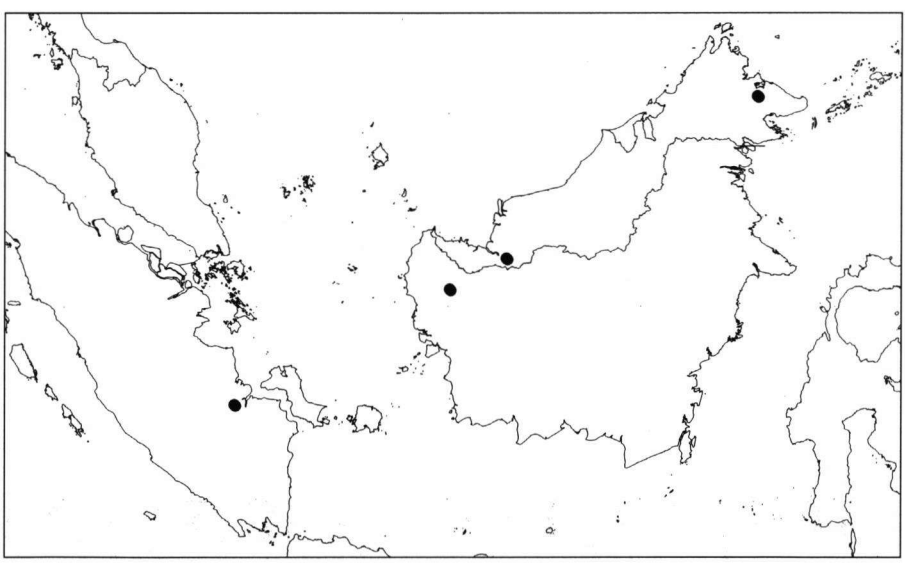


Map 3.5. Distribution of *Baccaurea carinata* Haegens in Papua New Guinea: E and W Sepik, Madang.

6. **Baccaurea costulata** (Miq.) Müll. Arg. — Map 3.6

Baccaurea costulata (Miq.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 464; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 68; S. Moore, J. Bot. Br. 63 (1925) 98; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 47; Kew Bull. 36 (1981) 261. — *Mappa costulata* Miq., Fl. Ned. Ind., Eerste bijv. (1861) 459. — *Pierardia costulata* (Miq.) Müll. Arg., Flora 47 (1864) 469. — Type: *Teijsmann HB 3655* (holo U), Sumatra, Palembang, near Tubuan, Oga-ulu.

Tree up to 10–30 m high, dbh up to 28 cm, buttresses absent; branchlets glabrous to sparsely hairy, densely hairy when young, Terminalia branching pattern weakly developed. *Indumentum* of simple and stellate hairs. *Bark* grey, flaky. *Leaves*: petiole 9–47 mm long, glabrous to densely hairy, transversal stripes sometimes present, brown when dry, raised glands absent; stipules 2.5–5.5 by 1–2.5 mm, densely hairy outside, glabrous inside, base inside densely hairy, margin ciliate, not hyaline; lamina ovate to obovate, 6.1–19.6 by 2.3–7 cm, l/w ratio 2–2.7, papery to slightly leathery; base rounded to cuneate; apex obtuse to cuspidate, up to 21 mm long; upper surface glabrous, raised glands absent, sometimes punctuate, (dark) brown to grey when dry; lower surface (sub)glabrous, densely hairy at secondary veins, discoid glands absent or present, if present in a row between two secondary veins, (light) brown when dry; secondary veins 5–8 per side, closed at margin or almost so; nervation reticulate to weakly scalariform. *Staminate inflorescences* axillary to somewhat ramiflorous, solitary, 1.5–4 cm long, c. 1 mm thick, densely hairy, many-flowered, flowers scattered along inflorescence; bracts 1–1.5 mm long, 1 per branchlet, margin ciliate, not hyaline, densely hairy outside, sparsely hairy inside, persistent; branchlets cylindrical, 1.5–3 mm long, densely hairy, 3–6-flowered. *Staminate flowers* 1–2.5 mm diam.; pedicel 1–1.5 mm long, upper part 0.5–1 mm, densely hairy; sepals 4 or 5, ovate, 1–1.7 by 0.6–1 mm,



Map 3.6. Distribution of *Baccaurea costulata* (Miq.) Müll. Arg. in Sumatra and Borneo.

outside and inside densely hairy; disc absent; stamens 5, c. 0.3 mm long, glabrous; filaments c. 0.15 mm long, straight; anthers c. 0.15 by c. 0.3 by c. 0.15 mm; pistillode, cylindrical to globose, 1.1–1.2 mm high, densely hairy, solid. *Pistillate inflorescences* axillary to ramiflorous, solitary. *Pistillate flowers*: sepals 4 or 5, persistent; ovary 3-locular; stigmas sessile, bifid, persistent. *Infructescences* 0.8–3.7(–13) cm long, 1.5–4 mm thick. *Fruits* 3- (or 4-)seeded, globose berries, 19–30 by 23–30 by 23–30 mm, 50 mm diam. when fresh, glabrous to sparsely hairy outside, subglabrous to sparsely hairy inside, raised glands usually absent; pericarp 1–4.5 mm thick; column 19–25 mm long, straight, persistent; pedicel 2–8 mm long, upper part 0.5–2 mm long. *Seeds* subglobose, laterally flattened, 12–19 by 11–16 by 3–8 mm; cotyledons c. 8.5–12.3 by 9.5–10.8 by 0.1 mm; radicle c. 1.5 mm long.

Distribution — Sumatra, Borneo.

Habitat & Ecology — Altitude: up to 450 m. Flowering: unknown. Fruiting: Feb., Apr., July, Aug.

Uses — Arillode edible, with a bitter aftertaste.

Vernacular names — Borneo: Kampul (Dayak).

Note — In *Baccaurea* the vegetative parts of male and female plants usually closely resemble each other. This species, however, causes some interpretation problems, because the similarity between male and female is not 100%. The male type specimen is clearly different from all other material. Three fruiting specimens resemble this male specimen most (they do not fit into other species). The female flowering and fruiting specimens, that traditionally have been included here, are hesitantly accepted by me.

7. **Baccaurea courtallensis** (Wight) Müll.Arg. — Map 3.7

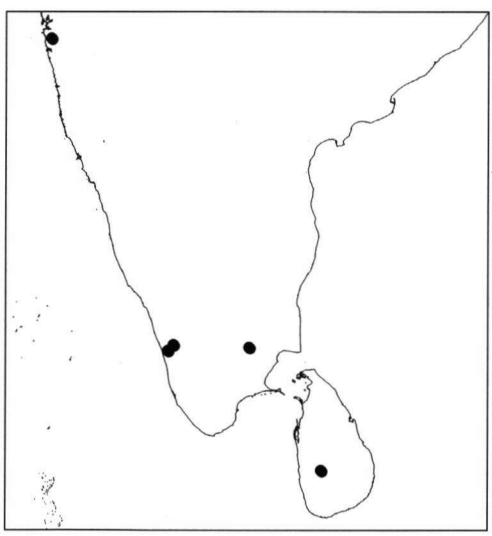
Baccaurea courtallensis (Wight) Müll.Arg. in DC., Prodr. 15, 2 (1866) 459; Hook.f., Fl. Brit. India 5 (1887) 367; Brandis, Indian Trees (1906) 563; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 54. — *Pierardia courtallensis* Wight, Icon. Pl. Ind. Orient. (1852) 30. — Type: *Wight KD 2675* (holo K; iso A, GH, L), India, Madras.

Tree 2–18 m high, dbh 7–18 cm, buttresses absent; branchlets subglabrous, densely hairy when young; young shoots (dark) brown to dark grey when dry, Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* pale brown when fresh. *Leaves*: petiole 7–41 mm long, glabrous to sparsely hairy, (dark) brown to green-brown when dry, transverse cracks absent to poorly developed, raised glands present; stipules 3–4.5 by 1–2.6 mm, glabrous to subglabrous outside, often densely hairy at base, midrib sparsely to densely hairy, inside glabrous, margin sometimes ciliate, sometimes hyaline; lamina elliptic to obovate, 6–18 by 2.6–7 cm, l/w ratio 2.2–3.1, papery; base cuneate to attenuate; apex acute to cuspidate to obtuse, up to 20 mm long; upper surface glabrous, raised glands often present, often granulate, (dark) brown to (shiny) grey when dry, nervation pale to dark brown; lower surface glabrous to sparsely hairy, nervation subglabrous to densely hairy, raised glands often present, discoid glands absent, green-brown to (pale) brown when dry, nervation (pale) brown to red-brown below; secondary veins 4–7 per side, often closed at margin; nervation reticulate. *Staminate inflorescences* axillary to cauline, solitary to many clustered together, 2–17.5 cm long, 0.4–1 mm thick, branching minute, sparsely hairy to velutinous,

many-flowered, flowers scattered along inflorescence or absent at base; bracts 1 (or 2) per branchlet, 0.4–1.3 mm long, subglabrous to densely hairy outside, (sub)-glabrous inside, margin ciliate, usually not hyaline; bracteoles absent or 2, up to 0.3 mm long; branchlets absent to cylindrical, 0–1 mm long, 3-flowered. *Staminate flowers* 1.5–3.5 mm diam., red to red-pink; pedicel 0.5–2.3 mm long, upper part 0.2–1 mm long, subglabrous to densely hairy; sepals 4–6, ovate to obovate, 1–1.7 by 0.4–1.3 mm, apex recurved, glabrous to densely hairy outside, subglabrous to densely hairy inside; stamens 5–8, 0.4–1 mm long, glabrous; filaments 0.2–0.7 mm long, straight; anthers 0.2–0.35 by 0.25–0.45 by c. 0.15 mm; disc absent; pistillode obtriangular, 0.3–0.8 mm high, densely short hairy, solid. *Pistillate inflorescences* probably ramiflorous to cauline, few clustered together, up to 28 cm long, 0.8–1.5 mm thick, subglabrous to densely hairy, many-flowered; pedicel 2.5–5 mm long, upper part 0.8–1 mm long, densely hairy; bracts 3 per branchlet, subglabrous outside, glabrous inside, margin ciliate. *Pistillate flowers* 3.5–7 mm diam.; sepals 4 or 5, ovate, 1.6–5 by 1–1.5 mm, subglabrous outside, densely hairy inside, caducous to rarely persistent; ovary cylindrical to globose, 2.5–5.5 by 3–4 mm, 3-locular, velutinous; style absent to 0.5 mm long, c. 1 mm wide, densely hairy; stigmas 0.7–1 mm long, cleft to halfway, caducous; lobes glabrous above with protuberances, densely hairy below. *Infructescences* 10.5–19 cm long, c. 2 mm thick. *Fruits* 3-seeded berries, globose, 26–42 by c. 35 by 35 mm, raised glands present, usually ruminate when dry, glabrous to sparsely hairy outside, glabrous inside, purple; pericarp 1–4 mm thick; column c. 30 mm long; pedicel c. 5 mm long. *Seeds* ellipsoid, laterally flattened, 13–19 by 8–15 by 4–12 mm; arillode probably yellow; cotyledons c. 12 by 10 by 0.1 mm; radicle 1.5 mm long; endosperm 2–2.5 mm thick.

Distribution — S and W India, Sri Lanka.

Habitat & Ecology — Secondary rain forest and swamp forest, and probably monsoon forest. Altitude: 750–1400 m. Flowering: Mar., May. Fruiting: June, Aug.



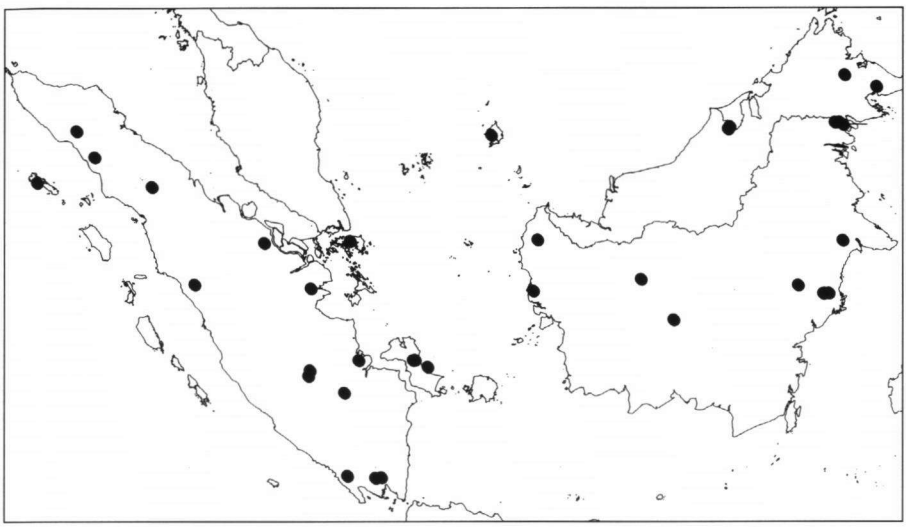
Map 3.7. Distribution of *Baccaurea courtallensis* (Wight) Müll. Arg. in S and W India and Sri Lanka.

8. Baccaurea deflexa Müll.Arg. — Fig. 3.7, Map 3.8

Baccaurea deflexa Müll.Arg. in DC., Prodr. 15, 2 (1866) 462; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 248; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 69; Merr., Univ. Calif. Publ. Bot. 15 (1929) 145; Backer & Bakh.f., Fl. Java 1 (1963) 454; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 37; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 47. — Type: *Zippelius s.n.* (lecto L, sheet 903.154-568, barcode L 0050885, selected here), probably Java.

Treelet or tree 6–25 m high, dbh 10–70 cm, buttresses rarely present, up to 1 m high; branchlets glabrous, densely hairy when young, Terminalia branching pattern weakly developed. *Indumentum* of simple and stellate hairs. *Bark* grey to brown reddish when fresh, brown when dry, up to 2 mm thick, smooth to rough, peeling off in strips of 5–10 mm long; inner bark red to brownish to yellowish. *Heartwood* reddish. *Leaves*: petiole 17–50 mm long, subglabrous to densely hairy, raised glands absent; stipules 3–6 by 1–2.5 mm, densely hairy outside, glabrous inside, margin ciliate, not hyaline; lamina ovate to obovate, 7.5–19.5 by 3.8–8.9 cm, l/w ratio 1.6–2.5, papery to slightly leathery; base acute to attenuate; marginal glands rarely as small indentations; apex acuminate to cuspidate, 4–14 mm long; upper surface glabrous, rarely granulate, brown to grey when dry; lower surface subglabrous to densely hairy, raised glands absent, few discoid glands sometimes present, (greyish) brown when dry; secondary veins (5 or) 6–8 (or 9) per side, closed at margin or almost so; nervation (weakly) scalariform, brown to white-brown when dry. *Staminate inflorescences* axillary to cauline, solitary to 4(–many) clustered together, 1–5 cm long, c. 1 mm thick, branched, densely hairy, many-flowered, flowers scattered along inflorescence; bracts 0.5–1 mm long, 1 or 3 (then 2 rudimentary) per branchlet, densely hairy outside, glabrous (to densely hairy?) inside, margin ciliate, not hyaline; branchlets cylindrical, 0.5–2.2 mm long, densely hairy, 3-flowered. *Staminate flowers* 1–2.5 mm diam., sessile, green; sepals 3 or 4, ovate, 0.5–1.5 by 0.5–1.5 mm, apex slightly recurved, outside and inside densely hairy; stamens (4–)6, 0.3–0.6 mm long, glabrous; filaments 0.3–0.5 mm long, straight; anthers 0.1–0.15 by 0.1–0.3 by 0.1–0.15 mm; disc absent; pistillode absent to present, globose, up to 0.3 mm high, velutinous, solid. *Pistillate inflorescences* axillary to ramiflorous, 1–3 clustered together, 3.5–9 cm long, 0.4–1 mm thick, densely hairy, many-flowered, yellow; pedicel 1–2.5 mm long, upper part 0.5–2 mm long, geniculate (90° bent), densely hairy; bracts 1 or 3 (2 very small) per branchlet, densely to sparsely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 1.6–3.1 mm diam., yellow-green; sepals (4 or) 5 or 6, ovate to triangular, 1–2 by 0.4–1.5 mm, outside and inside densely hairy, caducous to rarely persistent; ovary globose to cylindrical, 1.2–2 by 1–1.5 mm, 2-locular, densely hairy; style absent; stigmas 0.3–0.6 mm long, cleft, caducous; lobes 0.3–0.6 by c. 0.2 mm, glabrous above and below. *Infructescences* 5–17 cm long, 1–2.5 mm thick. *Fruits* subglobose to ellipsoid, but laterally flattened, usually 1- (or 2-)seeded fleshy capsules, 9–12 by 6–15 by 3–14 mm, loculicidally and often also septicidally dehiscent, raised glands absent, subglabrous to densely hairy outside, velutinous inside; pericarp 0.5–2 mm thick; column 7–12 mm long, curved to straight, persistent; pedicel 2–6 mm long, upper part 1–3 mm long. *Seeds* subglobose, laterally flattened, 5.8–12 by 4.5–8 by 2.5–4 mm; cotyledons 2.5–4 by 3–5 by c. 0.1 mm; radicle c. 1 mm long; endosperm up to 1 mm thick.

Fig. 3.7. *Baccaurea deflexa* Müll.Arg. a. Habit with male inflorescences; b. female inflorescences [Reproduced from E.J. Brill (ed.) Icones Bogorienses 4: tabula CCCX, f. 1. (1919)].



Map 3.8. Distribution of *Baccaurea deflexa* Müll. Arg. in Peninsular Malaysia, Sumatra and Borneo.

Distribution — Peninsular Malaysia, Sumatra, Borneo (the type is the only specimen from Java).

Habitat & Ecology — Primary rain forest. Altitude: sea level up to 450 m. Soil: sand, clay. Flowering: May, July to Nov. Fruiting: May, July to Sept., Nov.

Vernacular names — Sumatra: Bergang gaya, birah mato, djatikau, djentikan betima, djentikan merah, merah matu, tampoei. Simeuluë Island: Bolawah ontur, bolawah silai. Bangka: Kepris, ketjepat, masput, rankop, rankup. Borneo: Jelentikan (Kutai); keliwat'n (Benuag/Tunjun); lubi, tampoi.

Notes — Müller Argoviensis (1866) already noted that this species is very similar to *B. costulata*. Airy Shaw (1975) regarded the two as conspecific, with no further explanation. In my opinion, however, the two species are rather different, and the confusion must have been due to incomplete data. The leaves of *B. deflexa* tend to be larger than those of *B. costulata*; the midrib (lower surface) usually densely hairy, compared with usually sparsely hairy; the staminate inflorescences less lax, always densely hairy (often sparsely hairy in *B. costulata*), bracts 0.5–1 mm long, compared with 1–2.5 mm long; stamens (4–)6, compared with 4 or 5, 0.3–0.6 mm long, in contrary to 0.2–0.3 mm long. These differences together with the different appearance of both species in the herbarium material (*B. deflexa* dark brown, *B. costulata* more glossy, greyish brown) have me led to conclude that *B. deflexa* and *B. costulata* are not conspecific. I omitted the pistillate inflorescences and infructescences from the discussion because of insufficient knowledge of these characters in *B. costulata* (see note under *B. costulata*).

9. Baccaurea dolichobotrys Merr. — Map 3.9

Baccaurea dolichobotrys Merr., Univ. Calif. Publ. Bot. 15 (1929) 147; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 47. — Type: *Elmer 21676* (lecto L, selected here; isolecto DS, GH, K, US), Borneo, Sabah, Tawau.

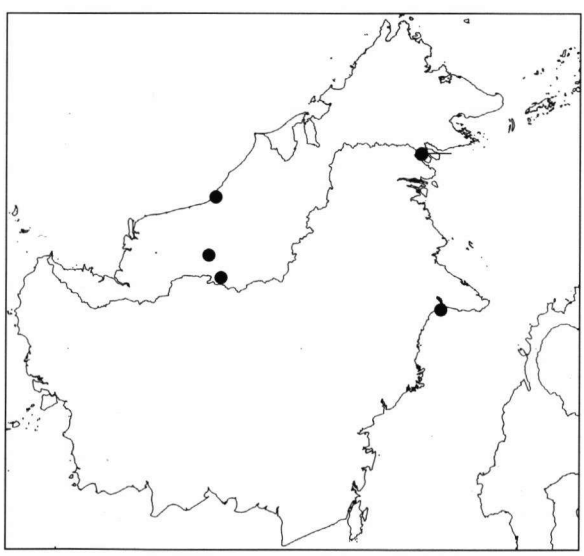
Tree 12–24 m high, dbh c. 29 cm, buttresses small; branchlets subglabrous to sparsely hairy; young shoots blackish when dry, Terminalia branching pattern weakly developed. *Indumentum* of simple and stellate hairs. *Bark* red-brown to dark reddish when fresh, brown when dry, scaly with cracks of 2 mm long; inner bark red-brown, c. 6 mm thick. *Leaves*: petiole 35–131 mm long, (sub)glabrous, dark brown to blackish when dry, raised glands usually absent; stipules 4–6 by c. 3 mm, densely hairy to velutinous outside, subglabrous to sparsely hairy inside, usually margin not ciliate, not hyaline; lamina ovate, (8.8–)10–30.3 by (5.7–)6.2–16.5 cm, l/w ratio 1.4–2.2, papery; base rounded to cordate; apex obtuse to acute, 2–15 mm long; upper surface glabrous, secondary veins glabrous to sparsely hairy, sometimes granulate; lower surface subglabrous to sparsely hairy, tuft of hairs present in nerve-axils, raised glands absent or present, discoid glands absent or present; secondary veins 10–12 per side, closed at margin; nervation scalariform. *Staminate inflorescences* unknown. *Pistillate inflorescences* ramiflorous to cauline. *Pistillate flowers* mainly unknown; sepals persistent to rarely caducous; ovary 3-locular, stigmas persistent. *Infructescences* 14–40 cm long, 1.7–2.5 mm thick. *Fruits* globose, usually 1- (or 2-)seeded, fleshy capsules, (9.5–)10–13 by 10–10.5 by 10–13.5 mm, loculicidally dehiscent, raised glands often present, subglabrous to sparsely hairy outside, sparsely to densely hairy inside, yellow to orange-brown; pericarp 0.1–0.3 mm thick; column 9–12 mm long, curved to straight, persistent; pedicel 4.5–9 mm long, upper part 2–5 mm long. *Seeds* globose, laterally flattened, 5.3–7.3 by 5–7.2 by 2–3 mm; arillode red to orange; testa pale brown; cotyledons 4.2–6.3 by 5–6.5 by c. 0.1 mm; radicle 0.3–1 mm long; endosperm 0.3–1.5 mm thick.

Distribution — Borneo.

Habitat & Ecology — Riverine rain forest. Altitude: 0–700 m. Soil: yellow sand, loam. Fruiting: Febr., July, Oct.

Uses — Arillode edible.

Vernacular names — Sarawak: Buah jelentik (Iban).



Map 3.9. Distribution of *Baccaurea dolichobotrys* Merr. in Borneo.

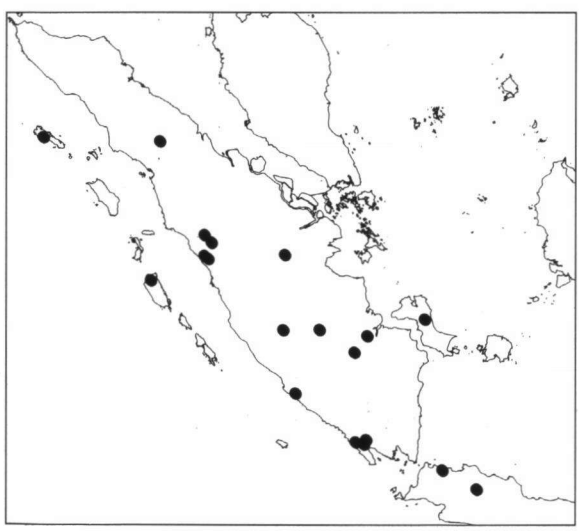
Note — Airy Shaw synonymised *B. dolichobotrys* with *B. hookeri* (= *B. polyneura*). *Baccaurea dolichobotrys* is in my opinion clearly different from *B. polyneura*. The indument on the branches is sparsely hairy in *B. dolichobotrys*, whereas *B. polyneura* is densely hairy (*B. dolichobotrys* is in general less hairy than *B. polyneura*); the petioles and leaves are on average longer in *B. dolichobotrys*; the fruits are 10–10.5 mm diam., compared with 12–26 in *B. polyneura*. Other characters (such as colour of the leaves when dry) differ in range but usually overlap.

10. **Baccaurea dulcis** (Jack) Müll.Arg. — Map 3.10

Baccaurea dulcis (Jack) Müll.Arg. in DC., Prodr. 15, 2 (1866) 460; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Koord., Exkurs. Fl. Java 2 (1912) 481; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 73; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 51; S. Moore, J. Bot. Br. 63 (1925) 98; Backer & Bakh.f., Fl. Java 1 (1963) 454; Soejarto, Bot. Mus. Leafl. (1965) 82; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 37; Airy Shaw, Kew Bull. 36 (1981) 261. — *Pierardia dulcis* Jack, Trans. Linn. Soc. 14 (1823) 120; Walp., Repert. Bot. Syst. 5 (1846) 367; Miq., Fl. Ned. Ind. 2, 1 (1859) 358; Fl. Ned. Ind., Eerste bijv. (1861) 441; Baill., Adansonia 3 (1863) 140. — Type: *Jack s.n.* (holo K), Sumatra, male flowering specimen.

Baccaurea suvrae Chakrab. & Gang., J. Econ. Taxon. Bot. 18 (1994) 423, syn. nov. — Type: *Forbes 3017* (holo CAL; iso L), Sumatra, Palembang, R. Rawas, Soeroelangoen.

Tree 3–30 m high, dbh 4–30 cm, buttresses absent; branchlets (sub)glabrous, hollow; young shoots (pale) red-brown to (pale) brown to grey when dry, Terminalia branching pattern weakly developed. *Indumentum* of simple hairs. *Bark* whitish-brown when fresh, grey when dry, c. 1 mm thick, rough; inner bark white, 2–3 mm thick. *Leaves*: petiole 8–68 mm long, glabrous to subglabrous, brown to red-brown when dry, raised glands usually present; stipules 6–15 by 2.5–6 mm, glabrous outside, but often densely hairy at base, glabrous to densely hairy at midrib, inside glabrous, margin not ciliate, not hyaline; lamina obovate, 7.8–30 by 3.7–11.6 cm, l/w ratio 1.5–3.3, papery to slightly leathery; base acute to attenuate; apex obtuse to acuminate, up to 11 mm long;



Map 3.10. Distribution of *Baccaurea dulcis* (Jack) Müll. Arg. in Sumatra and W Java.

upper surface glabrous, raised glands usually present, usually granulate, brown to reddish to grey to green when dry; lower surface glabrous, often subglabrous at midrib, discoid glands absent, brown to reddish to grey to green when dry; secondary veins 5–12 per side, closed at margin; nervation reticulate. *Staminate inflorescences* axillary to just below the leaves, solitary to few clustered together, 0.3–10 cm long, 0.5–1 mm thick, (glabrous to) subglabrous to densely hairy, many-flowered, flowers scattered along inflorescence; bracts 1 per branchlet, 1–2 mm long, (sub)glabrous outside, glabrous inside, margin ciliate, (not) hyaline; bracteoles 0–2, up to 0.3 mm long, sparsely hairy outside, glabrous inside; branchlets absent to cylindrical, 0–3 mm long, densely hairy, (2- or) 3-flowered. *Staminate flowers* 2–4.5 mm diam.; pedicel 1–3.8 mm long, upper part 0.5–1.5 mm long, densely hairy; sepals 4, ovate, 1.2–3.5 by 0.5–1.6 mm, apex (slightly) recurved, outside and inside densely hairy; staminodes 6–8; stamens 6–8, 0.4–0.9 mm long, glabrous; filaments 0.4–0.7 mm long, usually geniculate; anthers 0.1–0.15 by 0.15–0.2 by c. 0.1 mm; disc absent; pistillode absent to obtriangular, up to 1 mm high, densely hairy, hollow. *Pistillate inflorescences* axillary to ramiflorous (to cauline), solitary to few-clustered together, 2.5–12 cm long, 1–2.5 mm thick, (sub)glabrous, 8–30-flowered; pedicel, 2.5–10 mm long, upper part 0.3–4.2 mm, subglabrous to densely hairy; bracts inserted on rachis and pedicel, 3 per branchlet, (sub)glabrous outside, glabrous inside, ciliate. *Pistillate flowers* 5–10 mm diam., yellow; sepals 4 or 5, elliptic, 3–11 by 1.7–4.5 mm, sparsely to densely hairy outside, densely hairy inside, caducous, whitish when dry; ovary globose, 1.5–2.7 by 1.5–2.7 mm, 3-locular, (sub)glabrous; style absent; stigmas 0.4–0.8 mm long, not cleft to 90%, usually persistent; lobes 0.2–0.8 by 0.3–1 mm, glabrous and ruminate above and below. *Fruits* globose, 1–3-seeded berries, 24–35 by 11–26 by 11–26 mm when dry, raised glands present, ruminate when dry, (sub)glabrous outside, glabrous inside, yellow; pericarp 1.5–11 mm thick; column 21–24 mm long, straight; pedicel 8–17.5 mm long, upper part c. 1 mm long. *Seeds* globose to ellipsoid, laterally flattened, (10.6–)12.5–18 by (9–)10–12.5 by 3–5 mm; arillode purple; cotyledons 7–10.5 by 5.5–11.5 by c. 0.1 mm; radicle 1.5–2 mm long; endosperm c. 1 mm thick.

Distribution — Sumatra, W Java.

Habitat & Ecology — Primary rain forest, and cultivated. Altitude: 90–700 m. Flowering: June, Aug., Oct. Fruiting: May, June, Sept., Nov., Dec.

Uses — Fruits sweet to sour.

Vernacular names — Sumatra: Kapunduang (Minang); cupak, kaloe, ketoepa, menteng negri, toepa. Simeuluë Island: Pranggo.

11. **Baccaurea edulis** Merr. — Fig. 3.8; Map 3.11

Baccaurea edulis Merr., Univ. Calif. Publ. Bot. 15 (1929) 149; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 36; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 47. — Type: *Elmer 21783* (holo A; iso DS, L), Borneo, Sabah, Tawau.

Tree 8–33 m high, dbh 5–60 cm, buttresses absent to up to 4 m high by 1 m wide, thin; branchlets glabrous, densely hairy when young, Terminalia branching pattern weakly developed. *Indumentum* of simple and stellate hairs. *Bark* pale to red-brown when fresh, brown when dry, c. 0.5 mm thick, smooth, hard to soft; inner bark light red to red-brown to yellow to pale brownish, 2–10 mm thick, soft, sometimes brittle.

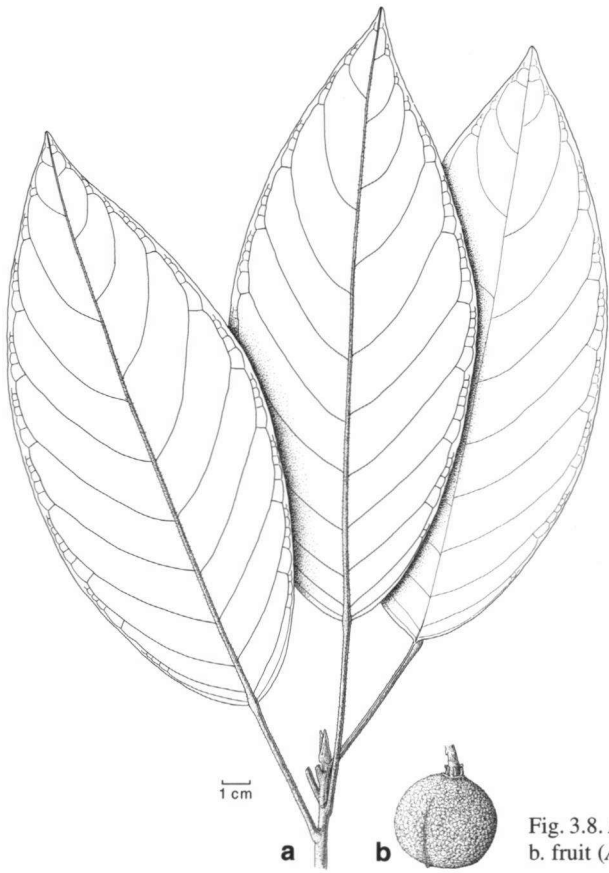


Fig. 3.8. *Baccaurea edulis* Merr. a. Habit; b. fruit (*Ambri & Arifin 708*).

Heartwood red-brown. *Leaves*: petiole 12–77 mm long, densely hairy, raised glands absent; stipules triangular to elliptic, 6–11 by 2.5–4.5 mm, sparsely to densely hairy outside, (sub)glabrous inside, margin ciliate, not hyaline; lamina usually elliptic, 8.3–29 by 3.2–11.8 cm, l/w ratio 2.3–3.8, papery; base rounded to cuneate; marginal glands often visible as small indentations; apex acute to cuspidate, 3–20 mm long; upper surface glabrous, midvein usually densely hairy, dark green when fresh, dark brown when dry; lower surface subglabrous to densely hairy, raised glands usually absent, discoid glands present, yellowish green when fresh, light brown (to green-brown) when dry; young leaves with yellowish brown indumentum; secondary veins (7 or) 8–10 per side, closed at margin; nervation reticulate, white (to light brown) above when dry. *Staminate inflorescences* axillary to just below the leaves, solitary to few clustered together, 1.5–12.5 cm long, c. 1 mm thick, branched, densely hairy, many-flowered, flowers scattered along inflorescence; bracts usually 1 per branchlet, spatulate, 1–4 mm long, densely hairy outside, (sub)glabrous inside, margin ciliate, not hyaline; bracteoles absent; cymules variable in shape, 3–18-flowered, densely hairy. *Staminate flowers* 1–2.5 mm diam., yellowish green to yellow to white; pedicel 0.5–1.7 mm long, upper part 0.3–1.5 mm long, densely hairy; sepals 4 or 5, ovate to

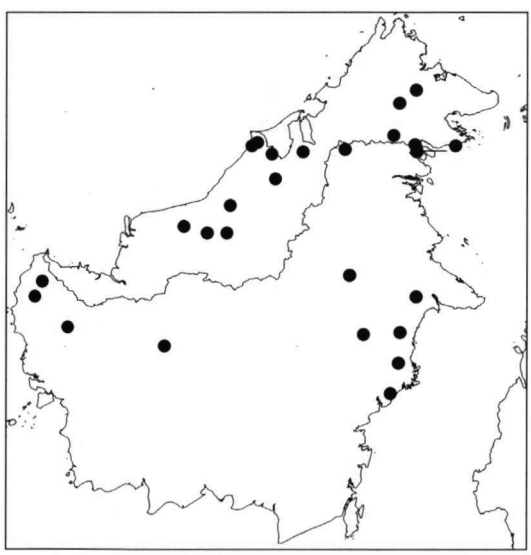
elliptic, 0.7–1.5 by 0.5–1 mm, apex recurved, outside and inside densely hairy; stamens (3 or) 4 or 5, 0.2–0.4 mm long, glabrous; filaments 0.1–0.3 mm long, straight; anthers 0.1–0.2 by 0.15–0.2 by c. 0.1 mm, pale yellow; pistillode absent to present, globose, up to 0.2 mm high, densely hairy, solid. *Pistillate inflorescences* ramiflorous to cauline, 2–6 clustered together, 2–18 cm long, 1–1.5 mm thick, densely hairy, 10–25-flowered, green; pedicel 3–7.8 mm long, upper part 0.5–1.5 mm long, densely hairy; bracts persistent, 1(–3) per branchlet, subglabrous to sparsely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 3–7 mm diam., greenish yellow; sepals 4 or 5, ovate, 2–3.5 by 1–2 mm, outside and inside densely hairy, persistent; ovary globose, 2–4 by 1.5–4 mm, 2-locular, densely hairy; style 1–2 by c. 1 mm, densely hairy; stigmas 1–2 mm long, cleft for upper 90%, caducous (to persistent); lobes 1–2 by c. 1 mm, glabrous above, densely hairy below. *Infructescences* 2–4 mm thick. *Fruits* globose, 2–4-seeded berries, 5–6 cm diam. when fresh, 23–60 by 23–60 by 23–60 mm when dry, raised glands absent, glabrous outside, densely hairy when young, subglabrous to densely hairy inside, (orange-)brown to whitish to yellow; pericarp 4–10 mm thick; column 19–25 mm long, straight; pedicel 5–14 mm long, upper part 1–6 mm long. *Seeds* globose to ellipsoid, laterally flattened, 13–20.5 by 8–21 by 2–8 mm; arillode white to yellow; cotyledons 11–12 by 10.5–16 by 0.1–0.4 mm; radicle 1–1.5 mm long; endosperm 1–2 mm thick.

Distribution — (Peninsular Malaysia), Borneo.

Habitat & Ecology — Primary and secondary rain forest, and swamp forest. Soil: sand. Altitude: up to 700 m. Flowering: Mar., June to Aug., Oct. Fruiting: Feb., Mar. to June, Aug., Sept.

Uses — Arillode and seed-coat edible, sweet to sour, sold in local markets.

Vernacular names — Borneo: Apor-apor (Bassap); pendal nyumbo, tampoi paya (Iban); pas, tampoi paya (Malay); boenjan, kapul, kapul putih, kelawat'n petik, kepsoet awoet, kulibon, puak burong.



Map 3.11. Distribution of *Baccaurea edulis* Merr. in Borneo.

12. **Baccaurea javanica** (Blume) Müll.Arg. — Fig. 3.9, Map 3.12

Baccaurea javanica (Blume) Müll.Arg. in DC., Prodr. 15, 2 (1866) 456; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 253; Koord., Exkurs. Fl. Java 2 (1912) 482; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 73; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 331; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 50; S. Moore, J. Bot. Br. 63 (1925) 98; Holth. & H.J. Lam, Blumea 5 (1942) 200; Backer & Bakh.f., Fl. Java 1 (1963) 254; Soejarto, Bot. Mus. Leafl. 21 (1965) 96; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 37; Whitmore, Tree Fl. Malaya 2 (1973) 65; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 48; Kew Bull. 36 (1981) 263; 37 (1982) 8; Chakrab. & Rao, J. Econ. Taxon. Bot. 5 (1984) 957; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 51. — *Adenocrepis javanica* Blume, Bijdr. (1825) 579; Baill., Etude Euphorb. (1858) 601; Adansonia 3 (1863) 134. — Type: *Blume s.n.* (lecto L, sheet 903.154-589, selected here), Java, Tjanjor, Parang.

Hedycarpus javanicus Miq., Fl. Ned. Ind. 1, 2 (1859) 359. — Type: *Hasskarl s.n.* (lecto L, sheet 909.25-49, barcode L 0059164, selected here), Java.

Microsepala acuminata Miq., Fl. Ned. Ind., Eerste bijv. (1861) 444. — *Baccaurea acuminata* (Miq.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 463; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281. — Type: *Diepenhuis s.n.* (lecto U, sheet -95/007-45, selected here), Sumatra, Priaman, Lubual-ang.

Baccaurea minutiflora Müll.Arg. in DC., Prodr. 15, 2 (1866) 463; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 257; Koord., Exkurs. Fl. Java 2 (1912) 482; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 58; Backer & Bakh.f., Fl. Java 1 (1963) 455; Airy Shaw, Kew Bull. 36 (1981) 260. — Type: *Zollinger 3048* (holo G), Java.

Baccaurea minahassae Koord., Meded. Lands Plantentuin 19 (1898) 625; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Koord., Syst. Verz. 3 (1914) 67; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 74. — Type: *Riedel s.n.* (holo K), North Celebes, Gorontalo.

Baccaurea sanguinea J.J. Sm., Icon. Bogor. 4 (1910) 25, t. 319. — Type: *Bogor Botanical Garden: VIII.F.3a* (lecto BO, selected here).

Aporosa dolichocarpa Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 98; S. Moore, J. Bot. Br. 63 (1925) 97; Airy Shaw, Kew Bull. 36 (1981) 264. — Type: *Forbes 3159* (lecto L, selected here), Sumatra.

Baccaurea leucodermis Hook.f. ex Ridl., Fl. Malay Penins. 3 (1924) 244; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 49. — Syntypes: *Kunstler s.n.* (K, n.v.), Malakka, Perak, Kinta; *Ridley s.n.* (K, n.v.), Johore, Castlewood.

