Systematics of *Aporosa*
(Euphorbiaceae)

PROEFSCHRIFT

ter verkrijging van
de graad van Doctor aan de Universiteit Leiden,
op gezag van de Rector Magnificus Dr. D.D. Breimer,
hoogleraar in de faculteit der Wiskunde en
Natuurwetenschappen en die der Geneeskunde,
volgens besluit van het College voor Promoties
te verdedigen op woensdag 3 november 2004
te klokke 15.15 uur

door

ANNE MARKETTA SCHOT
geboren te Leidschendam in 1966

PROMOTIECOMMISSIE:

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Systematics of *Aporosa* (Euphorbiaceae)

Anne Marketta Schot

BLUMEA Supplement 17

NATIONAAL HERBARIUM NEDERLAND, Universiteit Leiden branch

2004

Iq ta randayhet suk biqahuc
“Winter is not being the time for naked swimming”

Tad Williams – *To Green Angel Tower*

ISSN 0373-4293
ISBN 90-71236-58-7
NUR 941

BLUMEA Supplement 17

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SUMMARY

This study presents a monograph of the genus *Aporosa* (Euphorbiaceae). It is divided into three parts.

The **first part** describes the general aspects of the genus. The species of *Aporosa* are small dioecious trees, which occur in the tropical rain forests of Southeast Asia. Eighty-two species are recognized with 8 varieties; 7 insufficiently known taxa are also mentioned. The delimitation of the species is based on combinations of macromorphological characters. Notes on generic and species delimitation, a description of the macromorphological characters, the combinations of characters used to delimit species and species groups, and the micromorphological features are treated in Chapters 1 to 6. The leaf anatomy and pollen morphology of only a limited number of species was studied; however, the descriptions are completed with data from literature. An overview of wood anatomy and chemical compounds compiled from literature is also given. This is followed by a description of the known ecology of *Aporosa* and a compilation of uses mentioned for the various species.

The **second part** comprises the phylogeny reconstruction. It shows how a species-rich group can be partitioned into smaller sets using testing and consensus techniques. The study starts with a detailed description of the arguments used for selecting and coding the characters (Chapter 7). *Aporosa* has many species and the delimitation of the species using combinations of relatively few different characters, resulted in a relatively low number of characters available for coding.

In Chapter 8 the phylogenetic analyses are discussed. Many equally parsimonious cladograms are found, from which a general consensus pattern is extracted after weighting procedures. Higher confidence in this consensus pattern is established by testing, resulting finally in the acceptance of three subsets and the exclusion of several New Guinean taxa that are the main cause of the ambiguity found. The three subsets are analysed separately with redefined data sets.

A consensus pattern is compiled by combining the results of the analyses of the complete data set and of the subsets. Polytomies are a natural way to summarize multiple patterns; ambiguity in phylogenetic reconstructions should not be veiled, but accepted as a meaningful outcome.

Based on the consensus pattern, the character transformation series are traced for the better established relationships, and evolutionary processes are proposed to explain the relationships shown (Chapter 9). The top of the cladogram, with the taxa of the three accepted subsets, consists of often dichotomous and stable relationships. These patterns yield models for recent speciation events in *Aporosa*. These speciation hypotheses are compared with the distributions of the species and the geological history of Southeast Asia.

To explain the ambiguities in the relationships of the basal taxa it is argued that during the evolution of *Aporosa* possibly hybrid speciation or introgression and extinction have taken place. Geological and distributional data do not refute these hypotheses. Hybridization and introgression may be a way to keep genetic variability at a high level, which is favourable in unstable environments. However, the cladistic method, using parsimony and dichotomous depiction of relationships, is not suitable to study this process. It may also be that the relationships between the species of *Aporosa* cannot be solved on macromorphological characters only.

Based on the postulated phylogeny a new infrageneric classification is established in which five sections are recognized.

The **last part** of the study, Chapter 10, contains the taxonomic revision. A generic description, the new section classification, dichotomous keys to the species per area and a synoptical key to all species are given together with the descriptions, distributions, data on habitat, uses and interesting notes of all the species and a list of the specimens seen and their identification.

SAMENVATTING

Dit boekje bevat een monografie van het plantengeslacht *Aporosa*. *Aporosa* is een geslacht van kleine bomen, voorkomend in de tropische en subtropische oerwouden van Zuidoost-Azië. Het behoort tot de soortenrijke familie van de Wolfsmelkachtigen, de Euphorbiaceae.

De monografie is opgebouwd uit drie delen, een algemeen deel, een fylogenetisch deel en een taxonomisch deel.

Het **algemene deel**, bestaande uit de hoofstukken 1 tot en met 6, bevat de introductie (hoofdstuk 1), een beschrijving van de systematische positie van het geslacht *Aporosa* in de familie der Euphorbiaceae (hoofdstuk 2), een beschrijving van de macromorfologische kenmerken (hoofdstuk 3), een beschrijving van de micromorfologische kenmerken (hoofdstuk 4), een beschrijving van de ecologie, voor zover bekend (hoofdstuk 5) en de economische waarde van de diverse soorten (hoofdstuk 6).

Aporosa bestaat uit kleine, tweehuizige bomen. De meeste, gezien hun voorkomen in de tropen van Zuidoost-Azië zijn groenblijvend; een enkeling van de subtropische soorten heeft afvallend blad. Binnen de Euphorbiaceae wordt *Aporosa* gerekend tot de, vaak primitief geachte, basale subfamilie der Phyllanthoideae. Deze subfamilie wordt in het algemeen onderscheiden van de 'echte' Euphorbiaceae door het ontbreken van echte bijzondere eigenschappen. Alleen de aanwezigheid van twee ovula per hok tegen één ovulum per hok in de 'echte' Euphorbiaceae kan als positief kenmerk beschouwd worden. De soorten binnen het geslacht *Aporosa* zijn, gelijk deze definitie, dan ook vrij non-descript.

Er zijn momenteel 82 soorten bekend, met 8 variëteiten. Daarnaast bestaan een 7-tal exemplaren die niet plaatsbaar zijn in één van de bekende soorten en mogelijk nieuwe soorten vormen of afwijkende exemplaren van de bekende soorten. De soorten kunnen herkend worden op basis van combinaties van kenmerken. Deze kenmerken worden beschreven in hoofdstuk 3. Het belangrijkste kenmerk vormt het type bloeiwijze, d.w.z. de verspreiding van de bloemen over de bloeiwijze-as. Bij de mannelijke planten is tevens de vergroeiing van de sepalen en de relatieve lengte van de meeldraden t.o.v. de sepalen kenmerkend. De vrouwelijke planten kunnen vaak herkend worden aan de vorm van het ovarium en de stijlen.

Van de micromorfologie van *Aporosa* is weinig bekend. Tijdens de studie is onderzoek gedaan aan de bladanatomie en pollenmorfologie van enkele, representatief geachte soorten. Het micromorfologie deel (hoofdstuk 4) wordt verder aangevuld met uit de literatuur bekende waarnemingen betreffende de houtanatomie en chemische componenten.

De beschrijving van de ecologie in hoofdstuk 5 bestaat uit notities die werden gemaakt door J.V. LaFrankie (CTFS, Singapore) bij het opzetten van een onderzoeksproject in Pasoh, Malaysia. Het geheel is aangevuld met uit de literatuur gevonden overige summiere waarnemingen en de schaarse informatie genoteerd door verzamelaars op de labels. Het laatste hoofdstuk van het algemene deel, hoofdstuk 6, is een compilatie van in de literatuur genoemde gebruiken van de diverse *Aporosa*-soorten door de plaatselijke bevolking.

Het **tweede deel** van de monografie bevat de beschrijvingen van de opzet (hoofdstuk 7), de uitvoering en resultaten (hoofdstuk 8) en de theoretische toepassingen (hoofdstuk 9) van de fylogenetische reconstructie. De fylogenetische analyse van *Aporosa* is een voorbeeld van hoe een soortenrijk geslacht geanalyseerd kan worden. De reconstructie wordt in een aantal stappen uitgevoerd. Eerst wordt een globale analyse uitgevoerd, waarna op basis van de resultaten de dataset in stukken geknipt wordt en de losse groepen in een tweede ronde apart geanalyseerd worden.

In hoofdstuk 7 wordt uitgelegd welke kenmerken gekozen zijn en waarom, en de wijzes waarop de kenmerken gecodeerd zijn in voor de analyse bruikbare toestanden. Het opstellen van een goede datamatrix voor *Aporosa* is vrij lastig. Het probleem ligt in de hoeveelheid beschikbare kenmerken die omgezet kunnen worden naar kenmerktoestanden die niet of zo min mogelijk overlappen. In ideale omstandigheden zou een datamatrix van zo'n 100 taxa meer dan 200 binaire kenmerken moeten hebben. Dit is moeilijk realiseerbaar gezien het feit dat de *Aporosa* soorten onderscheiden worden op basis van diverse combinaties van een relatief klein aantal kenmerken. Hierdoor is de keuze aan geschikte eigenschappen beperkt, en zijn, om toch een redelijk geachte hoeveelheid kenmerken in de dataset te krijgen, via diverse omzettingen ook de moeilijk codeerbare gemiddelden, lengtes en polymorfismes opgenomen.

Na het opstellen van de datamatrix en het kiezen van de zustergroep worden de analyses uitgevoerd met behulp van het computerprogramma 'Hennig86' (hoofdstuk 8). Allereerst is de matrix in zijn geheel geanalyseerd. Dit resulteert in vele duizenden, zo niet vele miljoenen, even zuinige bomen. Om deze hoeveelheid te verkleinen is getracht de datamatrix te wegen. Dit houdt in dat aan elk kenmerk op basis van zijn invloed in de eerste analyse een weegfactor wordt toebedeeld, waarna de analyse opnieuw gedaan wordt, maar dan zodanig, dat patronen ondersteund door belangrijke kenmerken bevoordeeld worden boven de patronen ondersteund door minder belangrijke kenmerken. In het geval van *Aporosa* leidde het wegen echter tot vrij willekeurige resultaten, mogelijk veroorzaakt door de te grote verschillen tussen de diverse meest zuinige bomen. Daarom is besloten om liever de robuustheid van de in de ongewogen en gewogen analyse gevonden groepen te testen, zodat deze apart geanalyseerd konden worden. Het voordeel van een analyse met minder taxa is dat de verhouding tussen de hoeveelheid codeerbare kenmerken en de hoeveelheid taxa gunstiger is.

De diverse testen, waarbij wordt bepaald of de betreffende groepen overeind blijven als de kenmerken ofwel de taxa worden gemanipuleerd, toonden aan dat er binnen *Aporosa* drie stabiele groepen waren. Tevens werd uit de testen duidelijk dat een groot gedeelte van de eerder gevonden tegenstrijdigheden veroorzaakt wordt door een 14-tal Nieuw Guinese taxa. Door deze taxa uit de datamatrix te verwijderen, kunnen ook de verwantschappen van de drie groepen tot elkaar en van de basale taxa, die tot geen van de gevonden drie groepen behoren, beter bepaald worden. Na het analyseren van de diverse subsets is door combinatie een reconstructie gemaakt van de consensus tussen de diverse fylogenetische patronen in *Aporosa*. In dit uiteindelijke patroon is niet gestreefd naar volledige dichotomie; eerder naar de grootst mogelijke accuraatheid.