Shrub to tree 3–12 m high, dbh up to 30 cm, buttresses absent to up to 30 cm high, 10 cm long, c. 5 cm thick; branchlets glabrous, densely hairy when young, Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* (light) brown to pale grey to yellowish to white to silvery green, 1–2 mm thick, smooth, finely fissured; inner bark brown to yellow-brown, 2–4 mm thick, soft. *Heartwood* brown. *Leaves*: petiole 2–45 mm long, (sub)glabrous, sometimes with a tuft of short hairs at base, brown when dry; stipules 1–6 by 1–2 mm, densely hairy on both sides, margin ciliate, hyaline; lamina obovate (to ovate), 2.9–20 by 1.2–9.5 cm, l/w ratio 1.9–3.9, base cuneate; apex acuminate, up to 15 mm long; upper surface glabrous, sometimes granulate; raised glands sometimes present, (dark) green when fresh, yellowish green to brown when dry; lower surface glabrous, discoid glands rarely present, (dark) green when fresh, yellowish green to brown when dry; secondary veins 4–8 per side, ending open; nervation reticulate, red to brown when dry, slightly raised above; young leaves reddish brown when dry. *Staminate inflorescences* axillary to just below the leaves, solitary to 4 clustered together, 1.5–14 cm long, 0.5–1 mm thick, subglabrous to sparsely hairy, many-flowered, flowers scattered along inflorescence; bracts 1 per

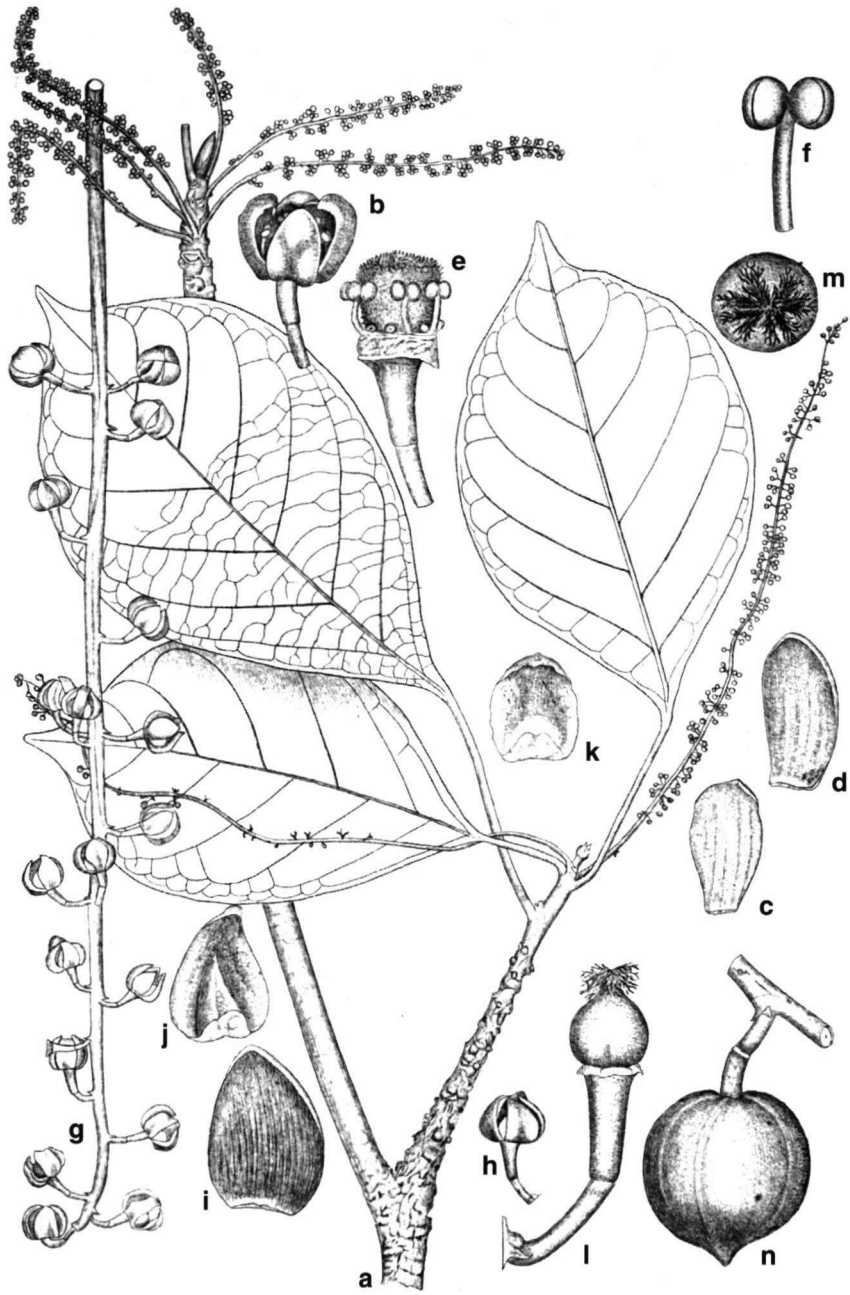
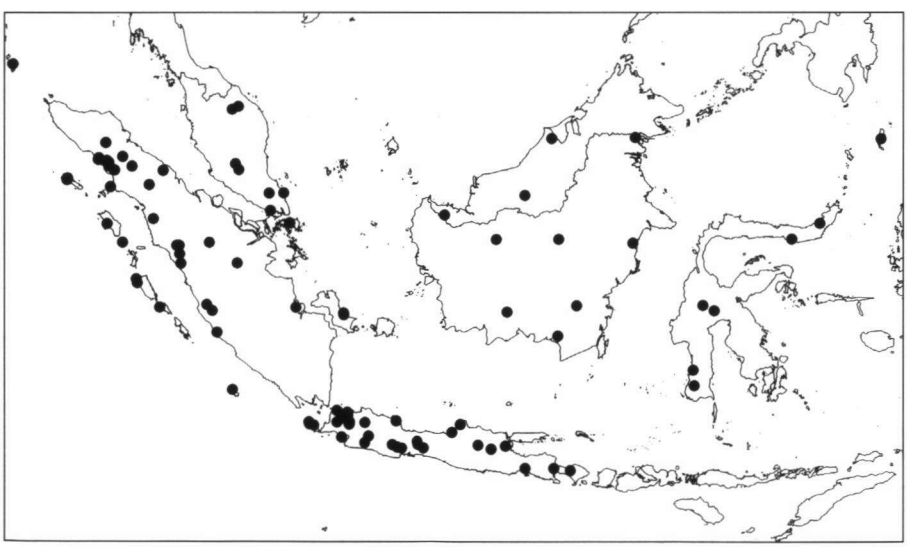


Fig. 3.9. *Baccaurea javanica* (Blume) Müll.Arg. a. Habit with male inflorescences; b. male flower; c. male sepal; d. male sepal; e. male flower without sepals; f. anther; g. female inflorescence; h. female flower; i. female sepal; j. female sepal; k. female sepal; l. female flower without sepals; m. stigma; n. fruit [Reproduced from E.J. Brill (ed.) Icones Bogorienses 4: tabula CCCIX, f. 1. (1919)].

branchlet, 0.5–1.1 mm long, persistent, glabrous on both sides, densely hairy at base outside, margin ciliate, hyaline; bracteoles 0 or 2, up to 0.5 mm long; branchlets cylindrical, 0–2.1 mm long, glabrous to densely hairy, (1–)3-flowered. *Staminate flowers* 1.7–3.7(–5.5) mm diam., green to white to light yellow to brownish; pedicel 1.2–4.2 mm long, upper part 0.9–2.2 mm long, glabrous to densely hairy; sepals 4 (or 5), ovate, 1.1–4.2 by 0.5–2.3 mm, apex recurved, outside glabrous except one side at margin densely hairy, densely hairy inside, brown outside when dry, whitish inside when dry; staminodes absent or 4–7; stamens 4–7, 0.4–1 mm long, glabrous; filaments 0.25–1 mm long, apically geniculate; anthers 0.1–0.4 by 0.1–0.2 by 0.1–0.2 mm; disc present, less than 0.1 mm thick; pistillode cylindrical, 0.3–1.1 mm long, densely hairy to velutinous. *Pistillate inflorescences* axillary to just below the leaves (to ramiflorous), solitary, up to 8.5 cm long, 1.2–1.4 mm thick, glabrous to sparsely hairy (to densely hairy), 1–17-flowered, brown to reddish brown when dry; pedicel 1.6–4 mm long, upper part 0.2–1.1 mm long, glabrous (to densely hairy); bracts 1 or 3 per branchlet, 0.7–0.8 by 0.7–0.8 mm, persistent, glabrous, margin ciliate; flowers up to 1 cm diam., green; sepals 4, ovate to lanceolate, 3–7.5 by 1.2–2.5 mm, outside glabrous, inside densely hairy, outside brown when dry, inside whitish when dry, caducous; ovary globose to cylindrical, 1.2–2.5 by 1–1.9 mm, 2-locular (2- or 3-locular in Borneo), pilose to velutinous, greenish-white; style absent or up to 0.1 mm; stigmas whitish, c. 0.5 mm diam., persistent, not lobed. *Fruits* globose to cylindrical, bivalved, 1- or 2 (–4-)seeded, fleshy capsules, 10–17 by 7–11 by 7–11 mm, not to loculicidally dehiscing, glabrous outside and inside, pale to dark orange to yellow; pedicel 1.5–5 mm long, upper part 0.5–2.5 mm long; pericarp 0.1–1.5 mm thick; column 7–11 mm long, curved when 1-seeded, caducous. *Seeds* ellipsoid to slightly globose, but laterally flattened, 5–9 by 5.5–7.4 by 1–5 mm; arillode purplish blue to dark purplish to violet; testa red to purplish red; cotyledons 5–6 by 6–6.5 by 0.1–2.5 mm thick.



Map 3.12. Distribution of *Baccaurea javanica* (Blume) Müll. Arg. in Andaman and Nicobar Islands, Peninsular Malaysia, Sumatra, Java, Borneo and Sulawesi.

Distribution — Andaman and Nicobar Islands, Peninsular Malaysia, Sumatra, Java, Borneo, Sulawesi (Talaud Island).

Habitat & Ecology — Primary or secondary rain forest, or freshwater swamps. Altitude: sea level up to 1800 m. Flowering and fruiting: throughout the year.

Uses — Arillode edible, sweet to sour.

Vernacular names — Sumatra: Bosi, toepak rawang. Simeuluë Island: Ahanang bala, ahalang bahok, ahanang bahok pajo, toeanang, toepa rawang. Java: Houtjit, hutjiet, huetjip, heuncit, heuntit. Borneo: Mata plantok (Tidong); sarakat. Bali: Kepinding.

13. Baccaurea lanceolata (Miq.) Müll. Arg — Fig. 3.10, Map 3.13, Photo 2, 3

Baccaurea lanceolata (Miq.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 457; Hook.f., Fl. Brit. India 5 (1887) 368; Stapf, Trans. Linn. Soc. London, Bot. 4 (1894) 224; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 280; Merr., Philipp. J. Sci., Bot. 4 (1909) 277; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 247; Koord., Exkurs. Fl. Java 2 (1912) 481; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 73; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 331; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 60; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 411; Ridl., Fl. Malay Penins. 3 (1924) 248; S. Moore, J. Bot. Br. 63 (1925) 98; Merr., Univ. Calif. Publ. Bot. 15 (1929) 150; Pax & K. Hoffm., Mitt. Staatsinst. Allg. Bot. Hamburg 7 (1931) 233; M.R. Hend., J. Malayan Branch Roy. Asiat. Soc. 17 (1939) 69; Corner, Wayside Trees Mal. 1 (1940) 240; Backer & Bakh.f., Fl. Java 1 (1963) 454; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 35; Airy Shaw, Kew. Bull. 26 (1972) 220; Whitmore, Tree Fl. Malaya 2 (1973) 65; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 49; Fernando, Philipp. J. Biol. 8 (1979) 302; Airy Shaw, Kew Bull. 36 (1981) 263; Enum. Euphorb. Philipp. (1983) 9. — *Hedycarpus lanceolatus* Miq., Fl. Ned. Ind. 1, 2 (1859) 359. — *Adenocrepis lanceolatus* (Miq.) Müll. Arg., Linnaea 32 (1863) 82. — Type: *Zollinger 3265* (holo U; iso K), Java.

Pierardia pyrrhodasya Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 441. — *Baccaurea pyrrhodasya* (Miq.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 462; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 65; Airy Shaw, Kew Bull. 36 (1981) 265, syn. nov. — Type: *Junghuhn s.n.* (lecto U, sheet 35998, the flowers only, selected here), Sumatra, Ankola.

Baccaurea glabriflora Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 59; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 411; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 50. — Type: *Merril 853* (holo US; iso K), Philippines, Island of Paragua, San Antonio Bay.

Tree 3–30 m high, dbh 5–60 cm, buttresses absent; trunk gnarled; branchlets (sub)-glabrous; young shoots green to grey-green to brownish when dry, Terminalia branching pattern usually weak. *Indumentum* of simple hairs. *Bark* grey to pale brown to yellowish to whitish to greenish when fresh, grey when dry, 0.2–3 mm thick, smooth, scaly, sometimes peeling off, soft; inner bark pale brown to white to grey to yellowish, 2–3.5 mm thick. *Heartwood* yellowish to brownish. *Leaves*: petiole 16–184 mm long, glabrous, apically and slightly basally pulvinate, green to grey to brown-green when dry, raised glands usually present; stipules (3–)5–16 by 2–6 mm, caducous (to late caducous), glabrous outside and inside, midrib often densely hairy above, margin (not) ciliate, usually hyaline (in Peninsular Malaysia not hyaline); lamina ovate to obovate, 9.2–45 by 3.7–26.5 cm, l/w ratio 1.7–3.4, papery; base attenuate to rounded; apex acute to cuspidate, (0–)3–20 mm long; upper surface glabrous, raised glands present, sometimes granulate, glossy dark green when fresh, (grey to brown to) green when dry; lower surface glabrous, sometimes sparsely hairy at midrib, raised glands present, discoid glands absent, (dull pale) green when fresh, (grey to brown to) green when dry, nervation paler; secondary veins 6–13 per side, closed at margin to almost so;

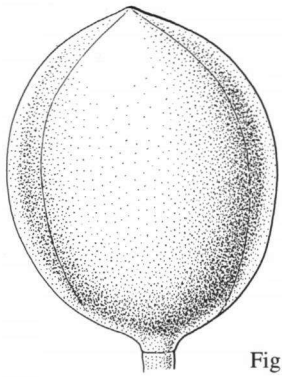
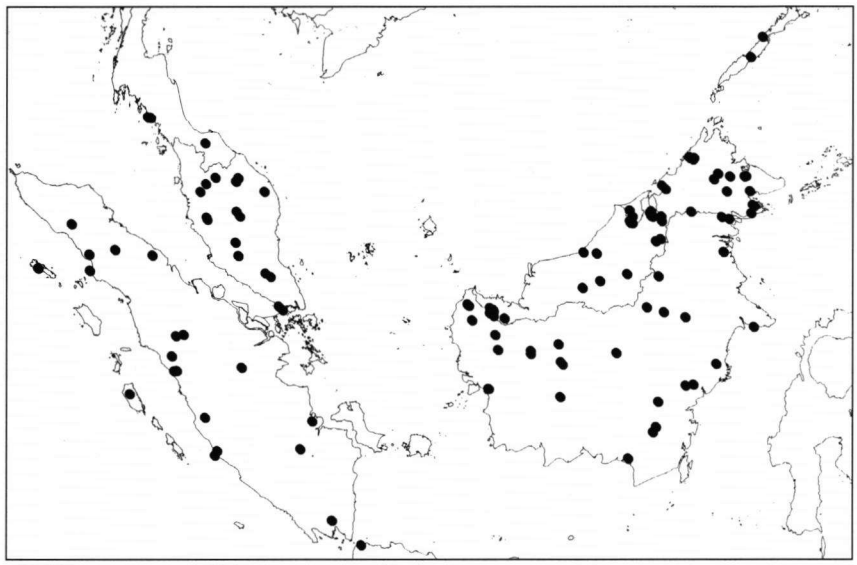


Fig. 3.10. *Baccaurea lanceolata* (Miq.) Müll.Arg. Fruit (*Hallier 475*).

nervation reticulate. *Staminate inflorescences* cauline, many clustered together, 3.5–18 cm long, 0.1–1 mm thick, glabrous to sparsely hairy, branching minute, many-flowered, flowers scattered along inflorescence, yellow to pink to cream-white; bracts 1 per branchlet, 0.4–1.5 mm long, densely hairy outside, (sub)glabrous inside, margin ciliate, hyaline; bracteoles 0.1–0.5 mm long, 2 per branchlet, glabrous outside, (sub)glabrous inside; branchlets absent, 3-flowered. *Staminate flowers* 2–7 mm diam., yellow to pink to purple to cream-white; pedicel 1.8–7 mm long, upper part 1.7–7 mm long, (sub)glabrous, densely hairy at base; sepals (3 or) 4 or 5, obovate to spatulate, often variable in size and shape, 1.1–5.5 by 0.6–2.7 mm, apex slightly recurved or straight, glabrous outside (densely hairy in Peninsular Malaysia), sparsely to densely hairy inside; petals often present, 3–5, rudimentary; staminodes 3–5; stamens (3 or) 4 or 5, 0.4–0.6 mm long, glabrous; filaments 0.1–0.3 mm long, straight; anthers 0.2–0.35 by 0.2–0.4 by 0.15–0.2 mm; disc absent; pistillode globose to cylindrical, 0.2–0.7 mm high, velutinous, solid. *Pistillate inflorescences* cauline, few clustered together, 8–33(–50) cm long, 1–5 mm thick, subglabrous to sparsely hairy (glabrous in Peninsular Malaysia), 20–25-flowered, yellowish brown to reddish; pedicel 0.8–4.5 mm long, thickened at abscission zone, upper part 0.1–1.5 mm long, subglabrous to densely hairy (glabrous in Peninsular Malaysia), pink; bracts 3 per branchlet, (sub)glabrous outside, glabrous inside, margin ciliate. *Pistillate flowers* 3.5–10 mm diam., yellow to orange to purple to reddish cream to whitish; sepals 4 or 5, ovate to obovate, 1–6 by 0.9–3.2 mm, densely hairy outside, (sub)glabrous inside, caducous; petals 2–8, reduced; ovary globose, 1.5–3.2 by 1.5–3.2 mm, 3- or 4-locular, sparsely to densely hairy, wings usually absent, rarely 3 or 4 poorly developed, purple to green; style absent; stigmas 0.7–1 mm long, cleft for upper 10–90%, reddish to ochre, persistent to caducous; lobes 0.7–1 by 0.2–0.6 mm, glabrous and ruminate above, glabrous to densely hairy below. *Fruits* globose to ellipsoid, 1–4-seeded berries, 24–54 by 16.5–41 by 16.5–41 mm when dry, 38 by 60 mm when fresh, raised glands present, ruminate when dry, glabrous outside and inside, purple or green when young, green to yellow to whitish to greyish to brownish when mature; pericarp 1–10 mm thick; column c. 32 mm long; pedicel (1–)2.5–17 mm long, upper part 0.5–11 mm long. *Seeds* ellipsoid, laterally flattened, 12.2–26 by 8–15 by 4.8–9 mm; arillode white to grey, translucent; testa yellow to whitish; cotyledons 10–11.5 by 8.9–13 by c. 0.1 mm; radicle 1–2.2 mm long; endosperm 1–2 mm thick.



Map 3.13. Distribution of *Baccaurea lanceolata* (Miq.) Müll. Arg. in Thailand, Peninsular Malaysia, Sumatra, N Java, Borneo and Palawan.

Distribution — Thailand, Peninsular Malaysia, Sumatra, N Java, Borneo, Palawan.

Habitat & Ecology — Primary and secondary rain forest, on slopes and in riverine forest. Soil: sandy clay, loam. Altitude: sea level up to 1300 m, common in lowland. Flowering: Mar. to Dec. Fruiting: throughout the year.

Uses — Against stomach-ache: the leaves are pounded in bamboo and mixed with water. Pericarp and arillode edible but sour and therefore eaten with sugar or salt. Rarely in cultivation in fruit gardens. Eaten with chicken rice.

Vernacular names — Peninsular Malaysia: Asam pahong, asam pahung, asam paung, limpanong, pahu asam, pahu temuangi. Sumatra: Tegeiluk (Mentawai); kaloe goegoer, langsat hutan, lempaong, lempaoe-oeng, peng. Java: Lingsoe. Borneo: Limpasu (Banjarese; Bundu tuhan); ampusu' (Bidayuh); asam pauh, empaong, lampaong, lampawong, lampong (Iban); buah lepasu, lipasu, nipassu (Dusun); kalampesu, lempahong (in Kalimantan); buah lipauh (Kelabit); kelepesoh (Kenyah); tampoy (Malay); buah lepesuh (Punan); empawang, lapahung, lempawong, paong.

Note — The type specimen is a mixtum, the leaves are *Terminalia* sp.

14. **Baccaurea macrocarpa** (Miq.) Müll. Arg. — Fig. 3.11, Map 3.14, Photo 4

Baccaurea macrocarpa (Miq.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 457; Hook.f., Fl. Brit. India 5 (1887) 375; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 280; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 73; Pax & K. Hoffm., Engl. Pflanzenr. IV.147.xv (1922) 49; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 35; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 50; Kew Bull. 36 (1981) 263. — *Pierardia macrocarpa* Miq., Fl. Ind. Bat., Eerste bijv. (1861) 441. — Type: *Teijsmann s.n.* (lecto U, sheet -95/007-35II36001, selected here), Sumatra, Dapoei, Mangala, Lampongs.

Mappa borneensis Müll.Arg., Flora 47 (1864) 468. — *Baccaurea borneensis* (Müll.Arg.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 460; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 280; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 330; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 62; Airy Shaw, Kew Bull. Add. .Ser. 4 (1975) 50. — Type: *Motley 199* (holo K), Borneo, near Bandjarmassing.

Baccaurea griffithii Hook.f., Fl. Brit. India 5 (1887) 371; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 66; Ridl., Fl. Malay Penins. 3 (1924) 248; Merr., Pap. Michingan Acad. Sci. 20 (1935) 100; Corner, Wayside Trees Mal. 1 (1940) 240; Whitmore, Tree Fl. Malaya 2 (1973) 66; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 50. — Type: *King's Collector 3266* (lecto K, selected here), Malakka, Perak, Larut.

Treelet or tree 5–27 m high, dbh 6–64 cm; bole sometimes fluted, up to 5 m high; buttresses absent to low to small; branchlets glabrous; young shoots blackish, Terminalia branching pattern weakly developed. *Indumentum* of simple hairs and small stellate. *Bark* dark to pale (red) brown to grey to orange when fresh, greyish-brown when dry, hard, c. 0.1 mm thick, smooth; inner bark red-brown to pale brown to orange to red to pinkish white, soft, 2.5–3 mm thick. *Leaves*: petiole (10–)22–145 mm long, glabrous to sparsely hairy, brown to blackish when dry, raised glands usually present; stipules 2–9 by 1–5 mm, glabrous to tomentose outside, glabrous inside, margin ciliate, not hyaline; lamina (ovate to) elliptic (to obovate), (7.2–)9–37 by 3.1–17.5 cm, l/w ratio (1.1–)1.6–2.8(–3.5), leathery to papery; base attenuate to cuneate (to rounded); apex (obtuse to) acuminate to cuspidate, up to 20 mm long; upper surface glabrous, sometimes granulate, brown to greenish when dry, nervation brown to rarely whitish when dry; lower surface (sub)glabrous, mostly sparsely hairy on midrib and secondary veins, raised glands absent or present, discoid glands in a row between secondary veins, green with brown nervation when fresh, brown to greenish when dry; secondary veins 6–10(–13) per side, not completely parallel, ending open at margin; nervation reticulate to weakly scalariform; young leaves blackish brown when dry. *Staminate inflorescences* (axillary to) ramiflorous to cauline, solitary to few clustered together, 0.5–13 cm long, c. 1 mm thick, densely to sometimes sparsely hairy, usually branched, many-flowered, flowers scattered along inflorescence; bracts 1 (or 3) per branchlet, 1–3 mm long, subglabrous to densely hairy outside, glabrous to densely hairy inside, margin ciliate, not hyaline; branchlets cylindrical, (0–)1–2 mm long, densely hairy, 3–12-flowered. *Staminate flowers* 0.7–2 mm diam., green to yellow to white; pedicel 1–2 mm, upper part 0.1–1.5 mm long, densely hairy; sepals 5, elliptic, 0.7–1.5 by 0.4–0.7 mm, apex straight, outside and inside densely hairy; stamens 5 (or 6), 0.1–0.25 mm long, glabrous, yellowish; filaments 0.1–0.2 mm long, straight; anthers c. 0.1 by 0.15 by 0.1 mm; disc absent; pistillode globose to obtriangular, c. 0.5 mm high, densely hairy, sometimes hollow. *Pistillate inflorescences* ramiflorous to cauline, solitary to 3 clustered together, 3.5–18 cm by 2–3 mm thick, subglabrous to densely hairy, 8–many-flowered; pedicel 3–7.5 mm long, upper part 0.4–0.5 mm long, geniculate or not, densely hairy, green; bracts 1 or 3 (then 1 big) per branchlet, sparsely to densely hairy outside, subglabrous to densely hairy inside, margin ciliate. *Pistillate flowers* 2–4.5 mm diam.; sepals 4–6, ovate, 1.5–2.8 by 1–1.3 mm, outside and inside densely hairy, persistent; ovary globose to cylindrical, c. 2 by 1.2–2 mm, 3- or 4-locular, tomentose; style 0.5–1.5 mm long, c. 1 mm wide, sparsely hairy; stigmas 0.5–1 mm long, cleft, persistent to caducous; lobes c. 1 by 0.4 mm, (sub)glabrous. *Infructescences* up to 15 cm long, 4–6 mm thick.

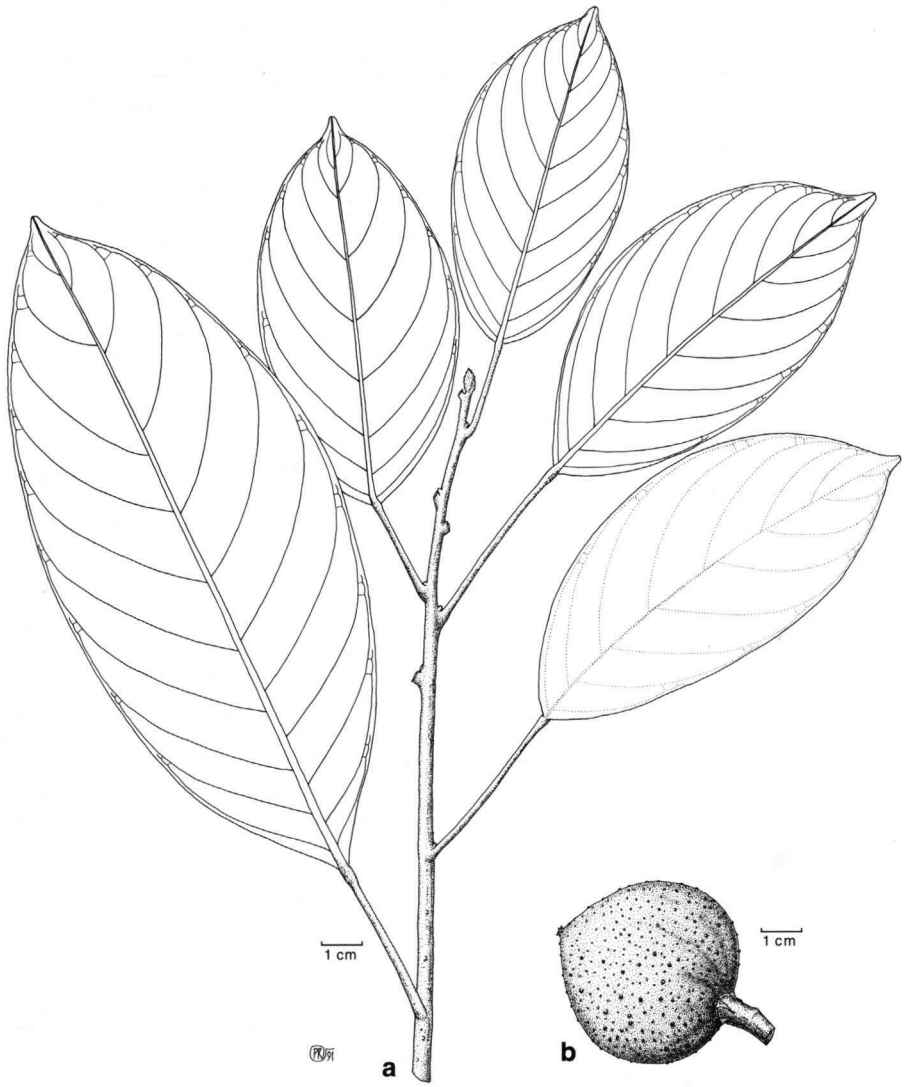
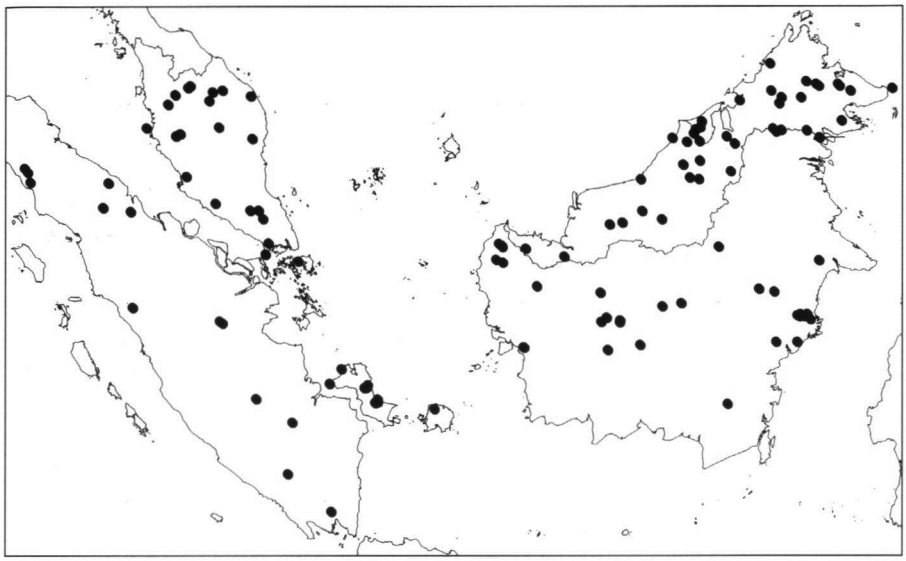


Fig. 3.11. *Baccaurea macrocarpa* (Miq.) Müll.Arg. a. Habit; b. fruit (*Sidiyasa 432*).

Fruits (sub)globose, (2- or) 3–6-seeded, fleshy capsules, 30–65 by 34–75 by 34–75 mm, up to 80 mm diam. when fresh, loculicidally (and also septicidally) dehiscent, (sub)glabrous outside, subglabrous to densely hairy inside, raised glands present, brown to yellow to orange to dull red to dark green; pericarp 4–11 mm thick; column 16–32 mm long, straight, caducous; pedicel 7–30 mm long, upper part 5–20 mm long, thickened at abscission zone. *Seeds* globose to ellipsoid, laterally flattened, (to triangular), 13–23 by 11–18.5 by 4–7 mm; arillode white to yellow to sometimes orange; testa yellow to brown; cotyledons 9–15 by 9–19 by up to 1 mm; radicle 1–2.3 mm long; endosperm c. 1 mm thick.



Map 3.14. Distribution of *Baccaurea macrocarpa* (Miq.) Müll. Arg. in Peninsular Malaysia, Sumatra and Borneo.

Distribution — Peninsular Malaysia, Sumatra, Borneo, (Ambon, Irian Jaya).

Habitat & Ecology — Primary rain forest, riverine rain forest and swamp forest, rarely also in secondary forest. Soil: granitic sand, sandy clay or red clay. Altitude: sea level up to 1600 m. Flowering and fruiting: throughout the year.

Uses — Arillode edible, sweet to sour. Sold in markets and cultivated in gardens.

Vernacular names — Peninsular Malaysia: Merkeh (Kelantan); ngeke (Malay); lara (Temuan); rambai, tampoi batang, tampoi, tampui. Sumatra: Tampoei daoen, tampoei benez. Bangka: Medang, tampui. Borneo: Pasin (Bassap Dyab); pegak (Dayak Tunjung); puak, tampoi (Iban); setai (Kenya); djentikan (Malay, Kutei); tampoi (Malay, Kedayan); buah setei, empak kapur, kapul, terai.

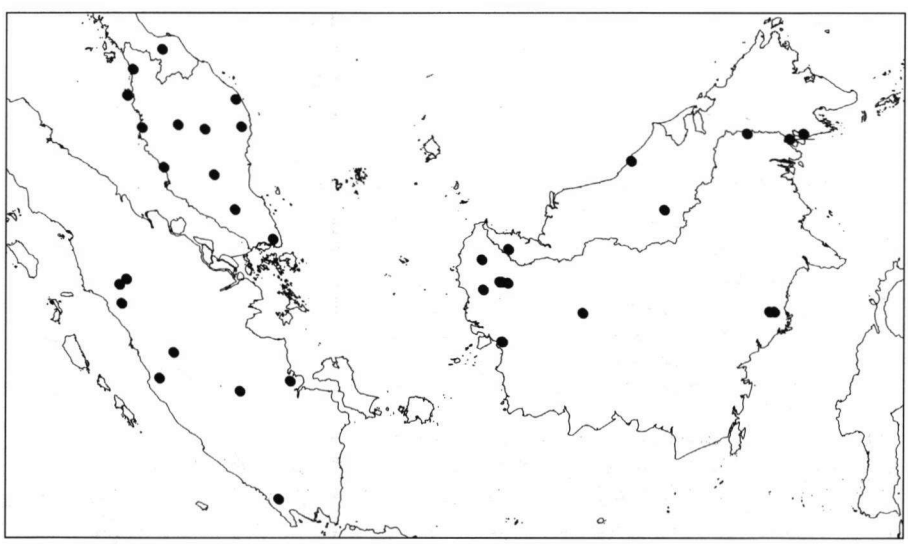
15. Baccaurea macrophylla (Müll.Arg.) Müll.Arg. — Map 3.15

Baccaurea macrophylla (Müll.Arg.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 460; Hook.f., Fl. Brit. India 5 (1887) 369; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 74; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 331; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 62; Ridl., Fl. Malay Penins. 3 (1924) 247; S. Moore, J. Bot. Br. 63 (1925) 98; Airy Shaw, Kew Bull. 26 (1972) 220; Whitmore, Tree Fl. Malaya 2 (1973) 66; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 51; Kew Bull. 36 (1981) 263. — *Pierardia macrophylla* Müll. Arg., Flora 47 (1864) 516. — Type: *Anonymous* (Hb Hook.f.; holo K), Malakka, Puolo-Penang.

Baccaurea beccariana Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 62; Airy Shaw, Kew Bull. 26 (1972) 220. — Type: *Beccari PB 3249* [holo FI (?, n.v.); iso G, K], Borneo. The type is to be expected in FI but cannot be found.

Tree 8–27 m high, dbh 14–63 cm; buttresses absent or small; bole sometimes fluted; branchlets glabrous, sparsely hairy when young; young shoots brown when fresh, brown to blackish when dry, Terminalia branching pattern weakly developed. *Indumen-*

tum of stellate hairs. *Bark* grey to dark red to red-brown when fresh, grey when dry, smooth, flaky; inner bark pale red to pinkish, thick, brittle, soft with sticky sap. *Heartwood* dark red-brown. *Leaves*: petiole 30–88 mm long, subglabrous to sparsely hairy, raised glands absent or present; stipules 2–11 by 3–11.5 mm, caducous (to late caducous), (glabrous to) subglabrous to sparsely (to densely) hairy outside, midrib sparsely to densely hairy, (sub)glabrous inside, margin ciliate, not to slightly hyaline; lamina (ovate to) elliptic (to obovate), 9.6–33 by 4.5–14.4 cm, l/w ratio 1.9–2.3(–2.9), papery; base rounded to cuneate; marginal glands not to slightly visible as indentation marks; apex acute, 2–10 mm long; upper surface glabrous, not granulate, dark brown when dry; lower surface glabrous to sparsely hairy, raised glands absent or present, discoid glands present below in a row between two secondary veins; brown when dry; secondary veins 6–13 per side, usually ending open at margin; nervation reticulate; young leaves yellowish green. *Staminate inflorescences* axillary to ramiflorous, solitary to few clustered together, 2.5–8.6 cm long, 0.5–1 mm thick, densely hairy, many-flowered, flowers clustered at the tip of inflorescence; bracts 1 per branchlet, 1.5–2.5 mm long, sparsely (to densely) hairy outside, (sub)glabrous inside, margin ciliate, usually not hyaline; bracteoles 2 per branchlet, 0.2–0.7 mm long; branchlets cylindrical, 0.7–3 mm long, densely hairy, 3-flowered. *Staminate flowers* 0.7–1.5 mm diam., green to yellow; pedicel 0–0.7 mm long, densely hairy; sepals 4 or 5, ovate, 0.4–0.9 by 0.4–0.6 mm, outside and inside densely hairy; staminodes absent to 4; stamens 4 or 5, 0.2–0.7 mm long, glabrous; filaments 0.1–0.7 mm long, straight; anthers 0.1–0.2 by 0.2–0.3 by c. 0.1 mm, yellow; disc absent; pistillode globose to cylindrical, 0.3–0.6 mm high, densely hairy, solid. *Pistillate inflorescences* ramiflorous, few clustered together, (4–)12–25 cm long, 1–1.5 mm thick, densely hairy to velutinous, few to many-flowered, green; pedicel 2–5 mm long, upper part c. 0.2 mm long, geniculate (90° bent), densely hairy; bracts 3 per branchlet, sparsely to densely hairy outside. *Pistillate*



Map 3.15. Distribution of *Baccaurea macrophylla* (Müll. Arg.) Müll. Arg. in Peninsular Malaysia, Sumatra and Borneo.

flowers 2–4 mm diam., green when fresh; sepals 4, lanceolate, c. 1.5 by 1–1.5 mm, outside and inside densely hairy, caducous (to persistent); ovary globose, 1.5–2 by 1–1.5 mm, (2- or) 3-locular, velutinous; stigmas sessile, c. 0.7 mm long, apically not lobed, glabrous, persistent. *Infructescences* up to 25 cm long. *Fruits* globose, 2- or 3-seeded, fleshy capsules, 10–16 by 9.5–15 by 9.5–15 mm, loculicidally dehiscent to irregularly splitting, ruminate when dry, raised glands present, (sub)glabrous outside, septa glabrous to densely hairy, usually green to sometimes light yellow to whitish violet to reddish to brown; pericarp 0.5–1.5 mm thick; column 10–14.5 mm long, straight; pedicel 3.5–14 mm long, upper part 0.3–7 mm long. *Seeds* globose, laterally flattened, 8–12.5 by 7.5–11 by 2–4 mm; arillode translucent; cotyledons 5–8.4 by 7–10 by 0.1–2 mm; radicle 0–1.3 mm long; endosperm cream.

Distribution — Peninsular Malaysia, Sumatra, Borneo, (Moluccas).

Habitat & Ecology — Primary and secondary rain forest, and peat swamp forest. Altitude: sea level up to 650 m. Flowering: Febr. to July, Oct., Nov. Fruiting: Mar., June to Oct.

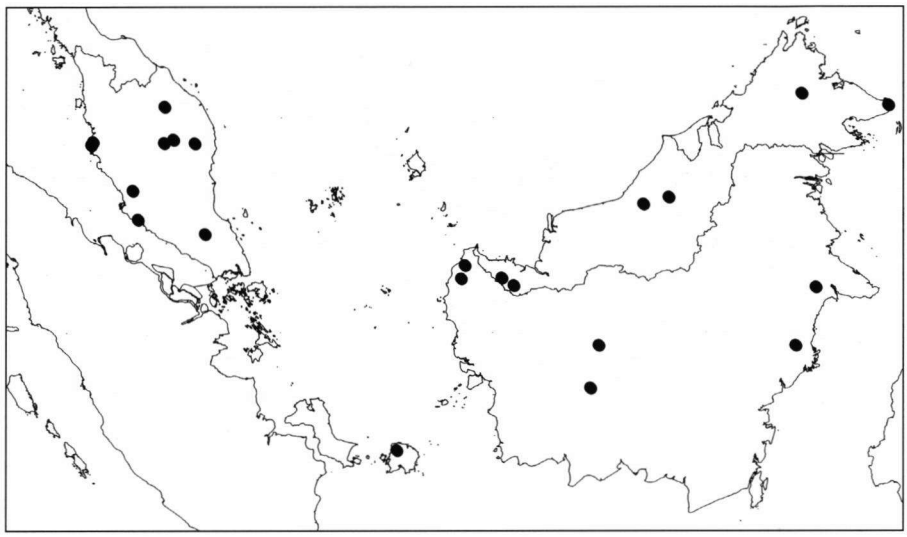
Uses — Arillode edible, sweet to sour.

Vernacular names — Peninsular Malaysia: Ampai ka, tampoi, tik. Sumatra: Rambai, rambaiklih lanang. Borneo: Jelenteh (Iban); keliw.

16. **Baccaurea maingayi** Hook.f. — Map 3.16

Baccaurea maingayi Hook.f., Fl. Brit. India 5 (1887) 370; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 63; Ridl., Fl. Malay Penins. 3 (1924) 246; Whitmore, Tree Fl. Malaya 2 (1973) 65; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 51. — Type: *Maingay KD 1415* (lecto K, selected here; isolecto L), Peninsular Malaysia.

Tree 10–22 m high, dbh 16–32 cm, buttresses absent; branchlets densely hairy, Terminalia branching pattern weakly developed. *Indumentum* of simple and stellate hairs. *Bark* red to brown when fresh, thin; inner bark red to pink. *Leaves*: petiole 31–120 mm long, glabrous to densely hairy, brown to black when dry, raised glands absent; stipules elliptic to ovate, 3–7.5 by 1.5–2.8 mm, velutinous outside, glabrous to rarely sparsely hairy inside, margin ciliate, not hyaline; lamina elliptic to ovate, 8–19.5 by 3.8–10.2 cm, l/w ratio 1.6–2.9, papery; base rounded to cordate to attenuate; apex cuspidate, 0–17 mm long; upper surface glabrous, raised glands normally present, often granulate, green to brown when dry; lower surface densely hairy, raised glands, normally present, absent, discoid glands absent to present, brown to green-brown when dry; secondary veins 8–11 per side, closed at margin; nervation scalariform; young leaves black when dry. *Staminate inflorescences* axillary to just below the leaves (to ramiflorous), solitary to 3 clustered together, 0.7–5 cm long, c. 1 mm thick, densely hairy to velutinous, 14–many-flowered, flowers clustered at the tip of inflorescence rarely somewhat scattered; branchlets cylindrical, 1.5–3 mm long, densely hairy to velutinous, 2-flowered; bracts absent. *Staminate flowers* 1–1.3 mm diam.; pedicel 0–1 mm long; sepals 4, ovate or variable in shape, 0.5–0.9 by 0.3–0.8 mm, straight, velutinous outside and inside; stamens 4, 0.2–0.5 mm long, glabrous; filaments 0.1–0.4 mm long, geniculate to straight; anthers c. 0.1 by 0.2 by 0.1 mm; pistillode absent. *Pistillate inflorescences* ramiflorous, solitary, c. 8.5 cm long, c. 1 mm thick, densely hairy to velutinous, 9–20-flowered; pedicel 3–3.5 mm long, upper part c. 0.5 mm



Map 3.16. Distribution of *Baccaurea maingayi* Hook.f. in Peninsular Malaysia, Simeuluë Island and Borneo.

long, geniculate (90° bent), densely hairy; bracts 3 per branchlet, densely hairy outside and inside, margin ciliate. *Pistillate flowers* 2–3 mm diam.; sepals 6, ovate, 1.8–3 by 0.9–1.4 mm, velutinous outside and inside, persistent; ovary globose, c. 1.3 by 1.3 mm, 3-locular, velutinous; style absent; stigmas small, persistent. *Infructescences* 6–19(–45) cm long, 1–3 mm thick. *Fruits* globose, 0–2-seeded, fleshy capsules, 10–20 by 14–22 by 13–20 mm, often loculicidally dehiscent, raised glands sometimes present, velutinous outside, densely hairy to velutinous inside, green to orange; pericarp c. 1 mm thick; column 9–15 mm long, curved to straight, caducous to persistent; pedicel 7.5–13 mm long, upper part 2.5–5 mm long. *Seeds* ellipsoid, laterally flattened, 8–16 by 7–14 by 2–4 mm; arillode amber; cotyledons 6.5–7.2 by 6–7 by < 0.1 mm.

Distribution — Peninsular Malaysia, Simeuluë Island, Borneo.

Habitat & Ecology — Primary rain forest and peat swamp forest. Altitude: 80–500 m. Flowering: Apr., May, Oct. Fruiting: Mar. to Aug., Dec.

Uses — Arillode edible, sweet.

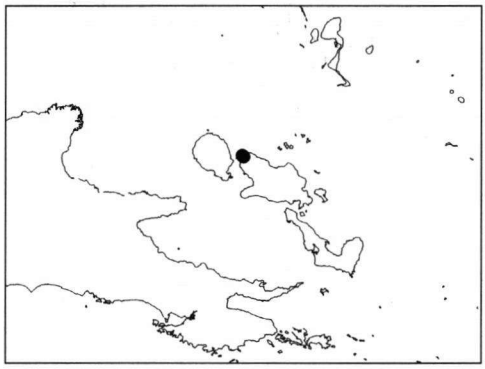
17. **Baccaurea microcarpa** (Airy Shaw) Haegens, *stat. nov.* — Fig. 3.12, Map 3.17

Baccaurea nesophila Airy Shaw var. *microcarpa* Airy Shaw, Kew Bull. 33 (1979) 530. — Type: *Brass 27290* (holo K; iso L, US), Papua New Guinea, Fergusson Island, Agamoia.