Met het in hoofdstuk 8 gereconstrueerde fylogenetische consensus patroon worden in hoofdstuk 9 de theoretische toepassingen besproken. Als eerste valt hieronder het opstellen van de transformatiereeksen van de kenmerken, en het uitwerken van de mogelijke evolutionaire patronen ervan. Slechts een klein deel van de kenmerken wordt besproken, hieronder vallen de belangrijk gebleken kenmerken van de bladklieren en de mannelijke en vrouwelijke bloeiwijzen en bloemen. In de evolutie hebben enkele groepen, voornamelijk de op het vaste land van Zuidoost-Azië voorkomende soorten, meer gespecialiseerde klieren gekregen. Verder valt op dat mannelijke bloemen in de loop van de geschiedenis eerder en anders gedifferentieerd zijn dan de vrouwelijke.

De tweede toepassing van de fylogenetische reconstructie is het afleiden van mogelijke speciatiepatronen. Voor enkele recentere groepen kan, met behulp van de verspreidingspatronen en de geologische geschiedenis van het gebied, vicariante soortvorming aannemelijk gemaakt worden. Om het ontbreken van consensus in de basis te verklaren, worden evolutionare processen die leiden tot discrepantie in fylogenetische bomen besproken. Zo is het mogelijk dat *Aporosa* op Nieuw Guinea hybrides heeft gevormd, wat een manier kan zijn om in instabiele omgevingen de genetische variatie hoog te houden. Echter, de parsimonie methode en een dichotome representatie van zo'n evolutionair patroon zijn niet verenigbaar met hybride soortvorming. Dit kan verklaren waarom het weglaten van een deel van de Nieuw Guinese soorten de oplossing van de analyse verbeterde. Echter, de door de westerse basale taxa gevormde polytomie werd alleen maar erger wanneer de aanwezige soorten uit de analyses verwijderd werden. Het is mogelijk dat hier een andere factor, bv. het ontbreken van de tussenvormen door snelle soortsvorming en gedeeltelijke uitsterving, heeft meegespeeld.

Als laatste toepassing van de fylogenetische reconstructie wordt een nieuwe infragenerische indeling in secties gedefiniëerd.

Het **derde en laatste deel** van de monografie bevat de genusbeschrijving, beschrijvingen van de nieuw gedefiniëerde secties en de soortsbeschrijvingen inclusief verspreidingskaarten. Tevens worden er per regio dichotome determinatiesleutels gegeven. Het betreft een sleutel voor: 1) Sri Lanka en Zuid India, 2) Noord India tot en met China en Thailand, 3) Maleisië, Singapore en de westelijke eilanden van en Indonesië, 4) Borneo, 5) de Fillippijnen, Sulawesi en de Molukken en 6) Nieuw Guinea en de Solomon eilanden. De regionale sleutels zijn, met uitzondering van de sleutel voor Nieuw Guinea, gesplitst in aparte sleutels voor de mannelijke en de vrouwelijk exemplaren. Ook wordt er voor het hele geslacht *Aporosa* een synoptische sleutel gegeven. Het geheel wordt afgesloten met een lijst van bestudeerde exemplaren in de diverse herbaria en een index naar de wetenschappelijke namen.

PART I

SYSTEMATICS

Chapter 1

INTRODUCTION

Within the framework of the long-term international Flora Malesiana project, the Leiden Universiteit branch of the Nationaal Herbarium Nederland focuses on the treatment of the large family Euphorbiaceae. *Aporosa* is one of the more speciose genera in Malesia. The species are small, dioecious trees, occurring in Sri Lanka and Kerala and southwards from the outskirts of the Himalaya and Southeast Asia throughout Malesia to the Solomon Islands. It is one of the more common genera in Malesia, and a revision was badly needed.

The present study has two main aims. Firstly, it provides a revision of *Aporosa* for Flora Malesiana and, as the whole genus is monographed, for adjacent areas. Secondly, phylogenetic relationships are reconstructed. With the cladistic patterns an infrageneric classification can be proposed for the 82 species. Additionally, the cladograms can indicate hypotheses for evolutionary pathways of characters and species, and, as a special application, be the base for a cladistic historical biogeographical analysis of the areas where the species occur.

The discussion of these subjects is presented in three parts. The first part, consisting of Chapters 2–6, provides general information on the systematic position of *Aporosa*, the macromorphological characters that are used to delimit the species and to build the phylogenetic data set, and a summary of other features of *Aporosa*, i.e., a compilation of available micromorphological and ecological information.

The second part, consisting of Chapters 7–9, deals with the cladistic analysis. Theoretical issues of defining the characters and character states and the coding of the characters that form the data set are found in Chapter 7. Next the phylogenetic reconstruction is treated. Since there are many taxa in *Aporosa*, the analysis is conducted in several phases following the practice of former workers with large data sets (e.g., Kellog & Watson, 1993). The paragraphs of Chapter 8 describe the results of these various steps. First analyses are conducted with all taxa with different manipulations of the characters. Their purpose is to find a general pattern and to test this pattern. The tests indicate which relationships and possibly monophyletic groups are reliable and which are not. These are the basis for the next step: excluding non-stable taxa and performing separate subanalyses of the stable monophyletic subsets. Finally, a general phylogenetic reconstruction is compiled using the patterns found in the general analysis and in the subanalyses. The theoretical issues and applications of the phylogenetic reconstruction are treated in the last chapter of the phylogenetic part, Chapter 9. First the character transformation series and speciation processes that can be hypothesized are described. Where possible, the models on speciation are coupled to historical and distributional data. Such reconstructions serve to strengthen the confidence in the pattern. In the last paragraph a new sectional classification is proposed on the basis of the phylogenetic results.

The third part of this monograph contains the revision (Chapter 10). Identification keys to the species per area, descriptions of the genus, the new sections and all species, the formal classification of the species into the proposed sections found in the phylogenetic reconstruction, and distribution maps of the species are given here.

Chapter 2

TAXONOMY

2.1 – **Taxonomic history of Aporosa**

Blume (1825: 514) established the genus *Aporosa* and its type species *A. frutescens* on a single staminate specimen from West Java. Its taxonomic affinities were unclear – *Aporosa* is derived from the Greek word απορουσα, meaning 'difficult' or 'confusing' – and, to honour the name, *Aporosa* was placed in the family Urticaceae. The pistillate specimens of the same *Aporosa frutescens* were classified correctly under the Euphorbiaceae as *Leiocarpus fruticosa* (Blume, 1825: 581).

In the years following, three further genera were described: *Scepa* and *Lepidostachys* by Lindley (1836), and *Tetractinostigma* by Hasskarl (1858). Lindley's two genera were placed in their own order with affinities to Betulaceae based on the staminate specimens and to Urticaceae based on the pistillate specimens. Baillon (1858) was the first to see the similarity of the staminate inflorescences of *Scepa* and *Lepidostachys* with those of *Aporosa frutescens*. He transferred them all to *Aporosa* and placed the genus in the Euphorbiaceae, but kept *Leiocarpus* separate. Hasskarl (1858) recognized the affinity of *Tetractinostigma* with *Leiocarpus,* but distinguished them on account of the difference in number of locules. A year later he unified his genus with *Aporosa* (Hasskarl, 1859).

Müller Argoviensis (1866) finally united *Leiocarpus* and *Aporosa* and provided a monograph of the then known 20 species. The next and only other complete survey of the genus was made by Pax & Hoffmann (1922) for Engler's Pflanzenreich. They recognized 62 species. Others have only revised *Aporosa* for local floras (e.g., Thwaites, 1861; Hooker, 1887; Ridley, 1924; Gagnepain, 1927; Whitmore, 1973; Airy Shaw, 1975, 1980a; Chakrabarty & Gangopadhyay, 1993). Especially the work of Airy Shaw has been of great value. He managed to revise the largest part of the genus and recognized approximately 80 species.

The present monograph builds largely on the revisions of Airy Shaw. There are a few differences resulting from the fact that it is a complete overview of the whole geographical range of the genus, and because of the acquisition of new material, especially from New Guinea. The major changes were already discussed by me (Schot, 1995). Currently, I recognize 82 species, with 8 varieties. Seven incompletely known species remain, which cannot be categorized systematically, and 6 informal forms are discussed but not distinguished. More material is needed to clarify their systematic status. I have also expressed a preference for the older spelling *Aporosa* instead of the later used *Aporusa* (Schot, 1995). Airy Shaw (1966b) argued in favour of the spelling *Aporusa* based on an assumption that *Aporosa* was a type-setting mistake. In my view the evidence for Blume's intended spelling is too scanty and the oldest variant should be preferred. *Aporusa* is considered a newer orthographic variant of *Aporosa* (see also Jongkind, 1991) and I will use the original spelling throughout this monograph.

2.2 – *Aporosa and the systematics of the Euphorbiaceae*

The taxonomic problems surrounding *Aporosa* mirror the controversies in the systematics of the family Euphorbiaceae and its subfamily Phyllanthoideae in particular. Euphorbiaceae constitute, with 334 genera and c. 8900 species, the world's sixth largest family (Radcliffe-Smith, 2001). It is diverse in appearance and also in the number of opinions on its taxonomy. Different views exist up to this day about the exact circumscription, the poly-, para-, or monophyly, and the affinities of the various tribes. The various opinions are based on differences in choosing important delimiting features and arguing what is primitive and derived. I will give a short overview of the main characteristics and systematics of the family. It is mostly summarized from the compilation of Webster (1994b), whose system I follow.

Euphorbiaceae show a great diversity in habit and macro- and micromorphology. Because of this, the monophyly of the Euphorbiaceae as a whole is still under discussion. Seeds (Stuppy, 1995), pollen (Punt, 1962; Köhler, 1965), gynoecia (Sutter & Endress, 1995), embryology (Tokuoka & Tobe, 1995), leaf anatomy (Rothdauscher, 1896; Levin, 1986), wood anatomy (Mennega, 1987), chemical compounds (Hemalatha & Radhakrishnaiah, 1994), and the molecular 18S rDNA, rbcL, and atpB sequences (Wurdack & Chase, 1999; Savolainen et al., 2000; Soltis et al., in prep) were studied in the hope to solve the relationships of the Euphorbiaceae. Alas, each set of characters points to another solution and a consensus has not yet been reached.

Most authors agree on a division between uni-ovulate and bi-ovulate taxa. Molecular studies have indicated that Euphorbiaceae s.l. is not monophyletic (Wurdack & Chase, 1999; Savolainen et al., 2000; Soltis et al., in prep), and should be separated into at least five lineages within the order. The uni-ovulates are called the Euphorbiaceae s.s., and are characterized by various, possibly apomorphic, characters. The bi-ovulate Euphorbiaceae are usually treated as ancestral to the uni-ovulates. They are divided into the subfamilies Oldfieldioideae and Phyllanthoideae and are mostly recognized by a lack of the characters typical for the Euphorbiaceae s.s.