Tree c. 10 m high, dbh 25–30 cm; branchlets densely hairy when young, blackish when dry, Terminalia branching pattern weakly developed. *Indumentum* of simple hairs. *Leaves*: petiole 11–26 mm long, densely hairy when young, sometimes longitudinal cracks present, raised glands absent; stipules c. 2.8 by 1.4 mm, densely hairy outside, margin ciliate, not hyaline; lamina obovate, 5.2–11.8 by c. 2–4.9 cm, l/w ratio 2.4–2.6, papery; base attenuate to cuneate; apex obtuse to acute, up to 5 mm long; upper surface glabrous to subglabrous, raised glands absent, granulate, greenish brown when

Fig. 3.12. *Baccaurea microcarpa* (Airy Shaw) Haegens. Habit with female inflorescence and infructescence (*Brass 27290*).

dry, nervation reddish brown, sometimes slightly sunken; lower surface subglabrous, sparsely hairy at veins, small raised glands present, discoid glands absent to present, reddish brown when dry; secondary veins 5–7 per side, closed at margin; nervation reticulate, brown. *Staminate inflorescences* unknown. *Pistillate inflorescences* axillary to just below the leaves, solitary, densely hairy, few to c. 20-flowered. *Pistillate flowers*: sepals caducous; ovary 2-locular; stigmas persistent. *Infructescences* 3–7 cm long, c. 1 mm thick. *Fruits* globose, 1- or 2-seeded, fleshy capsules, 9–10.5 by c. 10 by 10 mm, dehiscing irregularly, raised glands present, sparsely hairy outside, glabrous inside, green; pericarp c. 0.5 mm thick; pedicel 2.2–3.5 mm long, upper part 1–2 mm long. *Seeds* globose, laterally flattened, c. 6.5 by 7.5 by 4 mm; cotyledons c. 4.5 by 6 by 0.1 mm; radicle c. 1 mm long; endosperm c. 1 mm thick.



Map 3.17. Distribution of *Baccaurea microcarpa* (Airy Shaw) Haegens in Papua New Guinea: Ferguson Island.

Distribution — Papua New Guinea: Fergusson Island.
Habitat & Ecology — Altitude c. 200 m. Flowering: June.
Note — Only known from the type specimen.

18. **Baccaurea minor** Hook.f. — Fig. 3.13, Map 3.18

Baccaurea minor Hook.f., Fl. Brit. India 5 (1887) 370; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 64; Ridl., Fl. Malay Penins. 3 (1924) 245; Airy Shaw, Kew Bull. 16 (1963) 342; Soejarto, Bot. Mus. Leafl. 21 (1965) 71; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 37; Whitmore, Tree Fl. Malaya 2 (1973) 66; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 51; Kew Bull. 36 (1981) 264 — Type: *King's Collector 10287* (lecto L, selected here; isolecto K), Malakka, Perak.

Aporosa billitonensis Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 97; Airy Shaw, Kew Bull. 16 (1963) 342. — Type: *Van Rossum 28* (holo B†; lecto L, selected here; isolecto K), Billiton Isl.

Baccaurea pendula Merr., Univ. Calif. Publ. Bot. 15 (1929) 152; Airy Shaw, Kew Bull. Add. Ser. (1975) 51. — Type: *Elmer 21508* (holo PNH†; lecto L, selected here; isolecto DS, GH, K, US), Borneo, Tawau.

Tree 5–35 m high, dbh up to 8–70 cm; buttresses absent or present, up to 1 m high, 1 m long; branchlets subglabrous, Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* red-brown to brown or black, rarely greyish when fresh, brown to greyish brown when dry, up to 8 mm thick, smooth to rough, soft, flaking with small rectangular fibrous flakes, c. 1 cm wide, 6–7 mm thick; inner bark red to brown, up to 2.5 mm thick, fibrous. *Leaves*: petiole 7–35 mm long, glabrous, densely hairy when young, transverse cracks present; stipules lanceolate, 1–4 by 0.7–1.5 mm, densely hairy outside and inside, margin not ciliate, not hyaline; lamina ovate to obovate, 3.5–16.3 by 1.6–8.5 cm, l/w ratio 1.5–3.2(–4.2), papery; base (rounded to) cuneate to attenuate; apex acuminate to cuspidate, 1–20 mm long; upper surface glabrous, granulate, brown to greenish brown to white when dry, nervation brown; lower surface glabrous, midrib rarely densely hairy, discoid glands 0–13, often between two secondary veins or in a row at 0–5 mm distance of the midrib, (whitish to greenish) brown when dry; secondary veins 4–8 per side, closed at c. 3 mm from the margin; nervation reticulate to weakly scalariform, brown. *Staminate inflorescences* axillary to just below the leaves, solitary to 3 clustered together, 1–5 cm long, c. 1 mm thick,

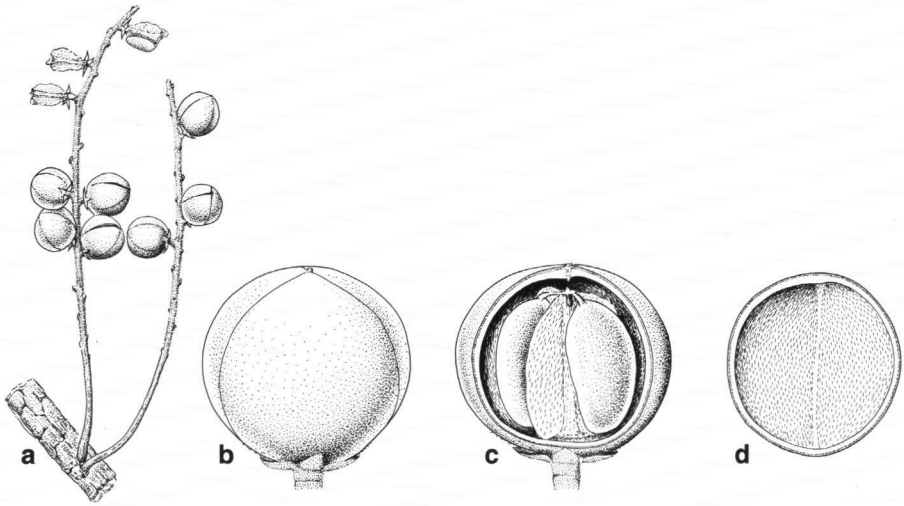
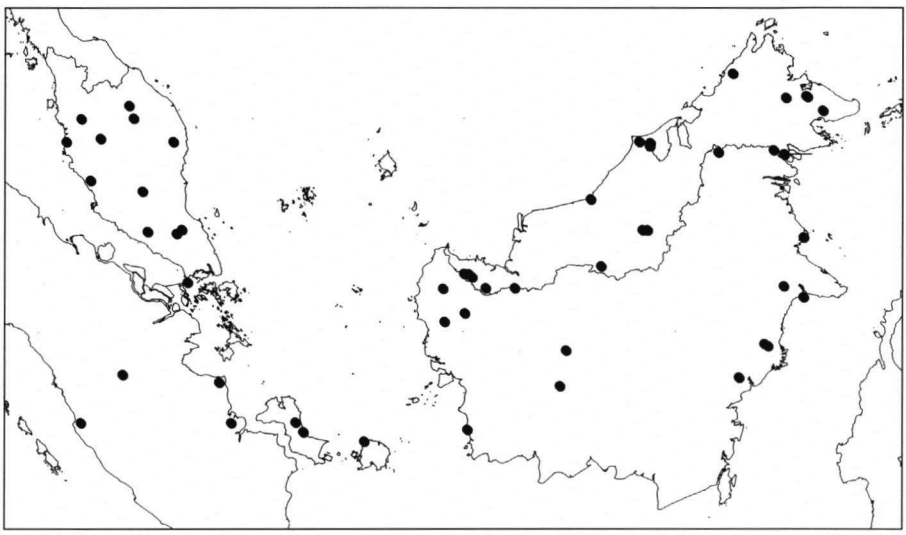


Fig. 3.13. *Baccaurea minor* Hook.f. a. Infructescence; b. fruit; c. dissected fruit showing seeds, column and hairy septa; d. dissected fruit, hairy inner pericarp and septum (*Ridsdale PBU 677*).

densely hairy, 25–60-flowered, flowers clustered at the tip of inflorescence; bracts 1 per branchlet, c. 4.5 mm long, caducous, sparsely to (densely) hairy outside, margin not ciliate; bracteoles 3 per branchlet, small; branchlets cylindrical to spatulate, 1.5–2 mm long, densely hairy, 1- or 2-flowered. *Staminate flowers* 0.8–2 mm diam., clustered at the tip of the branchlets, greenish yellow to yellow, rarely flushed pink; pedicel absent; sepals 4 (or 5), not uniform in shape, 0.3–1 by 0.3–1 mm, apex straight, densely hairy outside and inside; stamens 4 (or 5), 0.2–1 mm long, glabrous; filaments 0.2–1 mm long, laterally flattened, straight; anthers 0.1–0.2 by 0.1–0.2 by c. 0.1 mm when dehisced; disc absent; pistillode sometimes present, globose, up to 0.5 mm high, densely hairy, solid. *Pistillate inflorescences* ramiflorous, solitary to 4 clustered together, 4.5–28 cm long, 1–2 mm thick, densely hairy except at base, 3–20-flowered; pedicel 2–2.5 mm long, abscission zone present, upper part 1–1.5 mm long, densely hairy, pale green; bracts 3 per branchlet, persistent, densely hairy outside and inside, margin ciliate. *Pistillate flowers* 3–8 mm diam.; sepals 4, ovate to obovate, each with a different size and shape, 2.2–4.5 by 1–2.2 mm, densely hairy at both sides, green when fresh, brown when dry, persistent; staminodes rarely present; ovary cylindrical, 1.5–3 by 1.2–2.6 mm, 3-locular, densely hairy; style 0–3 mm long, tomentose; stigmas 0.8–1.4 mm long, apically cleft for upper 90%, persistent; lobes 0.7–1.3 by 0.3–0.6 mm, glabrous above, hirsute below, with rather long whitish hairs. *Fruits* globose, 3-seeded, fleshy capsules, 8–14 by 10–15 by 10–15 mm, dehiscing septicidally and loculicidally, raised glands absent, densely hairy outside, velutinous inside, orange to ochre; pericarp 0.8–1.7 mm thick; column 9–13 mm long, usually persistent, straight; pedicel 3–7 mm long, upper part c. 1 mm long. *Seeds* almost globose but strongly laterally flattened, 5.9–9.5 by 5.4–8.3 by 0.1–0.3 mm, flat; seed-coat red; arillode dull, yellow to orange; cotyledons 4–6 by 5–8 by c. 0.1 mm; radicle up to 2.2 by 1 mm.

Distribution — Peninsular Malaysia, Sumatra, Borneo.



Map 3.18. Distribution of *Baccaurea minor* Hook.f. in Peninsular Malaysia, Sumatra and Borneo.

Habitat & Ecology — Primary, old secondary, or bamboo forest, on ridges or slopes. Soil: granite, yellow sand or yellow sandy loam. Altitude: sea level up to 1200 m. Flowering: Mar. to Sept. Fruiting: June to Jan.

Uses — Used as timber in house construction. Arillode edible, sour-bitter.

Vernacular names — Peninsular Malaysia: Jentek-jentek, kaum tampoi, tampoi, rambai, tinlek-tinlek. Sumatra: Petik. Borneo: Sintak-nyabor (Iban); ubah merah (Malay); bua sarotic, djentikan, obar nasi.

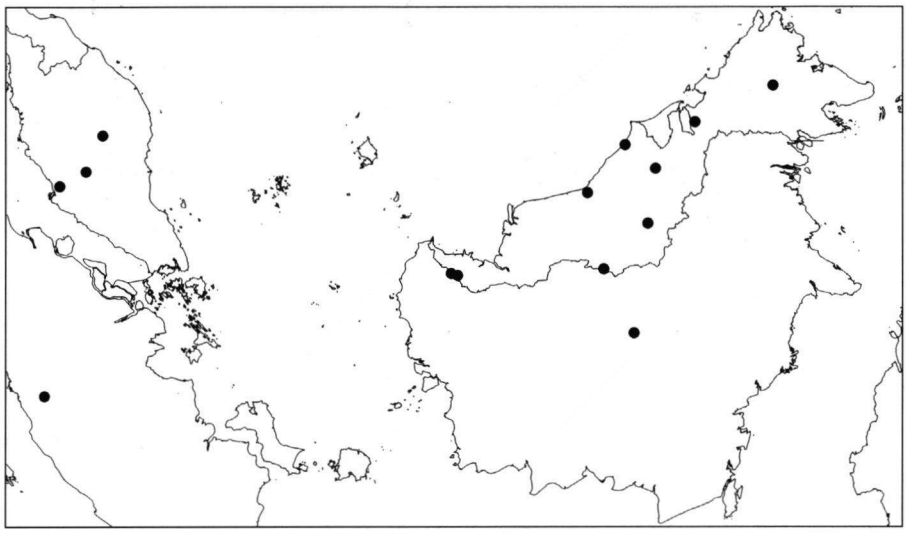
19. Baccaurea mollis Haegens, *spec. nov.* — Fig. 3.14, Map 3.19

> Ab omnibus congeneribus malesianis praeter combinationem charactorum sequentium stipulae serotine caducae ad persistentes 10.5–17 mm longa, petioli dense pubescentes, folia supra costa glabra, indumento et caespitibus stellatis et pilis simplicibus differt. — Typus: *S (Blicher, Rantai et al.) 60306* (holo L), Malaysia, Sarawak, Nanga Sebatu, Memgiong, Baleh.

Tree 9–16.5 m high, dbh 14–19 cm, buttresses low if present; branchlets sparsely hairy to velutinous, Terminalia branching pattern weakly developed. *Indumentum* of stellate and simple hairs. *Bark* red-brown when fresh; inner bark red. *Leaves*: petiole (34–)38–90 mm long, velutinous, raised glands absent; stipules 10.5–17 by 2.5–4 mm, late caducous, velutinous outside and inside, margin ciliate, not hyaline; lamina ovate to elliptic (to obovate), (8.8–)11.7–27.6 by (4.6–)6.3–12.1 cm, l/w ratio 1.6–2.9, papery; base truncate to acute; marginal glands as identification marks; apex acuminate to cuspidate, 4–16 mm long; upper surface (sub)glabrous, not granulate, nervation sunken; lower surface densely hairy, midrib and secondary veins velutinous, raised glands few to absent, discoid glands often present; secondary veins (6–)9–12 per side, closed at margin; nervation reticulate. *Staminate inflorescences* ramiflorous, soli-

Fig. 3.14. *Baccaurea mollis* Haegens. a. Habit with male inflorescences; b. habit; c. seed; d. dissected seed with cotyledon; e. infructescence (a: *KEP 3132*; b–e: *S 60306*).

tary to few clustered together, 3–4 cm long, 0.6–1.5 mm thick, velutinous, branching minute, many-flowered, flowers scattered along inflorescence; bracts 1 per branchlet, 1.2–2 mm long, densely hairy outside and inside, margin ciliate, not hyaline; bracteoles absent; branchlets cylindrical, 0.5–1 mm long, densely hairy, 3-flowered. *Staminate flowers* 1–1.5 mm diam., yellow-green; pedicel c. 0.1 mm long; sepals (3 or) 4 or 5, ovate, 0.6–1 by 0.6–1.2 mm, apex recurved, outside and inside densely hairy; stamin-



Map 3.19. Distribution of *Baccaurea mollis* Haegens in Peninsular Malaysia, Sumatra and Borneo.

odes absent or 4 or 5; stamens 4, c. 0.3 mm long, glabrous; filaments c. 0.15 mm long, straight; anthers c. 0.15 by 0.2 by 0.1 mm; disc absent; pistillode cylindrical, c. 0.4 mm high, densely hairy, solid. *Pistillate inflorescences* ramiflorous to cauline, solitary to 2 clustered together, 1.5–3 cm long, 1.5–3 mm thick, velutinous, more than 20-flowered; pedicel c. 2 mm long, upper part c. 1 mm, velutinous; bracts 3 per branchlet, velutinous outside and inside, margin ciliate. *Pistillate flowers* c. 5 mm diam.; sepals 4 of which 2 adnate, ovate, c. 2 by 1.5 mm, outside and inside densely hairy, persistent; disc absent; ovary globose, c. 3 by 3.5 mm, 2-locular, velutinous; style 0–0.1 mm long, c. 1 mm wide, densely hairy; stigmas 1.2–1.5 mm long, cleft for upper c. 80%, usually persistent; lobes c. 1 by 1 mm, subglabrous above, densely hairy below, protuberances above and below. *Infructescences* 1–4.5 cm long, 3–6 mm thick. *Fruits* globose, 1–4-seeded berries, 27–36 by 26–38 by 26–38 mm, raised glands usually absent, not ruminate, glabrous to sparsely hairy outside, subglabrous to sparsely hairy inside, light (yellow-)brown; pericarp (1–)2–6 mm thick; column 20–26.5 mm long, straight, persistent; pedicel 2–7 mm long, upper part 1–2 mm long. *Seeds* globose to ellipsoid, laterally flattened, 12–15 by 8.2–15 by 3.5–7 mm; arillode deep red; cotyledons 8.5–9.2 by 6–13 by 0.1–0.3 mm; radicle 1–1.5 mm long; endosperm 0.1–0.3 mm thick.

Distribution — Peninsular Malaysia, Sumatra, Borneo.

Habitat & Ecology — Rain forest. Altitude: 60–550(–1800) m. Flowering: Mar., Apr., July. Fruiting: Feb., Apr., June, July, Nov.

Uses — Arillode and pericarp edible, sweet-sour.

Vernacular names — Borneo (Sarawak): buah telok kejira, buah pekan (Iban); lebek (Kayan); tampoi (Malay).

Note — The species is named for its dense soft indumentum.

Specimens studied: *Haegens & Klazenga et al. 398*; *KEP FRI 1949, 2915, 3132*; *Meijer 7425*; *Shah & Noor MS 1953*; *Ridsdale PBU 70*; *S 3422, 32126, 38495, 46561, 60306, 69809*; *SAN 16789*.

20. Baccaurea motleyana (Müll.Arg.) Müll.Arg. — Fig. 3.15, Map 3.20, Photo 5, 6

Baccaurea motleyana (Müll.Arg.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 461; Hook.f., Fl. Brit. India 5 (1887) 371; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 74; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 331; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 53; Ridl., Fl. Malay Penins. 3 (1924) 250; Corner, Wayside Trees Mal. 1 (1940) 240; Backer & Bakh.f., Fl. Java 1 (1964) 454; Soejarto, Bot. Mus. Leafl. 21 (1965) 9, 10, 12, 73; Airy Shaw, Kew Bull. 26 (1972) 220; Whitmore, Tree Fl. Malaya 2 (1973) 66; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 52; 8 (1980) 35; Kew Bull. 36 (1981) 264. — *Pierardia motleyana* Müll.Arg., Flora 47 (1864) 516. — Type: *Motley 773* (holo K), Borneo, near Banjarmasin.

Baccaurea pubescens Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 61; Ridl., Fl. Malay Penins. 3 (1924) 250. — Type: *Wawra 297a* (holo W), Singapore.

Tree 8–20 m high, dbh 13–50 cm, buttresses short; branchlets densely hairy, Terminalia branching pattern weakly developed. *Indumentum* of simple hairs. *Bark* brown to red-brown to yellowish when fresh, thin, soft, scaly to flaky; inner bark cream, turning slightly reddish, hard. *Leaves*: petiole 23–84 mm long, densely hairy to velutinous, brown-grey when dry, raised glands absent; stipules 5–10 by 1.5–3.5 mm, glabrous to sparsely hairy outside, glabrous inside, midrib velutinous outside, margin ciliate, hyaline or not; lamina elliptic to obovate, 13.5–37 by 5.2–15 cm, l/w ratio 1.9–2.5, papery: base rounded to usually narrowly cordate; apex acute cuspidate, (0–)7–22 mm long; upper surface glabrous, not granulate, (dark) green when fresh, brown to green to grey when dry; lower surface densely hairy to sparsely hairy, midrib and secondary veins velutinous, raised glands absent, discoid glands absent, (dark) green when fresh, brown to green when dry; secondary veins 10–17 per side, open at margin; nervation scalariform; young leaves black when dry. *Staminate inflorescences* cauline to axillary, solitary to 5 clustered together, 2.5–24 cm long, up to 1.5 mm thick, velutinous, many-flowered, flowers scattered along inflorescence, greenish yellow; bracts persistent, elliptic, 1–2.5 mm long, 3 per branchlet, glabrous outside and inside, densely hairy at base inside, margin ciliate, not hyaline; bracteoles absent; branchlets absent to present, cylindrical, 0–3 mm long, densely hairy, 3-flowered. *Staminate flowers* 2–3 mm diam., green to yellow; pedicel 1.6–2.3 mm long, upper part 0.6–1.6 mm long, densely hairy; sepals 4 or 5, ovate, 0.7–1.4 by 0.5–1.4 mm, usually recurved, densely hairy outside and inside; stamens 5–10, 0.4–0.6 mm long, glabrous; filaments 0.4–0.6 mm long, geniculate to straight; anthers c. 0.1 by 0.2 by 0.1 mm; disc present, c. 0.1 mm thick; pistillode obtriangular, 0.4–0.5 mm high, velutinous, hollow. *Pistillate inflorescences* ramiflorous to cauline, solitary to 5 clustered together, 13–42 cm long, 1–2.5 mm thick, velutinous, more than 30-flowered, greenish yellow; pedicel 2–5.5 mm long, upper part 0.2–1 mm long, densely hairy to velutinous; bracts 3 per branchlet, persistent, velutinous outside, glabrous to densely hairy inside, margin ciliate. *Pistillate flowers* 4–10 mm diam., green to yellow; sepals 4 or 5, ovate, 4–8 by 1.5–3.5 mm, densely hairy outside and inside, persistent; ovary globose, 1.6–2.6 by 1.7–2.9 mm, 3-locular, velutinous; style 0–0.4 by 0.8–1.2 mm wide, velutinous; stigmas 0.5–1 mm long, glabrous above and below, persistent. *Fruits* globose to ellipsoid, 3-seeded berries, 22–45 by 15–25 by c. 25 mm, raised glands present, glabrous to densely hairy outside, glabrous inside, greenish yellow to white; pericarp 0.5–1.5 mm thick; column 18–23 mm long, straight, caducous; pedicel 4–10 mm long, upper part 1–2 mm long. *Seeds*

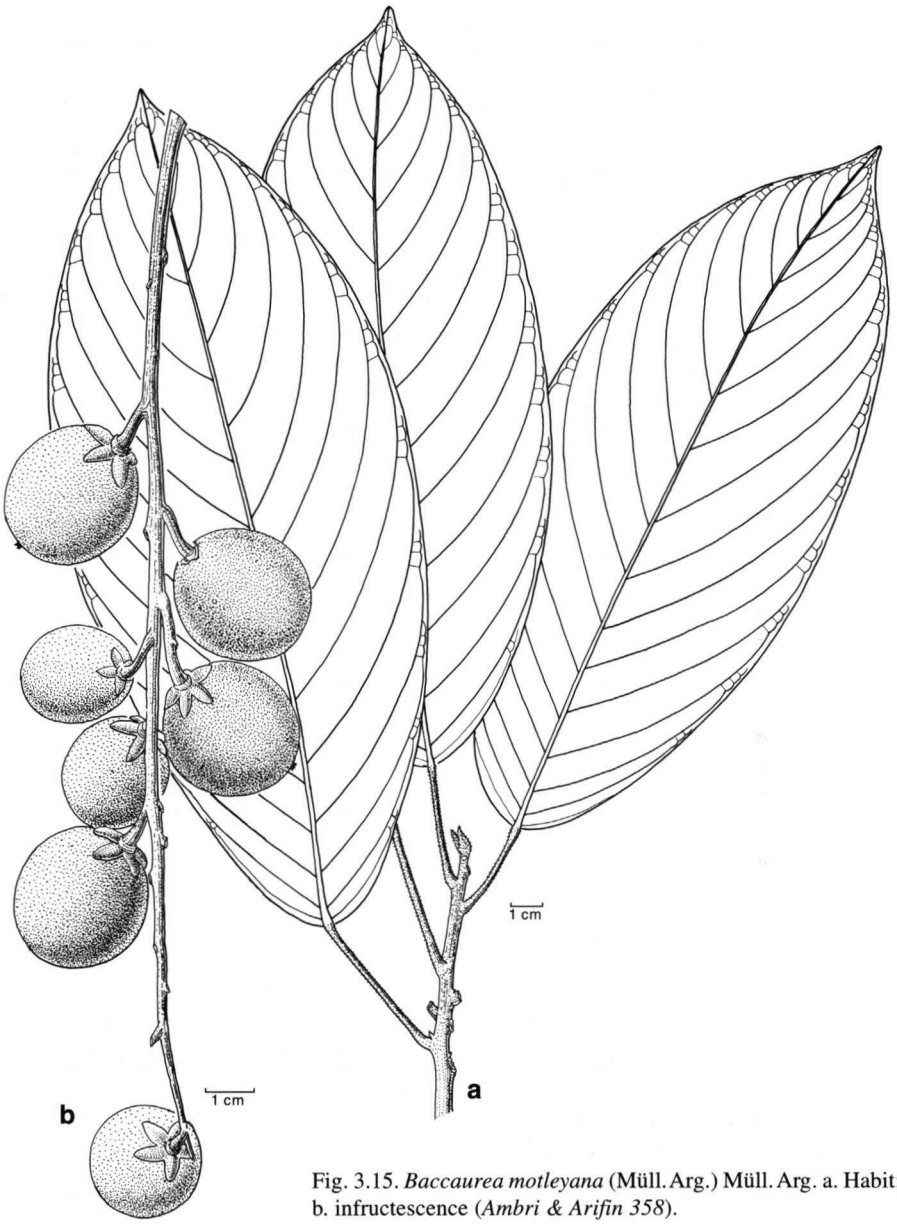
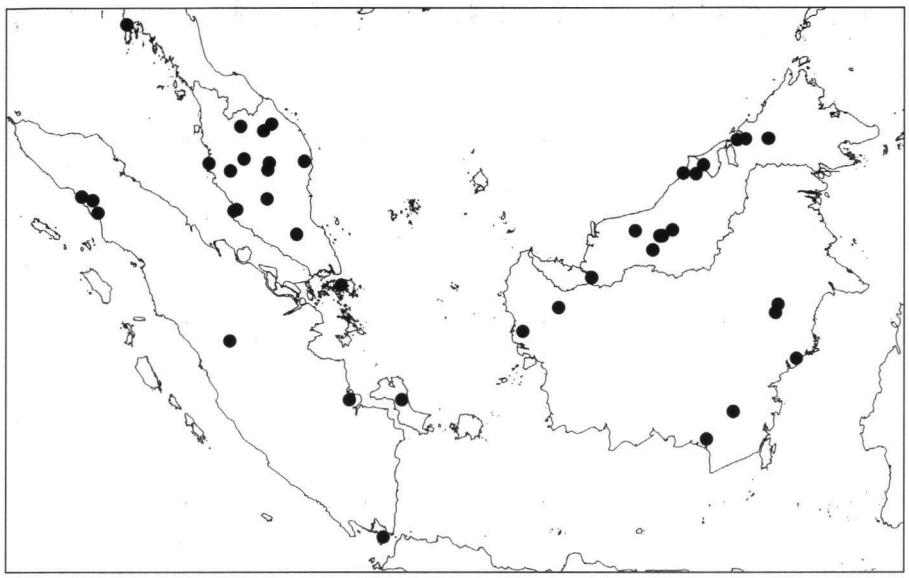


Fig. 3.15. *Baccaurea motleyana* (Müll. Arg.) Müll. Arg. a. Habit; b. infructescence (*Ambri & Arifin 358*).

ellipsoid, laterally flattened, 13–20 by 9–14.5 by 2.5–4 mm; arillode translucent white to rarely purple; cotyledons 5–9 by 5–9 by c. 0.1 mm; radicle 2–3 mm long.

Distribution — Peninsular Malaysia, Sumatra, Borneo, Halmahera.

Habitat & Ecology — Primary and secondary rain forest, and rarely riparian forest, often cultivated. Soil: yellow clay, sand or limestone. Altitude: 15–500 m. Flowering: Jan. to May, Aug., Oct., Nov. Fruiting: Jan., May, July to Sept., Nov., Dec.



Map 3.20. Distribution of *Baccaurea motleyana* (Müll.Arg.) Müll.Arg. in Peninsular Malaysia, Sumatra, Borneo and Halmahera.

Uses — Locally grown for fruits: arillode edible, sour to sweet. Squeezed cambium and inner bark used as a remedy for sore eyes.

Vernacular names — Peninsular Malaysia: Rambai. Sumatra: Rambai. Borneo: Pekan (Iban); rambai (Iban, Malay); ulup-lavai (Punan).

21. **Baccaurea multiflora** Burck ex J.J. Sm. — Fig. 3.16, Map 3.21

Baccaurea multiflora Burck ex J.J. Sm., Icon. Bog. 4 (1910) 37, t. 312; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 74; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 67; Airy Shaw, Kew Bull. 36 (1981) 264. — Type: *Teijsmann HB 3504* (lecto L, selected here), Sumatra, Bangka.

Tree c. 8 m high, dbh 10–20 cm, buttresses absent; branchlets glabrous to sparsely hairy, densely hairy when young; young shoots dark brown to blackish when dry, Terminalia branching pattern weakly developed. *Indumentum* of stellate and simple hairs. *Bark* grey-brown to dark brown when fresh, c. 2 mm thick; outer bark finely fissured; inner bark pale brown, c. 0.5 mm thick. *Leaves*: petiole 8–45 mm long, glabrous to sparsely hairy, transverse cracks present, dark brown to blackish when dry, raised glands often present; stipules 2.5–5 by 2–3 mm, densely hairy to velutinous outside, subglabrous inside, margin ciliate, not hyaline; lamina obovate, 6.7–13.2 by 2.5–5.9 cm, l/w ratio (1.3–)1.9–2.7(–3.1), (slightly) leathery; base cuneate to attenuate; apex obtuse to acute, up to 11 mm long; upper surface glabrous, raised glands usually present, green when fresh, dark (green-, or grey-)brown when dry; lower surface glabrous, nervation sometimes subglabrous, raised glands usually present, discoid glands absent, pale yellow-green when fresh, (pale) (yellow-)brown with darker nervation below when dry; secondary veins 4–7 per side, often closed at margin; nervation reticulate,

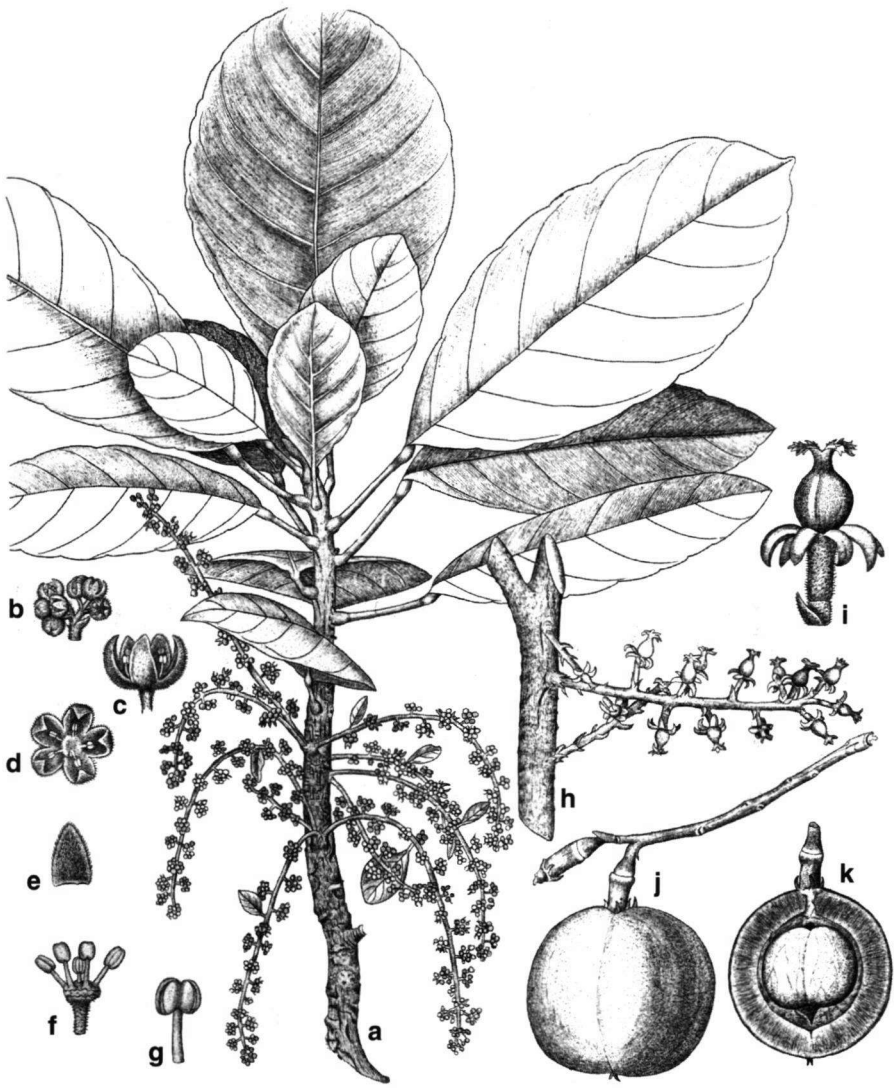
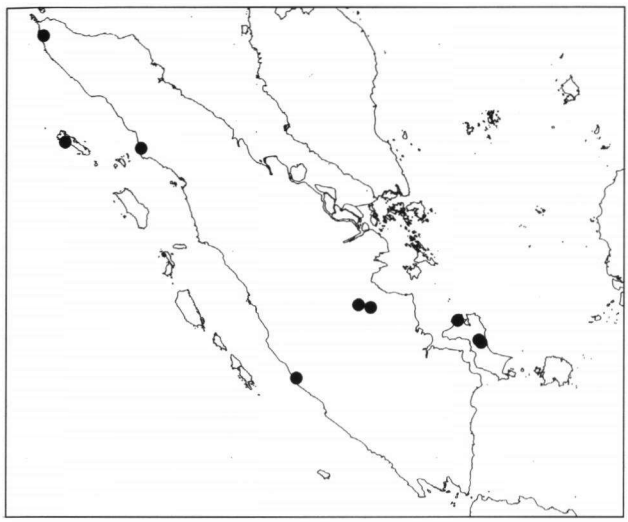


Fig. 3.16 *Baccaurea multiflora* Burck ex J.J. Sm. a. Habit with male inflorescences; b. male inflorescence detail; c. male flower; d. male flower; e. male sepal; f. male flower without sepals; g. anther; h. female inflorescence; i. female flower; j. infructescence; k. fruit in cross section, seeds covered by arillode [Reproduced from E.J. Brill (ed.) Icones Bogorienses 4: tabula CCCXII, f. 1. (1919)].

indistinct. *Staminate inflorescences* axillary to ramiflorous, solitary to few clustered together, 1–9.5 cm long, 0.5–1 mm thick, branched, subglabrous to densely hairy, many-flowered, flowers usually scattered along inflorescence, cream-yellow; bracts usually present, leaf-like; bracts 1 per branchlet, 1–3.5 mm long, sparsely to densely hairy outside, subglabrous to densely hairy inside, margin ciliate, not hyaline; bracteoles



Map 3.21. Distribution of *Baccaurea multiflora* Burck ex J.J. Sm. in Sumatra.

c. 0.5 mm long, subglabrous outside; branching cylindrical, 1.5–12 mm long, densely hairy, 3–10-flowered. *Staminate flowers* 1–2 mm diam., cream-yellow; pedicel 1–3.3 mm long, upper part 0.6–1.8 mm long, densely hairy; sepals 4 or 5, ovate to obovate, 0.5–1.8 by 0.4–0.9 mm, apex recurved, outside and inside densely hairy, cream-yellow; stamens 3–6, 0.2–0.5 mm long, glabrous; filaments 0.1–0.4 mm long, straight; anthers 0.1–0.15 by 0.2–0.3 by c. 0.1 mm; disc absent; pistillode globose, up to 0.2 mm high, velutinous, solid. *Pistillate inflorescences* probably ramiflorous, few clustered together, c. 3.3 cm long, 0.8–1 mm thick, densely hairy to velutinous, many-flowered; pedicel 1–4 mm long, upper part 0.7–3 mm, velutinous; bracts 3 per branchlet, 2 small, densely hairy outside, (sub)glabrous inside, margin ciliate. *Pistillate flowers* 2.5–6.8 mm diam.; sepals (4 or) 5, ovate to obovate, 2–3.5 by 1–1.9 mm, outside and inside velutinous, caducous; ovary fusiform to cylindrical, 1.8–4.5 by 1.5–3.6 mm, 2-locular, velutinous; style 0.3–0.9 by 0.9–1.2, densely hairy; stigmas 0.5–1.5 mm long, cleft for upper 0–50%, caducous; lobes 0.5–0.7 by 0.2–0.5 mm, glabrous above, densely hairy below, protuberances above and below. *Fruits* globose, berries, 24–28 by 22–23 by 22–23 mm when dry, raised glands present, velutinous outside and inside, peel brownish; pericarp 4–6 mm thick; column c. 20 mm long, straight; pedicel 8–9 mm long. *Seeds* only seen immature; arillode whitish.

Distribution — Sumatra.

Habitat & Ecology — Primary rain forest. Soil: yellow-red loam. Altitude: 50–900 m. Flowering: Aug. (and July, Nov. in cultivation). Fruiting: Dec.

Vernacular names — Sumatra: Rambay hutan, roesip, temoeleëng. Simeuluë Island: Bolawah anteu.

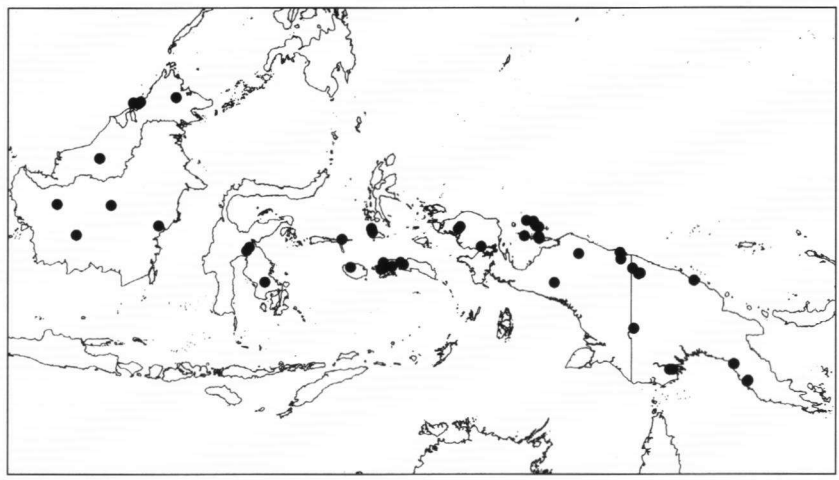
22. **Baccaurea nanihua** Merr. — Map 3.22

Baccaurea nanihua Merr., Interpr. Rumph. Herb. Amboin. (1917) 315; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 67; J.J. Sm., Bull. Jard. Bot. Buitenzorg 3 (1924) 94; K. Heyne, Nutt. Pl. Ned. Ind., 3rd ed., 1 (1950) 914; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 52; Kew

Bull 37 (1982) 8. — Type: *Robinson 331* (holo A; iso G, SING, US), Moluccas, Ambon, Koesoe-koesoe and Mahija.

Baccaurea tristis Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 69; Airy Shaw, Kew Bull. Add. Ser. 8 (1980) 37, syn. nov. — Type: *Ledermann 9811* (lecto L, selected here), Papua New Guinea.

Treelet or tree 5–25 m high, dbh 8–40 cm; bole sometimes fluted up to 1 m; mouldings 20 cm out, 10 cm thick; branchlets subglabrous, densely hairy when young; young shoots brown to grey when dry, Terminalia branching pattern weakly developed. *Indumentum* of stellate and simple hairs. *Bark* red to red-brown to grey-brown to dark brown when fresh, 0.2–2 mm thick, sometimes slightly peeling off; inner bark red to red-brown to yellowish red, 0.5–3 mm thick. *Heartwood* pale red to reddish yellow. *Leaves*: petiole 16–64 mm long, subglabrous to densely hairy, transverse cracks present, apically and sometimes basally pulvinate, raised glands rarely present; stipules 3.5–7.5 by 1–3 mm, velutinous outside, glabrous to densely hairy inside, margin ciliate, not hyaline; lamina ovate to elliptic (to obovate), 6.5–21(–25) by 2.5–10.8 cm, l/w ratio 1.4–2.9, papery to leathery; base attenuate to rounded; marginal glands sometimes visible as small indentations; apex (broadly) acuminate, up to 11 mm long; upper surface glabrous (to densely hairy at midrib), raised glands often present, sometimes granulate, dark brown to grey-brown when dry, nervation dark brown to grey-brown; lower surface glabrous to sparsely hairy (to densely hairy at midrib and veins), raised glands often present, discoid glands if present in a row between secondary veins, light brown when dry; secondary veins 6–10 per side, open at margin; nervation reticulate to weakly scalariform, (dark) brown; young leaves green. *Staminate inflorescences* axillary (to ramiflorous), solitary to few clustered together, 1–13.5 cm long, up to 1 mm thick, branching present, densely hairy, many-flowered, flowers scattered along inflorescence, rachis pale yellow, bracts leave-like (up to 2 cm long) usually present; bracts 1 per branchlet, 1.5–3 by 1–1.2 mm, densely hairy outside, subglabrous to densely hairy inside, margin ciliate, not to slightly hyaline; bracteoles 0.5–1.5 mm long, outside and inside densely hairy; branchlets cylindrical, 2–35 mm long, densely hairy, 3–many-flowered. *Staminate flowers* 1.5–2.5 mm diam., pale yellow to whitish; pedicel 1–2 mm long, upper part 0.6–1.2 mm long, densely hairy, reddish-brown; sepals 4–6, ovate, 0.9–1.5 by 0.3–1 mm, sometimes apically recurved, outside and inside densely hairy; stamens 4–6, 0.3–0.6 mm long, glabrous, brownish; filaments 0.15–0.5 mm long, straight; anthers 0.1–0.2 by 0.15–0.25 by up to 0.1 mm; disc absent; pistillode globose, 0.1–0.4 mm high, velutinous, solid. *Pistillate inflorescences* ramiflorous to axillary, solitary, 0.5–4 cm long, 1–2 mm thick, velutinous, few-flowered; pedicel c. 4.5 mm long, upper part 1–1.5 mm long, densely hairy; bracts 1 per branchlet, ovate, velutinous outside, densely hairy inside, margin ciliate. *Pistillate flowers* 3–7 mm diam.; sepals 5 (or 6), ovate, 1.5–3 by 1–1.5 mm, velutinous outside and inside, usually persistent; ovary globose to cylindrical, c. 2.5 by 2.5 mm, (2- or) 3- (or 4-)locular, velutinous; style c. 1 by c. 1.5 mm, velutinous; stigmas c. 0.1 mm long, persistent to caducous. *Fruits* globose to suppressed globose, 0–6-seeded, fleshy capsules, 14–25 by 25–29 by 25–29 mm, loculicidally dehiscent, raised glands usually present, densely short hairy outside, sparsely hairy to hirsute inside, septa densely long hairy, (yellowish to reddish) brown; pericarp 3–6.5 mm thick; column 11–13.5



Map 3.22. Distribution of *Baccaurea nanihua* Merr. in Borneo, Sulawesi, the Moluccas and New Guinea.

mm long, straight; pedicel 8.5–15 mm long, upper part 3.5–8 mm long. *Seeds* ellipsoid, laterally flattened, to long triangular, 7.5–11.5 by 3.8–7 by 3–4.7 mm; cotyledons 5–5.5 by c. 5 by 0.1 mm; radicle c. 0.7 mm long; endosperm 2–2.5 mm thick.

Distribution — Borneo, Sulawesi, Moluccas, New Guinea.

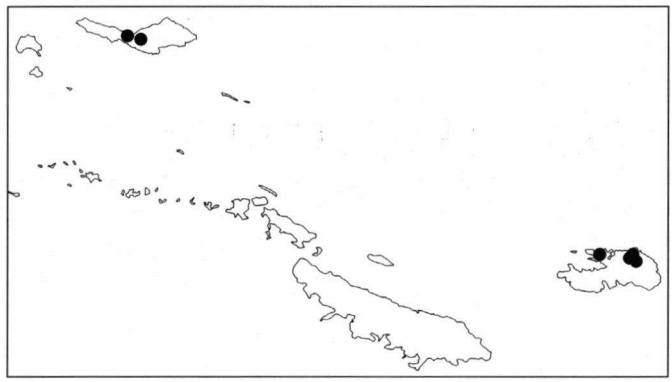
Habitat & Ecology — Primary rain forest, riverine rain forest, and edges of mangrove. Soil: sandy loam. Altitude: sea level up to 600 m. Flowering: June to Jan. Fruiting: Jan., Apr. to July, Sept., Nov., Dec.

Vernacular names — Moluccas: Maroontaboea. New Guinea: Garang kafak (Tehid); mabab (Biak); senesasau (Mekeo); pei (Biak).

23. **Baccaurea nesophila** Airy Shaw — Map 3.23

Baccaurea nesophila Airy Shaw, Kew Bull. 33 (1979) 529; Kew Bull. Add. Ser. 8 (1980) 35. — Type: *Brass 27665* (holo K; iso L, US), Papua New Guinea, Mimisa Island, Quark Mt.

Tree 8–20 m high, dbh 10–30 cm, slightly buttressed; branchlets densely hairy when young, brown to blackish when dry; Terminalia branching pattern weakly developed to sometimes strong. *Indumentum* of simple and rarely a few stellate hairs. *Bark* brown to reddish when fresh. *Heartwood* pinkish. *Leaves*: petiole 8–31 mm long, glabrous to sparsely hairy, densely hairy when young, raised glands absent; stipules 2.5–6 by 1.5–2 mm, glabrous on both sides, densely hairy when young, margin ciliate when young, (not) hyaline; lamina elliptic to obovate, 3.5–12.9 by 1.9–6.2 cm, l/w ratio 1.6–2.4, papery to slightly leathery, base attenuate to cuneate; apex (retuse to) obtuse to slightly acute, 0–3 mm long; upper surface (sub)glabrous, granulate above, nervation not to slightly sunken, glossy dark green when fresh, green to brown to reddish when dry; lower surface subglabrous, raised glands absent, discoid glands many, dark to pale green below when fresh, (light) green to brown below when dry; secondary veins 4–9 per side, closed at margin; nervation reticulate, brown to red when dry. *Staminate inflorescences* unknown. *Pistillate inflorescences* ramiflorous to axillary, solitary to



Map 3.23. Distribution of *Baccaurea nesophila* Airy Shaw in Louisiade Archipelago.

rarely 5 clustered together, few to c. 15-flowered. *Pistillate flowers*: sepals caducous; ovary 2-locular; stigmas persistent. *Infructescences* 2.6–7 cm long, 0.5–1.5 mm thick. *Fruits* globose to ellipsoid to pear-shaped, 2–4-seeded, fleshy capsules, 16–21 by 12–20 by 12–20 mm, dehiscing loculicidally, (sometimes septicidally also), raised glands absent to present, glabrous to sparsely hairy outside, glabrous to subglabrous inside, green to yellow; pericarp 1–1.8 mm thick; column 12–17 mm long, straight to slightly curved; pedicel 2.1–3.6 mm long, upper part 1–2.5 mm long. *Seeds* globose to ellipsoid, laterally flattened, 8.8–12.5 by 5.7–12 by 3–5 mm; arillode red to orange; testa cream to whitish; cotyledons 5.5–9 by 6–11 by c. 0.1 mm; radicle 1–2 mm long; endosperm c. 1.5 mm thick.

Distribution — Papua New Guinea: Louisiade Archipelago.

Habitat & Ecology — Swamp forest to ridge tops. Altitude: 0–510 m. Fruiting: Apr., June to Nov.

Vernacular names — Louisiade Archipelago: Dumi, tum.

24. **Baccaurea odoratissima** Elmer — Fig. 3.17, Map 3.24, Photo 7

Baccaurea odoratissima Elmer, Leafl. Philipp. Bot. 4 (1911) 1276; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 59; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 411; Fernando, Philipp. J. Biol. 8 (1979) 307. — Type: *Elmer 13160* (lecto L, selected here; isolecto GH, K, US), Philippines, Palawan, Puerto Princesa.

Baccaurea membranacea Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 49; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 54, syn. nov. — Type: *Hose 600* (lecto L, selected here; isolecto K), Borneo, Sarawak, Baram district, Miri River.

Baccaurea trunciflora Merr., Univ. Calif. Publ. Bot. 15 (1929) 151; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 37; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 56, syn. nov. — Type: *Elmer 21550* (lecto L, selected here; isolecto GH, US), Borneo, Sabah, Tawau.

Treelet to tree 2–17 m high, dbh 4.4–20 cm, buttresses absent; branchlets sparsely hairy, female plants rarely glabrous, Terminalia branching pattern well-developed. *Indumentum* of simple hairs, usually in combination with stellate hairs. *Bark* yellow to grey-brown when fresh, whitish grey when dry, 0.1–2.5 mm thick; inner bark yellow to orange-brown, 0.1–0.4 mm thick. *Leaves*: petiole 9–82 mm long, sparsely hairy,

Photo 1. *Baccaurea angulata* Merr. – Photo: A. Lamb (Sabah, Malaysia).

Photo 2. *Baccaurea lanceolata* (Miq.) Müll. Arg. – Photo: R. M. A. P. Haegens 473 (Sarawak, Malaysia).

Photo 3. *Baccaurea lanceolata* (Miq.) Müll. Arg. – Photo: R.M.A.P. Haegens (Sabah, Malaysia).

Fig. 3.17. *Baccaurea odoratissima* Elmer. a. Habit; b. infructescence; c. fruit; d. fruit, transverse section, showing two locules [a–d: *Sulit 3947*. Reproduced from E.S. Fernando in Kalikasan, Philipp. J. Bot. 8: 308, f. 3 (1979)].

female plants rarely glabrous, (green- or red-)brown when dry, raised glands present; stipules 1.7–8 by 0.5–2 mm, glabrous to sparsely hairy outside, but densely hairy when young, glabrous inside, midrib densely hairy outside, margin (not) ciliate; lamina obovate to elliptic (to ovate), 6.4–19 by 2–9.9 cm, l/w ratio 1.5–3.3, papery; base

acute to attenuate, apex rounded to cuspidate, up to 22 mm long; upper surface glabrous, raised glands usually present, green-brown when dry; lower surface glabrous, sparsely hairy at veins, raised glands usually present, discoid glands absent, brown when dry; secondary veins 3–8 per side, usually closed at margin; nervation reticulate to weakly scalariform; young leaves red-brown. *Staminate inflorescences* axillary to ramiflorous, solitary to few clustered together, 1.4–8 cm long, up to 1 mm thick, densely hairy, more than 30-flowered, flowers scattered along inflorescence; branchlets absent; bracts 3 per branchlet, c. 0.6 mm long, persistent, glabrous to densely hairy outside, glabrous inside, margin ciliate, sometimes hyaline. *Staminate flowers* 3 per branchlet, 1–2 mm diam., pale yellow; pedicel 0.8–2.5 mm long, upper part 0.6–2.1 mm long, densely hairy; sepals 4(–6), ovate, 0.9–1.2 by 0.7–0.9 mm, apex slightly recurved, densely hairy outside, glabrous inside; stamens 4–7, (0.2–)0.8–0.9 mm long, glabrous; filaments (0.2–)0.8 mm long, straight; anthers 0.1–0.3 by c. 0.1 by 0.1 mm; disc absent; pistillode subglobose to cylindrical, (0.2–)0.9 mm long, densely hairy, solid. *Pistillate inflorescences* cauline (to ramiflorous), solitary to 3 clustered together, 2–26.5 cm long, 0.5–1.5 mm thick, sparsely to densely hairy, 9–many-flowered, red; pedicel 1.2–3.5 mm long, upper part 0.5–1 mm long, densely hairy, light green to red; bracts 3 per flower, persistent, sparsely to densely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 5–11 mm diam.; sepals 4, obovate, 4–6 by 2–2.7 mm, sparsely hairy outside, densely hairy inside, greenish yellow when fresh, brown outside when dry, whitish inside when dry, caducous; ovary globose, 1.2–2.5 by 1.7–2.6 mm, 2-locular, densely hairy to velutinous, light green; style 0–0.1 mm long, c. 1 mm broad; stigmas white, 0.5–0.9 mm long, not lobed, glabrous on both sides, persistent, rarely caducous. *Fruits* subglobose to double globose, 0–2-seeded, fleshy capsules, 7.2–12 by 8–13.5 by (4–)6.8–11, irregularly splitting, glabrous on both sides, densely hairy when young outside, raised glands usually absent, red to shiny brown; pericarp up to 0.5 mm thick; column 6–10 mm long, caducous, straight; pedicel 2.5–9.5 mm long, upper part 0.5–3 mm. *Seeds* subglobose to ellipsoid, laterally flattened, 6.5–10 by 2.5–8 by 2.5–6 mm; arillode blue; cotyledons 5.5–7 by 6.8–7.2 by 0.1–0.3 mm; endosperm 1.5 mm thick; radicle 1.3–1.5 mm long.

Photo 4. *Baccaurea macrocarpa* (Miq.) Müll.Arg. – Photo: R.M.A.P. Haegens 328 (Sarawak Malaysia).

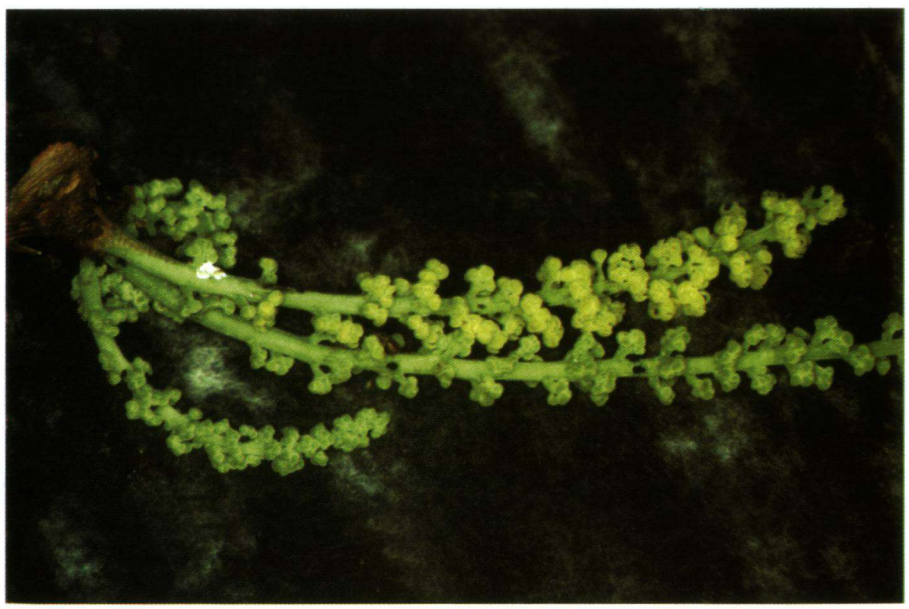


Photo 5. *Baccaurea motleyana* (Müll.Arg) Müll.Arg. – Photo: R.M.A.P. Haegens 640 (Sabah Malaysia).

Photo 6. *Baccaurea motleyana* (Müll.Arg) Müll.Arg. – Photo: J.L.C.H. van Valkenburg (Kalimantan, Indonesia).

Photo 7. *Baccaurea odoratissima* Elmer – Photo: A. Lamb (Sabah, Malaysia).

Distribution — Borneo.

Habitat & Ecology — Primary or secondary forest. Soil: basalt, yellow sandy clay, blackish sandstone. Altitude: sea level up to 1250(–1500) m. Flowering: Febr., Apr., July to Oct., Dec. Fruiting: Jan. to Mar., May to Aug., Oct., Nov.

Uses — Fruit edible.

Vernacular names — Borneo: Enkuni, kune madamayang (Iban); kukunal (Dusun Kinabatangan); kunau (Brunei, Dusun); kunau kunau (Malay); botung kratek, enkunig, enkuri, mata kunau, mata pelanduk, rambai tikus, sarotik, tampoi keli.

Note — Airy Shaw (1975) mentioned this species as a synonym of *B. parviflora* with a question mark. However, after studying the type material and the original descriptions, I am convinced that this species is conspecific with *B. membranacea* and *B. trunciflora*, and distinct from *B. parviflora*. Especially the fruit is utterly different, in the number of locules (*B. odoratissima* 2-locular, *B. parviflora* 3-locular) as well as in the fruit shape (globose in *B. odoratissima*, fusiform in *B. parviflora*).

25. **Baccaurea papuana** F.M. Bailey — Map 3.25

Baccaurea papuana F.M. Bailey, Proc. Roy. Soc. Queensland 18 (1904) 3: Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 57; Airy Shaw, Kew Bull. Add. Ser. 8 (1980) 36. — Type: *F.M. Barton s.n.* (holo BRI), Papua New Guinea, Mekeo District.

Baccaurea plurilocularis J.J. Sm., Nova Guinea 8 (1910) 228; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 60; S. Moore, J. Bot. Br. 61 (1923) 46; Airy Shaw, Kew Bull. Add. Ser. 8 (1980) 36. — Type: *Versteeg 1263* (lecto L, selected here; isolecto K, U), New Guinea, Irian Jaya, base of the Nepenthes Hills.

Baccaurea montana Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 55, syn. nov. — Type: *Schlechter 18537* (lecto K, selected here; isolecto A), Papua New Guinea, Kaiser Wilhelmsland, Bismarckgebiet.

Shrub to tree 4–20 m high, dbh 6–30 cm, buttresses absent; branchlets subglabrous, Terminalia branching pattern usually strong. *Indumentum* of simple hairs. *Bark* (light) brown to (light) grey when fresh, grey when dry, thin, papery; inner bark pale brown to pale yellow, thin, medium hard. *Heartwood* pinkish brown. *Leaves*: petiole 7–60 mm long, subglabrous to densely hairy, transverse cracks absent to some present, raised glands absent to present; stipules 3–6.5 by 1–2.3 mm, glabrous, densely hairy when young outside, glabrous inside, margin ciliate, (not) hyaline; lamina (ovate to) elliptic to obovate, 8–20.5 by 2.8–10.4 cm, l/w ratio 1.6–3.3, papery; base attenuate to cuneate to rarely rounded; marginal glands not to slightly visible as identification marks; apex (retuse to) obtuse to acute (to cuspidate), up to 13 mm long; upper surface glabrous, midrib glabrous to densely hairy, granulate, dull to shiny, pale to dark green when fresh, (greyish to greenish) brown when dry, nervation whitish to (dark) brown; lower surface subglabrous to sparsely hairy, subglabrous to densely hairy at veins, raised glands usually absent, discoid glands sometimes few present; dull to shiny, pale to dark green when fresh, (greyish to greenish) brown when dry; secondary veins 7–15 per side, closed at margin; nervation reticulate to weakly scalariform, grey-brown; young leaves reddish. *Staminate inflorescences* axillary to cauline, solitary to few clustered together, 0.5–23 cm long, c. 1 mm thick, sparsely to densely hairy, many-flowered, flowers scattered along inflorescence; bracts 3 (or 4) per branchlet, 0.3–1 mm long, subglabrous to densely hairy outside, glabrous inside, margin ciliate, hyaline;

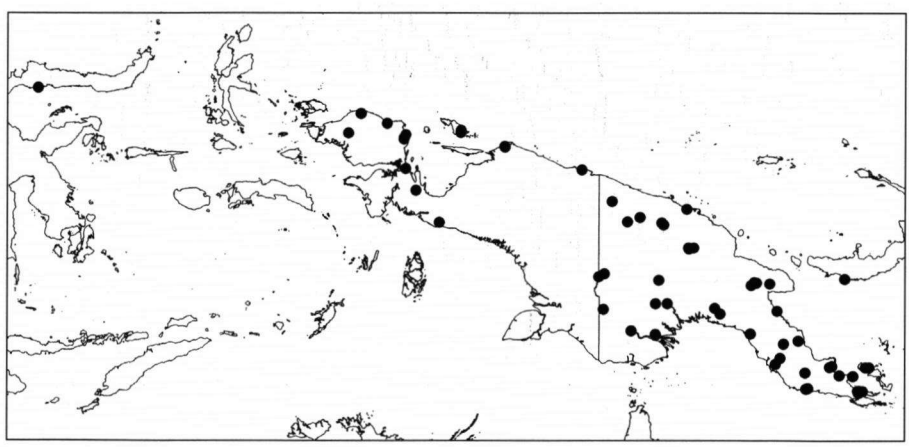
bracteoles absent; branchlets 0–0.4 mm long, 3-flowered. *Staminate flowers* 1.8–3.5 mm diam., cream to yellow, sweet scented; pedicel 1.2–4.2 mm long, upper part 0.6–3 mm, densely hairy, yellow; sepals 4 or 5, ovate to elliptic, 1–1.8 by 0.5–1.3 mm, apex straight, densely hairy outside and inside; staminodes 4–8; stamens 4–8, 0.3–0.8 mm long, glabrous; filaments 0.2–0.7 mm long, slightly geniculate to straight; anthers 0.1–0.2 by 0.2–0.3 by 0.1–0.15 mm; disc absent; pistillode globose to obtriangular, 0.3–0.6 mm high, densely hairy, hollow. *Pistillate inflorescences* cauline, solitary to few clustered together, 7.5–35 cm long, 0.5–2 mm thick, sparsely hairy to velutinous, 5–40-flowered, yellow; pedicel 2.5–10 mm long, upper part 0.5–2(–4) mm, densely hairy to velutinous; bracts 3 per branchlet, sparsely to densely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 4–18 mm diam., greenish to yellow to creamy yellow, fragrant; sepals 5–9, lanceolate to rarely obovate, 3–11 by 0.7–4.8 mm, densely hairy outside and inside, persistent; ovary globose, 1.2–3 by 1.5–3.3 mm, 3- (or 4-) locular, woolly; style absent to 0.01 mm long, c. 1 mm wide, glabrous; stigmas 0.7–1.2 mm long, cleft for upper 0–30%, persistent; lobes c. 0.7 by 0.4 mm, glabrous above and below, ruminate above and below. *Fruits* pear-shaped to globose, (3–)6-seeded berries, 27.5–43 by 24–40 by 24–40 mm, raised glands absent to present, not to slightly ruminate, glabrous to densely hairy outside, glabrous inside, brown to green to red to pink to purple; pericarp 1–7 mm thick; pedicel 5–8(–23) mm long, upper part 1–3(–4) mm long. *Seeds* ellipsoid to globose, laterally flattened, 9–22 by 9–12 by 3.5–7 mm; arillode yellow to white; cotyledons 5.5–8 by 5–8 by < 0.1–0.4 mm.

Distribution — New Guinea and (Sulawesi).

Habitat & Ecology — Primary and secondary rain forest, and swamp forest. Soil: laterite to clay. Altitude: sea level up to 1300 m. Flowering: throughout the year. Fruiting: Jan. to Oct.

Uses — Arillode edible, harsh but refreshing.

Vernacular names — New Guinea: Ngesby (Hattam); apo (Maipa; Mekeo); kniebieé (Manikiong); esino (Minufia); ani-abi (Noemfoer); kwame (Onjob); be(h)ga, tomarah (Orokaiva); cobo, gomo (Totubu); mapiok (Waskuk); motroka, nunuhabu, sakowgwo, yanak.



Map 3.25. Distribution of *Baccaurea papuana* F.M. Bailey in New Guinea.

Photo 8. *Baccaurea parviflora* (Müll.Arg) Müll.Arg. – Photo: R.M.A.P. Haegens (Peninsular Malaysia).

Photo 9. *Baccaurea ramiflora* Lour. – Photo: L.J.G. van der Maesen (Yunnan, China).

Photo 10. *Baccaurea sarawakensis* Pax & K. Hoffm. – Photo: J.L.C.H. van Valkenburg 1129 (Kalimantan, Indonesia).

26. **Baccaurea parviflora** (Müll.Arg.) Müll.Arg. — Fig. 3.18, Map 3.26

Baccaurea parviflora (Müll.Arg.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 462; Kurz, Forest Fl. Burma 2 (1877) 357; Hook.f., Fl. Brit. India 5 (1887) 368; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Brandis, Indian Trees (1906) 562; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 74; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 331; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 59; Ridl., Fl. Malay Penins. 3 (1924) 243; S. Moore, J. Bot. Br. 63 (1925) 98; Corner, Wayside Trees Mal. 1 (1940) 241; Soejarto, Bot. Mus. Leafl. 21 (1965) 89; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 37; Airy Shaw, Kew Bull. 26 (1971) 220; Whitmore, Tree Fl. Malaya 2 (1973) 64; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 52; Kew Bull. 36 (1981) 265; Enum. Euphorb. Philipp. (1983) 9. — *Pierardia parviflora* Müll.Arg., Linnaea 32 (1863) 82; Baill., Adansonia 3 (1863) 140. — Type: *Wallich 1849* (lecto K, selected here), Tavoy, India Orientalis (see note 2).

Pierardia dasystachya Miq., Fl. Ned. Ind. 1, 2 (1859) 358. — *Baccaurea dasystachya* (Miq.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 458; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 52; K. Heyne, Nutt. Pl. Ned. Ind., 3rd. ed., 1 (1950) 912; Airy Shaw, Kew Bull. 36 (1981) 260. — Type: *Zollinger 757z* (lecto U, selected here; isolecto A, BO, G), Sumatra.

Baccaurea affinis Müll.Arg. in DC., Prodr. 15, 2 (1866) 459. — Type: *Wallich 7759 B* (holo G-DC; iso ?K), Tavoy, India Orientalis (see note 2).

Baccaurea scortechinii Hook.f., Fl. Brit. India 5 (1887) 368; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 56; Ridl., Fl. Malay Penins. 3 (1924) 244; Corner, Wayside Trees Mal. 1 (1940) 242; Smitinand, Thai Forest Bull., Bot. 2 (1955) 25; Nat. Hist. Bull. Siam Soc. 20 (1961) 53; Airy Shaw, Kew Bull. 26 (1972) 221; Kiew, Gard. Bull. Sing. 49 (1997) 37. — Type: *Scortechini s.n.* (lecto K, selected by Kiew 1997), Malaysia, Perak. (The type bears ridged fruits.)

Baccaurea singaporica Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 54. — Type: *Ridley* (K?, n.v.), Singapore.

Baccaurea rostrata Merr., Univ. Calif. Publ. Bot. 15 (1929) 150; Airy Shaw, Kew Bull. 21 (1962) 355; Meijer, Bot. News Bull. Forest. Dept., Sabah 7 (1967) 37; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 52. — Type: *Elmer 21554* (lecto L, selected here; isolecto A, GH, K, US), Borneo, Sabah, Tawau.

Shrub to tree 3–15 m high, dbh 4–21 cm, buttresses absent, rarely fluted at base; branchlets glabrous, slightly thickened at tip, Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* greenish-grey to grey-black to light yellow-brown to brown, 1.5–3.5 mm thick, rough to smooth, minutely fissured in strips 5 mm wide, papery; inner bark yellow to light brown, 1.5–2 mm thick. *Leaves*: petiole glabrous, densely hairy when young, 4–55 mm long, brown to reddish when dry, raised glands usually present; stipules 2.5–7 by 1.5–2.5 mm, glabrous to rarely densely hairy, margin ciliate, one side with long hairs, hyaline, midrib hirsute above; lamina elliptic to obovate, 5–23 by 2–9.5 cm, l/w ratio 1.6–3.7, papery; base attenuate to cuneate; apex acuminate, up to 22 mm long; upper surface glabrous, rarely hair-domatia present at base, rarely granulate, (dark) green when fresh, red to brown to green when dry; lower surface (sub)glabrous, raised glands absent, discoid glands sometimes present, (greyish to light-)green when fresh, red to brown to green when dry; secondary veins (3–)5–10 per side, closed at 2–3 mm from margin; nervation reticulate to weakly scalariform, green to yellowish to red when dry; young leaves whitish to pinkish. *Staminate inflorescences* cauline, at base of trunk, many clustered together, 4–28 cm long, rachis up to 1.2 mm thick, densely hairy, many-flowered, flowers scattered along inflorescence, red to maroon to light yellow; bracts 1 per branchlet, 0.3–1.6 by 0.15–1 mm, subglabrous (to densely hairy) outside, glabrous inside, margin ciliate, sometimes hyaline; bracteoles 2, 0.2–0.4 mm long; branchlets cylindrical, 0.1–2.8 mm

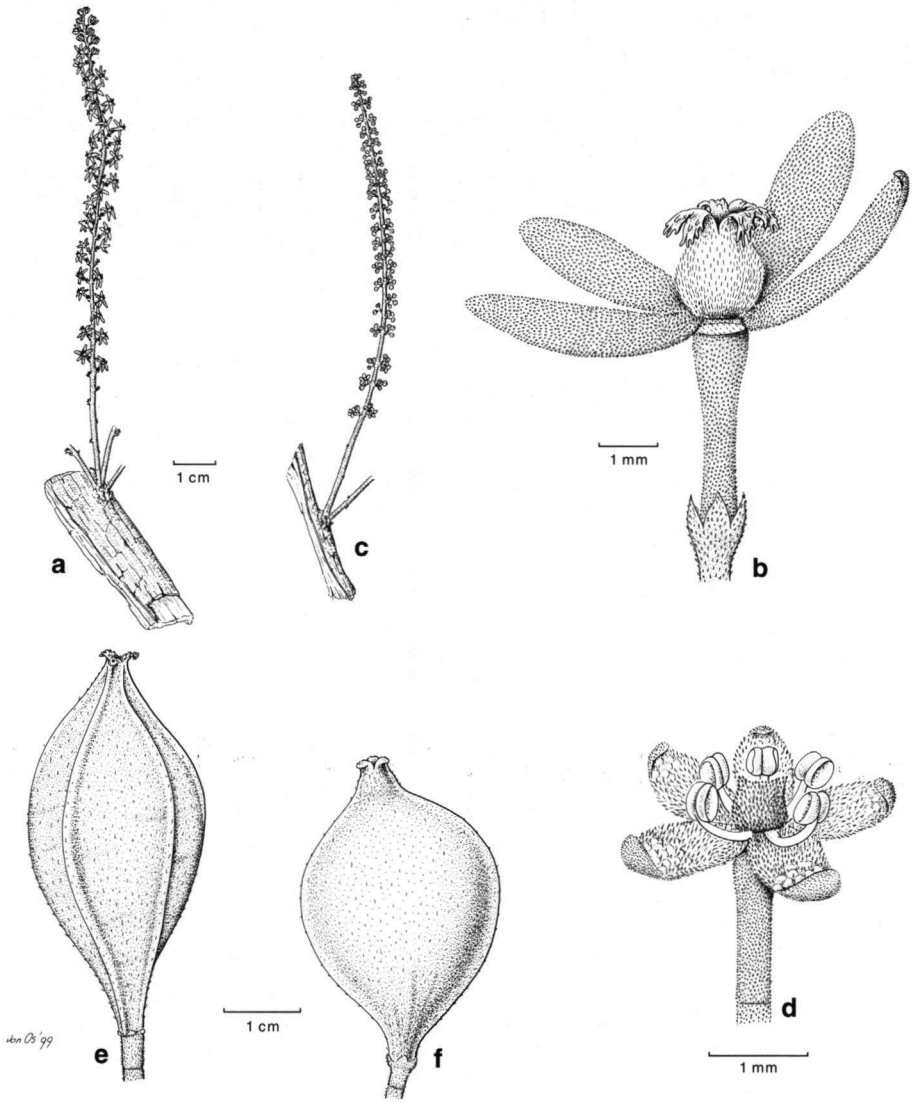


Fig. 3.18. *Baccaurea parviflora* (Müll. Arg.) Müll. Arg. a. Female inflorescence; b. female flower; c. male inflorescence; d. male flower; e. fruit; f. fruit (a, b: *KEP 8166*; c, d: *T&P 32*; e: *KEP 10581*; f: *KEP 8880*).

long, densely hairy, (1–)3-flowered. *Staminate flowers* 1–5 mm diam.; pedicel 0.4–6 mm long, upper part 0.2–3 mm, sparsely to densely hairy; sepals 4 or 5, obovate, each with a different size and shape, 0.5–3 by 0.5–1.2 mm, densely hairy outside, glabrous to densely hairy inside, maroon to yellow outside, cream to yellow inside when fresh, whitish outside, brownish white inside when dry; stamens 5–7, 0.5–0.9 mm long, glabrous, cream; filaments 0.4–0.8 mm long, straight; anthers 0.2–0.3 by 0.1–0.2 by 0.1–0.2 mm; rudimentary disc sometimes present; pistillode obtriangular, 0.3–1.2 mm

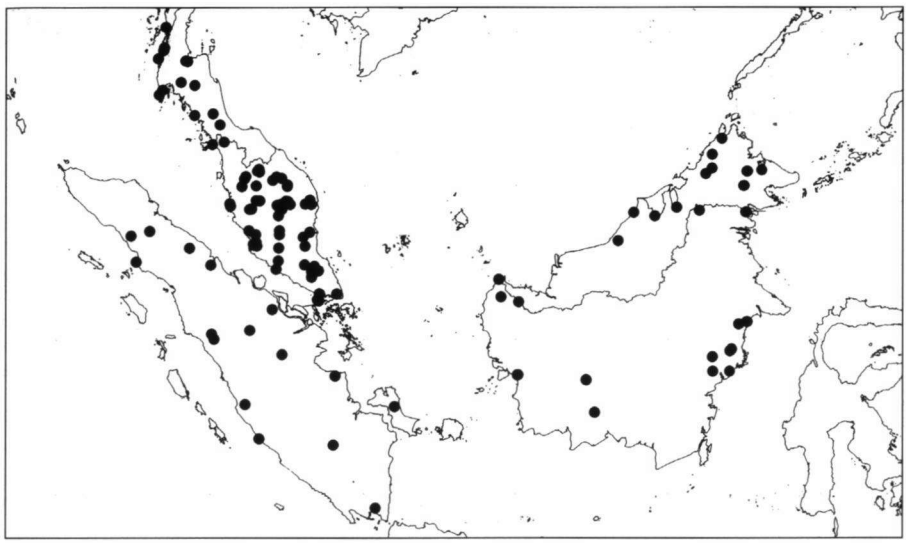
Photo 11. *Baccaurea sarawakensis* Pax & K. Hoffm. – Photo: J.L.C.H. van Valkenburg 1129 (Kalimantan, Indonesia).

Photo 12. *Baccaurea tetrandra* (Baill.) Müll.Arg. – Photo: R.M.A.P. Haegens 537 (Sarawak, Malaysia).

long, hirsute, hollow inside, cream. *Pistillate inflorescences* cauline, at base of trunk, many clustered together, up to 28 cm long, 1–4 mm thick, densely hairy (to glabrous), red when dry, fragrant; pedicel 2–6(–9) mm long, often without a clear abscission zone, upper part 0.2–3(–7.5) mm long, densely hairy, bright red; bracts 3, up to 1.2 (–1.6) by 1(–1.3) mm, persistent, sparsely to densely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 5–7.5 mm diam.; sepals 4 or 5, narrowly elliptic to obovate, 2.7–8 by 0.9–2 mm, densely hairy outside, glabrous to densely hairy inside, white to yellow to usually red when fresh, caducous to persistent; ovary almost globose, with or without 6 wings, 1.3–2.2 by 1–2.3 mm, (2- or) 3- (or 4-)locular, velutinous, yellow; style 0–2 by c. 1 mm, densely hairy, yellow; stigmas 0.1–1.5 mm long, cleft apically only or up to base, caducous to persistent; lobes 0.2–1.4 mm long, glabrous with protuberances above, sparsely to densely hairy below. *Fruits* fusiform, 1–3-seeded berries, with or without 4–6 narrow wings, 16–32 by 7–15 mm, glabrous to sparsely hairy outside, raised glands present, dull red to maroon turning purple to black when fresh; pericarp c. 1–2.5 mm thick, glabrous on both sides; column 10–18 mm long, straight. *Seeds* ellipsoid, laterally flattened, 9–16 by 4–8 by 1–5 mm; arillode red to purple to white; cotyledons orbicular to square, membranous, 5.5–11 by 4–6 by 0.5–3.5 mm, radicle up to 1.5 mm long.

Distribution — Thailand, Peninsular Malaysia, Sumatra, Borneo.

Habitat & Ecology — Primary and secondary evergreen forest, steep hillsides to dry parts of swamps to alluvial forest. Soil: sandstone, white sandy soil. Altitude: sea level up to 1250 m. Flowering: Nov. to June, Sept. Fruiting: Mar. to Dec.



Map 3.26. Distribution of *Baccaurea parviflora* (Müll.Arg.) Müll.Arg. in Thailand, Peninsular Malaysia, Sumatra and Borneo.

Uses — Wood used as box-wood. Pericarp and arillode edible, sour-sweet.

Vernacular names — Thailand: Som-fai Pah. Peninsular Malaysia: Tamun (Batec); kentamun ayer (Temuan); asam tambun, belembik, dedali, engkuni, setambun, tambun. Borneo: Bamotong-belaboh (Bassap-Mapulu); belembik plandoek, engkuni, konkuni, mata pelanduk.

Notes — 1. *Baccaurea parviflora* is rather heterogeneous in some characters, especially in the fruits. Kiew (1997) re-established the name *B. scortechinii*, based purely on material from the Peninsular Malaysia. She listed 19 differential characters. I checked all these characters, except for the fruit colour because this character is impossible to study when only herbarium material is available. She mentioned this as one of the problems of species delimitation in this complex (*B. parviflora* and *B. scortechinii*). All 19 characters listed overlap. The values given by Kiew are mean values only. Collections from Sumatra made by De Wilde & De Wilde-Duyfjes in Gunung Leuser Park overlap in all characters. According to Kiew, the most important difference is the position of the inflorescences in combination with fruit shape. *Baccaurea scortechinii* flowers at the trunk and branches, and has ridged fruits, while *B. parviflora* flowers at the base of the trunk, and has no ridges at the fruits. However, contrary to these observations, M. van Balgooy photographed a tree, which flowered at the base of the trunk, and had ridged fruits. In July 1998 I observed the same phenomenon in the FRIM campus in Kepong (Photo 8). My conclusion is that these two taxa are conspecific.

2. In 1997 Kiew erroneously typified *B. parviflora*. She mentioned *Wallich 7759B* (K) as the type specimen. This, however, is an isotype of *B. affinis*. In the original description of *Pierardia parviflora* Müller Argoviensis (1863) quoted: "Wall.! absque no. in hb. DC". I have checked G-DC on microfiche, but could not recover this

specimen. The lectotype *Wallich 1849* (K, selected here) has no original number and has been studied by Müller Argoviensis as notes in his handwriting are found on the sheet. Later the numbers 1849 and 7759B were added, of which number 7759B is crossed out again.

3. Another extremely closely related Burmese and Thai taxon is *B. ptychopyxis*. This species, however, always has axillary staminate inflorescences, and is ramiflorous to cauline only as an exception. *Baccaurea parviflora* is always strictly cauliflorous. The staminate inflorescences in *B. ptychopyxis* are solitary, whereas *B. parviflora* has dense clusters. Besides these differences there are some minor characters, such as the fruit length is in *B. ptychopyxis* 17–20.3 mm, and in *B. parviflora* 16–32 mm. The material of *B. ptychopyxis* is, however, very incomplete. Therefore *B. ptychopyxis* is here interpreted as a species separate from *B. parviflora*.

4. See note under *B. odoratissima*.

27. Baccaurea philippinensis (Merr.) Merr. — Fig. 3.19, Map 3.27

Baccaurea philippinensis (Merr.) Merr., Philipp. J. Sci., Bot. 10 (1915) 275; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 68; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 411; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 53; Fernando, Philipp. J. Biol. 8 (1979) 303; Airy Shaw, Kew Bull. Add. Ser. 8 (1980) 36; Enum. Euphorb. Philipp. (1983) 9. — *Everettiodendron philippinense* Merr., Philipp. J. Sci., Bot. 4 (1909) 279; Elmer, Leafl. Philipp. Bot. 3 (1910) 916. — Type: *Everett 7282* (lecto K, selected here; isolecto US), Philippines, Negros, Himugaan River.

Treelet to tree 4.5–12 m high, dbh 8–25 cm; branchlets subglabrous, velutinous when young, Terminalia branching pattern weakly developed. *Indumentum* of short stellate and usually longer simple hairs. *Bark* grey-brown when fresh; inner bark pale red-brown. *Leaves*: petiole 17–75 mm long, subglabrous to densely hairy, transverse cracks usually present, apically and sometimes basally pulvinate, raised glands rarely present; stipules 3–5.5 by 1.5–3 mm, velutinous outside, sparsely to densely hairy inside, margin ciliate, not hyaline; lamina ovate to elliptic (to obovate), (5–)7.2–18 by (2.4–)3.5–9 cm, l/w ratio 1.7–2.3, leathery to papery; base acute to cuneate (to rounded to attenuate); marginal glands sometimes visible as small indentations; apex acuminate to cuspidate, 2–18 mm long; upper surface glabrous, small raised glands sometimes present, rarely granulate, dark green when fresh, dark to grey-brown when dry, nervation slightly sunken; lower surface (sub)glabrous, subglabrous to densely hairy at midrib and veins, small raised glands sometimes present, discoid glands present, sometimes in a row between secondary veins, pale green when fresh, light to brown-green when dry, (dark) brown above and below when dry; secondary veins 4–7 per side, open at margin; nervation reticulate to weakly scalariform. *Staminate inflorescences* axillary, solitary to 3 clustered together, 1–6.5 cm long, c. 0.1 mm thick, branched, many-flowered, densely hairy to velutinous, flowers scattered along inflorescence; bracts 1 per branchlet, 1.2–3.5 mm long, velutinous outside, glabrous inside, margin ciliate, not to slightly hyaline; bracteoles (7–)9–12 per branchlet, 0.3–2 mm long; branchlets cylindrical, 1.2–8 mm long, velutinous, 9–12-flowered. *Staminate flowers* 1.2–2 mm diam., brownish; pedicel 0.2–1.3 mm long, upper part 0.1–0.6 mm long, velutinous; sepals 3 or 4, ovate to elliptic, 0.5–1.6 by 0.2–1.1 mm, apex slightly recurved, outside and velutinous inside; stamens (3 or) 4, 0.25–0.4 mm long, glabrous; filaments 0.1–0.2 mm long, straight; anthers 0.15–0.2 by 0.15–0.2 by 0.1–0.2 mm; disc absent; pistillode

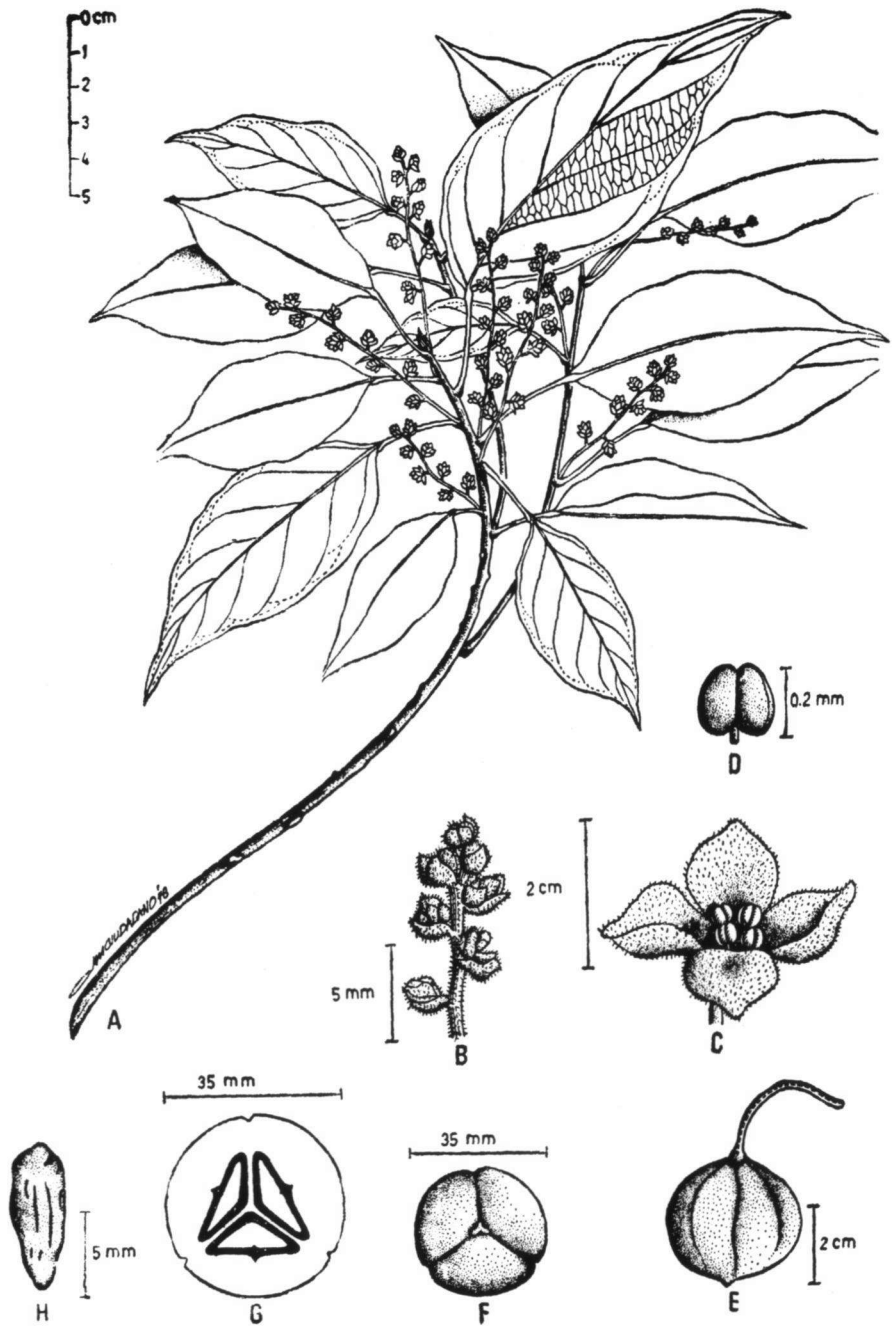
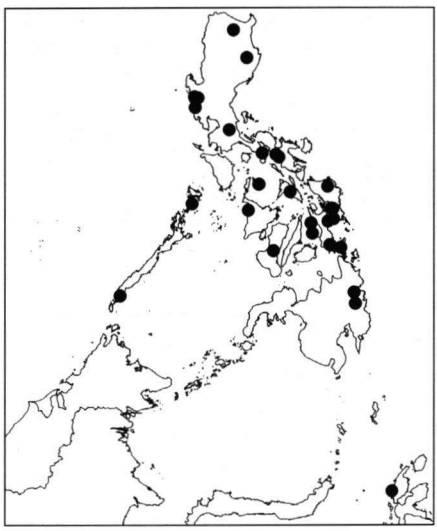


Fig. 3.19. *Baccaurea philippinensis* (Merr.) Merr. a. Habit with male inflorescences; b. male inflorescence; c. male flower; d. anther; e. fruit; f. fruit, basal view; g. fruit, transversal section, showing three locules; h. seed, lateral view [a–d: *Fernando 005*; e–h: *Lagrimas s.n. (PNH)*. Reproduced from E.S. Fernando in Kalikasan, Philipp. J. Bot. 8: 306, f. 2 (1979)].