Of these latter two subfamilies the Phyllanthoideae are regarded as most primitive. No single morphological character is present to delineate this subfamily with its 57 genera and ± 2000 species, unless the absence of derived characters, such as foliar glands or monoecy, is considered. However, many exceptional species are nested within this subfamily that do have such derived characters. These cause the disagreement among those who wish to call only the uni-ovulates Euphorbiaceae (e.g., Meeuse, 1990) and those who want to keep the bi-ovulates together with them. With the work of Webster (1994a, b) this last view seems to win, not because uni-ovulates and bi-ovulates are so much alike, but because more and more studies show that the derived characters of the uni-ovulate subfamilies also occur in the notoriously diverse Phyllanthoideae. This blurs the boundaries between the Phyllanthoideae and the uni-ovulates. Euphorbiaceae s.l. are recognizable on their overall similarity. They may be paraphyletic, but an extreme division, such as suggested by Meeuse (1990), or a more relaxed one, such as suggested by Airy Shaw (1980a), does not solve the problem. Euphorbiaceae is a diverse aggregate family that is extremely successful in the tropics. In my view, the family is best kept as broadly as described by Webster (1994b); though no character (set) is shared by all members and no unique characters are present to identify every part of the group, there is an indefinable coherence, even in the relatively primitive Phyllanthoideae.

Aporosa shares this description: no synapomorphy is possessed by all species, and only very few of the species are identified by a unique feature. But looking at overall similarity, all species are recognizable as *Aporosa*.

2.3 – **The taxonomic position of Aporosa**

Aporosa, having bi-ovulate locules, tricolporate pollen grains, and no latex or specialized trichomes, undoubtedly belongs to the Phyllanthoideae. Additional characters of (part of) the Phyllanthoideae are: simple indumentum, alternate leaves, axillary racemose inflorescences, often inconspicuous flowers without petals, few stamens, free styles, 2–5 locules, and capsular fruits. The level of variation is, however, quite high. *Aporosa* also bears many features that are uncommon to the rest of the Phyllanthoideae.

The racemose inflorescences, tanniniferous epidermal cells, and tricolporate pollen grains place *Aporosa* in the tribe Antidesmeae, a group of dioecious trees with ament-like inflorescences and only one of the two ovules per locule developing into a seed. Within the Antidesmeae, *Aporosa* is grouped by Webster (1994b) with seven other genera into the subtribe Scepinae. Of these, *Richeria* and *Jablonskia* are small, poorly known genera from tropical South America and *Protomegabaria* and *Apodiscus* are equally obscure genera from tropical Africa. *Ashtonia* is their small counterpart in tropical Asia. The three remaining genera, *Maesobotrya*, *Baccaurea*[1], and *Aporosa*, form the bulk of the subtribe with c. 20, 70, and 80 species, respectively. The eight genera are separated by sexuality, arrangement of the staminate flowers, presence and consistency of staminate and pistillate disc, number of stamens, size of the pistillode, persistence of pistillate sepals, style shape, and dehiscence of the fruit.

2.4 – **Generic delimitation**

Within the subtribe Scepinae, *Aporosa* is distinct from all other genera by its short inflorescences and tiny staminate flowers, with a minute or absent pistillode, up to 4 stamens, and absence of a disc. Its presumed nearest relatives are *Baccaurea*, *Ashtonia*, and *Maesobotrya*.

Of these, *Ashtonia* is nearest in leaf structure. The thick, shiny, greenish drying leaves with distinct basal glands are almost identical to those of the species around *Aporosa aurea*. The inflorescences, flowers, and fruits, however, are completely different and will never be confused with *Aporosa*.

Baccaurea, the presumed sister-group, is different in the larger staminate flowers and longer, often stem-borne, staminate and pistillate inflorescences. Furthermore, it is easily distinguished from *Aporosa* by the often candelabriform habit and the leaves with relatively long petioles. The caducous sepals of the pistillate flower also serve as a good delimiting feature. However, both *Baccaurea* and *Aporosa* are polythetic in their set of characters. On the one hand some species of *Aporosa*, e.g., *A. arborea* and *A. nervosa* have rather long inflorescences, *A. papuana* has relatively large staminate flowers, and *A. praegrandifolia, A. macrophylla*, and *A. arborea* have long petioles.

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[1] Haegens split *Baccaurea* into three genera, *Baccaurea*, *Distichir(r)ops*, and *Nothobaccaurea*.

On the other hand, species such as *Baccaurea racemosa* or *B. sumatrana* have smaller leaves, a less distinct candelabriform habit, and axillary inflorescences. In the New Guinean *Nothobaccaurea stylaris* (Müll.Arg.) Haegens the leaves are evenly spread and the pistillate sepals are persistent. Such examples blur the distinction between *Aporosa* and *Baccaurea*. Fortunately, most species are only deviating in one character and will usually be identified correctly.

The African *Maesobotrya* is intermediate between *Aporosa* and *Baccaurea* with its medium-sized leaves and smallish flowers. Closer inspection of the long, slender, often stem-borne inflorescences, however, indicates a greater resemblance to *Baccaurea* than to *Aporosa*.

Some genera outside the Scepinae are sometimes confused with *Aporosa*. But this resemblance is only superficial: *Aporosa* has a very common appearance and lacks unique characters. Especially specimens with inflorescences in bud are often misidentified as *Aporosa*. *Antidesma* is one of the genera most easily confused, probably because it also has no unique characters in the vegetative parts. The description of *Aporosa octandra* at one time as *Alnus* and *Myrica* may serve as an example of the similarity of the staminate inflorescences to these genera. But, as already said, such confusions go only skin-deep: once the flowers are fully developed such mistakes are quickly corrected.

2.5 – **Specific delimitation and species concept**[1]

2.5.1 – ***Specific delimitation***

Analogous to the generic delimitation, a combination of characters is more important than unique features for the specific delimitation in *Aporosa*. The 82 species are minimally distinct. There are only few distinctive characters, but the combinations in which they occur are constant within a particular species.

One of the most important delimiting characters is the inflorescence. Foliar glands are important too. With these two features, aided by less useful features such as the number of locules or the shape and persistence of the stipules, the species of *Aporosa* are grouped. Within these groups, characters such as size and indumentum of the various parts delimit the species. It is this hierarchical use of characters that produces the character combinations typical for one species.

The delimitation can be rather troublesome when a feature is sex-connected. For example, *A. latifolia* and *A. fusiformis* differ in number of locules and size of the pistillate flowers and fruits. Number of locules is one of the more important characters, and the two species are kept separate, even though the staminate specimens may not be assigned to one of them.

The place of a character in the hierarchy proved indicative for the relationship. For example, *A. prainiana* differs from *A. yunnanensis* in the inflorescence type and the two species are placed in different clades. On the other hand, the difference between *A. prainiana* and *A. whitmorei* lies in the indumentum of the leaves and the spe-

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1) References in this chapter to primitive and derived characters and relationships between species are based on the patterns shown by the phylogenetic analysis (Chapter 8).

cies proved to be closely related. The hierarchy of the characters can also be used to decide about the rank of a taxon: *A. symplocoides* differs from *A. symplocoides* var. *chalarocarpa* only in the minor feature of fruit shape. The two taxa are described as varieties.

The *A. octandra*-complex presented a difficult case. The hierarchical system could not be used to delimit species. This complex consists of three species: *A. wallichii*, *A. villosa*, and the variable *A. octandra* with four varieties. Important delimiting features such as inflorescence type, foliar glands, number of locules, stipules, etc. are constant. The less important characters are variable, e.g., indumentum, shape, and drying colour of the leaves. The complex has one member in the Malay Archipelago, *A. octandra* var. *malesiana*, which is rather uniform; only in mainland Asia the complex shows its variable face. Here all varieties of *A. octandra* co-occur together with *A. wallichii* and *A. villosa*. Intermediates are present between the last two species and *A. octandra* and all its varieties and also between the varieties of *A. octandra*, but not between *A. wallichii* and *A. villosa*. This has been the main reason to delimit three species in the complex: two extremes and one intermediate. The extremes, *A. villosa* and *A. wallichii* are strictly defined and recognizable; *A. octandra* contains all intermediate forms. Within *A. octandra*, the separation of the varieties is more or less based on geographical grounds.

The above paragraphs described a hierarchical use of the characters to delimit the species. However, this only works for West Malesia and the mainland of Asia. The New Guinean species are different: they have different combinations of characters and a different variability within a species. At first sight they look quite different, but when studied closer all the individual features that make up for the appearance of a West Malesian *Aporosa* are present, such as small flowers, dehiscent capsules, short inflorescences, and the conspicuous black dots in the dried leaves – which is more then can be said of some West Malesian species. The difference lies in the fact that the New Guinean species have retained a more primitive semblance: the flowers are present in higher numbers, they are larger, always pedicelled, and the pistillate flowers have styles. Furthermore, the New Guinean species vary in characters that are stable in West Malesia and are stable in characters that vary in West Malesia. This causes the disagreement between the character combinations of the New Guinean species and those of the West Malesian species.

In West Malesia species could be delimited using particular combinations of characters. In New Guinea this same basal argument may be used. Though the characters that constitute the combinations are different, the fact that there are still unique combinations also shows possibilities for delimitation of species in New Guinea. However, a different hierarchy of the characters is called for. Whereas inflorescence type and foliar glands were the first step in grouping the species in West Malesia, size differences are the prime factor for the New Guinean species.

Part of the species can be classified into two patterns. *Aporosa papuana* and similar species have big leaves, large inflorescences, relatively many and large flowers, large falcate, often persistent stipules, and a 3-locular ovary. The species of the *A. nigropunctata* affinity have small leaves, short inflorescences, relatively small flowers, small, slightly falcate, caducous stipules, and a 2-locular ovary. These two groups are connected by a range of species that have these characters in various mixtures and intermediate states, e.g., 2- and 3-locular ovaries, leaves and inflorescences of intermediate sizes, staminate flowers with small sepals but long stamens, large and falcate but caducous stipules. Combinations of these characters are enough to delimit the three groups. Within these groups the unique characters, the indumentum, and also foliar glands are useful to pinpoint the species.

In summary, all species of *Aporosa* – even in New Guinea – are distinct by unique combinations of characters. This means that the number of delimiting characters is small, which in its turn leads to a strict use of the characters in *Aporosa*.

2.5.2 – ***Species concept***

What is a species? Many books were written on this subject. Eloquent treatments can be found in, e.g., Kornet (1993) or Luckow (1995). Since this study is not on species concepts, I will only state my views on the species of *Aporosa*.

How to define a species is still a controversial subject. It often depends on the nature of the group studied and the study objectives. Practising taxonomists often rely on the morphological or phenetic species concept: the morphological characters that make a species recognizable are used as defining property. This sounds simple, but it is not. Species are often polytypic and some closely related ones tend to blend together, causing problems for the taxonomist.

Ever since Darwin another species concept has been discussed: species as evolving units that share a common evolutionary history. A difference between a taxonomic and evolutionary view is that in pure taxonomy a species is defined by its characters, while an evolutionary species is *recognized* by its characters (Baum & Donoghue, 1995). Because of this, aberrant specimens are allowed. Possession of a particular character(state) is neither necessary nor sufficient to classify an individual into a species (Kornet, 1993). This is characteristic for evolving communities. Aberrant specimens do not disrupt species boundaries, they only make recognition harder. The reticulating and hierarchical parent-offspring relations are what matters. This is the cladists' view.

How do I interpret the species of *Aporosa*? I have set two goals in my introduction to this study: 1) monographing the genus for the Flora Malesiana and 2) reconstructing the phylogeny and modelling an evolutionary pathway. The first aim calls for recognizability of species by – preferably – macromorphological characters, the second for identifying the correct evolving entities whose relationships can be traced using macromorphological characters. The latter is not a practical species concept. The species of *Aporosa* are evolving entities, but there is no way to know whether the entities I have recognized today equal those that play a role in speciation. Therefore, the only species concept that can be applied to daily taxonomic practice is the morphological one.

This brings me to a last topic: the status of the infraspecific taxa. Species such as *A. octandra, A. lucida*, or *A. subcaudata* are thought of as being in the process of speciation. I have described two levels of subspecific taxa: 1) the varieties, the geographically distinct entities without sharp boundaries to the common form; and 2) the erratic forms of unknown status, the informal forms. Neither of them are yet species, but the varieties are in my view more advanced in speciation than the aberrant small populations. Therefore, the geographical varieties are described and included in the phylogenetic analysis. The informal forms have no status: as possible evolving units they are included only in the phylogenetic part; in the revision they appear in the notes.

Chapter 3

MACROMORPHOLOGY

3.1 – **General**

This chapter provides a description of the more important macromorphological features of *Aporosa*. The genus description at the end of this monograph serves as a complete summing up of all characters. I will limit myself here to the features that deserve more detailed attention. I have tried to follow the terminology of Webster (1994b) as much as possible.

There are two categories of important characters. First, there are those that play a role in delimiting and grouping the species. One of the first features that draws attention is the large variability in inflorescence types. Extreme inflorescence types are connected by a large range of intermediate types. Notable are also the foliar glands and the variability in indumentum.

Second, there are the characters that are included in the phylogenetic analysis. Some will have more influence on the patterns in the cladogram than others. Furthermore, theories relating to what is primitive and what derived are one of the central discussion points in phylogenetic reconstruction. To facilitate the discussion on character evolution in paragraph 9.2, I will also discuss these aspects of the described morphological characters here.

3.2 – **Description of special features**

Habit

Most *Aporosa* species of the lowland rain forests are evergreen trees of about 10 to 25 m high. *Aporosa nervosa* and its allies can reach a height of more than 30 m, but this is exceptional. Some of the species in the more seasonal or montane areas, e.g., *A. microstachya*, *A. lanceolata*, and *A. nigropunctata*, seldom grow beyond 10 m tall. The species of the *A. octandra*-complex, inhabiting the mainland of Asia, are sometimes deciduous. Herbarium collections of flowering specimens are occasionally either leafless or have young leaves only.

The branchlets are smooth, with few protrusions where leaves or inflorescences have fallen off. In the deciduous species *A. octandra* and *A. villosa* this knobbiness is more pronounced.

Almost all species are dioecious. Sometimes herbarium specimens consist of both staminate and pistillate specimens, but there is usually no indication whether these were collected from the same tree or from different trees. In ecological studies no evidence for sex-change was reported (Thomas & LaFrankie, 1993). I have seen only two aberrant specimens with inflorescences bearing staminate flowers at the base of the rachis and pistillate flowers apically, one of *A. octandra* var. *chinensis* and one of *A. sarawakensis* (*Shiu Ying Hu 9960* and *Nooteboom 1112*, respectively). They might be aberrant, or evidence that species do change sex: if pistillate individuals are the larger trees and staminate ones the smaller trees, as Bawa (1980) has suggested, then there must be a moment when the staminate plants turn into pistillate ones.

Hermaphrodite flowers have evolved in a few species at higher altitudes in New Guinea. Two of these, *A. hermaphrodita* and *A. heterodoxa,* are complete hermaphrodites; strict staminate or pistillate specimens have not been found yet. Three other species – *A. brevicaudata*, *A. egregia*, and *A. carrii* – are facultative hermaphrodites; they seem to be both dioecious and androdioecious, or dioecious and subgynodioecious.

Indumentum

Only simple, unicellular hairs are present in *Aporosa*. Variation is found in type and density of indumentum: sericeous, tomentose, hirsute, or puberulous. Within the genus all parts vary from densely hairy to completely glabrous. There are no fixed combinations, so glabrous leaves can occur with tomentose branchlets and sericeous ovaries, or puberulous leaves can occur with subglabrous rachises.

Despite the large variability in type and density of hairs, indumentum is useful for species delimitation. Though some puberulous species are glabrescent and thus variable, the completely glabrous and the densely tomentose species are always easily picked out. The first separation of species into groups is based on inflorescence and foliar gland type; in the second instance the species within these groups can be recognized on differences in indumentum.

Using such characters in a phylogenetic analysis results in repeated reversals, and thus high homoplasy levels. Without them, however, it is hard to distinguish between species, or between minor diversification lines. Therefore, I have included indumentum characters not only in the identification keys, but also in the phylogenetic analysis.

Leaves

All species have simple, petiolate, alternate leaves. *Aporosa* has its leaves always scattered along the branchlets, in contrast to the often candelabriform clusters of *Baccaurea* (Haegens, 2000).

Stipules — The shape of the stipules is somewhat correlated with persistence. Caducous stipules are small and narrowly triangular. In the species of the *A. frutescens*-group and those related to *A. maingayi* the stipules become gradually larger and more oblique to almost falcate. The more oblique, the longer they persist. The large falcate stipules of, e.g., the species around *A. papuana* and the *A. benthamiana*-group are, with a few exceptions, persistent. In other genera and families, large and persistent stipules serve as hiding places for ants and other small insects, but an ecological study to confirm this for *Aporosa* has not been performed. An interesting fact is that large persistent falcate stipules are absent in the closest related genera of *Aporosa*, but present in less related genera.

Lamina — The shape and length of the lamina is very variable. Most species have approximately narrowly elliptic leaves, varying to elliptic, narrowly ovate, or narrowly obovate. The base varies from subcordate to attenuate. The margin ranges from subentire to slightly undulate to slightly crenate. Sometimes a (lowly) serrate margin, such as

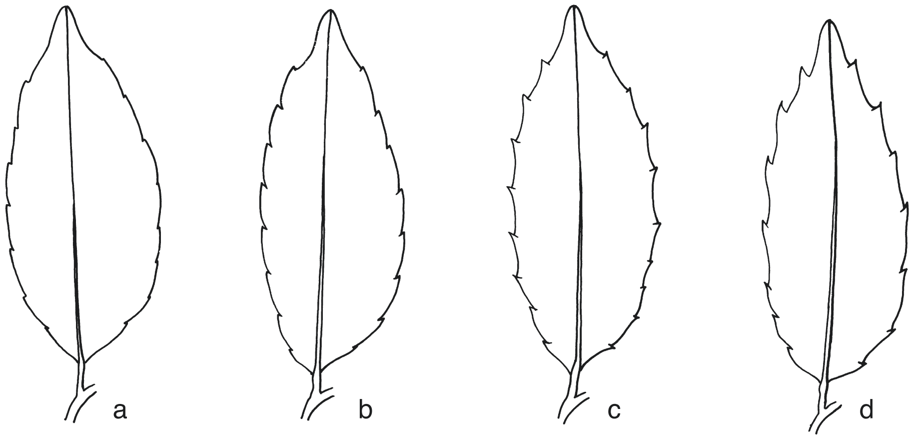


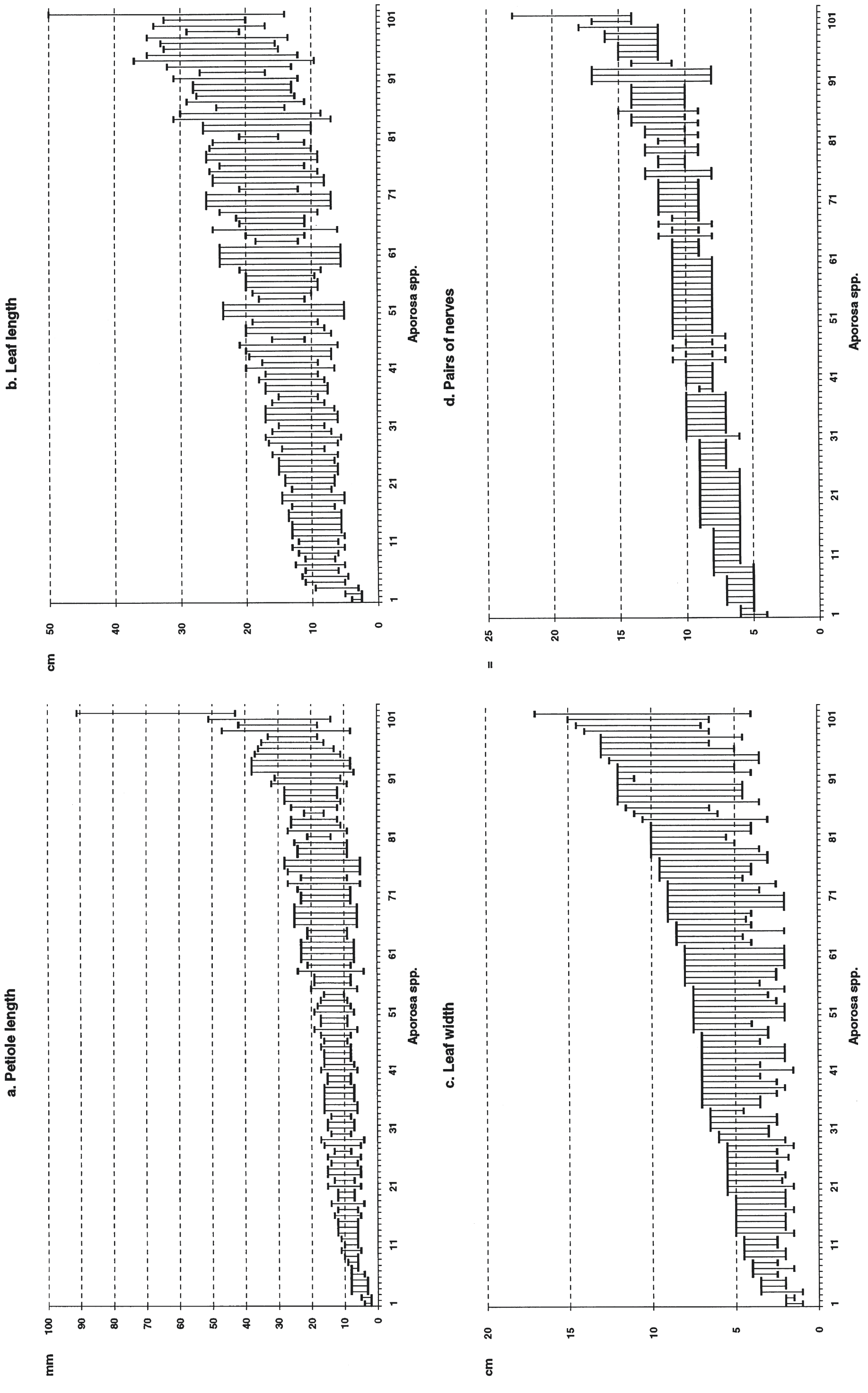
Fig. 3.1. Schematic overview of types of margin incision and the correlation with the placement of the marginal glands. — a. Lowly undulate; b. glandular-crenate; c. glandular-dentate; d. glandular-serrate.

in *A. octandra*, or a somewhat dentate margin, e.g., in *A. serrata*, is present (Fig. 3.1). The incision is correlated with the placing of the marginal glands. The apex is usually acuminate to cuspidate, but occasionally also caudate or acute. The length of the leaf ranges from up to 5 cm in, e.g., *A. parvula*, to more than 40 cm in, e.g., *A. lunata* or *A. benthamiana*. Figure 3.2 shows the size ranges of some leaf parts.