Map 3.27. Distribution of *Baccaurea philippinensis* (Merr.) Merr. in the Philippines and Halmahera.

globose, absent to 0.2 mm high, velutinous. *Pistillate inflorescences* axillary; sepals usually caducous; stigmas persistent to caducous. *Pistillate flowers*: ovary 3-locular. *Infructescences* 1.9–2 cm long, 1.3–2 mm thick. *Fruits* suppressed globose, (0–) 3–6-seeded, fleshy capsules, 21–34 by 26–38 by 26–38 mm, apparently loculicidally dehiscent, but normally not dehiscing, hard, raised glands usually present, subglabrous to densely hairy outside, sparsely to densely hairy inside, septa densely hairy, (yellowish) brown; pericarp 4–11 mm thick; column 16–23 mm long; pedicel 4.5–9 mm long, upper part 2–6 mm long. *Seeds* ellipsoid to triangular, laterally flattened, 9.5–11.5 by 5–7 by 3.5–5 mm; cotyledons 6–7 by 5–5.5 by c. 0.1 mm; radicle 1–1.5 mm long; endosperm 0.5–1 mm thick.

Distribution — Philippines, Moluccas (Halmahera).

Habitat & Ecology — Primary and secondary rain forest. Altitude: 80–450 m. Flowering: Apr. to Aug. Fruiting: Jan. to June, Aug., Oct., Dec.

28. **Baccaurea polyneura** Hook.f. — Map 3.28

Baccaurea polyneura Hook.f., Fl. Brit. India 5 (1887) 369; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 65; Ridl., Fl. Malay Penins. 3 (1924) 248; S. Moore, J. Bot. Br. 63 (1925) 98; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 37; Whitmore, Tree Fl. Malaya 2 (1973) 67; Airy Shaw, Kew Bull. 36 (1981) 265. — Type: *Griffith KD 4910* (lecto K, selected here), Peninsular Malaysia.

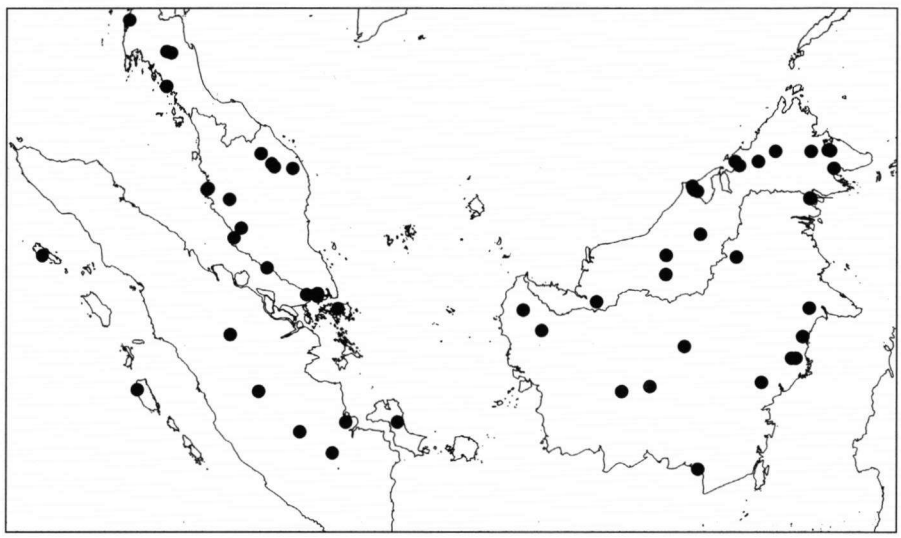
Baccaurea kunstleri King ex Gage, Rec. Bot. Surv. India 9, 2 (1922) 230; Ridl., Fl. Malay Penins. 3 (1924) 248; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 36; Airy Shaw, Kew Bull. 26 (1972) 219; Whitmore, Tree Fl. Malaya 2 (1973) 65; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 49; Kew Bull. 36 (1981) 263; Chakrab. & Gang., J. Econ. Taxon. Bot. 18 (1994) 425, syn. nov. — Type: *King's Collector 8139* (lecto CAL, selected by Chakrab. & Gang. 1994), Malakka, Perak (see note), n.v.

Baccaurea hookeri Gage, Rec. Bot. Surv. India 9 (1922) 232; Ridl., Fl. Malay Penins. 3 (1924) 247; Whitmore, Tree Fl. Malaya 2 (1973) 67; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 48; Kew Bull 37 (1982) 8. — Type: *King's Collector 6240* (lecto K, selected here), Malaysia, Perak, Larut.

Baccaurea cordata Merr., Univ. Calif. Publ. Bot. 15 (1929) 147; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 36; Airy Shaw, Kew Bull. 26 (1971) 219; Kew Bull. Add. Ser. 4 (1975) 47. — Type: *Elmer 21513* (lecto A, selected here; isolecto BO, DS, K, L, US), Borneo, Sabah, Tawau.

Tree (5–)11–30 m high, dbh 10–32 cm, buttresses small; branchlets velutinous, Terminalia branching pattern weakly developed. *Indumentum* of simple and stellate hairs. *Bark* brown to white-brown to red-brown when fresh, brown when dry, 3–5 mm thick, smooth; inner bark red to brown, 2–5 mm thick. *Heartwood* red to brown. *Leaves*: petiole 7–78 mm long, velutinous, raised glands usually absent; stipules elliptic to ovate, 2.2–10 by 0.5–2 mm, caducous (to late caducous), velutinous outside, subglabrous to velutinous inside, margin ciliate, not hyaline; lamina ovate to elliptic, 5.5–21.5 by 3.1–12.5 cm, l/w ratio 1.4–2.7, papery to slightly leathery; base rounded to cordate (to attenuate); apex (retuse to) acute, up to 11 mm long; upper surface glabrous to densely hairy, midrib and veins sparsely hairy to velutinous, sometimes granulate; lower surface sparsely hairy to velutinous, raised glands absent to present, discoid glands absent; dark green when fresh, green to brown when dry, black when young when dry; secondary veins 7–14 per side, closed at margin or almost so; nervation scalariform, brown to white-brown when dry. *Staminate inflorescences* axillary to just below the leaves (to ramiflorous), solitary to 5 clustered together, 1–7 cm long, c. 1 mm thick, velutinous, many-flowered, flowers clustered at the tip of inflorescence, rarely somewhat scattered; bracts 0 or 3 per branchlet, 0.2–1.3 mm long, persistent, velutinous outside, glabrous to rarely velutinous inside, margin ciliate, not hyaline; branchlets cylindrical to spatulate, 1–4 mm long, velutinous, 3-flowered. *Staminate flowers* 1.1–3.3 mm diam., green to yellow to greenish-white; pedicel 0–0.5 mm long, velutinous; sepals 4–6, ovate, 0.7–1.5 by 0.5–1.5 mm, apex straight, outside and inside velutinous; stamens 4–8, 0.3–0.7 mm long, glabrous, cream to brown; filaments 0.2–0.6 mm long, geniculate to straight; anthers c. 0.1 by 0.2–0.3 by 0.1 mm; pistillode absent to present, globose, 0–0.3 mm high, velutinous, solid. *Pistillate inflorescences* axillary to ramiflorous, solitary to 3 clustered together, 1–34.5 cm long, 0.5–4 mm thick, velutinous, 5–50-flowered, yellow; pedicel 2–5.8 mm long, upper part 0.5–2 mm long, geniculate or not, velutinous to sparsely hairy; bracts 0–3 per branchlet, persistent to caducous, velutinous outside, glabrous to velutinous inside, margin ciliate. *Pistillate flowers* 2.5–6.5 mm diam.; sepals 4 or 5, ovate, 0.5–5.9 by 0.3–3.5 mm, outside and inside velutinous, persistent (or caducous), ochre; ovary subglobose to pyriform, 2.5–4.5 by 2.2–4 mm, 3-locular, velutinous; style 0.1–0.2 mm by 0.5–0.8 mm, velutinous; stigmas 0.6–0.9 mm long, cleft for upper 60–90%, persistent or caducous; lobes 0.5–0.9 by c. 0.2 mm, glabrous above, glabrous to sparsely hairy below. *Fruits* globose to subglobose, 1–3-seeded, fleshy capsules, 10–26 by 12–26 by 12–26 mm, loculicidally dehiscent, raised glands often present, sparsely hairy to velutinous outside and inside, yellow to orange; pericarp 0.1–4 mm thick; column 9.5–19 mm long, almost straight, persistent; pedicel 5–11(–35) mm long, upper part 1–7 mm long, 80% bent present at abscission zone. *Seeds* ellipsoid, laterally flattened, 7.8–11 by 5–9.8 by 2–5 mm; arillode red; testa orange; cotyledons 5–9 by 5–7.5 by c. 0.1 mm; radicle 0.5–2 mm long; endosperm c. 0.5 mm thick.

Distribution — Thailand, Peninsular Malaysia, Sumatra, Borneo.



Map 3.28. Distribution of *Baccaurea polyneura* Hook.f. in Thailand, Peninsular Malaysia, Sumatra and Borneo.

Habitat & Ecology — Primary, secondary and swamp rain forest. Soil: sand, clay, loam, granite. Altitude: 20–600 m. Flowering and fruiting throughout the year.

Uses — Arillode edible, sweet to sour.

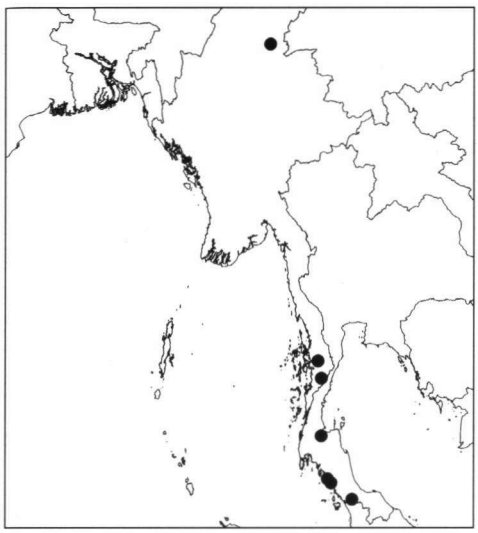
Vernacular names — Thailand: Chum rai. Peninsular Malaysia: Jentik-jentik, rambai, rambai hutan. Simeuluë Island: Sirawi, sirawi uding, sirawi pajo. Sumatra: Djetikan betina, djentikan, djenti ompang, méràh mata, pétèkan. Borneo: Jelintik, kayu masam, simpak nyabor (Iban); enyak beruk, kapul burung, tampoi.

Note — Although I had no opportunity to study the lectotype, I am convinced that *B. kunstleri* is conspecific with *B. polyneura*. The following paratypes of *B. kunstleri* were studied by me: *Ridley 6670*, *6163*, and *Goodenough 5084*. I was unable to separate the numerous other specimens I have studied into two taxonomic entities.

29. **Baccaurea ptychopyxis** Airy Shaw — Map 3.29

Baccaurea ptychopyxis Airy Shaw, Kew Bull. 21 (1968) 354. — Type: *Parker 2517* (holo K), Burma, Mergui District, Pawut.

Shrub to tree 2.5–9 m high, buttresses absent; branchlets glabrous, sparsely hairy when young, Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* grey when dry. *Leaves*: petiole 9–46 mm long, (sub)glabrous, grey to dark brown when dry, raised glands present; stipules 4.3–6.5 by 1.7–3 mm, subglabrous outside, midrib densely hairy, glabrous inside, margin ciliate, hyaline; lamina (ovate to) elliptic to obovate, 7.4–20 by 3.3–7.8 cm, l/w ratio 1.6–2.8, papery; base attenuate to cuneate; apex obtuse to cuspidate, up to 22 mm long, brown to (dark) green when dry; upper surface glabrous, usually granulate, raised glands usually absent; lower surface subglabrous, raised glands usually present, discoid glands absent, brown to (dark) green



Map 3.29. Distribution of *Baccaurea ptychopyxis* Airy Shaw in Bangladesh, Burma and Thailand.

when dry; secondary veins 6–8 per side, sometimes closed at margin; nervation reticulate, (pale) green to whitish when dry. *Staminate inflorescences* axillary to cauline, many-flowered, 2.1–15 cm long, 1–1.5 mm thick, solitary, branches minute, densely hairy, flowers scattered along inflorescence; branchlets 3-flowered; flowers 2.6–3.1 mm diam., red; pedicel 1.4–2.6 mm long. *Pistillate inflorescences* cauline to ramiflorous, many clustered together, 13.8–36 cm long, 1–3.9 mm thick, densely hairy, many-flowered, reddish; pedicel 1.5–5 mm long, upper part 1–1.6 mm long, densely hairy; bracts 3, densely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 4.2–9 mm diam., reddish; sepals 5, elliptic to obovate, 4–9 by 1–2 mm, densely hairy outside and inside, caducous; ovary globose, 6-winged, 2.1–2.6 by 1.6–2 mm, 3-locular, densely hairy to velutinous; style c. 1 by 1 mm, densely hairy; stigmas c. 1.2 mm long, cleft for upper 80%, persistent; lobes c. 1 by 0.3 mm, glabrous above, sparsely hairy below, protuberances above and below. *Fruits* fusiform, berries, 17–20.3 by 7.2–11.6 by 7.2–11.6 mm, rugose between narrow wings, glabrous outside and inside, raised glands present.

Distribution — Bangladesh, Burma, Thailand.

Habitat & Ecology — Altitude: 50–100 m. Flowering: Jan. to Mar., Dec. Fruiting: Jan.

Vernacular names — Burma: Kakwauka (Shan).

30. **Baccaurea pubera** (Miq.) Müll.Arg. — Map 3.30

Baccaurea pubera (Miq.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 448; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 280; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 70; K. Heyne, Nutt. Pl. Ned. Ind., 3rd ed., 1 (1950) 914; Airy Shaw, Kew Bull. 36 (1981) 265. — *Pierardia pubera* Miq., Fl. Ned. Ind., Eerste bijv. (1861) 442. — Type: *Teijsmann HB 3503* (lecto U, selected here), Indonesia, Sumatra, Bangka.

Baccaurea latifolia King ex Hook.f., Fl. Brit. India 5 (1887) 373; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 65; Ridl., Fl. Malay Penins.

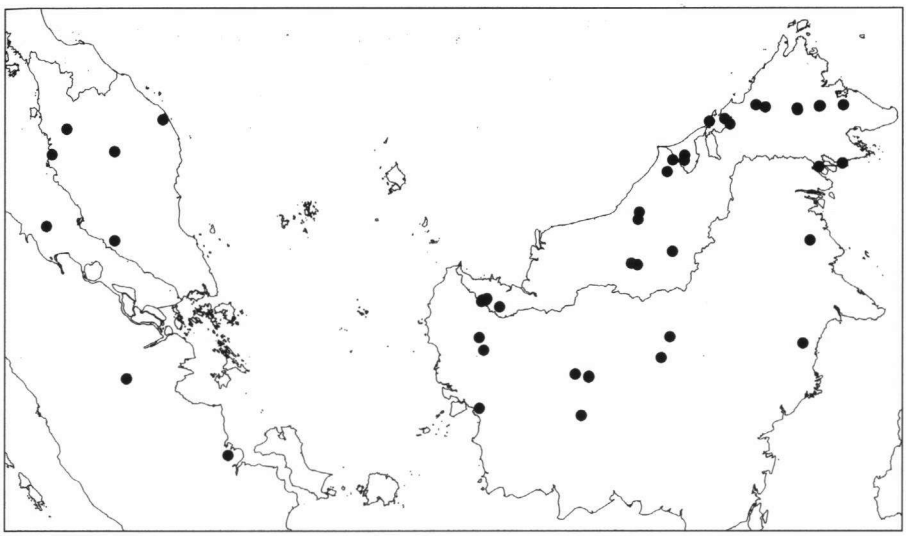
3 (1924) 249; Whitmore, Tree Fl. Malaya 2 (1973) 67; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 50; Kew Bull. 36 (1981) 265; Chakrab. & Gang., J. Econ. Taxon. Bot. 18 (1994) 425, syn. nov. — Type: *King's Collector 3955* (lecto CAL, selected by Chakrab. & Gang., 1994; iso K), Malakka, Perak.

Baccaurea puberula Merr., Univ. Calif. Publ. Bot. 15 (1929) 145; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 36; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 50. — Type: *Elmer 21284* (holo GH; iso DS, K, L), Borneo, Sabah, Tawau.

Baccaurea elmeri Merr., Univ. Calif. Publ. Bot. 15 (1929) 146; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 48. — Type: *Elmer 21509* (lecto US, selected here; isolecto A, DS, K, L), Borneo, Sabah, Tawau.

Tree 5.7–25 m high, dbh 5–40 cm; bole sometimes fluted, rarely with buttresses up to 30 cm out, up to 6 cm thick; branchlets densely hairy to sometimes sparsely hairy, Terminalia branching pattern weakly developed. *Indumentum* of stellate and simple hairs. *Bark* pale brown to greyish when fresh, brown to brown-red when dry, smooth; inner bark red to brown, c. 2 mm thick. *Leaves*: petiole 34–130 mm long, usually densely hairy, raised glands rarely present; stipules 5.5–11 by 4–8.5 mm, densely hairy outside and inside, margin ciliate, not hyaline; lamina (ovate to) elliptic (to obovate), 13–36 by 5.4–14.9 cm, l/w ratio 1.7–2.4, papery to somewhat leathery; base rounded to attenuate; apex acuminate, 4–10 mm long; upper surface (sub)glabrous, raised glands absent (to present), usually granulate, dark (grey-)brown to blackish when dry, nervation light (to dark) brown to whitish, (slightly) sunken; lower surface densely hairy, raised glands absent (to present), discoid glands (hairy) in a row between secondary veins, yellowish-brown when dry; secondary veins (5–)8–13 per side, usually closed at margin, not completely parallel; nervation reticulate to weakly scalariform, (yellowish) brown. *Staminate inflorescences* axillary to just below the leaves, solitary to 3 clustered together, 0.5–16.5 cm long, c. 1 mm thick, branched, densely hairy, many-flowered, flowers scattered along inflorescence; bracts 1 per branchlet, triangular to lanceolate, 1.5–4 mm long, densely hairy outside and inside, margin ciliate, not hyaline; bracteoles usually absent, or 1–few; branchlets cylindrical, 4–11 mm long, densely hairy, 5–16-flowered. *Staminate flowers* 1.3–2.5 mm diam., lime green to whitish yellow to pale green; pedicel 0.5–2.1 mm long, upper part 0.1–0.9 mm long, densely hairy; sepals 4 or 5, ovate to obovate, 0.8–1.3 by 0.3–0.7 mm, apex slightly recurved to straight, densely hairy outside and inside; staminodes 4 or 5, < 1 mm long; stamens 4 or 5, 0.1–0.6 mm long, glabrous; filaments 0.15–0.5 mm long, straight; anthers 0.1–0.3 by 0.2–0.25 by c. 0.1 mm; disc absent; pistillode flat, 0.1–0.3 mm high, densely hairy. *Pistillate inflorescences* ramiflorous to cauline; sepals persistent; stigmas caducous. *Pistillate flowers*: sepals 5, yellow; ovary 3-locular. *Infructescences* 4–16 cm long, 1–2.5 mm thick. *Fruits* pear-shaped to (sub)globose, 5- or 6-seeded, fleshy capsules, 25–34 by 29–35 by 29–34 mm, c. 4 cm diam. when fresh, usually not dehiscent; raised glands present to absent, ruminate when dry, densely hairy to sparsely hairy outside, subglabrous inside, brown to yellow ochre; pericarp 2–5 mm thick; column 19–24 mm long, straight, persistent; pedicel 11–14 mm long, upper part 2.5–4 mm long. *Seeds* globose to ellipsoid, laterally flattened, 13–17.5 by 8.3–14.3 by 5.5–8 mm; arillode yellowish to orange; testa brown; cotyledons 10–12.2 by 9.5–11.2 by 0.1–2 mm; radicle 0–1.5 mm long.

Distribution — Peninsular Malaysia, Sumatra, Borneo.



Map 3.30. Distribution of *Baccaurea pubera* (Miq.) Müll.Arg. in Peninsular Malaysia, Sumatra and Borneo.

Habitat & Ecology — Primary, rarely secondary, rain forest. Soil: yellow sand, clay. Altitude: sea level up to 660(–1650) m. Flowering: Jan. to Mar., May, Sept. to Dec. Fruiting: Mar. to Dec.

Uses — Fruit edible, sweet.

Vernacular names — Sumatra: Sebenggang, sibongang. Borneo: Puak (Dusun); tampui (Kedayan); pugi (Murut); silu buang (Sebob); kunkurad, monyak buruk, paih, tampoi.

Note — I have identified *Elmer 21306* (A, DS, K, L, US), one of the syntypes of *B. elmeri* as *B. nanihua*. The remaining syntype, *Elmer 21509*, is chosen as lectotype of *B. elmeri*.

31. Baccaurea purpurea Haegens, *spec. nov.* — Fig 3.20, Map 3.31

> Ab omnibus congeneribus malesianis praeter combinationem charactorum sequentium truncus non nodosus, petioli bipulvinati, folia papyracea brunnea i.s., supra costa glabra, indumento simplici, infra (sub)glabra, flores masculini purpurei, fructus inalati loculicide dehiscentes differt. — Typus: *NGF (Henty & Lelean) 41916* (holo L; iso A), New Guinea, Central Province, Abau Subdistrict, Cape Rodney.

Tree 6–8 m high, dbh 6.3–10 cm, buttresses absent; branchlets glabrous, grey to blackish when dry, Terminalia branching pattern well-developed to weak. *Indumentum* of simple hairs. *Bark* grey to brown when fresh, corky; inner bark cream to light brown; sapwood cream. *Leaves*: petiole 17–65 mm long, (sub)glabrous, apically and basally pulvinate, light to black-brown when dry, raised glands present; stipules 5–9 by 1.5–2 mm, glabrous outside and inside, midrib subglabrous to sparsely hairy outside, margin (slightly) ciliate, often hyaline; lamina elliptic (to ovate), 7.4–17.5 by 3.2–7 cm, l/w ratio 2.2–3.2, papery to slightly leathery; base cuneate to rounded; apex

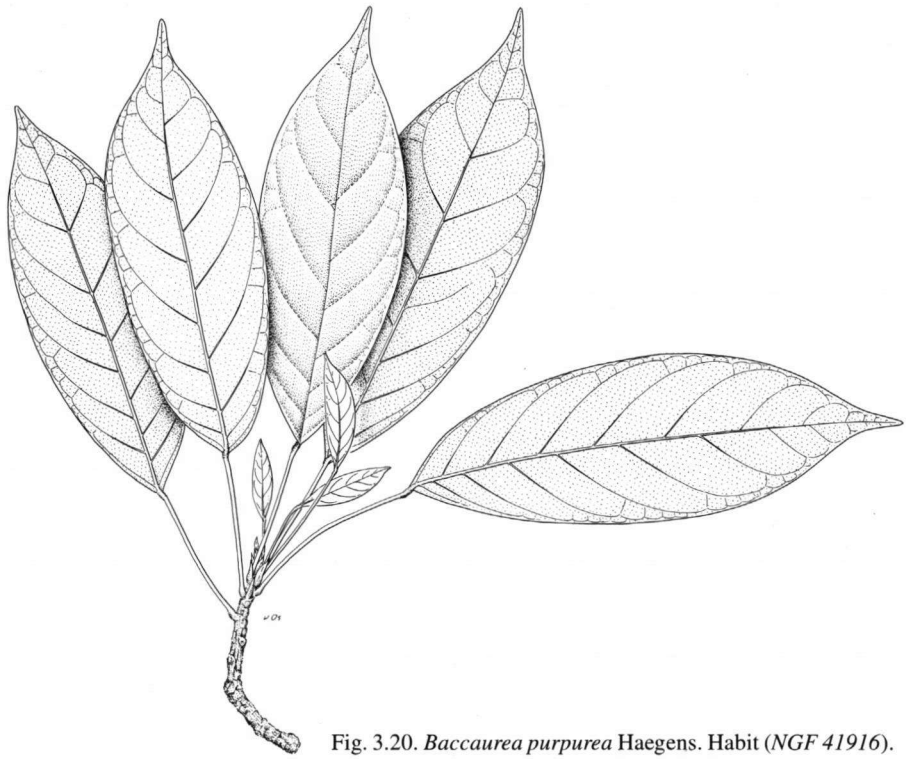
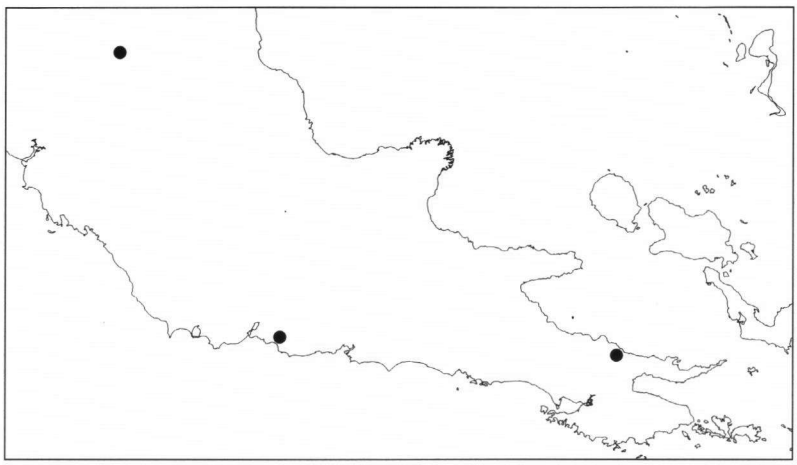


Fig. 3.20. *Baccaurea purpurea* Haegens. Habit (*NGF 41916*).

(rounded to) obtuse to acuminate, up to 15 mm long, dark green when fresh, (grey) green to dark brown when dry; upper surface glabrous, usually not granulate; lower surface (sub)glabrous, raised glands usually present, discoid glands sometimes present, dark green when fresh, greenish to brown when dry; secondary veins 6–11 per side, sometimes closed at margin; nervation reticulate. *Staminate inflorescences* cauline, many clustered together, 2–24 cm long, up to 1 mm thick, branches minute, subglabrous to sparsely hairy, many-flowered, flowers scattered along inflorescence; bracts 3 per branchlet, 1 large, 0.2–1 mm long, subglabrous outside, glabrous inside, margin ciliate, hyaline; bracteoles absent. *Staminate flowers* 3 per branchlet, c. 1.5 mm diam., (purplish) pink; pedicel 1–2 mm long, upper part 0.2–0.5 mm long, sparsely hairy to densely hairy; sepals 4 (or 5), ovate to triangular, 0.8–1.5 by 0.5–1 mm, sparsely to densely hairy outside, densely hairy inside, apex straight; staminodes 5 or 6; stamens 5, 0.4–0.6 mm long, glabrous; filaments 0.2–0.4 mm long, straight; anthers c. 0.2 by 0.25 by 0.1–0.2 mm; disc absent; pistillode globose, c. 0.3 mm long, densely hairy, solid. *Pistillate inflorescences* probably cauline to ramiflorous. *Pistillate flowers*: sepals caducous; ovary 3-locular; stigmas persistent. *Fruits* globose, 3-seeded, fleshy capsules, 16–19 by 14–19 by 14–19 mm, loculicidally dehiscent, subglabrous to sparsely hairy outside, glabrous inside, few raised glands present, ochre; pericarp 1.5–2 mm thick, slightly ruminate when dry, column 13–14 mm long, straight pedicel 7–9 mm long. *Seeds* globose, laterally flattened, 9.3–10.3 by 9.2–10.3 by 3.5–5 mm; cotyledons c. 5.5 by 7–7.7 by 1 mm; radicle c. 1 mm long; endosperm c. 1 mm thick.



Map 3.31. Distribution of *Baccaurea purpurea* Haegens in Papua New Guinea.

Distribution — Papua New Guinea: Prov.: Central, Northern, Milne Bay.

Habitat & Ecology — Soil: thin soil over limestone. Altitude: 240–400 m. Flowering: Feb., Nov. Fruiting: Mar.

Note — The species is named for its purple (to pink) colour of the male flowers.

Specimens studied: *Carr 16270*; *LAE 62274*; *NGF 41916*.

32. **Baccaurea pyriformis** Gage — Fig. 3.21, Map 3.32

Baccaurea pyriformis Gage, Rec. Bot. Surv. India 9 (1922) 233; Ridl., Fl. Malay Penins. 3 (1924) 249; S. Moore, J. Bot. Br. 63 (1925) 98; Corner, Wayside Trees Mal. 1 (1940) 241; Whitmore, Tree Fl. Malaya 2 (1973) 67; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 53; Kew Bull. 36 (1981) 265; Chakrab. & Gang., J. Econ. Taxon. Bot. 18 (1994) 426. — Type: *Goodenough 1992* (lecto CAL, n.v., selected by Chakrab. & Gang., 1994), Malakka, Ayer Panas (see note).

Baccaurea platyphylla Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 67; Whitmore, Tree Fl. Malaya 2 (1973) 67; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 53. — Type: *Ridley 6491* (lecto K, selected here), Singapore, Krangi and Bot. Garden Jungle (both localities are mentioned on the specimen label).

Baccaurea platyphylloïdes Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 68. — Type: *Ridley 6492* (holo K), Singapore, Tanglin.

Baccaurea pubera (Miq.) Müll.Arg. var. *tomentella* Miq., Fl. Ned. Ind., Eerste bijv. (1861) 442; Müll.Arg. in DC., Prodr. 15, 2 (1866) 458. — Type: *Teijsmann s.n.* (n.v.), Indonesia, Sumatra, Bangka.

Tree 7–30 m high, dbh 8–50 cm, buttresses small if present; branchlets velutinous when young, Terminalia branching pattern weakly developed. *Indumentum* of stellate and simple hairs. *Bark* brown to grey-brown to red-brown when fresh, brown when dry, 2–5 mm thick, smooth to rough, soft, flaky; inner bark brown to red-brown or pink, c. 2 mm thick. *Heartwood* red-brown. *Leaves*: petiole 14–72 mm long, densely hairy, apically and often basally slightly pulvinate, brown hairy when fresh, raised glands absent; stipules lanceolate to elliptic to triangular, 2–8 by 1.5–2 mm, velutinous outside, glabrous to sparsely hairy (to velutinous) inside, margin ciliate, not hyaline;

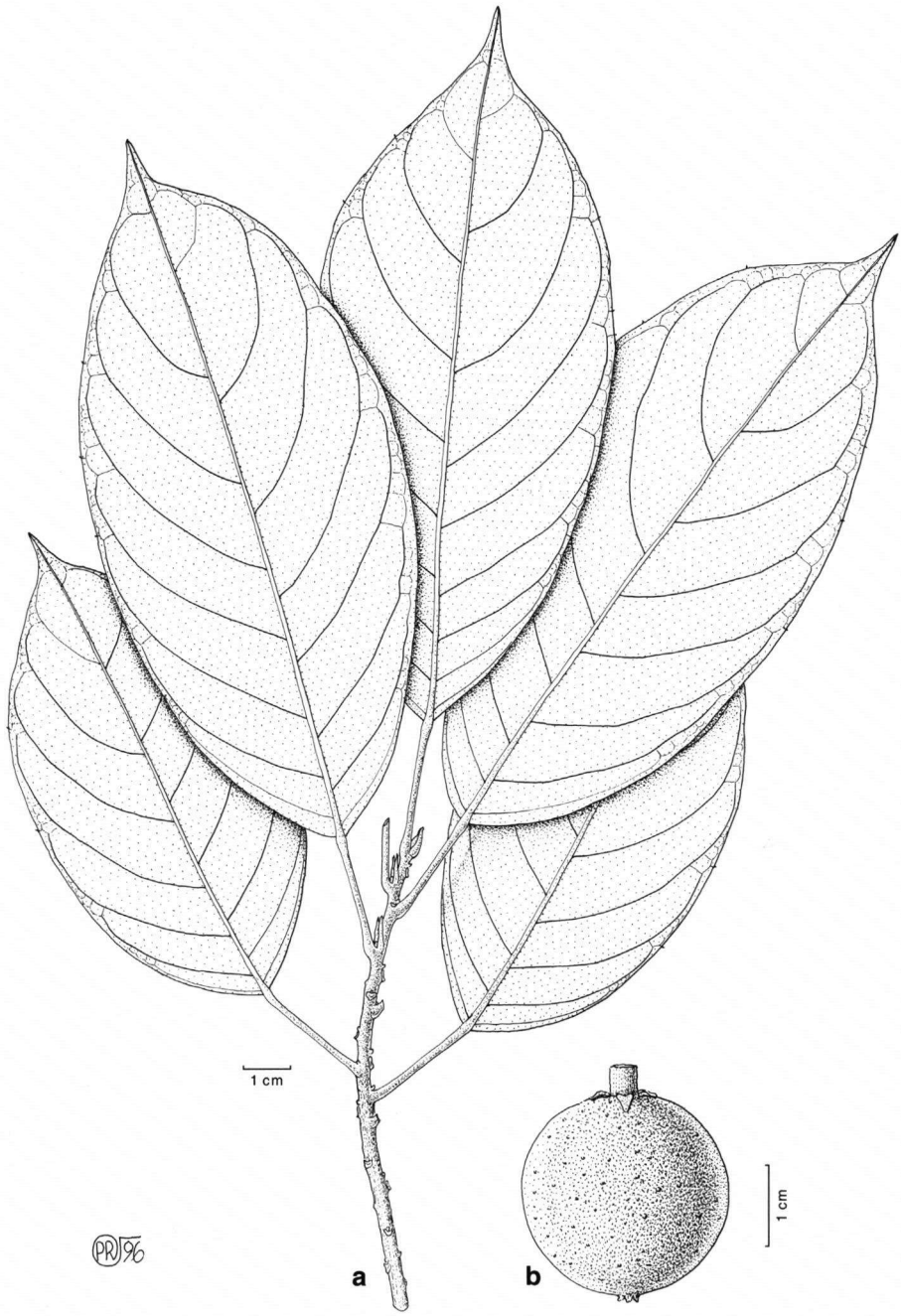
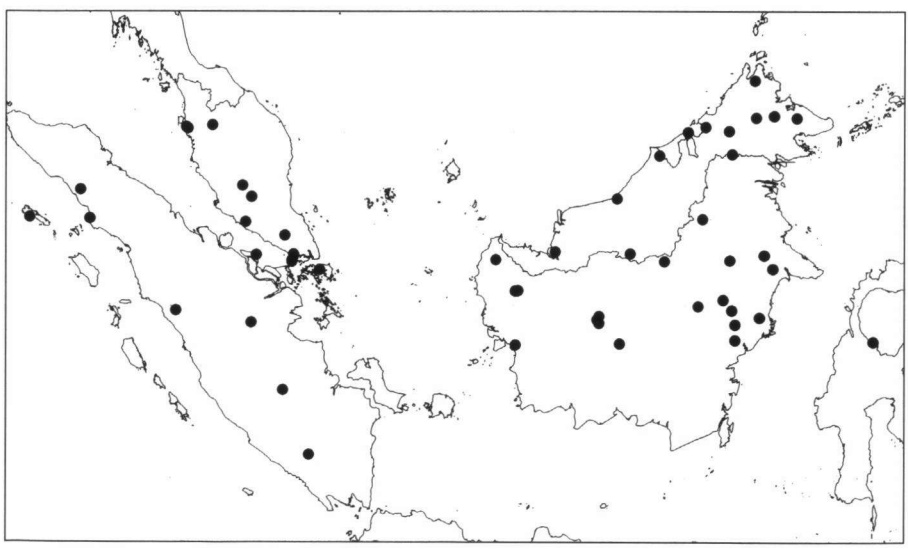


Fig. 3.21. *Baccaurea pyriformis* Gage. a. Habit; b. fruit (*Van Valkenburg 1420*).

lamina elliptic to obovate, 6.8–18 by 2.7–8.4 cm, l/w ratio 1.9–3.8, papery to leathery; base (rounded to) acute to cuneate; marginal glands visible as identification marks; apex acuminate to cuspidate, (0–)1–17 mm long; upper surface glabrous, not granulate, dark to yellowish green when fresh, dark brown when dry, nervation slightly sunken; lower surface (subglabrous to) densely hairy, midrib and veins (sparsely hairy to) velutinous, raised glands absent, discoid glands present, dark to yellowish green when fresh, light brown when dry; secondary veins 6–9 per side, closed at margin; nervation reticulate. *Staminate inflorescences* (axillary to) just below the leaves to ramiflorous, solitary to few clustered together, 1–7.5 cm long, up to 1.5 mm thick, velutinous, many-flowered, flowers scattered along inflorescence; bracts absent or 1 per branchlet, 0.3–1.5 mm long, densely hairy outside, glabrous inside, margin ciliate, hyaline or not; bracteoles, 1–1.5 mm long, c. 1 per branchlet, velutinous; branchlets cylindrical to spatulate, 0.4–4 mm long, densely hairy, 3–12-flowered. *Staminate flowers* 1–2 mm diam., yellowish to pale brown; pedicel 0–0.8 mm long; sepals 4 or 5, ovate, 0.4–0.9 by 0.3–0.8 mm, apex recurved, densely hairy outside and inside, yellowish to pale brown; stamens 4 or 5, 0.3–0.6 mm long, glabrous; filaments 0.2–0.5 mm long, geniculate to straight; anthers c. 0.1 by 0.1–0.2 by 0.1 mm; disc absent; pistillode cylindrical, 0.4–0.5 mm high, velutinous, solid. *Pistillate inflorescences* ramiflorous (to axillary), solitary, 1.5–3 cm long, c. 1.2 mm thick, velutinous, c. 10-flowered; pedicel c. 1 mm long, abscission zone not clear, velutinous; bracts 3 per branchlet, velutinous outside, sparsely hairy inside, margin ciliate. *Pistillate flowers* 2.5–3.5 mm diam., dirty brown; sepals 4 or 5, ovate, 1.3–2 by 1–1.4 mm, velutinous outside and inside, persistent; ovary cylindrical, 2–2.5 by 1.5–2 mm, (2- or) 3-locular, velutinous; style c. 0.2 by c. 1 mm, velutinous; stigmas c. 1.3 mm long, cleft for upper c. 70%, persistent; lobes c. 1 by 0.5 mm, glabrous above, densely hairy below, protuberances present above. *Infructescences* 1.5–9.8 cm long, 1.5–3.5 mm thick. *Fruits* pear-shaped (to globose), (2- or) 3-seeded berries, c. 38 by 34 by 34 mm when fresh, 18–24



Map 3.32. Distribution of *Baccaurea pyriformis* Gage in Peninsular Malaysia, Sumatra and Borneo.

by 14–22 by 14–22 mm when dry, rarely irregularly splitting, raised glands absent, not ruminate, densely hairy outside, subglabrous to densely hairy inside, (yellowish to orange-)brown; pericarp 1.5–2.5 mm thick; column 13–19 mm long, straight; pedicel 3–9 mm long, upper part 0.5–4.5 mm long. *Seeds* ellipsoid, laterally flattened, 8–17.5 by 5–12 by 2–7 mm; testa red; arillode cream to orange; cotyledons 9–12 by 6.2–11.5 by 1–2 mm (endosperm included); radicle up to 1 mm long.

Distribution — Peninsular Malaysia, Sumatra, Borneo.

Habitat & Ecology — Primary rain forest. Soil: sandstone, sandy loam. Altitude: sea level up to 1000 m. Flowering: Mar. to Oct. Fruiting: Jan., Feb., June to Nov.

Uses — Arillode edible.

Vernacular names — Simeuluë Island: Bolawah iteung falah. Borneo: Papar pingan (Bussup); tampoi hutan (Dusun Ramu); tampoi (Iban); tampoi merah (Malay); bukut.

Note — The following former syntypes have been studied: *Derry 66*; *Griffith 4901*; *Maingay 1361*; *Ridley 6491, 6492, 6669*; *SF 28, 2766, 2949*.

33. **Baccaurea racemosa** (Reinw. ex Blume) Müll.Arg. — Fig. 3.22, Map 3.33

Baccaurea racemosa (Reinw. ex Blume) Müll.Arg. in DC., Prodr. 15, 2 (1866) 461; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 249; Koord., Exkurs. Fl. Java 2 (1912) 481; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 75; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 331; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 51; Merr., Univ. Calif. Publ. Bot. 15 (1929) 150; Backer & Bakh.f., Fl. Java 1 (1964) 454; Soejarto, Bot. Mus. Leafl. (1965) 74; Whitmore, Tree Fl. Malaya 2 (1973) 64; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 53; Kew Bull. 36 (1981) 266; Lemmens et al., Prosea 3 (1991) 16. — *Coccomelia racemosa* Reinw. ex Blume, Catal. Gew. Buitenzorg (1823) 110; Reinw., Flora 8, 1 (1825) 103; Syll. Ratisb. 2 (1828) 5. — *Pierandia racemosa* (Reinw. ex Blume) Blume, Bijdr. (1825) 579. — *Pierardia racemosa* (Reinw. ex Blume) Miq., Fl. Ned. Ind. 1. 2 (1859) 358; Fl. Ned. Ind., Eerste bijv. (1861) 442; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281. — Type: *Blume s.n.* (lecto L, sheet 903.154-627, barcode L 0059160, selected here), Java.

Baccaurea wallichii Hook.f., Fl. Brit. India 5 (1887) 375; K. Heyne, Nutt. Pl. Ned. Ind. 3 (1917) 95; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 53; Ridl., Fl. Malay Penins. 3 (1924) 245; Soejarto, Bot. Mus. Leafl. (1965) 99. — Type: *King's Collector 7634* (lecto G, selected here), Peninsular Malaysia, Perak.

Baccaurea bhaswatii Chakrab. & Gang., J. Econ. Taxon. Bot. 18 (1994) 420; syn. nov. — Type: *Forbes 1653* (lecto CAL, selected by Chakrab. & Gang., 1994; isolecto L), Sumatra.