As can be deduced from the ranges in Fig. 3.2, sizes are of restricted use in species delimitation. The smallest and the largest leaved species are clearly distinct from each other, but they are connected by all possible intermediates. The shape of the base, apex, and lamina is an analogous story. Extreme shapes like the elliptic leaves of *A. elmeri* or the acute apex of *A. tetrapleura* are conspicuously different from the narrowly obovate leaves of *A. bourdillonii* or the caudate apex of *A. maingayi*, but neither of them is separable from, e.g., the narrowly elliptic leaf with acuminate to cuspidate apex of *A. nervosa*. Nevertheless, the extremes can be delimitated on size and shape, even if the intermediates remain problematic. Therefore, I have used both size and shape for identification and phylogeny.

Some of the species of the *A. frutescens*-group carry on the upper surface of the leaf small white granules; *A. chondroneura* bears many of these scattered over the veins on the lower side. These granules might be caused by druses in the mesophyll (paragraph 4.2, cf. Fig. 4.6).

The thickness of the leaves is a continuously varying character that is hard to define. It is more a comparative character. When a species with thick, shiny leaves is placed side by side with a species with dull, papery (dried) leaves, then the distinction is obvious. In this way, mature leaves of, e.g., *A. prainiana* and *A. symplocoides*, *A. chondroneura* and *A. nitida*, *A. cardiosperma* and *A. latifolia*, or *A. octandra* var. *yunnanensis* and *A. villosa*, are separated. The difference between papery and leathery leaves helps in these cases to delimit the species, and I have thus used it as an diagnostic and phylogenetically informative character. It is, however, variable and only reliable in mature leaves.


a. Petiole length
mm
0
10
20
30
40
50
60
70
80
90
100
b. Leaf length
cm
0
10
20
30
40
50
c. Leaf width
cm
0
5
10
15
20
d. Pairs of nerves
n
0
5
10
15
20
25
1
11
21
31
41
51
61
71
81
91
101
Aporosa spp.

One of the more useful characters in the herbarium is the colour of the dried leaves. Herbarium specimens of *Aporosa* have either greenish or brownish leaves, depending on the aluminium content of the leaf (Chenery, 1948). High concentrations of aluminium result in shiny yellow to yellowish green leaves, e.g., in *A. aurea*, *A. symplocifolia* or related species. Slightly lower concentrations of aluminium in the leaves are reflected in a more greyish green drying colour; examples are *A. alia*, *A. globifera*, and all the species in the *A. frutescens*-group. Species with low concentrations of aluminium dry a variable kind of brown. The phenomenon is independent of the method used for drying. In the field all species have (dark) green leaves.

A distinctive feature of *Aporosa* – and according to Webster (1994b) also of other members of the tribe Antidesminae – is the presence of small black dots on the upper surface of dried leaves, only to be observed with a hand-lens. The arrangement of these dots is rather specific. They can be more or less densely scattered, more or less distinct, large or small, blackish to greyish or brownish.

Foliar glands — Three types of glands are found in *Aporosa* leaves. In transverse view they have a similar anatomical structure consisting of elongated epidermal cells (cf. Fig. 4.3b). In surface view, however, the three appear different because of their various positions. They can be arranged a) at the base of the leaf on the transition between the petiole and the lamina; b) along the margin; c) on the lower side of the lamina.

a) One pair of basal glands is sometimes present on the edge of either side of the lamina at the apex of the petiole. They look like small, brownish to greyish, or large, black protrusions, or appear as bunches of hairs. They occur typically in a majority of the species of the *A. octandra*-group, and occasionally in others as well.
b) The marginal glands are found at the apex of the veinlets where these reach the margin. Usually, they just look like tiny indentations. Depending on the size and distinctiveness of these glands, the margin is undulate to glandular crenate, with the veinlet-ends at the indentations (Fig. 3.1). In other cases, the marginal glands are more pronounced or densely hairy. Then the margin is more glandular-dentate or glandular-serrate, with the veinlet-ends on the outer curve of the indentations. All species of *Aporosa* except *A. aurea* have marginal glands.
c) The third type of glands occurs on the lower surface of the leaf. They are disc-shaped, slightly sunken, and brownish when dry. These disc-like glands are positioned in various configurations (Fig. 3.3). *Aporosa nervosa*, *A. frutescens*, and their relatives have disc-like glands occasionally present near the margin. They are neither always present on all leaves, nor in a symmetric pattern: occurrence of disc-like glands along the margin of one leaf has no relation with presence, number, and position of the glands along the other margin of the same or another leaf (Fig. 3.3b). The five species in the *A. benthamiana*-group have many, distinct, disc-like glands scattered along the margin (Fig. 3.3c). This feature is shared by some of the New Guinean species, especially *A. laxiflora*. Most New Guinean species, however, have disc-like glands concentrated at the base of the leaf (Fig. 3.3a). The third possibility, disc-like glands unevenly scattered within the arches

←

Fig. 3.2. Variation in size ranges of various leaf parts. — a. Petiole length; b. leaf length; c. leaf width; d. pairs of nerves.

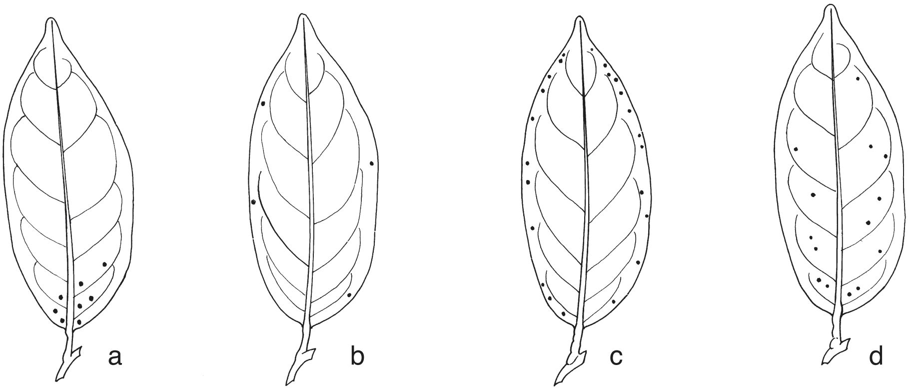


Fig. 3.3. Schematic overview of the placement of the disc-like glands on the lower side of the leaves. — a. Scattered at the base; b. occasionally few along the margin; c. regular along the margin; d. scattered within the marginal arches.

of the marginal veins throughout the lamina, is shown by *A. ledermanniana* and all species of the *A. octandra*-group, with the exception of *A. nigricans* (Fig. 3.3d).

The function of the glands is unknown. Extra-floral nectaries are reported to be common in leaves of other Euphorbiaceae (Metcalfe & Chalk, 1957).

Foliar glands are often classified as a derived character within the Euphorbiaceae. Webster (1994a) reports a restricted occurrence of foliar glands in the Phyllanthoideae and Oldfieldioideae, but does not mention *Aporosa* or the Scepinae. This study shows that at least *Aporosa* has a variety of glands. Other genera may also have foliar glands that have gone unnoticed because of their relatively unspecialized type. A revision of *Baccaurea* has indicated that foliar glands are also common in this genus (Haegens, 2000). This raises question marks on what is primitive and derived.

Nervation — The nervation of the various species of *Aporosa* is rather uniform. Group-specific variation lies largely in the degree of protrusion of the nervation, but is only perceptible when species are compared. *Aporosa lunata*, *A. bullatissima*, *A. ficifolia*, and to a lesser extent also *A. decipiens*, are recognizable by their strongly sunken nervation on the upper side.

Slight differences are also present in the number of pairs of nerves. There are usually 7–13 pairs of nerves (Fig. 3.2d). *Aporosa microstachya* is striking with its 4–6 pairs of nerves, *A. grandistipula* with its 17–23 pairs. Only these extremes can be defined.

Inflorescences

The inflorescences are basically cymes, as usual in Euphorbiaceae. However, as the side axes are completely reduced, the inflorescences appear to be simple spikes. Typically, *Aporosa* carries its inflorescences axillary or just below the leaves. *Aporosa benthamiana* is usually ramiflorous. A couple of other species, e.g., *A. arborea*, *A. lunata*, *A. nitida*, and a number of New Guinea species often combine ramiflory with inflorescences just below the leaves.

There is a continuous range in length and diameter of inflorescences, ranging from a short and thin rachis (c. 4 by 0.2 mm) to a long and thick rachis (up to c. 100 by 5 mm). Comparable with leaf sizes, the extremes are distinct, but connected by a range of intermediates (Fig. 3.4). Despite the evident overlap, however, a particular combination of length and diameter is, at least in West Malesian species, characteristic for the more derived sections (see the description of the staminate and pistillate inflorescences). The same is true for the indumentum. The extremes in length, diameter, and indumentum of the inflorescences are, just like those of the leaves, distinct and thus useful, while the intermediates are all alike.

The staminate and pistillate inflorescences are similar in the above aspects: differences are found in the number of flowers and their position. Staminate inflorescences have many small flowers packed in clusters, the glomerules, along the rachis, enclosed by one bract, which is usually as long as the glomerule. Bracteoles are absent. Pistillate inflorescences carry single flowers along the rachis, each accompanied by one bract and two bracteoles. The inflorescences are categorized into five types based on arrangement of the glomerules or pistillate flowers along the rachis. Within each type one class of length, diameter, and indumentum of the rachis is pre-eminent, but exceptions are quite common. Especially the New Guinean species show different combinations.