Treelet to tree 3–15(–20) m high, dbh 5–24 cm, buttresses absent; branchlets glabrous to sparsely hairy; young shoots reddish-black to reddish-brown when dry, Terminalia branching pattern well-developed. *Indumentum* of simple hairs and rarely stellate hairs. *Bark* whitish to grey to pale brown to fawn when fresh, greyish to brown when dry, up to 3 mm thick, smooth, papery, flaky, soft; inner bark white to yellow to creamy to ochre to brown, 1–2 mm thick, soft. *Heartwood* yellowish-brown to yellowish-ochre to brown, hard. *Leaves*: petiole 12–77 mm long, glabrous to sparsely hairy, red to brown when dry; stipules elliptic to triangular, 3–7.5 by 1–1.5 mm, glabrous to sparsely hairy, densely hairy when young outside, glabrous inside, margin ciliate, usually hyaline; lamina (ovate to) elliptic to obovate, 5.8–22 by 2.3–18.8 cm, l/w ratio 2.2–4.6, papery; base cuneate; apex acuminate to cuspidate, up to 25 mm long; upper surface glabrous, sometimes granulate, raised glands usually present, dark green when fresh, (white to green)-brown when dry; lower surface glabrous, rarely densely

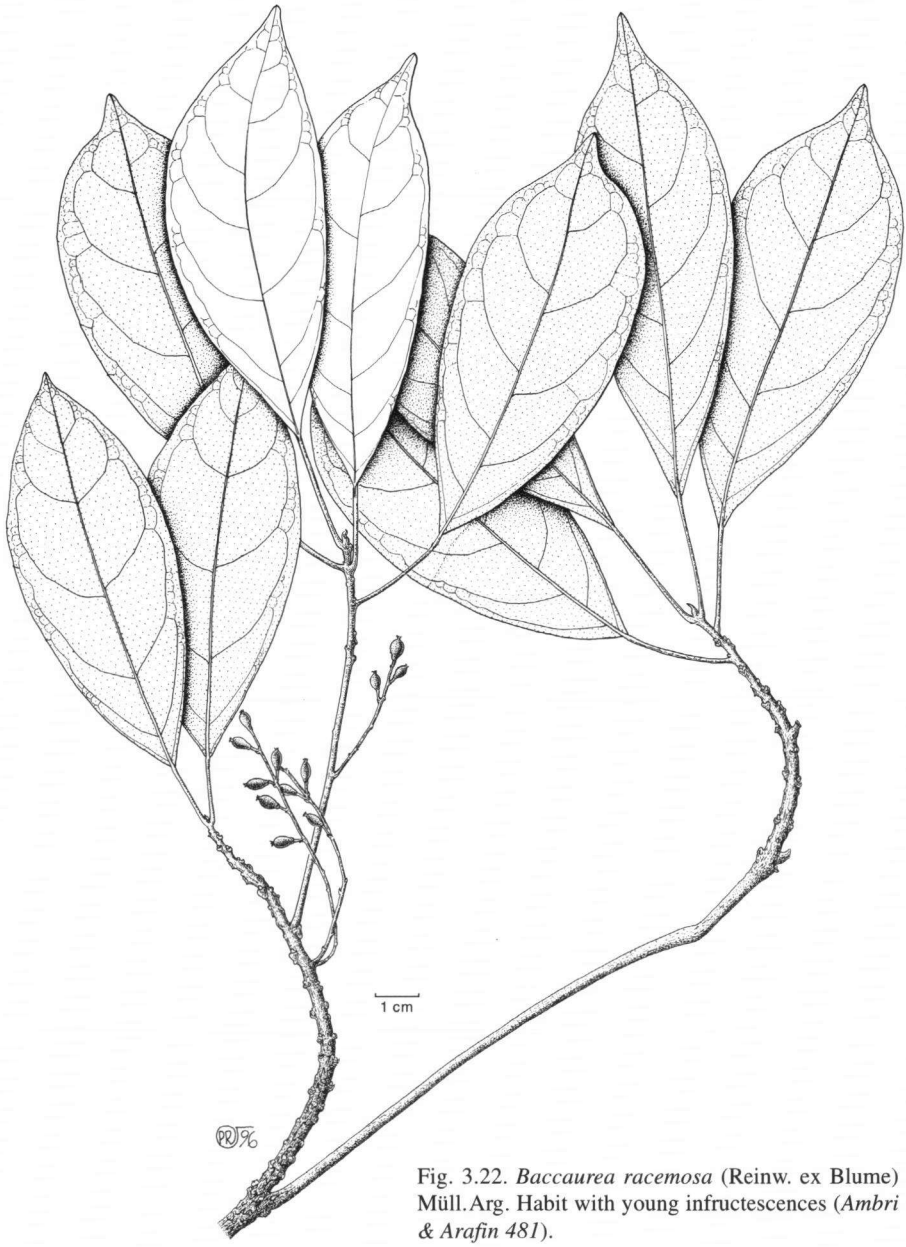
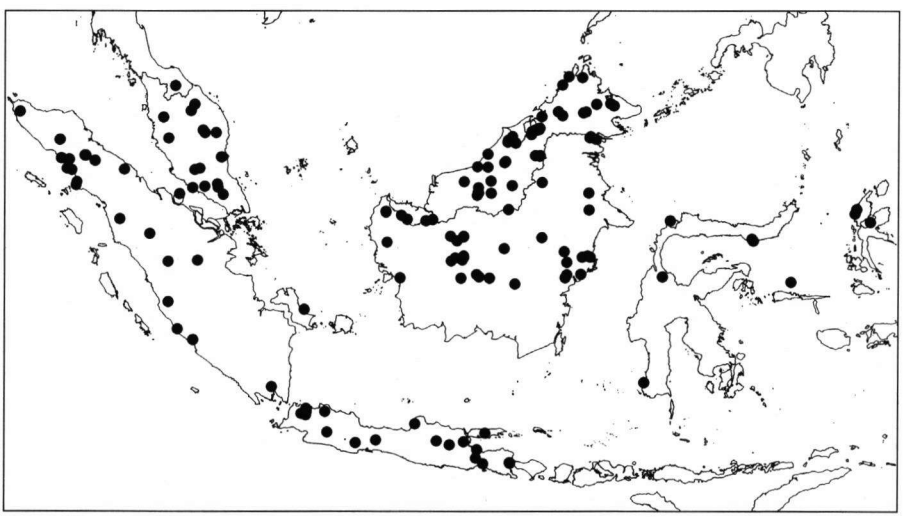


Fig. 3.22. *Baccaurea racemosa* (Reinw. ex Blume) Müll.Arg. Habit with young infructescences (*Ambri & Arafin 481*).

hairy at veins, discoid glands rarely present, light green when fresh, brown when dry, yellowish green to pink when young: nervation reddish to brown to black when dry; secondary veins 4–10 per side, almost closed at margin; nervation reticulate to weakly scalariform. ***Staminate inflorescences*** cauline to just below the leaves, solitary to 5 clustered together, 3–10 cm long, up to 1.3 mm thick, densely hairy, many-flowered,

flowers scattered along inflorescence; bracts 3 per branchlet, of which two very small, 0.2–1.1 mm long, persistent, glabrous to densely hairy outside, glabrous inside, margin ciliate, rarely hyaline; branchlets triangular, 0.1–2.5 mm long, densely hairy, (2- or) 3-flowered. *Staminate flowers* 1–3 mm diam., creamy yellow to white; pedicel 0.4–2.5 mm long, upper part 0.4–1.9 mm long, densely hairy; sepals 4 (or 5), ovate to obovate, 0.9–1.8 by 0.7–1.5 mm, apex usually recurved, densely hairy on both sides; stamens 5–7, 0.5–0.8 mm long, glabrous; filaments 0.4–0.6 mm long, straight; anthers white, c. 0.15 by 0.2–0.25 by 0.1 mm; disc present or absent; pistillode cylindrical, 0.3–0.9 mm long, densely hairy, hollow. *Pistillate inflorescences* cauline to axillary, solitary (to few clustered together), 3–28 cm long, c. 1 mm thick, densely hairy, 4–many-flowered, reddish-green when fresh, reddish to brown when dry; pedicel 1–2.9(–6.7) mm long, upper part up to 1.9(–2.5) mm long, densely hairy, green to brown to pinkish; bracts 3 per branchlet, persistent, densely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 3–9.2 mm diam., greenish yellow when fresh; sepals 4 (or 5), obovate to lanceolate, 2–6 by 1–2.7 mm, densely hairy on both sides, indumentum of silvery hairs when dry, caducous; ovary subglobose, 1.5–1.9 by 1.4–1.7 mm, (2- or) 3- (or 4-)locular, velutinous; style 0.2–0.4 by c. 1 mm, velutinous; stigmas c. 0.3 mm long, not lobed, persistent. *Fruits* (sub)globose, 1–3-seeded, berries or fleshy capsules, 14–30 by 16–25 by 16–25 mm, outer pericarp loculicidally dehiscing, inner pericarp not dehiscent, glabrous to sparsely hairy outside, glabrous inside, raised glands present, yellow to orange (to pink to red); pericarp 0.8–4.5 mm thick; column 12–15 mm long, caducous, straight; pedicel reddish when dry, 3–9 mm long, upper part 1–4.5 mm long. *Seeds* obovoid to ellipsoid, laterally flattened, 9–11.5 by 6.5–9.2 by 2.5–6 mm; testa reddish-purple to blue to black; arillode blue to purple to violet; cotyledons 5–7 by 6–7 by 0.1–1 mm, radicle 0–0.3 mm long.

Distribution — Thailand, Peninsular Malaysia, Sumatra, Java, Bali, Borneo, Sulawesi and (Halmahera).



Map 3.33. Distribution of *Baccaurea racemosa* (Reinw. ex Blume) Müll.Arg. in Thailand, Peninsular Malaysia, Sumatra, Java, Bali, Borneo and Sulawesi.

Habitat & Ecology — Primary and secondary rain forest, riverine forest, or fresh water swamp forest. Soil: granite to yellow or red sandy clay. Altitude: 50–1550 m. Flowering: Mar. and May to Oct. Fruiting: throughout the year.

Uses — Arillode edible, sour to sweet.

Vernacular names — Peninsular Malaysia: Asam tambun, rambi, tamut, tampoi. Sumatra: Roesip, kisip. Java: Menteng. Borneo: Kokonau (Dusun); engkuni, enkunik, kayu masam, longkuno, moho liox.

34. **Baccaurea ramiflora** Lour. — Map 3.34, Photo 9

Baccaurea ramiflora Lour., Fl. Cochinch. (1790) 661; Müll.Arg. in DC., Prodr. 15, 2 (1866) 458; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 71; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 551; Merr., Trans. Amer. Philos. Soc. 24, 2 (1935) 232; Airy Shaw, Kew Bull. 26 (1971) 221; Whitmore, Tree Fl. Malaya 2 (1973) 65; Airy Shaw, Kew Bull. 36 (1981) 266. — Type: *Loureiro s.n.* (lecto BM, sheet 31252, selected here), Hortis Cochinchinae (see note 1).

Baccaurea cauliflora Lour., Fl. Cochinch. (1790) 661; Müll.Arg. in DC., Prodr. 15, 2 (1866) 458; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 70; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 551; Merr., Trans. Amer. Philos. Soc. 24 (1935) 233. — Type: *Fleury 32043* (neo P, selected here), Vietnam, Cochinchina, Bien Hoa Province, Trañg Bône Forest Reserve (see note 2).

Pierardia sapida Roxb., Fl. Ind. 2 (1832) 254; Hortus Bengalensis (1814) 28. — *Baccaurea sapida* (Roxb.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 459; Bedd., Fl. Sylv. S. India (1869) 280; Kurz, Forest Fl. Burma 2 (1877) 356; Hook.f., Fl. Brit. India 5 (1887) 371; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Williams, Bull. Herb. Boissier. 2 (1905) 30; Brandis, Indian Trees (1906) 562; Craib, Aberdeen Univ. Stud. 57 (1911) 461; Koord., Syst. Verz. (1914) 67; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 52; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 548; Merr., Trans. Amer. Philos. Soc. 24 (1935) 233; Corner, Gard. Bull. Straits Settlem. 10 (1939) 290; Wayside Trees Mal. 1 (1940) 241, syn. nov. — Type: *Wallich 8072* (lecto K, selected here), Burma?.

Baccaurea flaccida Müll.Arg. in DC., Prodr. 15, 2 (1866) 459; Hook.f., Fl. Brit. India 5 (1887) 370; Brandis, Indian Trees (1906) 563; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 50, syn. nov. — Type: *Wallich 8074* (lecto K, selected here), Burma.

Baccaurea propinqua Müll.Arg. in DC., Prodr. 15, 2 (1866) 463. — Type: *Wallich 8071* (lecto G, selected here) India Orientali, Silhet.

Baccaurea wrayi King ex Hook.f., Fl. Brit. India 5 (1887) 374; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 53; Ridl., Fl. Malay Penins. 3 (1924) 244; S. Moore, J. Bot. Br. 63 (1925) 98; Airy Shaw, Kew Bull. 14 (1960) 354; Kew Bull. 26 (1971) 221. — Type: *King's Collector s.n.* (lecto K, selected here), Peninsular Malaysia, Perak.

Baccaurea oxycarpa Gagnep., Bull. Soc. Bot. France 23 (1923) 431; Fl. Gén. Indo-Chine 5 (1927) 549, f. 69; Airy Shaw, Kew Bull. 14 (1960) 354; Kew Bull. 26 (1971) 221; Vu Van Dung, Vietnam Forest Trees (1996) 191. — Type: *Pierre 614* (lecto K, selected here; isolecto P), Cambodia, Mt Knang-krepeuh.

Gatnaia annamica Gagnep., Bull. Soc. Bot. France 24 (1924) 870; Fl. Gén. Indo-Chine 5 (1927) 540; Pax & K. Hoffm. in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 50. — Type: *Eberhardt 3042* (lecto P, selected here; isolecto K, L), Annam, Thua-thien Prov.

Baccaurea sylvestris auct. non Lour.: Lour., Fl. Cochinch. (1790) 662, p.p., inflorescences; Müll.Arg. in DC., Prodr. 15, 2 (1866) 457; Pellegr., Fl. Indo-Chine (1911) 766; A. Chev., Cat. Pl. Jard. Bot. Saigon (1919) 64; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 61; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 551; Merr., Trans. Amer. Philos. Soc. 24, 2 (1935) 233; Mabb. et al., Fl. Males. ser. 1, 12 (1995) 316; Vu Van Dung, Vietnam Forest Trees (1996) 192 (see note 3).

Tree 5–13 m high, dbh 5–33 cm, buttresses absent; branchlets glabrous to sparsely hairy; young shoots greenish white when fresh, brown to greenish white when dry,

Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* greyish-brown to grey when fresh, 1–2 mm thick, smooth; inner bark white. *Leaves*: petiole 10–63 mm long, glabrous to sparsely hairy, raised glands present; stipules 2.5–6 by 1–2.5 mm, caducous (to late caducous), glabrous to sparsely hairy outside, midrib densely hairy to velutinous, glabrous inside, margin ciliate, usually hyaline; lamina elliptic to obovate, 7.1–25.5 by 2.9–8.8 cm, l/w ratio 1.8–4, papery; base attenuate to cuneate; apex acute to cuspidate, 2–12 mm long; upper surface: glabrous, raised glands present, not granulate, glossy dark green when fresh, greenish brown to greyish brown when dry; lower surface glabrous to sparsely hairy, raised glands present, discoid glands absent, green when fresh, greenish brown when dry; secondary veins 4–9 per side, closed at margin or almost so; nervation reticulate to weakly scalariform. *Staminate inflorescences* axillary to cauline, solitary to many clustered together, 3–8.5 (–15.5) cm long, up to 1 mm thick, densely hairy, many-flowered, flowers clustered at the tip of inflorescence, greenish; bracts conspicuous, 1 (or 3) per branchlet, (1.5–) 3–4 mm long, persistent, sparsely to densely hairy outside, glabrous inside, but densely hairy at base, margin ciliate, sometimes hyaline; bracteoles absent; branchlets cylindrical, absent to 1.8 mm long, densely hairy, 3-flowered. *Staminate flowers* 1.1–4 mm diam., yellow; pedicel 0.8–2.6 mm long, upper part 0.7–2.4 mm long, densely hairy; sepals 4 or 5, different in shape, 1–2.4 by 0.5–1.4 mm, sometimes apically recurved, densely hairy outside and inside; stamens 5–8, 0.7–1.1 mm long, glabrous; filaments 0.5–0.9 mm long, straight; anthers 0.2–0.3 by 0.2–0.4 by c. 0.2 mm, yellow; pistillode present, obtriangular, 0.9–1.1 mm high, densely hairy, solid. *Pistillate inflorescences* just below the leaves to cauline, solitary to many clustered together, c. 10 cm long, c. 1 mm thick, densely hairy, 10–15-flowered, red; pedicel 1.5–3 mm long, upper part 0.1–1 mm long, densely hairy; bracts 1 per branchlet, persistent (to caducous), sparsely hairy outside, densely hairy at midrib, glabrous inside, margin ciliate. *Pistillate flowers* 3–8 mm diam., yellow; sepals 4 or 5, elliptic, 3.5–5 by 1–2 mm, densely hairy outside and inside, caducous; ovary globose, 2–2.3 by 2–2.3 mm, (2- or) 3- (or 4-)locular, woolly, green; style absent; stigmas c. 0.5 mm long, not lobed, glabrous, cream, caducous (to persistent). *Infructescences* 12–20 cm long, 1–2.5 mm thick. *Fruits* globose to ovoid to pear-shaped, 2–4-seeded berries, 19–37 by 14–28 by 14–28 mm, raised glands absent, glabrous to sparsely hairy outside, glabrous inside, red to orange to pink to purplish outside, cream inside; pericarp 1–3 mm thick; column fragile; pedicel 1–10(–15) mm long, upper part 0.5–3 mm long. *Seeds* globose to ellipsoid, but laterally flattened, 9–15 by 9–11 by 1.5–6 mm; arillode white; testa purplish red; cotyledons 5.5–9 by 5.2–8.5 by c. 0.1 mm; radicle 0.5–1.8 mm long; endosperm 1.5–7 mm thick.

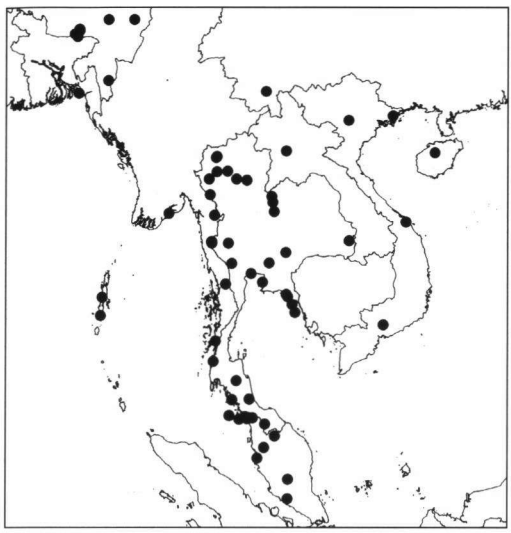
Distribution — India (Assam), Burma, China (Yunnan, Hainan), Vietnam, Laos, Thailand, Andaman and Nicobar Islands, Peninsular Malaysia.

Habitat & Ecology — Primary rain forest and cultivated. Soil: sand, granite. Altitude 50–1700 m. Flowering: Dec. to June, Sept. Fruiting: throughout the year.

Uses — Arillode edible, sweet to sour.

Vernacular names — Burma: Kanaso. Thailand: Mahphie. Peninsular Malaysia: Tampoi.

Notes — 1. The front side of the type sheet (BM: 31252) of *B. ramiflora* refers to page 662 of Fl. Cochinch. and *B. sylvestris*. This is certainly wrong, because the



Map 3.34. Distribution of *Baccaurea ramiflora* Lour. in India, Burma, Thailand, Laos, China, Vietnam, Peninsular Malaysia, and the Andaman and Nicobar Islands.

specimen does not correspond with the description of *B. sylvestris*. The back side of this sheet refers to page 661 of Fl. Cochinch., where *B. ramiflora* is described.

2. The type of *B. cauliflora* is probably lost. There is no original illustration. It is therefore not possible to lectotypify this name. From the description it is however obvious that this name is conspecific with *B. ramiflora*. It is here therefore neotypified. *Fleury 32043* is chosen as neotype, because it is a collection from Cochinchine, and it is a fruiting specimen like the original specimen described by Loureiro.

3. The type sheet of *B. sylvestris* is a mixture. The leaves on this sheet are *Lancium domesticum* Corrêa, see Mabberley et al. (1995). The description of Loureiro is also congruent with *Lancium domesticum*. The fruits, for example, contain 5 locules, and each locule has one ovule only (both features not present in *Baccaurea*). The inflorescences on the type sheet, on the other hand, belongs to *B. ramiflora*. The fact that the type specimen is a mixture has probably caused the confusion about the taxonomical status of *B. sylvestris*.

35. **Baccaurea reticulata** Hook.f. — Fig. 3.23; Map 3.35

Baccaurea reticulata Hook.f., Fl. Brit. India 5 (1887) 373; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 65; Ridl., Fl. Malay Penins. 3 (1924) 246; Corner, Wayside Trees Mal. 1 (1940) 241; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 36; Whitmore, Tree Fl. Malaya 2 (1973) 67; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 54; Kew Bull. 36 (1981) 266; Chakrab. & Gang., J. Econ. Taxon. Bot. 18 (1994) 424. — Type: *Scortechini s. n.* (lecto L, sheet 903.154-630, barcode L 0039846, selected here), Peninsular Malaysia, Perak, Goping.

Tree or treelet 6–28 m high, dbh 21–60 cm, bole sometimes fluted to up to 2 m high; branchlets subglabrous, densely hairy when young, Terminalia branching pattern weakly developed. *Indumentum* of stellate and simple hairs. *Bark* red to red-brown to orange-brown when fresh, brown when dry, thin, rugose, fibrous to flaky; inner bark

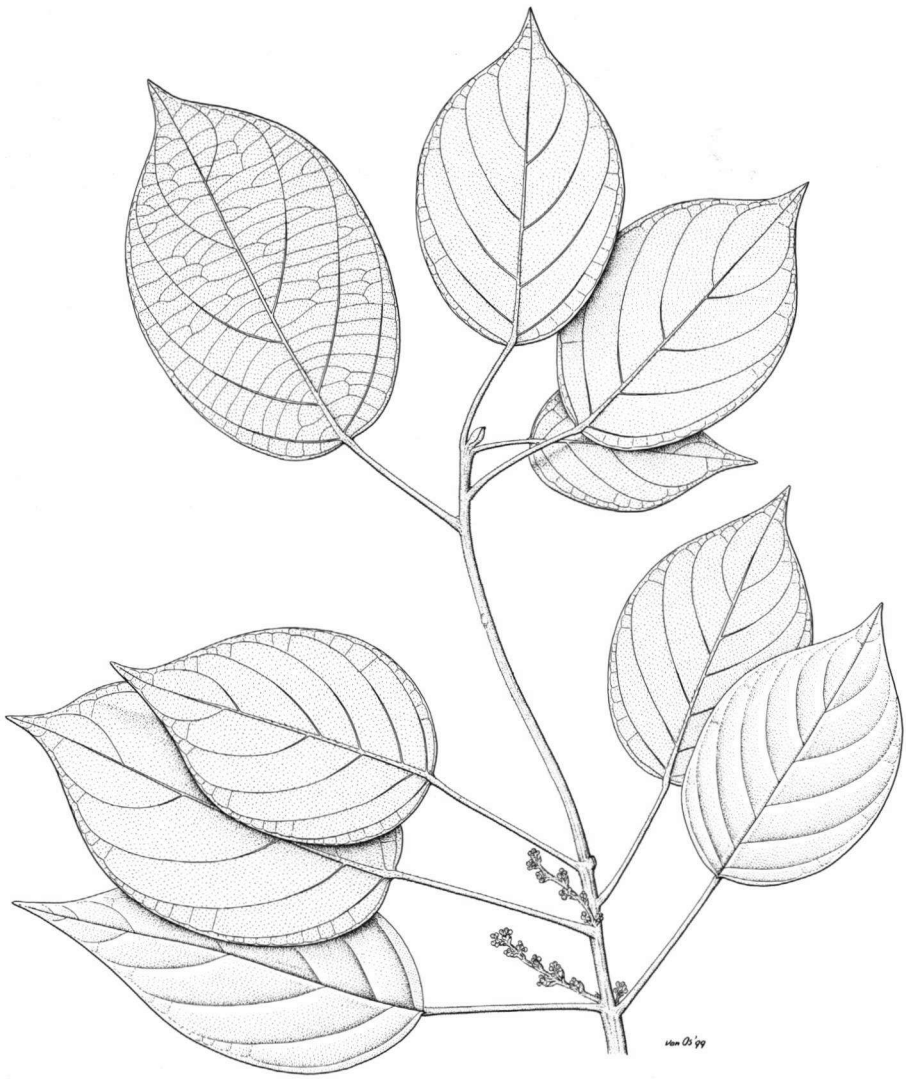


Fig. 3.23. *Baccaurea reticulata* Hook.f. Habit with male inflorescences (*S 25377*).

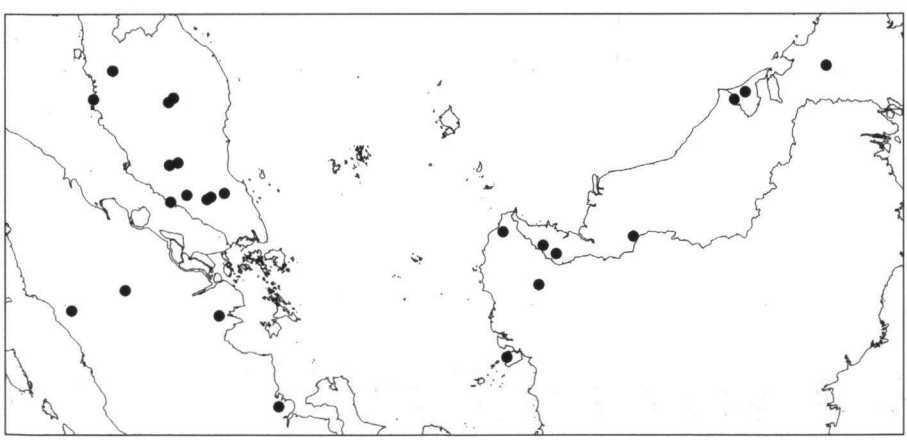
red to pink to light brown, 2–5 mm thick. *Heartwood* red-brown to yellow-brown. *Leaves*: petiole 18–87 mm long, subglabrous to velutinous with short stellate hairs and long simple hairs, transverse cracks usually, apically and slightly basally pulvinate, raised glands sometimes present; stipules 4–7.5 by 1.5–3.5 mm, velutinous outside and inside, margin ciliate, not hyaline; lamina (ovate to) elliptic to obovate, 5.4–14.5 by 2.8–6.6 cm, l/w ratio 1.6–2.9, papery to slightly leathery; base acute to cuneate (to attenuate); marginal glands sometimes visible as small indentations; apex (obtuse to) acuminate to cuspidate, up to 16 mm long; upper surface glabrous, raised glands often present, sometimes granulate, grey-green to green-white to brown-white, nerva-

tion whitish to grey-green, slightly sunken; lower surface subglabrous, densely hairy at midrib and veins, raised glands often present, discoid glands if present in a row between secondary veins, light (yellowish) brown when dry; secondary veins 4–8 per side, closed at margin; nervation (weakly) scalariform, (dark) brown. *Staminate inflorescences* axillary (to ramiflorous), solitary to 3 clustered together, 1–7 cm long, c. 0.1 mm thick, branched, velutinous, many-flowered, flowers scattered along inflorescence; bracts 1 per branchlet, 1–5 mm long inserted, densely hairy outside and inside, margin ciliate, not to slightly hyaline; bracteoles 0.5–2.5 mm long, 1–3 (or 4) per branchlet; branchlets cylindrical, 1–4 mm long, densely hairy, (3–)9–15-flowered. *Staminate flowers* 0.8–2.5 mm diam., pale yellow to greenish white to white; pedicel 0.6–1.5 mm long, upper part 0.3–1.2 mm long, densely hairy; sepals 4 (or 5), ovate to elliptic, 0.7–1.8 by 0.2–0.9 mm, apex recurved, densely hairy outside and probably also inside; stamens 4 (or 5), 0.2–0.3 mm long, glabrous; filaments up to 0.2 mm long, straight; anthers 0.1–0.2 by 0.15–0.2 by c. 0.1 mm; disc absent; pistillode absent to small, up to 0.15 mm high, velutinous. *Pistillate inflorescences* ramiflorous to just below the leaves. *Pistillate flowers*: ovary 3- (or 4-)locular. *Infructescences* 2–5 cm long, 2–3 mm thick. *Fruits* globose, 3–6-seeded, fleshy capsules, 25–38 by 29–51 by 29–51 mm, loculicidally dehiscent, raised glands present, subglabrous to tomentose outside, subglabrous inside, septa sparsely hairy, green to dirty orange to brown; pericarp 3–6.5 mm thick; column 19–25 mm long, straight; sepals usually persistent; stigmas usually caducous; pedicel 12–21 mm long, upper part 8–15 mm long. *Seeds* globose to ellipsoid, laterally flattened, 10–13.5 by 8–14.5 by 3–4 mm; arillode whitish yellow, translucent; cotyledons 8–11 by 6.5–12 by up to 0.1 mm; radicle up to 0.1 mm long.

Distribution — Peninsular Malaysia, Sumatra, Borneo.

Habitat & Ecology — Secondary rain forest. Soil: yellow sandy loam. Altitude: sea level up to 330 m. Flowering: Jan., Mar., Apr., Aug., Sept. Fruiting: June to Sept., Nov.

Uses — Arillode edible, sweet.



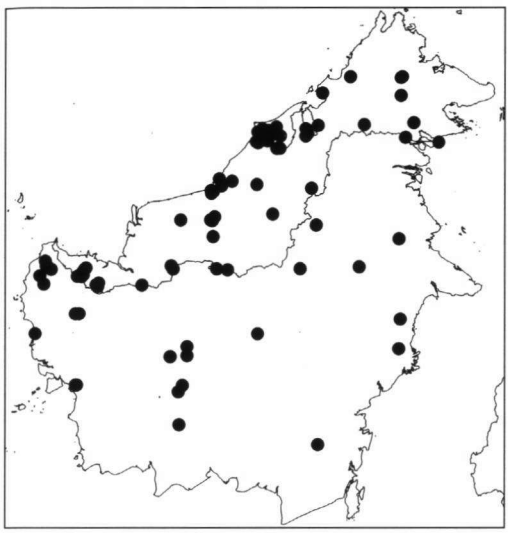
Map 3.35. Distribution of *Baccaurea reticulata* Hook.f. in Peninsular Malaysia, Sumatra and Borneo.

Vernacular names — Peninsular Malaysia: Tampoi, tampoy, tampui. Sumatra: Kaloe merah, tampoei simba.

36. **Baccaurea sarawakensis** Pax & K. Hoffm. — Map 3.36, Photo 10, 11

Baccaurea sarawakensis Pax & K. Hoffm. in Engl., Pflanzenr. VI.147.xv (1922) 53; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 54. — Type: *Hose 43* (lecto K, selected here; isolecto L), Borneo, Sarawak, Baram.

Tree 3–18(–21) m high, dbh 4–21 cm, buttresses absent; branchlets glabrous; young shoots greyish-white when dry, slightly thickened at tip, Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* whitish to green to grey to brown when fresh, greyish-white to brown when dry, c. 1–2.5 mm thick; inner bark yellowish to pale brown or pale red, up to 2 mm thick, soft. *Leaves*: petiole brown when dry, 10–56 mm long, sparsely hairy, raised glands present; stipules caducous to late caducous, lanceolate, 2.5–9 by 1–2.8 mm, sparsely to densely hairy outside, glabrous inside, margin ciliate, sometimes hyaline; lamina obovate to elliptic, 7–20 by 3–8 cm, l/w ratio 2.3–3, firm papery to leathery; base cuneate to acute; apex (rounded to) acuminate, up to 17 mm long; upper surface glabrous, sometimes granulate, glossy green when fresh, whitish brown when dry; lower surface glabrous, rarely sparsely hairy at midrib and veins, raised glands usually present, discoid glands sparse or absent, shiny pale green when fresh, whitish green to brown when dry; secondary veins 5–8 per side, closed at margin; nervation reticulate to weakly scalariform, (whitish) brown when dry. *Staminate inflorescences* axillary to just below the leaves, solitary to 5 clustered together, 3–12 cm long, less than 1 mm thick, densely hairy, more than 60-flowered, flowers scattered along inflorescence, bright yellow; branchlets 0–0.2 mm long; bracts 3 per branchlet, 0.4–1.5 mm long, glabrous to densely hairy outside, (sub)glabrous inside, margin ciliate. *Staminate flowers* 3 per branchlet, 1–1.4 mm diam.; pedicel 1.9–4.5 mm long, upper part 1–2.8 mm long, densely hairy; sepals ovate to obovate, 4 or 5, apically recurved, 0.8–1.2 by 0.4–0.8 mm, glabrous to densely hairy inside and outside; stamens 4 or 5, 0.15–0.2 mm long, glabrous; filaments c. 0.1 mm long, straight; anthers c. 0.2 by 0.2–0.3 by 0.1 mm; disc present, 0.1–0.15 mm thick; pistillode globose, 0.25–0.3 mm high, densely hairy, solid. *Pistillate inflorescences* axillary to ramiflorous, solitary to few clustered together, 5–10 cm long, c. 1 mm thick, densely hairy, 9–16-flowered; bracts 3, usually persistent, densely hairy outside, glabrous inside, margin ciliate; pedicel 2–4.1 mm long, upper part c. 0.2 mm long, densely hairy. *Pistillate flowers* 2–9 mm diam.; sepals 4 or 5, lanceolate, 1.5–9 mm by 1–2.6 mm, glabrous to densely hairy on both sides, caducous; ovary (sub)globose, 1.5–3.5 by 1.5–3.2 mm, 3-locular, woolly; style (0–)0.5–1 mm by 1–2 mm, glabrous to densely hairy; stigmas c. 1 mm long, slightly lobed apically, caducous; lobes above glabrous with protuberances, below densely hairy. *Fruits* subglobose to triangular, 0–3-seeded, fleshy capsules, 18–28(–30) by 16–30 by 13–30 mm, dehiscing loculicidally, outside sparsely to densely hairy, inside glabrous, raised glands present, red to yellowish red-pink; pericarp 0.5–3.5 mm thick, column 13–16 mm long, caducous; pedicel 2–11 mm long, upper part 1–2 mm long. *Seeds* obovoid, laterally flattened, 10–14 by 7–11.5 by 1–5.7 mm; arillode blue to pinkish. *Seeds* coat blue to purple; cotyledons 6–8 by c. 6 by 0.1 mm.



Map 3.36. Distribution of *Baccaurea sarawakensis* Pax & K. Hoffm. in Borneo.

Distribution — Borneo.

Habitat & Ecology — Primary rain forest. Altitude: up to 800(–1600) m. Soil: loam. Flowering: Mar., Apr., June to Sept. Fruiting: Jan., Feb., May to Dec.

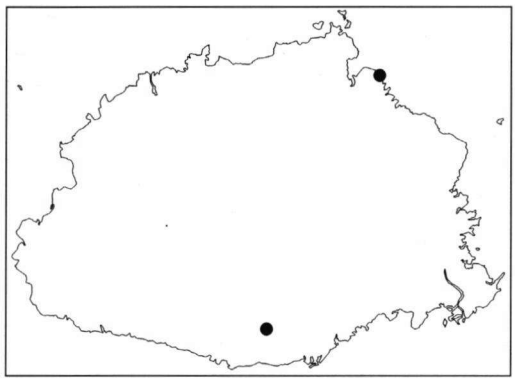
Vernacular names — Borneo: Ankuni (Brunei, Dayak); engkuni, gune (Iban); kunau-kunau (Malay); mata kunau (Brunei, Dusun); Ng'kokonau (Dusun Rongos); asam kuning, enkunyit, kayu masam, peladuk.

37. **Baccaurea seemannii** (Müll. Arg.) Müll. Arg. — Map 3.37

Baccaurea seemannii (Müll. Arg.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 462; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 55; A. C. Sm., Allertonia 1 (1978) 378. — *Pierardia seemannii* Müll. Arg., Flora 47 (1864) 469. — Type: *Seemann 390* (holo BM; iso K), Fiji.

Baccaurea wilkesiana Müll. Arg. in DC., Prodr. 15, 2 (1866) 461; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 62. — Type: *Wilkes 75125* (holo US; iso GH), Fiji.

Shrub or tree 3.6–10 m high, buttresses absent; branchlets densely hairy to velutinous, Terminalia branching pattern usually weak. *Indumentum* of simple hairs. *Bark* grey when dry. *Leaves*: petiole 12–41 mm long, velutinous, transverse cracks often present, small raised glands sometimes present; stipules 2–3.5 by 0.8–1 mm, sparsely hairy to velutinous outside, glabrous inside, margin ciliate, not hyaline; lamina ovate to obovate, 5–14.5 by (2–)3–6.9 cm, l/w ratio 1.4–2.3, papery; base rounded to cuneate (to attenuate); apex (retuse to) obtuse to acuminate (to cuspidate), up to 11 mm long; upper surface glabrous, midrib sometimes subglabrous at base, small raised glands often present, sometimes granulate, glossy green when fresh, (dark) brown when dry; lower surface subglabrous to sparsely hairy, veins sparsely hairy to velutinous, small raised glands often present, discoid glands present, glossy green when fresh, (green to pale) brown when dry; secondary veins 5–8 per side, open at margin; nervation reticulate. *Staminate inflorescences* axillary to just below the leaves (to ramiflorous), solitary to 5 clustered together, 0.5–6 cm long, 0.5–1 mm thick, velutinous, branching minute,



Map 3.37. Distribution of *Baccaurea seemannii* (Müll.Arg.) Müll.Arg. in Fiji.

45–many-flowered, flowers scattered along inflorescence; bracts 1 (or 3, then 2 small), (0.2–)0.5–1 mm long, densely hairy outside, glabrous to sparsely hairy inside, margin ciliate, not hyaline; bracteoles absent; branchlets absent to 0.3 mm long, densely hairy, 3-flowered. *Staminate flowers* 1–2.5 mm diam., (pale to brown)-yellow; pedicel 0.5–1.3 mm long, upper part 0.2–0.5 mm long, densely hairy; sepals 3–5, ovate, 0.4–1.3 by 0.15–1 mm, densely hairy outside and inside; stamens 5 or 6 (or 7), 0.4–0.9(–1.5) mm long; filaments 0.2–0.7(–1.3) mm long, straight; anthers c. 0.2 by 0.2–0.25 by 0.1–0.15 mm; disc absent; pistillode cylindrical to obtriangular, 0.5–0.9 mm high, densely hairy, often hollow. *Pistillate inflorescences* axillary to ramiflorous, solitary to 3 clustered together, 0.5–3.5 cm long, 0.5–1.5 mm thick, velutinous, 3–15-flowered; pedicel 0.7–2 mm long, not to geniculate at abscission zone, upper part 0.6–1.2 mm long, velutinous; bracts 3, inserted on base, densely hairy outside, probably sparsely hairy inside, margin ciliate. *Pistillate flowers* 1.5–2.2 mm diam., pink; sepals 4, ovate, 0.5–1.3 by 0.3–1 mm, densely hairy on both sides, caducous; ovary cylindrical to globose, 1–1.3 by 0.6–1.3 mm, 2-locular, velutinous; style c. 1 by 0.6–1 mm; stigmas c. 0.6 mm long, cleft for upper c. 80%, persistent; lobes c. 0.5 by 0.8–1 mm, many protuberances present above and below, glabrous above, densely hairy below. *Fruits* globose, 2-seeded, fleshy capsules, 12.5–14 by c. 14 by 12.2 mm, dehiscing loculicidally, raised glands absent, subglabrous outside, glabrous inside, septa sparsely hairy; pericarp c. 1 mm thick. *Seeds* globose, but laterally flattened, 9–9.5 by 10–11.5 by 5–6.5 mm; testa hard, not easily dehiscing.

Distribution — Fiji.

Habitat & Ecology — Primary forest. Altitude: 0–210 m. Flowering: Oct., Dec.

Vernacular names — Fiji: Koka.

38. Baccaurea simaloerensis Haegens, *spec. nov.* — Fig. 3.24, Map 3.38

Ab omnibus congeneribus malesianis praeter combinationem charactorum sequentium pili et caespites stellati et simplices, ramuli (sub)glabri, stipulae caducae, folia ovata ad elliptica, 5 vel 6 (vel 7) nervis utrius lateris venis reticulatis, supra costa glabra, infra sine glandula nigra pilorum basi, inflorescentiae masculae ramosae multifasciculatae, flores (sub)clausi, bracteis inflorescentiis partialibus maioribus amplectentibus, flores pistillati 8–14 mm diam., ovarium (2? vel) 3-loculare, fructus indehiscentes 15–24 mm diam. differt. — Typus: *Achmad 728* (holo L), Sumatra, Simeuluë Island.

Tree; branchlets glabrous to sparsely hairy, densely hairy when young, Terminalia branching pattern weakly developed. *Indumentum* of simple and usually short stellate hairs. *Bark* dark brown when dry, thin. *Leaves*: petiole 12–40 mm long, subglabrous to sparsely hairy, rarely densely hairy, apically and basally pulvinate, blackish to dark reddish brown when dry, raised glands usually absent; stipules 2–4 by 1–1.5 mm, sparsely to densely hairy outside, midrib densely hairy, glabrous inside, margin ciliate, not hyaline; lamina ovate to elliptic, 6.2–18 by 3.4–9.1 cm, l/w ratio 1.5–2.1, papery; base truncate to acute (to attenuate); apex obtuse to acuminate, up to 13 mm long; upper surface glabrous, small raised glands present, usually granulate, dark brown, nervation sunken; lower surface (sub)glabrous, subglabrous to sparsely hairy at midrib, raised glands present, discoid glands usually present, scattered, pale brown when dry; secondary veins 5 or 6 (or 7) per side, open at margin; nervation reticulate. *Staminate inflorescences* axillary to just below the leaves, solitary, 3–10 cm long, 0.6–1 mm thick, branched, sparsely to densely hairy, many-flowered, flowers scattered along inflorescence; bracts 1 per branchlet, (broadly) ovate, 2.2–3.5 mm long, usually caducous, densely hairy outside, glabrous inside, margin ciliate, not hyaline; bracteoles usually 4, 1.5–2.5 mm long; branchlets cylindrical, 2–3.5 mm long, 6–20-flowered, densely hairy. *Staminate flowers* 1.5–2 mm diam., caducous before dehiscence; pedicel 0.3–1 mm long, densely hairy; sepals 4 or 5, ovate, 1–1.3 by 0.7–1.2 mm, apically slightly recurved, velutinous outside and inside; stamens 4–7, 0.3–0.4 mm long, glabrous; filaments 0.1–0.2 mm long,

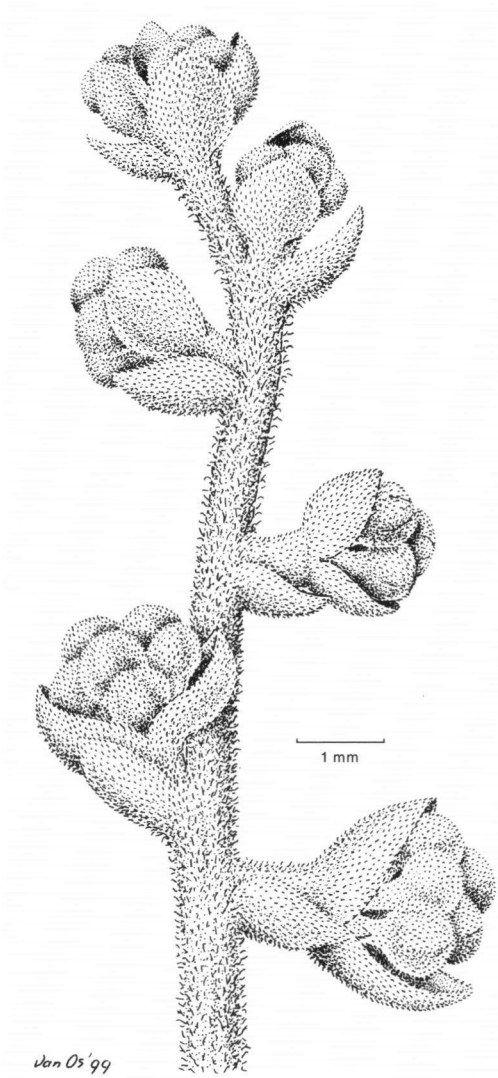


Fig. 3.24. *Baccaurea simaloerensis* Haegens. Detail of male inflorescence (*Achmad 728*).

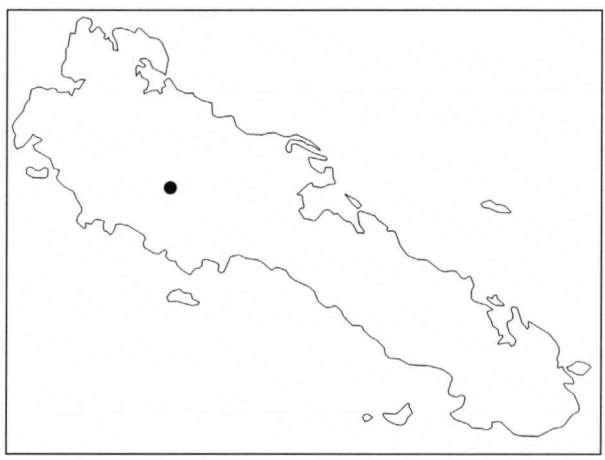
straight; anthers 0.15–0.1 by 0.15–0.2 by c. 0.1 mm; disc absent; pistillode present, cylindrical to obtriangular, c. 0.5 mm high, velutinous, solid. *Pistillate inflorescences* axillary, solitary, 2–4.2 cm long, 1–2 mm thick, densely hairy, few-flowered; pedicel 2–8.5 mm long, upper part 1–4.5 mm long, densely hairy; bracts probably 3 per branchlet, spatulate, persistent, subglabrous outside, sparsely hairy at base, glabrous inside, margin ciliate. *Pistillate flowers* 8–14 mm diam.; sepals 5, lanceolate to elliptic, 5–7.5 by 1.2–1.5 mm, densely hairy outside and inside, caducous to persistent; ovary globose, 2–4 by 2–5 mm, (2-? or) 3-locular, velutinous; style c. 0.5 by 1.5 mm, velutinous; stigmas c. 2.8 mm long, cleft for upper 60–70%, persistent; lobes c. 2 by 0.5 mm, glabrous above, protuberances small, below densely hairy, protuberances strong. *Fruits* globose, usually 2–4-seeded, berries or fleshy capsules, 15.5–18 by 15.8–23.5 by 15.8–23.5 mm, only outer layer loculicidally dehiscent, raised glands absent, sparsely to densely hairy outside, (sub)glabrous inside, septa subglabrous; pericarp 1.5–6.5 mm thick; column 9–12 mm long, straight. *Seeds* ellipsoid, laterally flattened, 7–8.5 by 3.5–4.5 by 1.5–3.5 mm; cotyledons 2.8–3 by 2–3 by c. 0.1 mm; radicle 0.6–2 mm long; endosperm 0.2–0.5 mm thick.

Distribution — Sumatra: Simeuluë Island.

Habitat & Ecology — Flowering: June, Sept., Nov., Dec. Fruiting: Feb., May.

Vernacular names — Simeuluë Island: Awa-batoe-fatoeh, bolahna itung, bolawah-iteung-delok, bolawah ontur, bolawah palo, bolawah pajo-oeding, bolawah silai, soerai-datan, toetoen bolafah.

Notes — 1. In this species all staminate flowers in herbarium material fall off before anthesis. In *B. bracteata*, a close relative, a part of the staminate flowers show the same phenomenon. However, despite the fact that the staminate flowers remain closed, pollination takes place because in the fruit bearing specimen seeds are produced. A possible explanation for the successful pollination could be that the breaking off of the unopened flowers is an artifact, and that the flowers do open in the wild. Another explanation could be that fertilisation is performed by thrips, who are able to enter the closed flowers.



Map 3.38. Distribution of *Baccaurea simaloerensis* Haegens in Simeuluë Island.

2. This species is named for its restricted distribution on Simeuluë Island, off the coast of Sumatra. All studied collections of this species were made by Achmad, and he spelled the island as Simaloer.

Specimens studied: *Achmad 244, 428, 484, 620, 728, 751, 788, 881, 1331, 1507.*

39. **Baccaurea sumatrana** (Miq.) Müll.Arg. — Fig. 3.25, Map 3.39

Baccaurea sumatrana (Miq.) Müll.Arg. in DC., Prodr. 15, 2 (1866) 466; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 281; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 63; S. Moore, J. Bot. Br. 63 (1925) 98; Merr., Univ. Calif. Publ. Bot. 15 (1929) 151; K. Heyne, Nutt. Pl. Ned. Ind. 1, 3rd ed. (1950) 915; Soejarto, Bot. Mus. Leafl. 21 (1965) 71, 99; Meijer, Bot. News Bull. Forest Dept., Sabah (1967) 36; Whitmore, Tree Fl. Malaya 2 (1973) 65; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 55; Kew Bull. 36 (1981) 267; Chakrab. & Rao, J. Econ. Taxon. Bot. 5 (1984) 957; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 51. — *Calyptroon sumatranum* Miq., Fl. Ned. Ind., Eerste bijv. (1861) 472. — Type: *Teijsmann s.n.* (lecto U, sheet 35994, selected here) Sumatra.

Baccaurea kingii Gage, Rec. Bot. Surv. India 9 (1922) 231; Hook.f., Fl. Brit. India 5 (1887) 373; Ridl., Fl. Malay Penins. 3 (1924) 245; Whitmore, Tree Fl. Malaya 2 (1973) 65; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 54. — Type: *Wray 1364* (lecto SING, selected here), Malakka, Perak, Tapa.

Baccaurea bivalvis Merr., Univ. Calif. Publ. Bot. 15 (1929) 148; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 56. — Type: *Elmer 21510* (holo US; iso DS, GH, K, L), Borneo, Sabah, Tawau.

Tree (4–)15–43 m high, dbh (5–)15–35 cm, buttresses if present up to 1 m high, c. 6 cm thick; branches glabrous, young shoots dark brown to black, Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* greyish-brown to brown

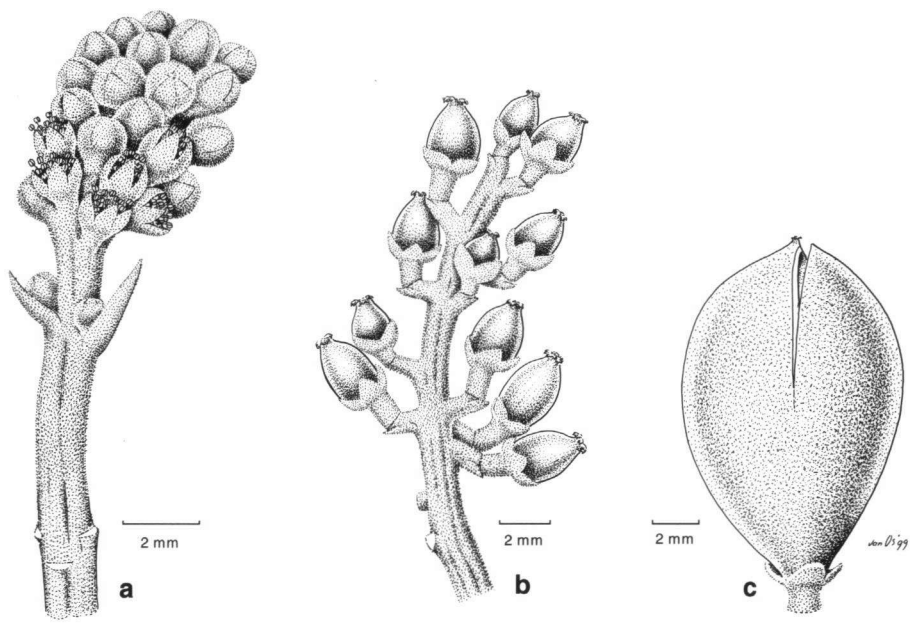
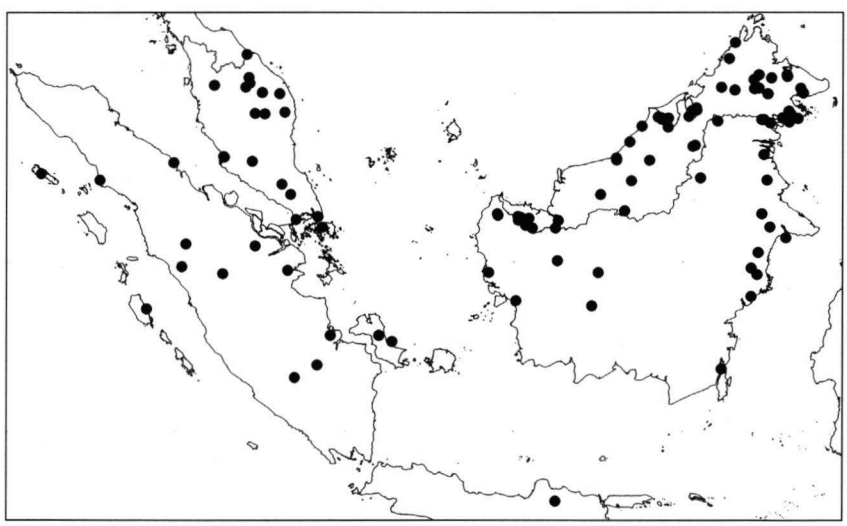


Fig. 3.25. *Baccaurea sumatrana* (Miq.) Müll.Arg. a. Male inflorescence; b. female inflorescence; c. fruit (a: *SAN 15398*; b: *SAN 117460*; c: *SAN 37064*).

to black, 2–16 mm thick, smooth to rather rough, hard, fibrous, peeling off with longitudinal flakes of c. 1 cm long, raised glands present, (exudate watery, red); inner bark white to red brown to pink, 1.5–2 mm thick, fibrous, hard, scaly. *Heartwood* reddish to dark brown. *Leaves*: petiole 5–48 mm long, glabrous; stipules 1–7 by c. 1 mm, sparsely hairy on both sides, densely hairy at midrib outside, margin not ciliate; lamina ovate to sometimes obovate, 3–19 by 1.2–7.5 cm, l/w ratio 1.1–2.9(–3.75), papery; base attenuate to cuneate (to rounded); apex obtuse to acuminate, up to 18 mm long; upper surface glabrous, rarely granulate, a few discoid glands rarely present; lower surface glabrous, a few discoid glands present; green to red when dry, red when young; secondary veins, 5–8(–10) per side, sometimes closed at margin; nervation reticulate. *Staminate inflorescences* axillary to somewhat ramiflorous, solitary (to 3 clustered together), up to 2.3(–5.4) cm long, densely hairy, 30–75-flowered, flowers grouped at upper part of inflorescence; branchlets spatulate, 2–3.8 mm long, densely hairy, with (2 or) 3 (or 4) flowers; bracts 1 per branchlet, c. 1 mm long, glabrous outside. *Staminate flowers* sessile, 0.9–1.8 mm diam., yellow-green; sepals 3–5, each with a different size and shape, 0.3–1.2 by 0.3–1 mm, glabrous; stamens 4–6, 0.4–1 mm long, glabrous; filaments 0.4–0.9 mm long; anthers 0.1–0.15 mm; pistillode ligulate, up to 0.5 mm high, densely hairy. *Pistillate inflorescences* axillary to ramiflorous, solitary (to 4 clustered together), 0.7–6.5(–9) cm long, 1–2 mm thick, densely hairy except at base, 2–20-flowered; pedicel geniculate (90° bent) at the abscission zone, 2.2–2.5 mm long, upper part c. 1.2 mm, densely hairy; bracts absent. *Pistillate flowers* 1.5–2 mm; sepals 4 or 5, ovate to obovate, each with a different size and shape, 0.5–1.3 by 0.5–1.4 mm, densely hairy on both sides; ovary cylindrical, 1.8–2.5 by 1–1.4 mm, 2-locular, sparsely hairy to velutinous; style absent or up to 0.1 mm long; stigmas not lobed to apically lobed up to the base, lobes up to 0.5 mm long, glabrous. *Fruits* ellipsoid, laterally flattened, usually 1-seeded, fleshy capsules, 9–17 by 4–10 mm,



Map 3.39. Distribution of *Baccaurea sumatrana* (Miq.) Müll.Arg. in Thailand, Peninsular Malaysia, Sumatra and Borneo.

dehiscing loculicidally, outside subglabrous, inside glabrous, septa rarely sparsely hairy, yellow to orange to reddish; pedicel straight, 2–8 mm long, upper part 0.5–2 mm; pericarp c. 1 mm thick; column often persistent, 6–12 mm long, curved, flattened; sepals persistent, small. *Seeds* ellipsoid, laterally flattened, 6–9 by 4–7.5 by 2–4 mm; arillode orange; testa red; cotyledons 3.5–6 by 4–6.5 mm, thin; radicle up to 0.8 mm long.

Distribution — Thailand, Peninsular Malaysia, Sumatra, Borneo and (Java).

Habitat & Ecology — Primary and secondary rain forest. Soil: sand or sandy clay. Altitude: sea level up to 1550 m. Flowering: Mar., May to Nov. Fruiting: throughout the year.

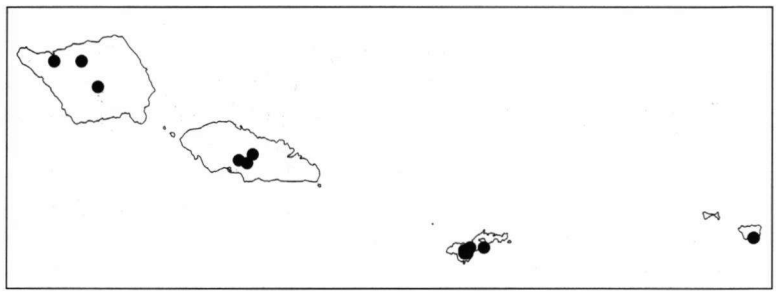
Uses — Used as timber.

Vernacular names — Peninsular Malaysia: Tampoi. Sumatra: Ketjipot, semasam, semasam pris. Sumatra (Banka): Masput (Malay). Sumatra (Simeuluë Island): Toetoen bolawak iteung pajo, toetoen bolawah kèhè-pajo. Borneo: Perepat (Malay); kayu massam, sangkurat.

40. **Baccaurea taitensis** Müll. Arg. — Map 3.40

Baccaurea taitensis Müll. Arg. in DC., Prodr. 15, 2 (1866) 463; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 63; A.C. Sm., Allertonia 1 (1978) 380. — Type: *Wilkes s.n.* (holo US; iso GH, K), Tahiti.

Shrub to tree 3–6 m high, buttresses absent; branchlets glabrous, densely hairy when young, Terminalia branching pattern usually weak. *Indumentum* of simple hairs. *Bark* grey when dry. *Leaves*: petiole 13–60 mm long, subglabrous to sparsely hairy, brown to red-brown to dark grey when dry, raised glands usually present; stipules 2–5 by 0.8–1.5 mm, sparsely hairy to velutinous outside, glabrous inside, margin ciliate, usually not hyaline; lamina obovate to elliptic, 5.4–19 by 3.2–11 cm, l/w ratio 1.1–2.2, papery; base cuneate to rounded; apex retuse to acute, up to 5 mm long; upper surface glabrous, midrib sometimes subglabrous at base, raised glands present, often granulate, (red-) brown when dry; lower surface subglabrous to sparsely hairy, raised glands often present, discoid glands present, (red-)brown when dry; secondary veins 5–9 per side, usually open at margin; nervation reticulate. *Staminate inflorescences* axillary to sometimes ramiflorous, solitary to few clustered together, c. 8 cm long, 0.5–1 mm thick, densely hairy, branches minute, many-flowered, flowers scattered along inflorescence; bracts usually absent; bracteoles 3 per branchlet, 0.7–1 mm long, subglabrous to densely hairy outside, glabrous inside, margin ciliate, sometimes hyaline; branchlets cylindrical to spatulate, 1.5–4.5 mm long, densely hairy, (1–)3- (or 4-)flowered. *Staminate flowers* 2–3 mm diam., white; pedicel 0.2–0.5 mm long, upper part 0.3–0.5 mm long, sparsely to densely hairy; sepals 4–8, ovate to obovate, 1–1.3 by 0.2–1.5 mm, (sub)glabrous outside and inside; stamens 5–9, 0.5–1 mm long, glabrous; filaments 0.1–0.8 mm long, straight; anthers 0.25–0.4 by c. 0.3 by 0.2–0.25 mm; disc absent; pistillode cylindrical, 0.5–1 mm high, densely hairy. *Pistillate inflorescences* axillary to sometimes ramiflorous, few clustered together, few-flowered. *Pistillate flowers*: sepals usually caducous; ovary 2- (or 3-)locular; stigmas persistent. *Infructescences* 1.1–6 cm long, 1–2 mm thick. *Fruits* globose, 2(–4)-seeded, woody berries, 11–16 by 9.5–16 by 9.5–14.5 mm, raised glands present, subglabrous to sparsely hairy outside, glabrous



Map 3.40. Distribution of *Baccaurea taitensis* Müll. Arg. in the Samoan Islands.

inside, septa sparsely to densely hairy, green; pericarp 0.5–1 mm thick; column 11–12 mm long, straight; pedicel 3–8 mm long, upper part 1–2 mm long. *Seeds* globose to ellipsoid, laterally flattened, 10–12 by 5.7–12.7 by 4.5–6.5 mm; arillode orange-yellow; cotyledons sometimes folded, 4.8–6.5 by 8.7–9.5 by c. 0.1 mm; radicle 0.9–1.2 mm long; endosperm thin to 0.25 mm thick.

Distribution — Samoan Islands.

Habitat & Ecology — Altitude: 250–700 m. Flowering: Feb., Mar., Aug., Sept. Fruiting: Feb., Mar., June, July, Oct., Nov.

Vernacular names — Samoa: fua feti'i (see note).

Note — The label of the type specimen indicates Tahiti as collecting locality. Smith (1978) questioned the reliability of the specimen label, because many geographic errors are known to have been made on the U.S. Exploring Expedition labels. I follow his reasoning and do not trust the locality on the type label. Therefore, although the name of the species is *B. taitensis*, it is considered to be a Samoan endemic.

41. **Baccaurea tetrandra** (Baill.) Müll. Arg. — Fig. 3.26, Map 3.41, Photo 12

Baccaurea tetrandra (Baill.) Müll. Arg. in DC., Prodr. 15, 2 (1866) 465; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 49; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 411; Fernando, Philipp. J. Biol. 8 (1979) 307; Airy Shaw, Enum. Euphorb. Philipp. (1983) 10. — *Adenocrepis tetrandra* Baill., Étude Euphorb. (1858) 601; Adansonia 4 (1863) 135. — Type: *Cuming 982* (lecto L, selected here; isolecto P, US), Philippines.

Baccaurea stipulata J.J. Sm., Icon. Bog. 4 (1910) 32, t. 311; Merr., J. Straits Branch Roy. Asiat. Soc. (1921) 331; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 56; Merr., Univ. Calif. Publ. Bot. 15 (1929) 151; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 55; Kew Bull. 36 (1981) 266, syn. nov. — Type: *Hallier 3445* (lecto L, selected here), Borneo, Amai Ambit.

Baccaurea terminalifolia Elmer, Leafl. Philipp. Bot. 4 (1911) 1277. — Type: *Elmer 13089* (lecto DS, selected here; isolecto GH, K, L, US), Philippines, Palawan, Puerta Princesa, Mt Pulgar.

Baccaurea brevipedicellata Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 55; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 54. — Type: *Hose 48* (lecto L, selected here; isolecto K) Borneo, Sarawak, Baram District.

Shrub or tree 2–20 m high, dbh 3–29 cm, sometimes fluted, buttresses absent; branchlets (sub)glabrous, often thickened at tip, Terminalia branching pattern well-developed. *Indumentum* of simple hairs. *Bark* brown to grey to whitish green when fresh, brown to grey when dry, 0.1–2 mm thick, smooth to slightly rough, corky, peeling off in 5–8 long cm strips, soft; inner bark red to purple to brown to yellow to white, c. 1.5

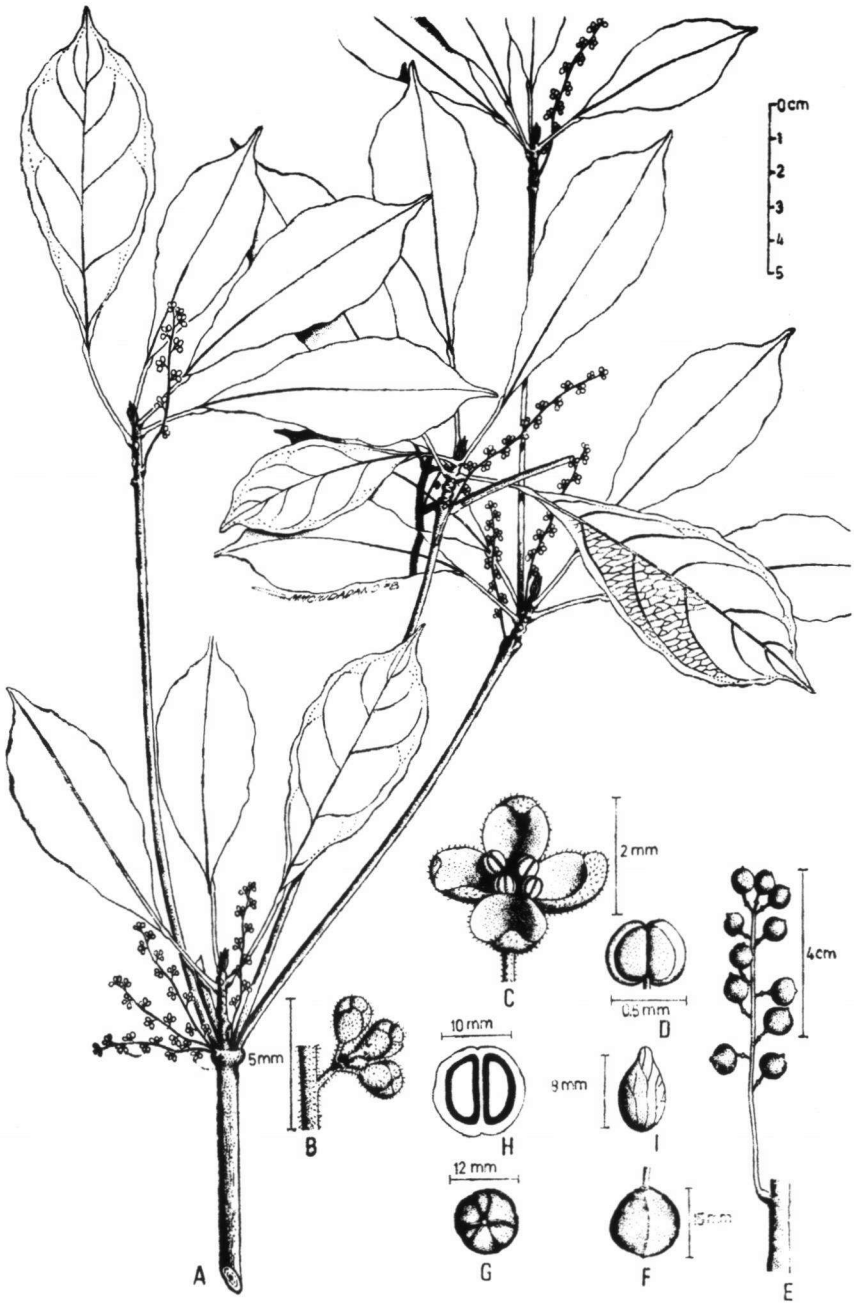
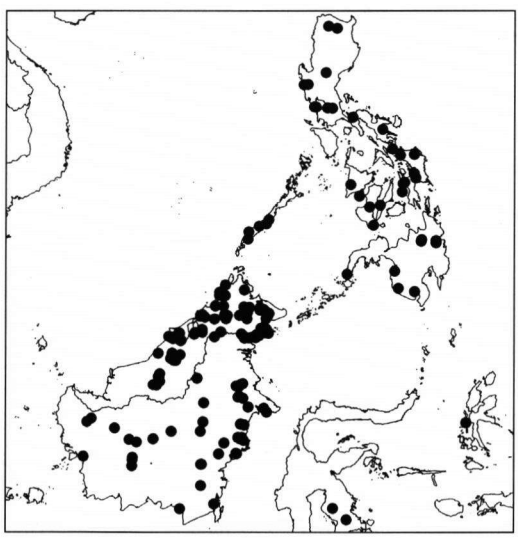


Fig. 3.26. *Baccaurea tetrandra* (Baill.) Müll.Arg. a. Habit with male inflorescence; b. detail of male inflorescence, showing one branchlet; c. male flower; d. anther; e. young infructescence; f. fruit; g. fruit, basal view; h. fruit, transverse section, showing two locules; i. seed [a–d: *Fernando 15*; e: *Sulit 3990*; f–i: *Mendosa 92*. Reproduced from E. S. Fernando in Kalikasan, Philipp. J. Bot. 8: 310, f. 4 (1979)].

mm thick, soft. *Heartwood* brown. *Leaves*: petiole 4–75 mm long, (sub)glabrous, transverse cracks at base and tip, brown to grey when dry, raised glands present; stipules 3–11 by 1.2–4.5 mm, caducous (to late caducous), glabrous to densely hairy outside, glabrous inside, margin often ciliate, sometimes hyaline; lamina obovate to elliptic, (3.2–)5–21 by 1.5–12.3 cm, l/w ratio 1.4–3.4, papery; base rounded to cuneate; apex (retuse to) obtuse to acute, up to 20 mm long; upper surface glabrous, raised glands usually present, often granulate, (light yellow-)green when fresh, (greenish to brownish) white, nervation slightly raised; lower surface glabrous, nervation subglabrous, raised glands usually present, discoid glands absent, light green when fresh, (pale greenish to greyish) brown when dry; secondary veins (2–)4–9 per side, often closed at margin; nervation reticulate to weakly scalariform, white to brown when dry; young leaves red. *Staminate inflorescences* axillary to just below the leaves, solitary to 3(–many) clustered together, 1.5–17 cm long, 0.5–1.5 mm thick, sparsely to densely hairy, many-flowered, flowers scattered along inflorescence, rachis white to red to purple; bracts 1 per branchlet, 0.3–2 mm long, persistent to caducous, glabrous to densely hairy outside, (sub)glabrous inside, margin ciliate, not hyaline; bracteoles (0–)2, up to 1 mm long, subglabrous to densely hairy outside, glabrous inside; branchlets cylindrical, 0–2.5 mm long, densely hairy, 3-flowered. *Staminate flowers* 1.6–4.5 mm diam., yellow to white; pedicel 0.8–3 mm long, upper part 0.3–2 mm long, densely hairy; sepals 4 or 5, spatulate to sometimes ovate, 0.9–3 by 0.6–1.3 mm, sometimes apically recurved, sparsely to densely hairy outside, densely hairy inside; staminodes absent or 4 or 5; stamens (3 or) 4 or 5, 0.6–1.4 mm long, (sub)glabrous; filaments glabrous to subglabrous, 0.5–1.3 mm long, often apically geniculate; anthers 0.15–0.25 by 0.15–0.3 by c. 0.1 mm; pistillode obtriangular to cylindrical, 0.6–1.3 mm high, densely hairy, usually hollow. *Pistillate inflorescences* axillary to just below the leaves (to ramiflorous), solitary to 3 clustered together, 2.5–30 cm long, 0.1–2 mm thick, sparsely to densely hairy, 5–50-flowered, rachis red; pedicel 0.5–7.5 mm long, upper part 0–1.3 mm long, sparsely hairy to densely hairy; bracts (1 or) 3 per branchlet,



Map 3.41. Distribution of *Baccaurea tetrandra* (Baill.) Müll. Arg. in Borneo, Philippines, Sulawesi and Halmahera.

glabrous to densely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 3–12 mm diam., yellow to green (to red); sepals 4–6, obovate to elliptic, 1.5–5.9 by 0.2–2.4 mm, sparsely to densely hairy outside, densely hairy inside, caducous; ovary globose, 1.2–2.4 by 1–2.1 mm, 2-locular, sparsely to densely hairy, pale green; style absent to 0.4 by 0.7–1 mm, densely hairy; stigmas 0.4–1 mm long, cleft for upper up to 90%, white, persistent to caducous; lobes 0.4–0.7 by 0.2–0.7 mm, glabrous with protuberances above, below glabrous to densely hairy with protuberances. *Infructescences* to 45 cm long, purple. *Fruits* globose to ellipsoid, laterally flattened, 1- or 2- or 4-seeded, fleshy capsules, 7–17 by 6.5–15 by 6.5–15 mm, loculicidally dehiscent to irregularly splitting, raised glands sometimes present, glabrous to sparsely hairy outside, glabrous inside, red (to yellow to pink to greenish white); pericarp 0.1–1.5 mm thick; column 8–14 mm long, straight, caducous; pedicel 0.5–8 mm long, upper part 0.2–5.5 mm long, red. *Seeds* globose to obovoid, laterally flattened, 7–13 by 5–9.5 by 3–6.5 mm; arillode blue to purple; testa red; cotyledons often folded, (3–)3.5–7.5 by 4–8.7 by c. 0.1 mm; radicle 0.9–1.8 mm long; endosperm 0.2–1 mm thick.

Distribution — Borneo, Philippines, Sulawesi, Moluccas (Halmahera only).

Habitat & Ecology — Primary and secondary rain forest, and swamp forest. Soil: sand, clay, loam. Altitude: up to 1500 m. Flowering and fruiting: throughout the year. Flowers odourless.

Uses — Arillode edible, sweet to sour.

Vernacular names — Borneo (Brunei): Kunau; mata kunau (Malay). Borneo (Sabah): Kunau-kunau, mata-pelandok. Borneo (Sarawak): Enkuni(k), kunau (Iban); sekunau (Dusun); kuni, mata pelandok. Borneo (Kalimantan): Pundung undang (Dayak); konkuning, mata pelandoeh. Philippines: Katag, saket.

Note — In the type of *B. stipulata* the leaf blades are 13–19 cm long and whitish when dry, whereas in the type of *B. tetrandra* the leaf blades are 6–14 cm long and brown when dry. However, intermediates between these characters are found frequently. The same variability is found in the leaf anatomical characters (Bodegom et al., in prep.). *Baccaurea stipulata* is therefore considered to be conspecific with *B. tetrandra.*

42. **Baccaurea trigonocarpa** Merr. — Fig. 3.27, Map 3.42

Baccaurea trigonocarpa Merr., Univ. Calif. Publ. Bot 15 (1929) 152; Meijer, Bot. News Bull. Forest Dept., Sabah 7 (1967) 38; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 54. — Type: *Elmer 21525* (holo A; iso DS, K, L, US), Borneo, Sabah, Tawau.

Tree or shrub 4–15 m high, dbh 5–38 cm, buttresses absent; branchlets glabrous to rarely densely hairy, Terminalia branching pattern usually weak. *Indumentum* of simple and rarely stellate hairs. *Bark* white-brown to brown to blackish-brown when fresh, brown to grey when dry, thin, smooth; inner bark yellow to rarely yellowish-red to grey. *Leaves*: petiole 10–57 mm long, subglabrous to densely hairy, slightly apically and sometimes slightly basally pulvinate, raised glands sometimes present; stipules lanceolate to triangular, 4–9 by 1–3 mm, glabrous to densely hairy outside, (sub)glabrous inside, margin usually not ciliate, usually not hyaline; lamina obovate to elliptic, 7–16.5 by 3.9–8 cm, l/w ratio 1.7–2.9, papery; base cuneate to attenuate; marginal glands usually visible as small indentations; apex acuminate to cuspidate, 3–18 mm long; upper surface glabrous, rarely granulate, dark green when fresh, dark (green)-

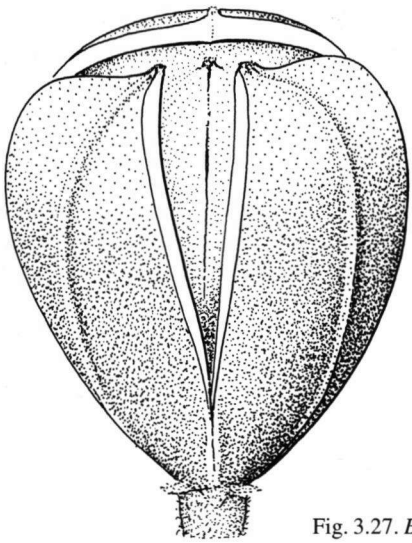
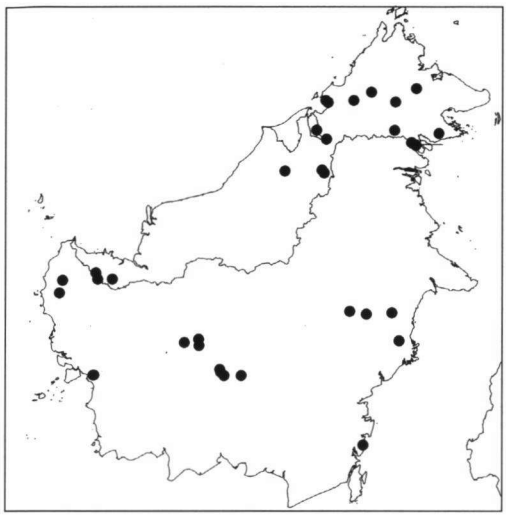


Fig. 3.27. *Baccaurea trigonocarpa* Merr. Fruit (*Veldkamp 8437*).

brown when dry; lower surface (sub)glabrous, glabrous to densely hairy at veins, raised glands usually absent, discoid glands present, sparse to in a row between the secondary veins, dark green when fresh, green to brown when dry; secondary veins 6–10 per side, closed at margin; nervation reticulate to weakly scalariform. *Staminate inflorescences* axillary to just below the leaves, solitary, 1–3 cm long, c. 1 mm thick, densely hairy, many-flowered, flowers clustered at the tip of inflorescence; bracts absent; bracteoles usually 1 per branchlet, c. 1 mm long, densely hairy outside, subglabrous inside, margin ciliate, not hyaline; branchlets cylindrical, c. 1 mm long, densely hairy, 3-flowered. *Staminate flowers* 1–2.2 mm diam., pale yellow, sessile; sepals (5 or) 6, obovate, 0.5–1 by 0.4–0.8 mm, apically straight, densely hairy outside and inside; stamens 6, 0.9–1 mm long, glabrous; filaments c. 0.9 mm long, straight; anthers c. 0.1 by 0.2 by 0.1 mm; pistillode obtriangular, c. 0.5 mm high, velutinous, solid. *Pistillate inflorescences* usually ramiflorous (to axillary or cauline), solitary (to 4 clustered together), 1.5–3 cm long, c. 1 mm thick, densely hairy, 7–many-flowered; pedicel 1–1.5 mm long, upper part 0.2–0.5 mm long, geniculate (90° bent), densely hairy; bracts (1–)3 per branchlet, persistent, glabrous to densely hairy outside, densely hairy inside, margin ciliate. *Pistillate flowers* 1–2 mm diam., yellow; sepals (5 or) 6, 0.5–1.2 by 0.2–0.9 mm, ovate, densely hairy outside and inside, persistent; ovary globose, 1–1.4 by 0.7–0.9 mm, (2- or) 3- or 4-locular, velutinous, wings usually present, 6 or 8, small; style absent; stigmas c. 0.5 mm long, glabrous, persistent. *Infructescences* 4–50 cm long, 1–2 mm thick. *Fruits* 3- or 4-angular (to globose), 1- or 2-seeded, fleshy capsules, 8–15 by 9–14.5 by 9–14.5 mm, dehiscing loculicidally, raised glands usually absent, (sub)glabrous outside, glabrous inside, subglabrous at column, yellow to orange to purple; pericarp 0.5–1.5(–2) mm thick; column 7–11 mm long, straight, sometimes caducous; pedicel 4–10(–17) mm long, upper part 0.5–3 mm long. *Seeds* globose to ellipsoid, laterally flattened, 6.2–9 by 6–8 by 3.5–5 mm; arillode orange to purple to reddish; testa white; cotyledons 5–7 by 5.5–7 by 0.1–1; radicle 0.1–0.2 mm long; endosperm thin.



Map 3.42. Distribution of *Baccaurea trigonocarpa* Merr. in Borneo.

Distribution — Borneo, Singapore but probably only in cultivation.

Habitat & Ecology — Primary rain forest and kerangas forest. Soil: sand, clay, loam. Altitude: 30–1200 m. Flowering: June, Aug., Sept. Fruiting: Jan., Apr. to Nov.

Uses — Firewood.

Vernacular names — Borneo: Engkuhi (Iban); tikak cabo (Murut); butoh pranuk, ngiboruok, ombak pahung, pugé laboh, rambai hutan.

43. **Baccaurea velutina** (Ridl.) Ridl. — Map 3.43

Baccaurea velutina (Ridl.) Ridl., J. Bot. 62 (1924) 300; Fl. Malay Penins. 5 (1925) 331; Whitmore, Tree Fl. Malaya 2 (1973) 67. — *Baccaurea reticulata* Hook.f. var. *velutina* Ridl., Fl. Malay Penins. 3 (1924) 246; Smitinand, Nat. Hist. Bull. Siam Soc. 22 (1967) 170. — Type: *Burkill HMB.11319* (lecto K, selected here; isolecto A, SING).

Shrub or tree (2.1–)9–15(–18) m high, dbh 6.4–24 cm, buttresses absent; branchlets sparsely hairy to velutinous; young shoots pale to red-brown when dry, Terminalia branching pattern well-developed. *Indumentum* of stellate and simple hairs. *Bark* brown to grey-brown to orange-brown when fresh, smooth; inner bark red to brown, thin, fibrous. *Leaves*: petiole 18–80 mm long, velutinous with long and short hairs, often with longitudinal cracks when old, light to blackish brown when dry, raised glands or lenticels often present; stipules 3–7 by 1.5–3 mm, velutinous outside, glabrous inside, margin ciliate, not hyaline; lamina ovate to obovate, 5.2–19.3 by 3.5–11.2 cm, l/w ratio 1.4–2.8, papery to somewhat leathery; base cuneate to attenuate (to rounded); apex rounded to acuminate, up to 11 mm long; upper surface glabrous, raised glands present, sometimes granulate, (dark to grey)-brown when dry; lower surface subglabrous to sparsely hairy, nervation sparsely hairy to velutinous, raised glands present, discoid glands present, hairy, if many then in a row between secondary veins, brown when dry; secondary veins 5–7 per side, usually open at margin; nervation reticulate; young leaves yellowish brown when fresh. *Staminate inflorescences* axillary, solitary

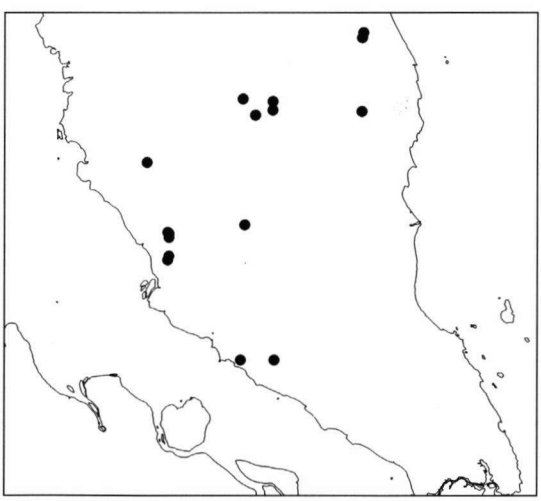
or in pairs, 2.5–9 cm long, rachis 1–1.8 mm thick, branches minute, velutinous, many-flowered, flowers scattered along inflorescence; bracts 1 per branchlet, 4–7.3 mm long, densely hairy outside, (sub)glabrous inside, margin ciliate, not hyaline; bracteoles 4(–8), small; branchlets, cylindrical, 0.5–1 mm long, velutinous, 4–12-flowered. *Staminate flowers* 2.5–5 mm diam., yellow to brown; pedicel 0.5–1.3 mm long, upper part 0.2–0.9 mm long, velutinous; sepals 4 (or 5), ovate, 1.8–4 by 1–1.8 mm, recurved to straight at apex, velutinous outside and inside; stamens 5 or 6, 0.3–0.9 mm long, glabrous; filaments 0.1–0.7 mm long, straight; anthers 0.15–0.2 by 0.2–0.25 by 0.1–1.15 mm; disc absent; pistillode cylindrical to obtriangular, 0.6–1.3 mm high, velutinous. *Pistillate inflorescences* axillary, solitary, 2.5–5.5 cm long, 1.2–1.5 mm thick, velutinous, few-flowered; pedicel 1.5–3.5 mm long, upper part 0.5–2 mm long, velutinous; bracts 2 per branchlet, ovate, velutinous outside, glabrous inside, margin ciliate. *Pistillate flowers* 5–10 mm diam., yellow; sepals 4 (and a small 5th), ovate, (3–)6–10 by (1–)2–3 mm, velutinous outside and inside, persistent to caducous; ovary cylindrical, 2.5–4 by c. 2.5 mm, 3-locular, velutinous, dark brown; style 0.5–1 by 1–1.5 mm, white velvety; stigmas 1.2–2.2 mm long, cleft for upper c. 50%, persistent and up to 3 mm long; lobes 0.6–1.1 by 0.2–0.4 mm, glabrous above, velutinous below. *Fruits* globose, 2–6-seeded, berries to fleshy capsules, 23–28 by 25–31 by 25–31 mm, 2.5 cm diam. when fresh, usually only 1 layer dehiscing loculicidally when dry, raised glands present, (slightly) ruminate when dry, velutinous outside, (sub)glabrous inside, septa subglabrous, (red-)brown; pericarp 3–7.5 mm thick; column 15–17 mm long, straight; pedicel 4–5 mm long, upper part 2–3 mm long. *Seeds* ellipsoid, laterally flattened, 7.5–10 by 4.6–8 by 3–5 mm; arillode yellow to orange; cotyledons 5.2–6 by 5–6.9 by 0.1–0.5 mm; radicle 1–1.5 mm long.

Distribution — Peninsular Malaysia.

Habitat & Ecology — Rain forest, on ridges, rarely in swamps. Altitude: 330–1450 m. Flowering: Apr., Aug., Sept. Fruiting: Feb. to May, Sept.

Uses — Arillode edible, sour.

Vernacular names — Peninsular Malaysia: Tampoi, tampoy tungau.



Map 3.43. Distribution of *Baccaurea velutina* (Ridl.) Ridl. in Peninsular Malaysia.

3.2.5 – *Species dubiae*

No original material of the following taxa could be traced or obtained so that their taxonomic status could not be evaluated.

1. *Baccaurea airyshawii* Chakrab. & Gang., J. Econ. Taxon. Bot. 18 (1994) 419. — Type: *Kunstler 1408* (holo CAL, n.v.).
2. *Baccaurea celebica* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 69; Airy Shaw, Kew Bull. 37 (1982) 8. — Type: *Warburg 15565* (n.v.).
3. *Baccaurea henii* Thin, J. Biol. (Vietnam) 9, 2 (1987) 37. — Type: *Duong van Hen s.n.* (holo HM, n.v.).
4. *Pierardia macrostachys* Wight & Arn., Icon. Pl. Ind. Orient. (1852) 30; Baill., Adansonia 3 (1863) 140. — Type: *Wight* (lecto plate 1912 in Wight & Arn., Icon. Pl. Ind. Orient. (1852) 28, selected here).

   Hooker (1885) has considered this name a synonym of *B. sapida* (= *B. ramiflora).* The original description and plate of *B. macrostachys* are, however, not congruent with Hooker's description of *B. sapida.* The original description and plate of *B. macrostachys* are also incongruent with the modern description of *B. ramiflora* (see no. 34). In *B. macrostachys* (5–)8–10 stamina are present, whereas *B. ramiflora* has 5–8 stamina. In my opinion, the plant with staminate inflorescences depicted in Wight & Arn. (1852: plate 1912) is a true *Baccaurea*, but is maybe not conspecific with *B. ramiflora.* The drawing is too crude to establish the exact identity of the depicted plant. Two oddities appear in the description and on plate 1913 (Wight & Arn., 1852) of the plant with pistillate inflorescences and infructescence: the seed has no arillode; the leaves are opposite (but Wight & Arn. were not sure if the leaves belonged to the fruits). For these reasons it is extremely questionable if the female plant is a *Baccaurea.* The plate with the staminate flowers is therefore chosen as lectotype.
5. *Baccaurea reniformis* Chakrab. & Gang., J. Econ. Taxon. Bot. 19 (1995) 449. — Type: *King's Collector 10196* (holo CAL, n.v.).

3.2.6 – *Excluded names*

1. *Baccaurea cavaleriei* H. Lév., Fl. Kouy-Tchéou (1914) 158; Rehder, J. Arnold Arbor. 18 (1937) 281; Airy Shaw, Kew Bull. 19 (1965) 314. — Type: *Cavalerie 3299* (holo E), China, Kweichow, Lo Fou. = **Cleidiocarpon cavaleriei** (H. Lév.) Airy Shaw.
2. *Baccaurea esquirolii* H. Lév., Fl. Kouy-Tchéou (1914) 158; Rehder, J. Arnold Arbor. 18 (1937) 281. — Type: *Cavalerie 3458* (lecto A, selected here), China, Nom-You-Se-Ki-Fou. = **Sapium rotundifolium** Hemsl.