Staminate inflorescences (Fig. 3.5) — The five arrangements of the glomerules along the rachis are: a) continuous; b) continuous, but leaving the base of the rachis bare; c) variable; d) interrupted; and e) massed in an apical head. Within these types a subdivision is possible based on the compactness of the glomerules, i.e., the number of flowers in it and their density, and the general shape of the glomerule. The relative size of the bract compared with the size of the glomerule can also be used. These differences in compactness of the glomerules and size of the bracts, however, show more overlap then the type of inflorescence. Therefore, for specific delimitation, the latter is the more important character; the former can only be used in combination with this.

The types are defined to include the New Guinean species, though they often look different. This is caused by different combinations of indumentum, size, and type of inflorescence.

The types and subtypes in combination with size and indumentum of the rachis are:

a) glomerules continuously set; rachis floriferous to the base (Fig. 3.5a, b). The rachis is often average in length, i.e., 15–25 mm, and c. 2 mm in diameter, and (densely) tomentose or sericeous, but this is often invisible under the densely and continuously set glomerules. There are two subtypes: inflorescences with the glomerules separated by distinct bracts, such as in the species of the *A. octandra*-group, and with the glomerules indistinct, like in *A. planchoniana* or *A. microstachya*. The distinction between these subtypes is not always clear. The New Guinean intermediate species *A. misimana, A. leptochrysandra*, and *A. spec. C* are also of this type. They differ in a thinner diameter and very laxly set flowers (Fig. 3.5m).

(*Text continued on page 31*)

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Fig. 3.4. Variation in the size ranges for various reproductive organs. — a. Staminate inflorescence length; b. staminate inflorescence diameter; c. pistillate inflorescence length; d. pistillate inflorescence diameter; e. staminate flower length; f. stigma length; g. fruit length; h. pericarp thickness.

Fig. 3.4.

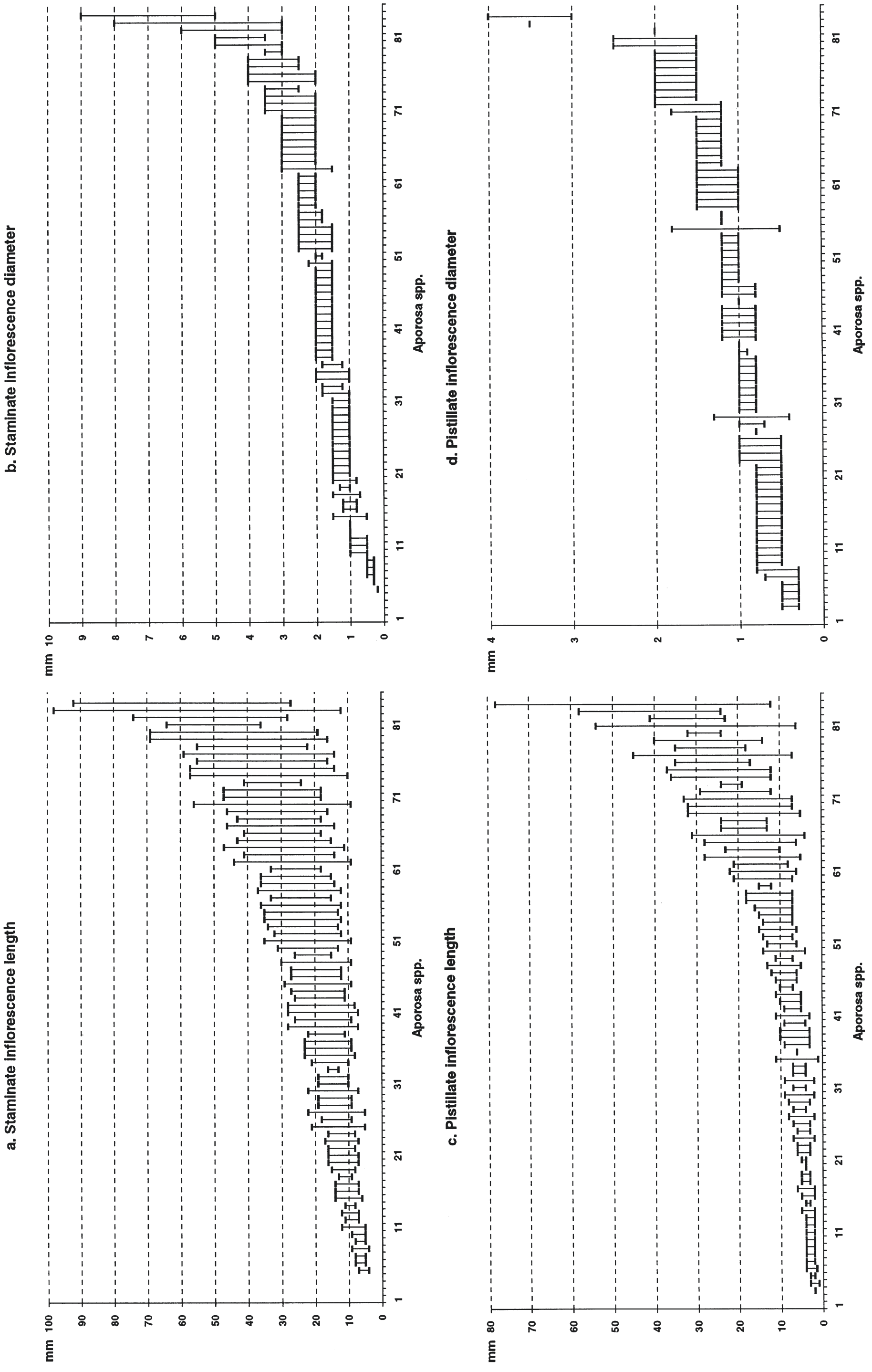
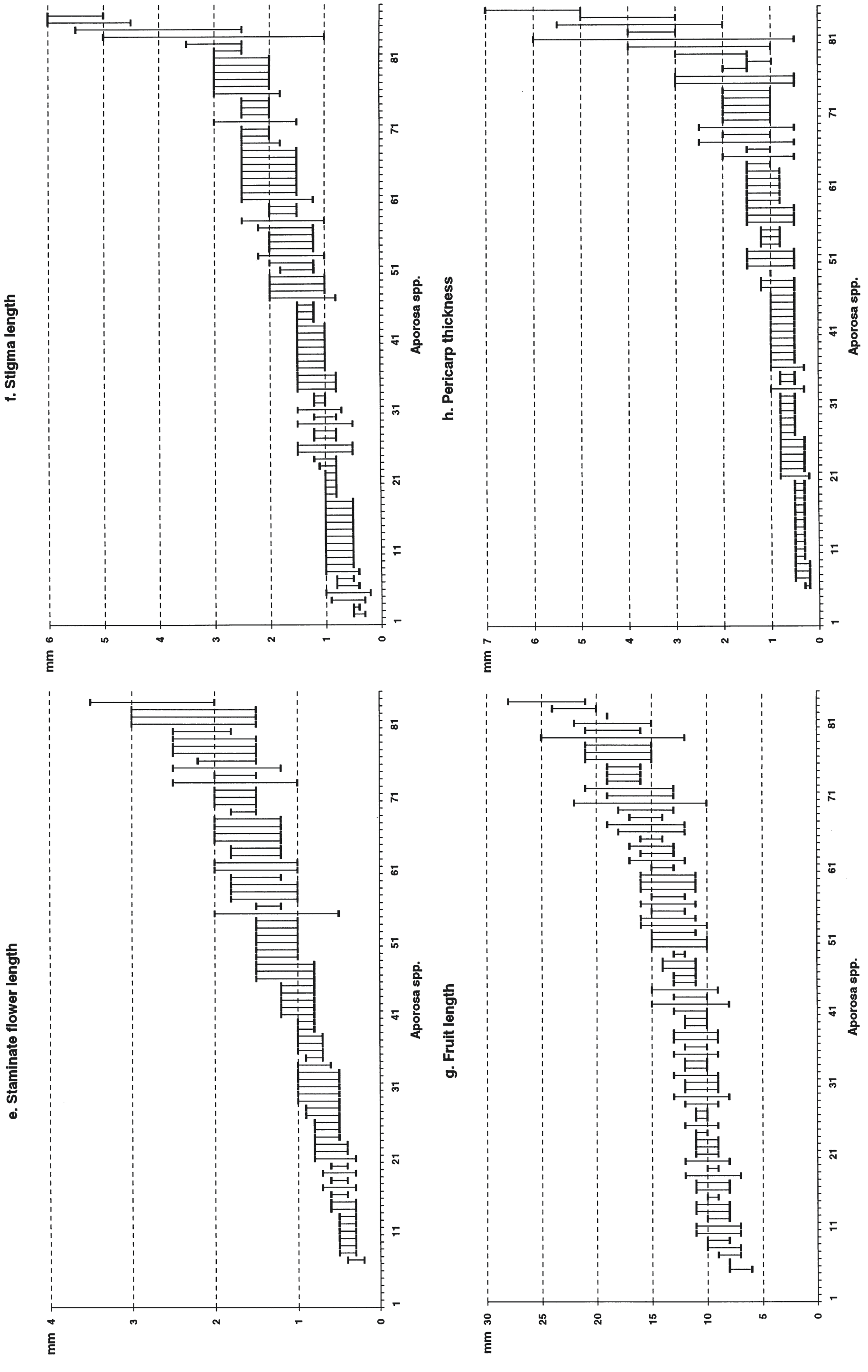

a. Staminate inflorescence length
mm
100
90
80
70
60
50
40
30
20
10
0
1
11
21
31
41
51
61
71
81
Aporosa spp.
b. Staminate inflorescence diameter
mm
10
9
8
7
6
5
4
3
2
1
0
1
11
21
31
41
51
61
71
81
Aporosa spp.
c. Pistillate inflorescence length
mm
80
70
60
50
40
30
20
10
0
1
11
21
31
41
51
61
71
81
Aporosa spp.
d. Pistillate inflorescence diameter
mm
4
3
2
1
0
1
11
21
31
41
51
61
71
81
Aporosa spp.