3.3 – **Distichirhops** Haegens, *gen. nov.*

3.3.1 – *Genus description*

> Aporosae similis, ramulis foliisque non in architecturae Terminaliae modo dispositis, foliis distichis, pedicellis articulatis, disci feminei absentia differt. — Typus: *Distichirhops mitsemosik* Haegens.

Shrub to tree, dioecious, Terminalia branching pattern absent. *Indumentum* of simple hairs. *Bark* finely fissured. *Leaves* simple, alternate, distichous; petiole apically pulvinate, transverse cracks often present; stipules triangular, caducous, ciliate; blade: base rounded to attenuate; margin entire, marginal glands present; apex acuminate to cuspidate; upper surface glabrous, sometimes densely hairy on veins, raised glands often present, sometimes granulate; lower surface sparsely to densely hairy, raised glands often present, discoid glands absent; nervation raised, secondary veins curved. *Inflorescences* axillary to cauline, reduced thyrses, solitary to few clustered together; flowers hypogynous, actinomorphic; pedicel with abscission zone. *Staminate inflorescences* unknown. *Pistillate inflorescences* not branched, 5–10-flowered; bracts inserted on rachis, 3 per flower, triangular. *Pistillate flowers* 1.5–2 mm diam.; sepals 4 or 5, caducous to persistent; petals absent; staminodes absent; disc absent; ovary cylindrical to globose, 2–4-locular, ovules 2 per locule, attached at apex of column, wings usually absent; stigmas not cleft to completely so; protuberances often present. *Fruits* 0–4-seeded berries to late dehiscing fleshy capsules; raised glands often present; arillode enclosing seed totally.

Distribution — Three species in Borneo and New Guinea.

Habitat & Ecology — Secondary forest. Soil: clay. Altitude: sea level up to 350 (–1980 m). Flowering: June, Aug. Fruiting: Apr., July, Aug., Oct.

Notes — 1. *Distichirhops* is a poorly known genus. It closely resembles *Aporosa*. However, as long as the staminate inflorescences of *Distichirhops* remain unknown, it is desirable to understand it as a distinct genus within the subtribe Scepinae. *Distichirhops* differs from *Baccaurea*, *Nothobaccaurea*, and *Maesobotrya* in the following characters: absence of the Terminalia branching pattern; distichous (not spiral) arrangement of the leaves. The main differences between *Distichirhops* and *Aporosa* are: three instead of one bract per pistillate flower; absence of the small pistillate disc present in *Aporosa*; presence of an abscission zone in the pedicel. Furthermore, all species have character combinations that are absent in *Aporosa*

2. This genus is named for its distichous leaf arrangement and shrubby habit (the Greek word distichos = in two rows; the Greek word rhopo = shrub).

3.3.2 – *Key to the species of Distichirhops*

1a. Leaves glabrous above 2
b. Leaves sparsely to densely hairy above ..... **1. D. megale**
2a. Petioles glabrous to subglabrous. Leaf lamina ovate, leathery, glabrous to subglabrous below ..... **3. D. mitsemosik**
b. Petioles very hairy. Leaf lamina elliptic to obovate, papery to slightly leathery, sparsely to densely hairy below ..... **2. D. minor**

3.3.3 – *Species descriptions*

1. Distichirhops megale Haegens, *spec. nov.* — Fig. 3.28, Map 3.44

Speciebus alioribus foliis supra pubescentibus, fructibus grandis c. 4 cm diam., pericarpio comparate tenui differt. — Typus: *NGF (Streimann & Katik) 28659* (holo L), New Guinea, Milne Bay Prov., Junction Ugat and Mayu Rivers, near Mayu I.

Tree c. 10 m high, dbh c. 8 cm, branchlets velutinous. *Leaves*: petiole 4–12 mm long, velutinous, raised glands absent; stipules 2–3.5 by c. 1 mm, densely hairy outside, glabrous inside, not hyaline; lamina elliptic, 12–15.7 by 5.3–6.8 cm, l/w ratio 1.9–2.7, slightly leathery; base attenuate to cuneate; marginal glands present as small indentations; apex obtuse to cuspidate, (0–)14 mm long; upper surface sparsely hairy, velutinous at veins, small raised glands present, granulate, dull green when fresh, nervation not to slightly raised; lower surface glabrous, densely hairy on veins, discoid glands absent, green when fresh; secondary veins 7–10 per side, closed at margin;

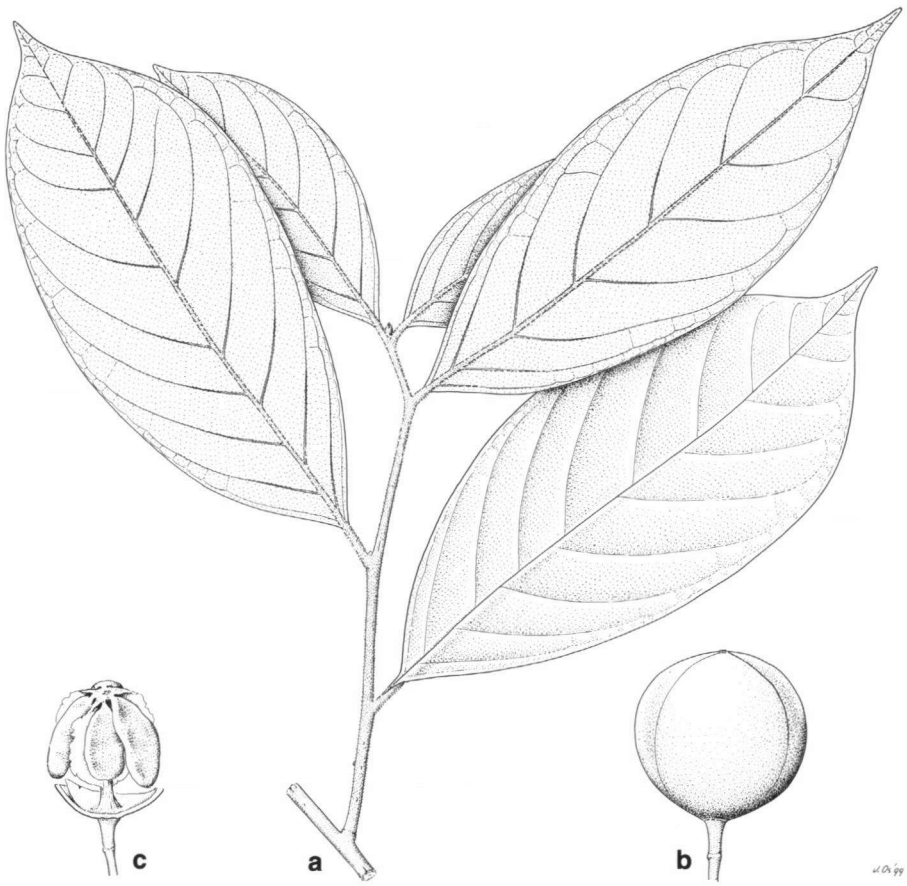
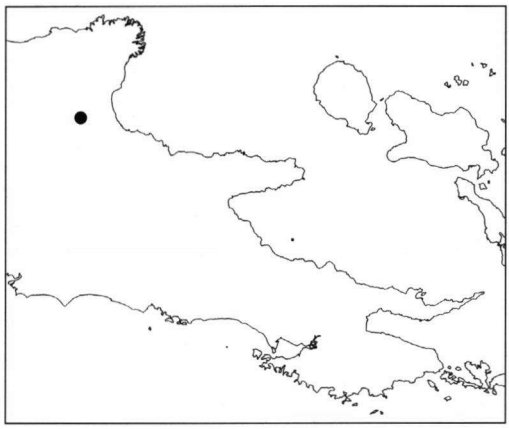


Fig. 3.28. *Distichirhops megale* Haegens. a. Habit; b. fruit; c. dissected fruit with seeds (*NGF 28659*).



Map 3.44. Distribution of *Distichirhops megale* Haegens in Papua New Guinea.

nervation reticulate to weakly scalariform. *Staminate inflorescences* unknown. *Pistillate inflorescences* cauline. *Pistillate flowers*: sepals caducous; ovary 3-locular. *Fruits* globose, 3-seeded, fleshy capsules, c. 40 by 40 by 40 mm, irregularly dehiscent, slightly ruminate when dry, raised glands present, sparsely hairy outside, glabrous inside; septa subglabrous, dark brown; pericarp 2.5–3 mm thick, inner layer up to 0.1 mm thick; column 34–38 mm long, straight, persistent; pedicel c. 20 mm long, slightly thickened at abscission zone, upper part 6–12 mm long. *Seeds* globose, laterally flattened, 25–30 by 13–29 by 5–10 mm; arillode yellow; cotyledons 12–13 by 16–17 by c. 0.1 mm; radicle 4–4.5 mm long; endosperm c. 1.5 mm.

Distribution — Papua New Guinea, Milne Bay Prov.

Habitat & Ecology — Altitude c. 350 m.

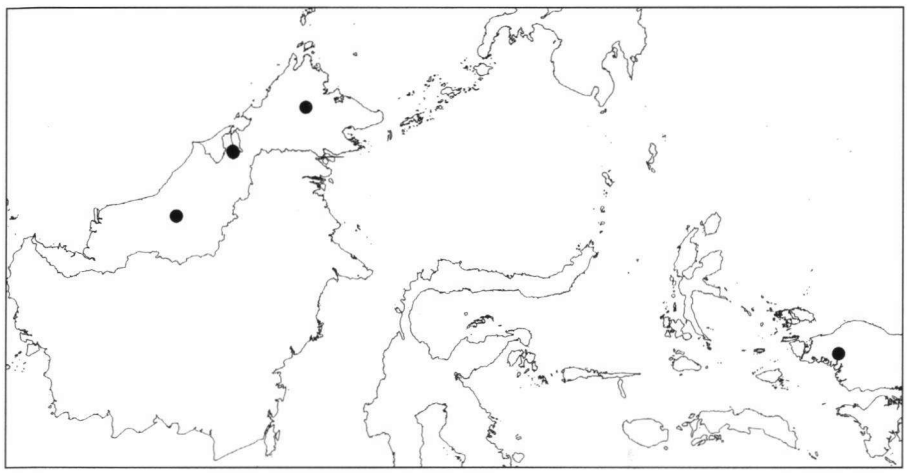
Notes — 1. The species is named for its big fruits (the Greek word megas = big).

2. Only known from the type specimen.

2. Distichirhops minor Haegens, *spec. nov.* — Map 3.45

> Haec species foliis relative minutis ellipticis ad obovatis papyraceis ad leniter coriaceis 6–13.5 cm longis, supra glabris, infra dense pubescentibus, fructibus quoque minutis 4.5–8.5 mm diam. notata. — Typus: *SAN (Sigin et al.) 99863* (holo L; iso K), Malaysia, Sabah, Ulu sungei Padau Madau.

Tree 4–15 m high, dbh 2.5–10.2 cm, buttresses absent; branchlets subglabrous to densely hairy. *Bark* pale brown to grey when fresh, smooth; inner bark (pale) brown. *Sapwood* pale yellow to pale brown. *Leaves*: petiole 3.5–8(–11 in New Guinea) mm long, velutinous, transverse cracks present when old, dark to grey-brown when dry, blackish in New Guinea, raised glands rare; stipules triangular to lanceolate, 2–7.5 by 0.4–0.8 mm, sparsely to densely hairy outside, inside subglabrous, densely hairy at base; lamina obovate to elliptic, 6–13.5 by 1.5–4.5 cm, l/w ratio 2.3–3.8, papery to slightly leathery; base rounded to attenuate; apex acuminate to cuspidate, 4–25 mm long; upper surface glabrous, usually granulate, raised glands usually present; lower surface glabrous to sparsely hairy, velutinous on veins, discoid glands absent, raised glands usually present; grey to brown above, pale brown to green-brown below when



Map 3.45. Distribution of *Distichirhops minor* Haegens in Borneo and Irian Jaya.

dry; nervation whitish to grey to (dark) brown when dry; secondary veins 4–7 per side, looped and closed at margin (or ending open in New Guinea); nervation reticulate. *Staminate inflorescences* unknown. *Pistillate inflorescences* axillary to just below the leaves, solitary to 5 clustered together, 0.5–4.5 cm long, 0.5–1 mm thick, densely hairy to velutinous, 5–10-flowered, red; pedicel 1–3 mm long, abscission absent, densely hairy; bracts 3 per flower (1 large, 2 small), subglabrous to sparsely hairy outside, (sub)glabrous inside, margin ciliate. *Pistillate flowers* 1.5–2 mm diam.; sepals 4 or 5, ovate to triangular, 0.2–0.4 by 0.2–0.3 mm, subglabrous to sparsely hairy outside, (sub)glabrous inside, persistent; ovary globose to cylindrical, 1.5–2 by 1.3–1.7 mm, 2-locular, sparsely hairy (densely hairy at base); style absent; stigmas 0.4–0.5 mm long, cleft for upper 50–100%, persistent; lobes 0.3–0.4 by 0.3–0.4 mm, glabrous above, (sub)glabrous below, protuberances small, on both sides. *Fruits* globose to ellipsoid, laterally flattened, 0–2-seeded fleshy capsules, 9.6–10.5 by 5.5–7.4 by 4.5–8.5, dehiscing loculicidally, glabrous on both sides, subglabrous when young outside, raised glands absent; pericarp 0.6–1.3 mm thick; column 8–9 mm long, straight. *Seeds* ellipsoid, laterally flattened, c. 7 by 5.1 by 3.5 mm; cotyledons c. 5 by 0.5 by 0.1 mm.

Distribution — Borneo, Irian Jaya (Vogelkop).

Habitat & Ecology — Secondary forest. Altitude: 10–200 m. Flowering: June, Aug. Fruiting: Apr., Aug., Oct.

Note — The species is named for the small size of the leaves and fruits.

Specimens studied: *BW 4933*; *S 43466*; *SAN 99863* (type); *Wong Khoon Meng 1190, 1974.*

3. **Distichirhops mitsemosik** Haegens, *spec. nov.* — Fig. 3.29, Map 3.46

Haec species alioribus petiolis brevibus 5–18 mm longis (sub)glabris, foliis ovatis, supra glabris, infra (sub)glabris differt. In zona medio-montana (c. 1980 m altitude) habitat. — Typus: *LAE (Stevens) 55701* (holo L; iso LAE), New Guinea, Scarp of Tantam Plateau, overlooking Mayu River, Mt Suckling.

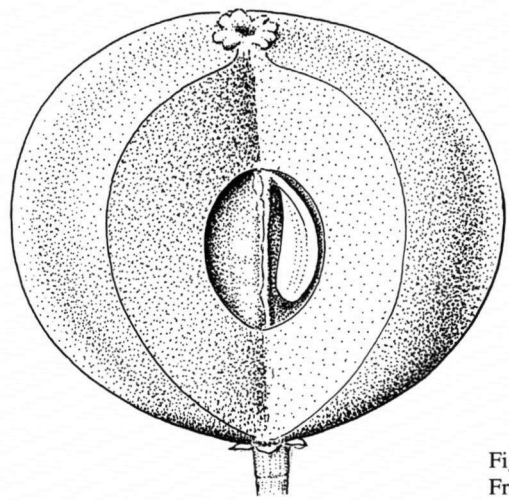
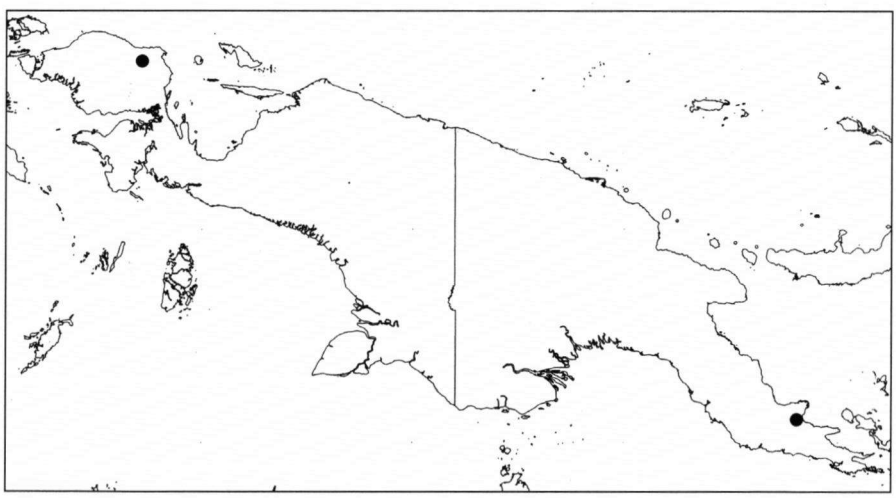


Fig. 3.29. *Distichirhops mitsemosik* Haegens. Fruit (*LAE 55701*).

Shrub to tree 2–10 m high; branchlets glabrous. *Bark* grey-brown when fresh; inner bark red. *Sapwood* pale yellowish. *Leaves*: petiole 5–18 mm long, (sub)glabrous, transverse cracks present, raised glands present; stipules caducous; lamina ovate, 10.5–14 by 3.8–6.2 cm, l/w ratio 1.8–2.8, leathery; base attenuate; margin lowly undulated; apex acute, c. 7 mm long; upper surface glabrous, small raised glands present, not granulate, dull green when fresh, grey-green when dry, nervation not to slightly raised; lower surface (sub)glabrous, small raised glands present, discoid glands absent, shiny green when fresh, light brown when dry; secondary veins 5–7 per side, almost closed at margin; nervation reticulate. *Staminate inflorescences* unknown. *Pistillate flowers*: sepals persistent; ovary 3- or 4-locular; stigmas persistent. *Fruits* globose, 3- or 4-seeded berries, 31–33 by 33–35 by 33–35 mm, few raised glands present, glabrous



Map 3.46. Distribution of *Distichirhops mitsemosik* Haegens in Papua New Guinea.

outside and inside; septa subglabrous to sparsely hairy, yellowish; pericarp 9–13 mm thick, not dehiscent; column c. 19 mm long, straight; pedicel, upper part c. 2 mm long. *Seeds* ellipsoid, laterally flattened, c. 8 by 5.5 by 2.5 mm.

Distribution — Papua New Guinea: Milne Bay Prov.

Habitat & Ecology — Mixed montane forest. Altitude: c. 1980 m. Fruiting: July.

Vernacular names — Papua New Guinea: Mitsemosik (Hattam).

Note — The species is named for its vernacular name 'Mitsemosik' in the Hattam Language.

Specimens studied: *BW 12623*; *Hartley 12711*; *LAE 55701* (type).

3.4 – **Nothobaccaurea** Haegens, *gen. nov.*

3.4.1 – *Genus description*

> Baccaureae et Maesobotryae fide methodi cladistici nullo dubio proxima, praecipue sepalis basaliter connatis, staminibus multo longioribus, pistillodiis glabris differt. Ramuli foliaque in architecturae Terminaliae modo dispositi, inflorescentiae masculae (sub)-glabrae, stamina sepalis multo longiora. — Typus: *Nothobaccaurea stylaris* (Müll. Arg.) Haegens.

Shrub to tree, dioecious, Terminalia branching pattern present. *Indumentum* of simple hairs. *Bark* finely fissured. *Leaves* simple, alternate to opposite, spirally arranged; petiole apically pulvinate; stipules triangular or foliaceous, caducous, often ciliate; lamina: base rounded to attenuate; margin entire, marginal glands present; apex usually retuse to cuspidate; upper surface (sub)glabrous, raised glands often present, sometimes granulate; lower surface glabrous to sparsely hairy, raised glands often present, discoid glands present, nervation raised; secondary veins curved, usually closed at margin. *Inflorescences* axillary to ramiflorous to rarely cauline, reduced thyrses, solitary to many clustered together; flowers hypogynous, actinomorphic; pedicel with or without abscission zone. *Staminate inflorescences* distinctly branched, many-flowered, flowers scattered along inflorescence; bracts triangular to ovate; branchlets 1–5-flowered. *Staminate flowers* 1–2.5 mm diam.; sepals 3–7, fused at base; petals absent; disc absent; stamens 5–7, longer than sepals, glabrous; anthers basifixed to dorsifixed, opening with an apical slit; staminodes or disc glands absent; pistillode present, small, glabrous. *Pistillate inflorescences* not branched, few to many-flowered; bracts inserted on rachis and along pedicel, 1–2 per flower, triangular. *Pistillate flowers* 0.8–2 mm diam.; sepals 5 or 6, slightly imbricate, persistent; petals absent; staminodes present, c. 7; disc absent; ovary ovoid, 2-locular, ovules 2 per locule, attached at apex of column, wings absent; stigmas apically cleft, almost completely divided into 2 lobes; protuberances present. *Fruits* 1- (or 2-)seeded late dehiscing fleshy capsules, raised glands present; arillode enclosing seed totally.

Distribution — Two species in the Pacific.

Habitat & Ecology — Primary or secondary rain forest. Altitude: sea level up to 1100 m, usually in lowland. Flowering and fruiting throughout the year.

Notes — 1. *Nothobaccaurea* closely resembles *Baccaurea* and *Maesobotrya*. It is also placed within the subtribe Scepinae. *Nothobaccaurea* differs in a reasonable number of characters from *Baccaurea*: the sepals of the staminate flowers are fused at

base, whereas in *Baccaurea* they are free; the stamens are longer than the sepals; the presence of staminodes, which is a very rare feature in *Baccaurea* (*B. lanceolata*); the stipules are usually foliaceous, instead of triangular. The differences between *Nothobaccaurea* and the African genus *Maesobotrya* are less profound: pistillode glabrous in *Nothobaccaurea*, hairy in *Maesobotrya*; staminodes absent in *Nothobaccaurea*, present in *Maesobotrya*; stigmatic lobes with protuberances in *Nothobaccaurea*, without protuberances in *Maesobotrya*; anthers purple in *Nothobaccaurea*, yellow in *Maesobotrya*; somewhat longer anthers in *Nothobaccaurea*. Because of these differences and the enormous gap in distribution, *Nothobaccaurea* is treated here as a genus distinct from *Maesobotrya*.

2. The genus is named for its false resemblance with *Baccaurea*.

3.4.2 – *Key to the species of Nothobaccaurea*

1a. Stipules with petioles, 5–14 mm long (petiole included). Leaves spirally arranged. Fruits indehiscent ..... **1. N. pulvinata**

b. Stipules sessile, 1–4.5 mm long. Leaves spirally arranged to opposite. Fruits loculicidally dehiscent ..... **2. N. stylaris**

3.4.3 – *Species descriptions*

1. Nothobaccaurea pulvinata (A.C. Sm.) Haegens, *comb. nov.* —
Fig. 3.30, Map 3.47

Baccaurea pulvinata A.C. Sm., Allertonia 1 (1978) 386. — Type: *O. Degener 14905* (holo A; iso BISH, K), Fiji, Nandroga & Navosa Prov.

Tree 4–10.5 m high, dbh 6–8 cm, buttresses absent; branchlets glabrous to sparsely hairy; young shoots (pale to red)-brown when dry, Terminalia branching pattern weakly developed. *Bark* pale grey when dry, 1 mm thick. *Leaves*: petiole 11–47 mm long, sparsely hairy, red to grey-brown when dry, small raised glands often present; stipules leaf-like, 5–14 by 2.5–7.5 mm, glabrous to sparsely hairy (densely hairy when young) outside, midrib glabrous to densely hairy, (sub)glabrous inside, margin (slightly) ciliate, not hyaline; lamina: elliptic to obovate, 7–18.3 by 4.7–10.6 cm, l/w ratio 1.4–2.0, (thick) papery to slightly leathery; base rounded to attenuate; apex obtuse to acuminate, up to 12 mm long; upper surface glabrous, midrib (sub)glabrous, raised glands often present, often granulate, (dark to red to green)-brown when dry, nervation (pale to red)-brown when dry; lower surface glabrous, veins (sub)glabrous, raised glands often present, discoid glands many present (not precisely circular in appearance), (green)-brown when dry; secondary veins 5–9 per side, almost closed at margin; nervation reticulate, (pale to red)-brown when dry. *Staminate inflorescences* axillary to ramiflorous (to cauline), solitary to many clustered together, 1–5 cm long, 0.2–0.5 mm thick, branches minute, glabrous to sparsely hairy, dark to pink-red; bracts 1 per branchlet, ovate, 0.9–1.5 mm long, glabrous to subglabrous outside and inside, margin (slightly) ciliate, often hyaline; bracteoles absent; branchlets absent to 0.3 mm long, subglabrous, c. 3-flowered. *Staminate flowers* 1.5–2.5 mm diam., (dark to pink)-red; pedicel 1–2.2 mm long, upper part c. 2.2 mm long, (sub)glabrous; sepals slightly

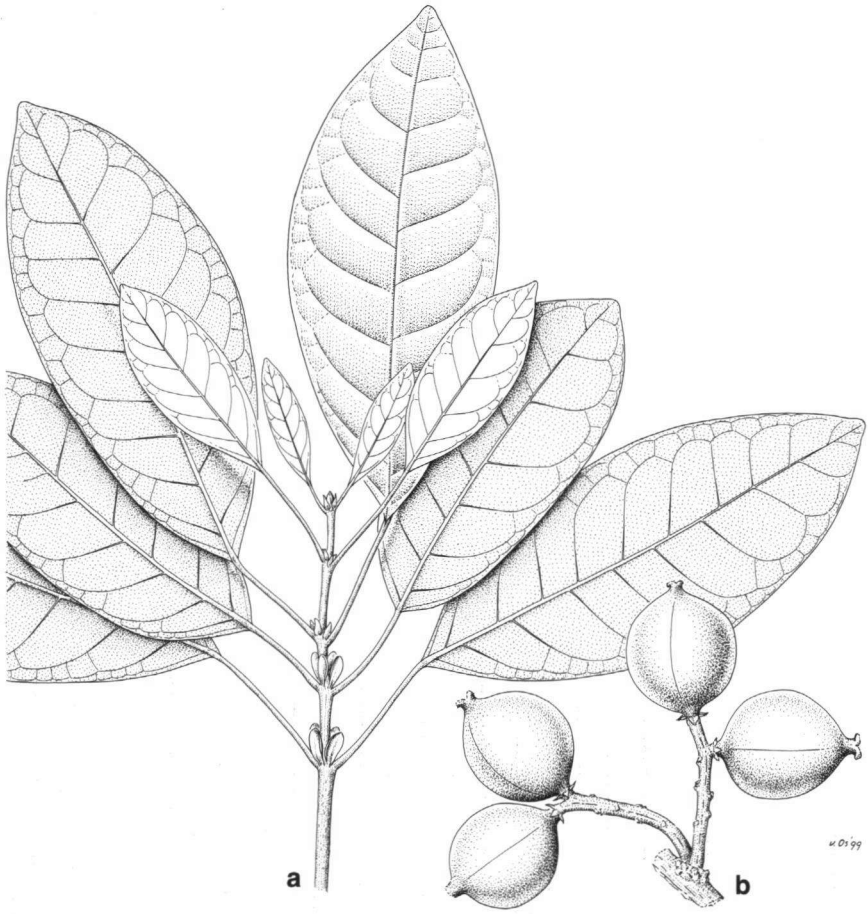
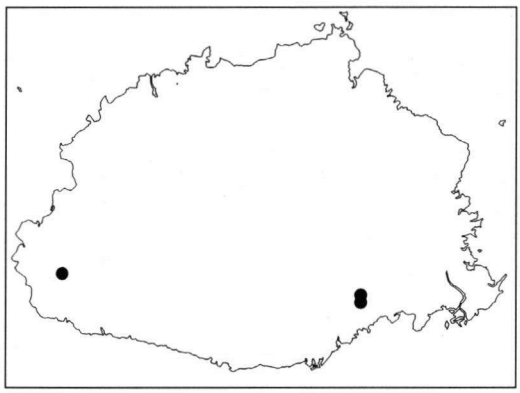


Fig. 3.30. *Nothobaccaurea pulvinata* (A.C. Sm.) Haegens. a. Habit; b. infructescences (*Gillespie 2409*).

imbricate, 5–7, fused at base, ovate, 0.5–1.4 by 0.2–1.3 mm, (sub)glabrous outside, glabrous inside, translucent brown to pinkish when dry; stamens 6 or 7, 1.4–2.3 mm long, glabrous; filaments 1–1.9 mm long, straight; anthers 0.25–0.4 by 0.3–0.6 by 0.15–0.25 mm; pistillode cylindrical, 0.3–0.5 mm high, glabrous, usually hollow. *Pistillate inflorescences* axillary to ramiflorous, solitary to few clustered together, 10–20-flowered; bracts persistent. *Pistillate flowers*: sepals 4–6, persistent; stigmas persistent. *Infructescences* 1–4 cm long, 0.5–1.2 mm thick. *Fruits* globose to ovoid, 1-seeded berries, 7–10 by 6–6.3 by 6–6.3 mm, raised glands present, glabrous outside and inside, red to green-pink; pericarp 0.6–0.8 mm thick; column c. 6 mm long, curved; pedicel 1–4 mm long, upper part 0.2–0.6 mm long. *Seeds* globose, 4.3–5.2 by 4–5 by 4–4.6 mm; cotyledons c. 3 by 3 by 0.1 mm; endosperm 0.5–1 thick.

Distribution — Fiji.

Habitat & Ecology — Rain forest. Altitude: sea level up to 750 m. Flowering: Jan., Mar., Nov. Fruiting: Apr., May.



Map 3.47. Distribution of *Nothobaccaurea pulvinata* (A.C. Sm.) Haegens in Fiji.

2. Nothobaccaurea stylaris (Müll.Arg.) Haegens, *comb. nov.* — Fig. 3.31, Map 3.48

Baccaurea stylaris Müll.Arg. in DC., Prodr. 15, 2 (1866) 465; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 46; A.C. Sm., Allertonia 1 (1978) 383. — Type: *Wilkes 75126* (lecto US, selected here; isolecto GH, K), Fiji .

Baccaurea obtusa A.C. Sm., Bernice P. Bishop Mus. Bull. 141 (1936) 84. — Type: *A. C. Smith 420* (lecto US, selected here; isolecto GH), Fiji, Vanua levu, Thakaundrove, Mt Mariko.

Baccaurea sanctae-crucis Airy Shaw, Kew Bull. 35 (1980) 383, syn. nov. — Type: *Kajewski 673* (holo K; iso BRI, US), Santa Cruz Islands.

Shrub or tree 2–20 m high, dbh 19–48 cm, buttresses rarely present, up to 45 cm high; branchlets subglabrous to sparsely hairy, densely hairy when young; young shoots grey to red to dark-brown when dry, Terminalia branching pattern usually weak. *Bark* white to grey to brown when fresh, brown to grey when dry, 0.2 mm thick, smooth, hard to soft; inner bark (pale) brown. *Sapwood* white to cream to brownish, hard. *Leaves* alternate and/or opposite; petiole 3–41 mm long, glabrous to sparsely hairy, transverse cracks usually absent, (greyish to reddish to blackish)-brown when dry, small raised glands present; stipules triangular (to foliaceous), 1–4.5 by 0.5–1.5 mm, sparsely hairy to velutinous outside, midrib densely hairy to velutinous, glabrous to densely hairy inside, margin often ciliate, not hyaline; lamina ovate to obovate, 2.3–15 by 1.2–8.5 cm, l/w ratio 1.1–2.8, papery to slightly leathery; base rounded to at-tenuate; apex retuse to cuspidate, up to 15 mm long; upper surface glabrous, small raised glands often present, often granulate, (dark) green when fresh, (dark to red to green)-brown when dry; lower surface (sub)glabrous, veins glabrous to sparsely hairy, small raised glands often present, discoid glands present, often in a row parallel to midrib and/or between the secondary veins, (dark) green when fresh, (green to pale)-brown when dry; secondary veins 4–9 per side, almost closed at margin; nervation reticulate. *Staminate inflorescences* axillary to just below the leaves, solitary to few clustered together, 0.3–4.5 cm long, 0.2–0.5 mm thick, sometimes branched, subglabrous to densely hairy, many-flowered, usually less than 36, dark red to reddish pink; bracts absent or 1, 0.9–1 mm long, subglabrous to densely hairy outside, glabrous inside, margin usually ciliate, not hyaline; bracteoles (0 or) 1(–5), 0.5–1.5 mm long, glabrous to densely hairy outside, glabrous inside; branchlets cylindrical, 1–6 mm

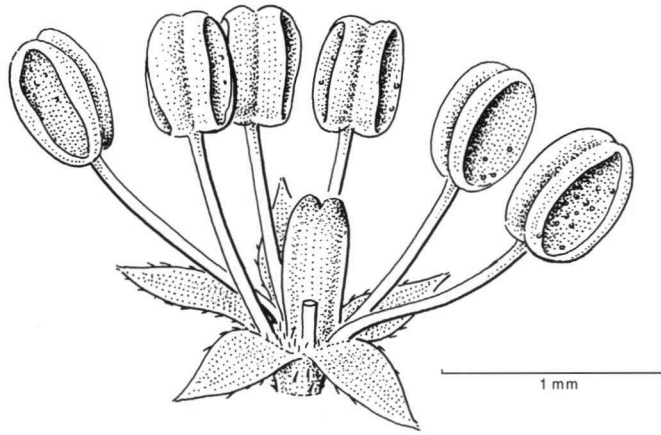
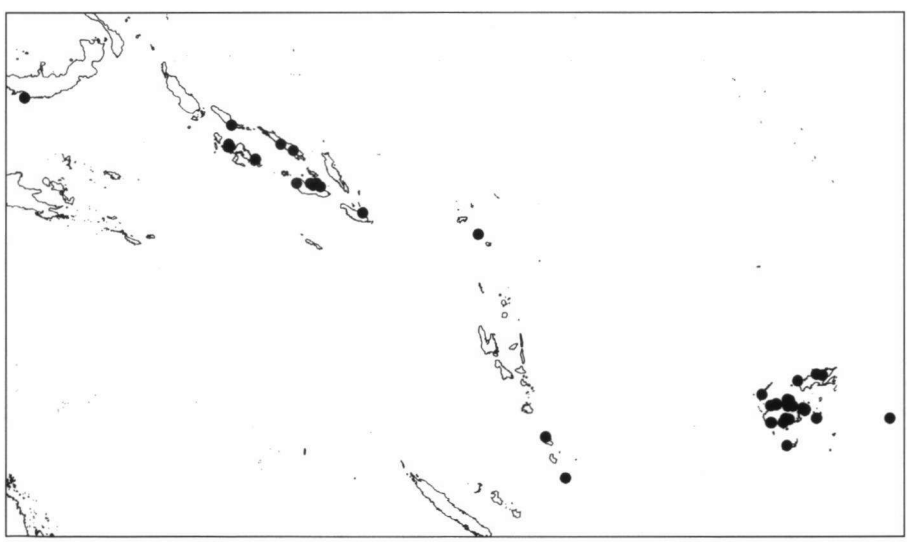


Fig. 3.31. *Nothobaccaurea stylaris* (Müll.Arg.) Haegens. Male flower (*Bernardi 13310*).

long, glabrous to sparsely hairy, 1–5-flowered. *Staminate flowers* 1–3 mm diam., reddish brown to dark red to whitish; pedicel 0–1.8 mm long, abscission zone often hardly visible, upper part 0–0.5 mm long, glabrous to sparsely hairy; sepals 3–6, (ob)ovate, 0.5–1.2 by 0.2–0.9 mm, glabrous outside and inside, margin ciliate; stamens 5–7, 0.9–2.5 mm long, glabrous, purple; filaments 0.5–2.1 mm long, straight; anthers 0.25–0.6 by 0.25–0.6 by 0.2–0.4 mm, purple; pistillode obtriangular to cylindrical, 0.3–0.8 mm high, glabrous, hollow. *Pistillate inflorescences* axillary to ramiflorous, solitary to few clustered together, 0.5–3 cm long, 0.3–0.5 mm thick, subglabrous to densely hairy, 3–20-flowered; petiole 0.2–1.7 mm long, geniculate (90° bent) at abscis-



Map 3.48. Distribution of *Nothobaccaurea stylaris* (Müll.Arg.) Haegens in the Solomon Islands, Vanuatu and Fiji.

sion zone, upper part 0.1–0.4 mm long, subglabrous; bracts 1 or 2, subglabrous to densely hairy outside, glabrous inside, margin ciliate. *Pistillate flowers* 0.8–2 mm diam., (dark) red; sepals 5 or 6, ovate, 0.5–1.2 by 0.2–0.5 mm, (sub)glabrous outside, glabrous inside, persistent; staminodes c. 7, small; ovary 1–2.5 by 0.5–1.2 mm, subglabrous at tip, base sparsely to densely hairy, style 0.1–1.2 by 0.25–0.5 mm, (sub)glabrous; stigmas 0.3–0.8 mm long, cleft for upper c. 90%, persistent; lobes 0.3–0.7 by 0.2–0.8 mm, protuberances present above and below, glabrous above, subglabrous below. *Fruits* globose to ovoid, 1- (or 2-)seeded, fleshy capsules, (5–)8–12.5 by (2–)6–9 by (2–)5–9 mm, loculicidally dehiscent, small raised glands present, (sub)glabrous outside, glabrous inside, septa rarely subglabrous, (light) green to red to brown; pericarp 0.2–1 mm thick; column 5–9.5 mm, caducous to persistent, usually curved; pedicel 0.4–4 mm long, upper part 0.1–1.2 mm long. *Seeds* globose, sometimes laterally flattened, 4–6.8 by 3.8–5.3 by 3.3–5 mm; arillode dull purple; testa red; cotyledons 2–3.2 by 2.2–3 by 0.02–0.1; radicle 0.5–1 mm; endosperm papery to c. 1 mm thick.

Distribution — Solomon Islands, Vanuatu, Fiji.

Habitat & Ecology — Primary or secondary rain forest. Altitude: sea level up to 1100 m. Flowering and fruiting throughout the year. Fruits eaten by pigeons.

Vernacular names — Fiji: Innoka, kailoa, midra, sinumbuta, vurevure.

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GLOSSARY

acuminate	:	terminating in a short point
arillode	:	additional fleshy layer covering of the seed
attenuate	:	gradually and concavely tapering to a point
axillary	:	inserted in leaf axil
bract	:	scale-like leaf in whose axil a flower develops
bracteole	:	a small secondary bract or bractlet
caducous	:	falling off early
cauline	:	flowering from the trunk
cordate	:	heart-shaped
cuneate	:	tapering to a point in a straight line
cuspidate	:	terminating in a long sharp point
dehiscent	:	opening
discoid glands	:	small glands on leaf blades, usually black and c. 1 mm diam.
elliptic	:	widest in middle
fusiform	:	spindle-shaped, tapering gradually at both ends
geniculate	:	bent like a knee and thickened
glabrous	:	without hairs
loculicidal	:	dehiscing down the back of the locule (= chamber containing the seeds), not at the septa
obovate	:	inversely egg-shaped and attached by the narrow end (widest above middle)
obtuse	:	blunt
ovate	:	egg-shaped and attached by the broader end (widest below middle)
pedicel	:	flower stalk
petiole	:	leaf stalk
pistillate	:	'female' flowers bearing pistils but no stamens
protuberance	:	bulging outgrowth
pulvinate	:	swelling in petiole, usually accompanied with a bent
rachis	:	inflorescence axis
raised glands	:	white glands producing a crystalline excretion
reticulate	:	like a network
retuse	:	obtuse with a broad shallow notch in the middle
scalariform	:	ladder-like
septicidal	:	dehiscing at the septum
septum	:	a partition separating two carpels
staminate	:	'male' flowers containing stamens but no carpels
staminode	:	rudimentary stamen
stellate	:	star-shaped
Terminalia branching	:	branching scheme as in the genus *Terminalia*; the branches do not develop continuously in time, but show every year a period of fast development and a period of slow development. The leaves are grouped at the tip of the branch.

IDENTIFICATION LIST

Only those specimens with a clearly identified collector and collection number are listed.
B. = *Baccaurea*; *D.* = *Distichirhops*; *N.* = *Nothobaccaurea*

1 = *B. angulata*
2 = *B. annamensis*
3 = *B. bracteata.*
4 = *B. brevipes*
5 = *B. carinata*
6 = *B. costulata*
7 = *B. courtallensis*
8 = *B. deflexa*
9 = *B. dolichobotrys*
10 = *B. dulcis*
11 = *B. edulis*
12 = *B. javanica*
13 = *B. lanceolata*
14 = *B. macrocarpa*
15 = *B. macrophylla*
16 = *B. maingayi*
17 = *B. microcarpa*
18 = *B. minor*
19 = *B. mollis*
20 = *B. motleyana*
21 = *B. multiflora*
22 = *B. nanihua*
23 = *B. nesophila*
24 = *B. odoratissima*
25 = *B. papuana*
26 = *B. parviflora*
27 = *B. philippinensis*
28 = *B. polyneura*
29 = *B. ptychopyxis*
30 = *B. pubera*
31 = *B. purpurea*
32 = *B. pyriformis*
33 = *B. racemosa*
34 = *B. ramiflora*
35 = *B. reticulata*
36 = *B. sarawakensis*
37 = *B. seemannii*
38 = *B. simaloerensis*
39 = *B. sumatrana*
40 = *B. taitensis*
41 = *B. tetrandra*
42 = *B. trigonocarpa*
43 = *B. velutina*
44 = *D. megale*
45 = *D. minor*
46 = *D. mitsemosik*
47 = *N. pulvinata*
48 = *N. stylaris*

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Character-number combinations refer to the species as used in this revision. Genus names (and their synonyms) to page number. New names are in **bold**, accepted names in roman, and synonyms in *italics*. The following abbreviations have been used: *Baccaurea* (B), *Distichirhops* (D), *Nothobaccaurea* (N), species dubiae (*dub.*), excluded names (*excl.*).

CURRICULUM VITAE

Raoul Martin Anne Peter Haegens werd geboren op 13 juni 1969 te Weesp. In 1987 behaalde hij het Gymnasium-b diploma aan het Katholiek Gymnasium 'Rolduc' te Kerkrade. Vervolgens maakte hij een aanvang met de studie werktuigbouwkunde te Eindhoven. In 1988 stapte hij over naar de studie biologie te Wageningen. Deze opleiding heeft hij met goed gevolg afgesloten in 1994. Tijdens zijn biologiestudie waren plantensystematiek, -fysiologie en -morfologie zijn voornaamste aandachtspunten. Gedurende 6 maanden verrichtte hij een plantensystematische stage in Kameroen en Gabon. In 1994 is hij begonnen met zijn promotieonderzoek aan het onderzoeksinstituut Rijksherbarium/Hortus Botanicus te Leiden, begeleid door dr. P.C. van Welzen en prof. dr. P. Baas. Dit onderzoek is uitgevoerd in het kader van het onderzoeksprogramma 'Pathways from Asia to New Guinea, the origin of the non-Australian elements', van de Stichting Levenswetenschappen (SLW) van NWO.

Op dit ogenblik is hij werkzaam als plantentaxonoom bij de Vaste Keuring Commissie (VKC) te Aalsmeer gedurende drie dagen per week en bij de Naktuinbouw te Roelofarendsveen gedurende twee dagen per week.

Van zijn hand verschenen de volgende publicaties:

Haegens, R.M.A.P. 1994. Revision of Cylindropsis Pierre and Vahadenia Stapf, Series of revisions of Apocynaceae XXXV in Bull. Jard. Bot. Nat. Belg. / Bull. Nat. Plantentuin Belg. 63: 313–328.

Vonk, G.J.A., A.J.M. Leeuwenberg & R.M.A.P. Haegens. 1994. Revision of Ancylobotrys Pierre, Series of revisions of Apocynaceae XXXVII in Wageningen Agricultural University Papers 94.3: 1–44.

Haegens, R.M.A.P. (accepted). Systematics and phylogeny of Baccaurea Lour. (Euphorbiaceae) in Plant Diversity in Malesia IV, Proceedings of the Flora Malesiana Symposium 1998.

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