Fig. 3.4 (*continued*)



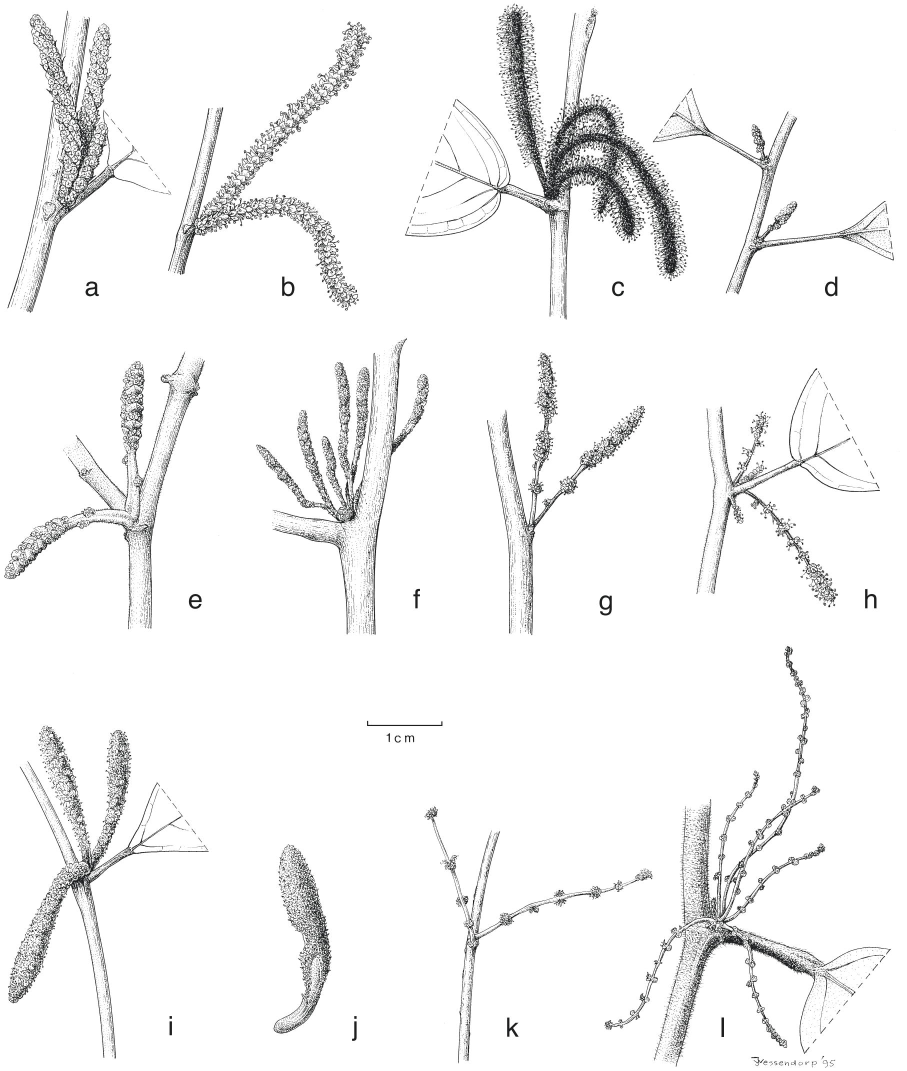
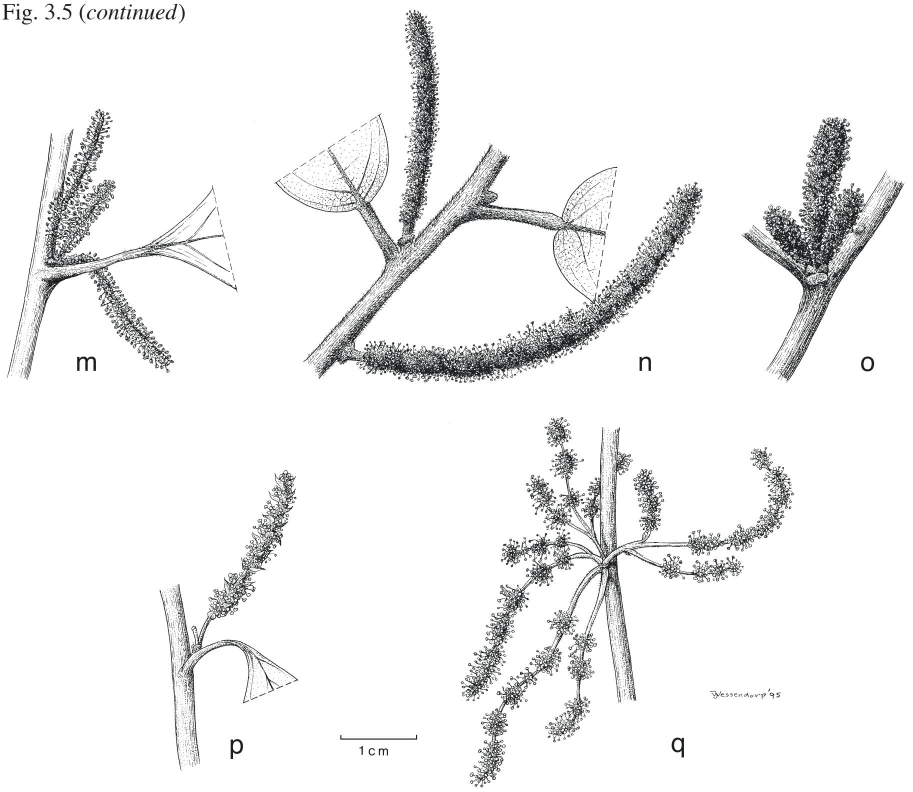


Fig. 3.5. Types of staminate inflorescence. a, b, m: glomerules continuously set; c, d, n–p: glomerules continuously set but with a bare rachis; e–h, q: intermediate types; k, l: glomerules interruptedly set; i, j: glomerules massed in an apical head. — a. *Aporosa octandra* (Buch.-Ham. ex D. Don) Vickery var. *malesiana* Schot (*Meijer 6707*); b. *A. yunnanensis* (Pax & K. Hoffm.) F.P. Metcalf (*Put 3529*); c. *A. falcifera* Hook.f. (*Hose 40*); d. *A. granularis* Airy Shaw (*Ambriansyah & Arifin AA 157*); e. *A. subcaudata* Merr. (*S 23379*); f. *A. stellifera* Hook.f. (*KEP FRI 7981*); g. *A. banahaensis* (Elmer) Merr. (*FB 7279*); h. *A. lagenocarpa* Airy Shaw (*Jacobs 5102*); i. *A. frutescens* Blume (*Maxwell 82-35*); j. *A. nitida* Merr. (*Jacobs 5196*); k. *A. prainiana* King ex Gage (*KLU 1183*); l. *A. elmeri* Merr. (*SAN 29685*); m. *A. leptochrysandra* Airy Shaw (*Darbyshire & Hoogland 8375*) n. *A. papuana* Pax & K. Hoffm. (*Schlechter 18654*); o. *A. vagans* Schot (*Brass 32343*); p. *A. brevicaudata* Pax & K. Hoffm. (*Eyma 4303*) q. *A. ledermanniana* Pax & K. Hoffm. (*NGF 35127*). All specimens from L.

Fig. 3.5 (*continued*)



b) glomerules continuously set at the apical 3/4th to 7/8th of the rachis; the lower part, the peduncle, is sterile (Fig. 3.5c, d). This type is either average in length and c. 2 mm in diameter, and (densely) tomentose to sericeous (Fig. 3.5c: the *benthamiana*-group) or less than 15 mm long, average in diameter, and sparsely puberulous to subglabrous (Fig. 3.5d: the species around *A. maingayi*). The sericeous inflorescences are also characterized by ellipsoid glomerules with up to 10 densely set flowers, and the sparsely puberulous ones by globose glomerules with up to 5 laxly set flowers. The two distinct groups of New Guinean species follow in this type their West-Malesian relatives, though with longer and thicker rachises and more and larger flowers (Fig. 3.5n–p: the species around *A. papuana* and around *A. brevicaudata*, respectively).

c) intermediates (Fig. 3.5e–h). The glomerules are interruptedly set at the base of the rachis, and continuously at the apex. Size and indumentum are variable. This group is hard to define, for it is actually characterized as ‘not type a, b, d, or e’. This type is also divided into those with ellipsoid and those with globose glomerules, but no particular combination is common. Most of the intermediate New Guinean species show this type. They are very variable in the placement of the glomerules, but consistent in the laxly set subglobose flowers and exserted stamens (Fig. 3.5q).

d) glomerules interruptedly set along the whole rachis (Fig. 3.5k, l). The rachis is often rather long, 30–70 mm, slender, with a diameter of about 0.8 mm, and sparsely puberulous to subglabrous. This type has small globose, lax glomerules, except for the ellipsoid ones of *A. stenostachys*. It is characteristic for the more primitive species of the *frutescens*-group, but also found in a couple of other species. Strictly speaking, the New Guinean *A. nigropunctata* and *A. laxiflora* belong to this type, but are more similar to the intermediate type because of the laxly set flowers with exserted stamens.

e) glomerules massed in an apical head (Fig. 3.5i, j). The rachis is clavate, with the apical part broadened, up to 9 mm in diameter. The glomerules are densely packed on this part. This is a specialized type, found only in *A. confusa*, *A. nitida*, and *A. quadrilocularis*. *Aporosa frutescens* is a borderline case. The typical forms of Java, Sumatra, the Malay Peninsula, and partly Borneo, are distinctly clavate; but at the periphery of the range – in Thailand and the Philippines – the inflorescences of *A. frutescens* are nearly cylindrical.

Pistillate inflorescences (Fig. 3.6) — The pistillate inflorescences are, analogous to the staminate ones, divided into five types based on the setting of the flowers along the rachis: a) densely set; b) densely set, but leaving the base of the rachis bare; c) intermediate between a–d; d) laxly set; and e) uniflorous. Similar to the staminate inflorescences, there is a correlation between inflorescence type and length, diameter, and indumentum of the rachis. Besides this, the pedicel length and number of carpels are also usually consistent within one type of pistillate inflorescence. New Guinean species are either laxly set or show a likeness to type b, and I have defined this type in a manner to accommodate for these species.

The five types and their common associations with size, indumentum, pedicels, and locularity are:

a) flowers continuously and densely set; rachis floriferous to the base (Fig. 3.6a–d). As in staminate type a, the rachis is often average in length, c. 2 mm in diameter, and (densely) tomentose or sericeous. Furthermore, the flowers are sessile – except in *A. cardiosperma* – and often 2-locular.

b) flowers densely set at the apical 3/4th to 7/8th of the rachis; the lower part is barren (Fig. 3.6e–h, l). The flowers are mostly (sub)sessile. This type is either small and sparsely puberulous to subglabrous or large and tomentose. The small ones bear often 2-locular flowers, the large ones 3-locular flowers. The difference between type a and b seems slight, but in comparison it is distinct. The lower part of the rachis in type a bears bracts and the scars of fallen flowers or fallen bracts; in type b the lower part of the rachis shows no sign of ever having carried flowers, only sterile bracts are occasionally present. In fruit this is also the distinction between these two types (cf. Fig. 3.6i with 3.6j, k). Part of the New Guinean species have apically clustered subsessile flowers (Fig. 3.6w, x) and are included in this type. The length of the rachis can, however, be longer than in the Sundanese species. Since the number of flowers placed along the rachis is equal, it appears that these New Guinean species have more laxly set flowers. In the phylogenetic analysis I have coded these as 'rather densely' set, but the difference is a slight one.

c) intermediates (Fig. 3.6m–q). The flowers are more or less densely set, often less so at the base of the rachis, and more so at the apex. Size, indumentum, pedicel length, and locularity are variable and no particular combination exists. This group contains those inflorescences that are best characterized as 'somewhat like type x, but not quite, and not always'. Their characters might partly fit in some type, but then, e.g., the size or locularity would be wrong. They are often also rather variable. The New Guinean intermediate species fit best into this type.

d) flowers laxly set along the rachis (Fig. 3.6r–t). As in staminate type d, the rachis is often rather long, slender, with a diameter of about 0.8 mm, and sparsely puberulous to subglabrous. The flowers are distinctly pedicelled. Both 2- and 3-locular flowers occur. Some of the New Guinean species also belong here (Fig. 3.6y, z).

e) uniflorous (Fig. 3.6u, v). Only the topmost flower develops, the axillary buds are dormant. They develop only when the top one is lost. The length of the rachis is variable, but the diameter is usually about 1 mm. The flower is pedicelled and 3- or more locular. This type has no parallel within the staminate inflorescences and is found only in the species around *A. frutescens*.

The inflorescence type proved to be one of the characters with a high consistency index in the phylogenetic analysis, and is thus also one of the fundamental characters for the new classification (see paragraph 9.4).

Flowers

The flowers of *Aporosa* are small and unisexual, except for the exceptional hermaphroditic species of New Guinea. They are sessile or pedicelled, and consist of one whorl of 3–5(–7) sepals, usually 0.5–1 mm long, and either one whorl of 2–4 stamens and a pistillode or a pistil. Petals and disc are absent, though petal-like structures can sometimes occur. The indumentum is variable as in many other organs in *Aporosa*.

Staminate flower — The small, usually sessile, staminate flower with 2–4 stamens is typical for genus *Aporosa* (Fig. 3.7). The slight differences between the species are mostly found in the length of the pedicel, the number, length, and indument of the sepals and stamens, and the size of the pistillode. Only the more interesting features and their connection with the type of inflorescence are discussed here.

The staminate flower is mostly sessile. Some species, e.g., *A. ficifolia*, *A. papuana*, or *A. macrophylla*, regularly have a distinct pedicel. Other species, such as *A. sphaeridiophora*, *A. basilanensis*, or *A. grandistipula*, sometimes have a broad protrusion at the base of the sepals that may be interpreted as a pedicel. The length of the pedicel is very variable and correlated with the size of the glomerule. The distinctly pedicelled flowers occur only in large glomerules; the more apically placed flowers in the glomerule have the longest pedicels. In species with smaller glomerules the pedicel is short or absent. This pattern in length might be a way to increase the accessibility of the anthers to pollinators.

The number of sepals fluctuates around 4 or 5. When checking all flowers in one glomerule, the majority has 4 or 5 sepals, but often one or two flowers have either one sepal more or less. *Aporosa praegrandifolia* and *A. fulvovittata* seem to have up to 10 sepals, but as these particular flowers also have double numbers of stamens, it is more likely a case of an accidental doubling.

(*Text continued on page 37*)

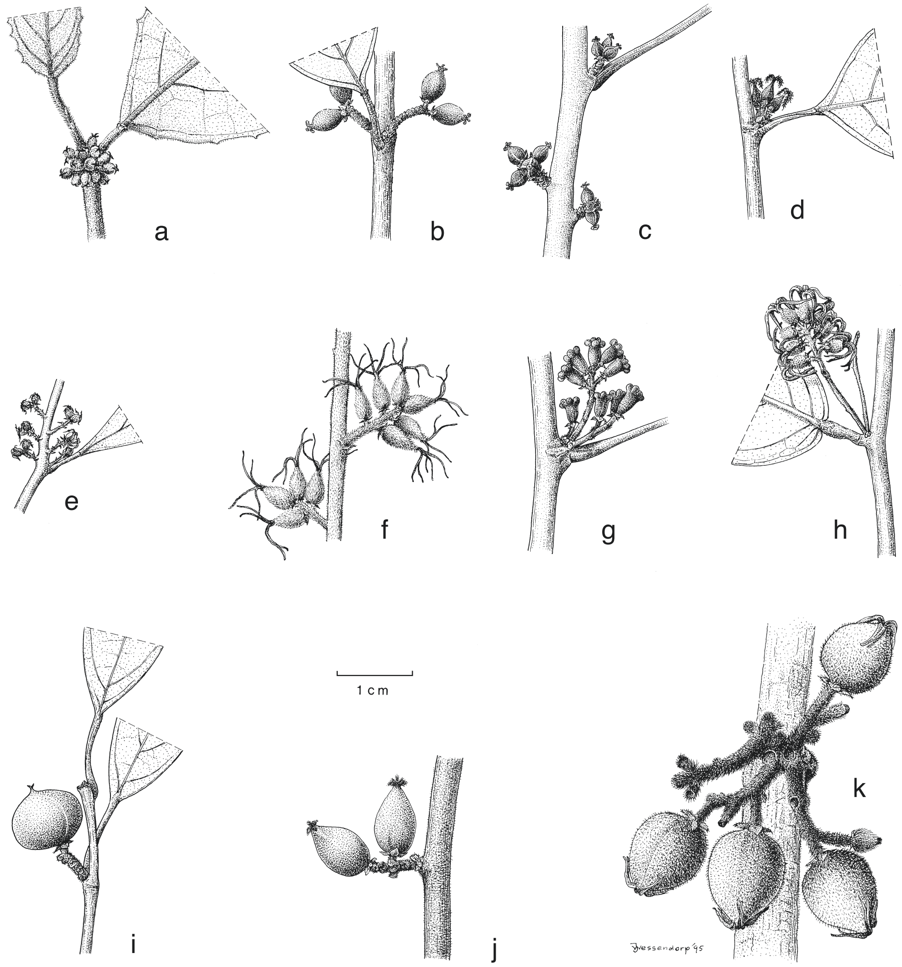
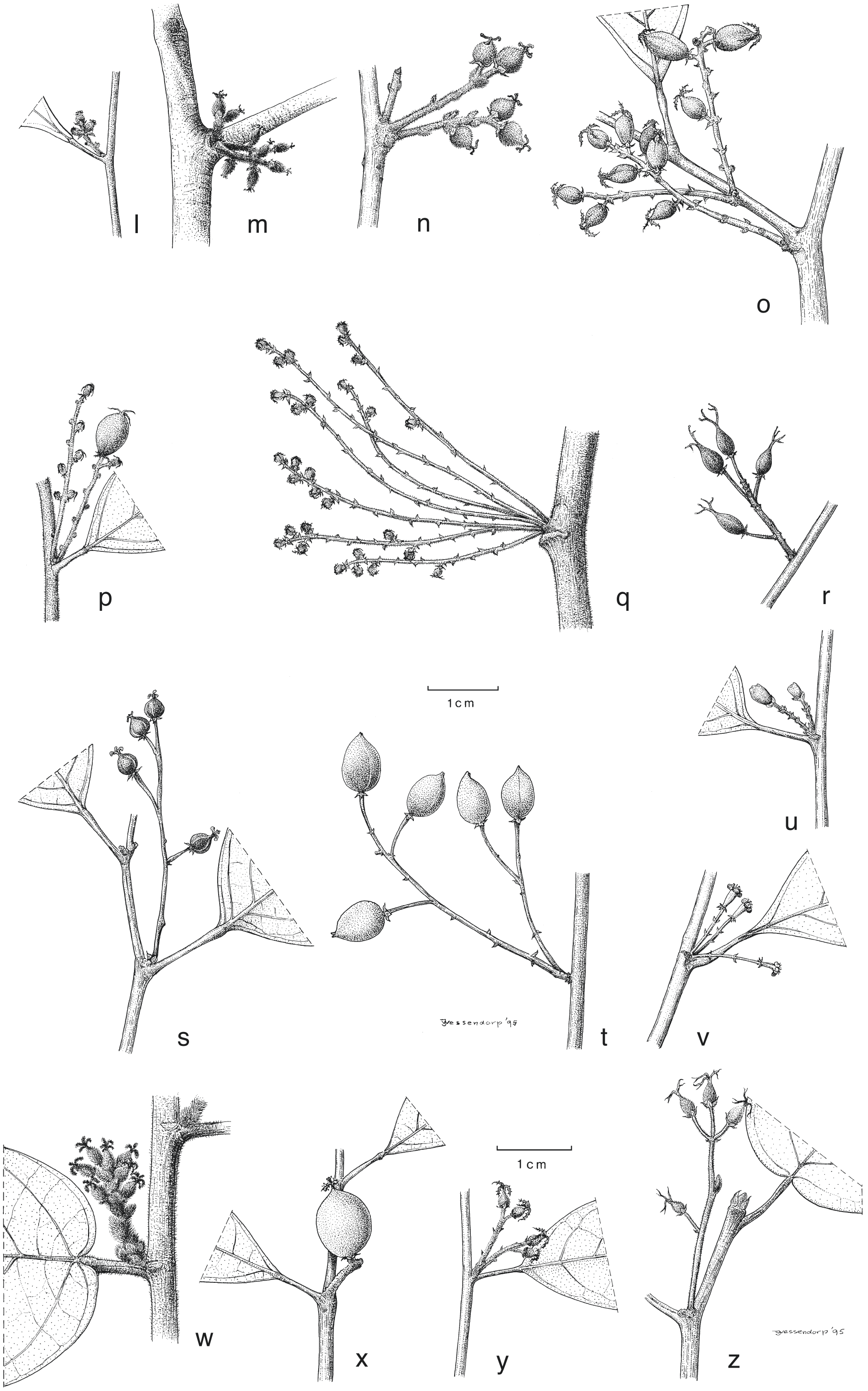


Fig. 3.6. Types of pistillate inflorescence. a–d: Flowers continuously and densely set; e–l, w, x: flowers densely set apically; m–q: intermediate types; r–t, y, z: flowers laxly set throughout the rachis; u, v: uniflorous. — a. *Aporosa serrata* Gagnep. (*Kerr 8776*); b. *A. octandra* (Buch.-Ham. ex D. Don) Vickery var. *malesiana* Schot (*Meijer 7094*); c. *A. aurea* Hook.f. (*KEP 105136*); d. *A. yunnanensis* (Pax & K. Hoffm.) F.P. Metcalf (*BKF 14382*); e. *A. granularis* Airy Shaw (*Jacobs 5193*); f. *A. lagenocarpa* Airy Shaw (*SAN 49765*); g. *A. stellifera* Hook.f. (*KEP FRI 14705*); h. *A. falcifera* Hook.f. (*Hose 92*); i. *A. lucida* (Miq.) Airy Shaw (*KEP FRI 10721*); j. *A. subcaudata* Merr. (*KEP FRI 14434*); k. *A. lunata* (Miq.) Kurz (*De Wilde & De Wilde-Duyfjes 12913*); l. *A. maingayi* Hook.f. (*KEP 105120*); m. *A. nervosa* Hook.f. (*Maxwell 86-277*); n. *A. leytensis* Merr. (*Wenzel 614*); o. *A. basilanensis* Merr. (*SAN 65446*); p. *A. rhacostyla* Airy Shaw (*S 28797*); q. *A. elmeri* Merr. (*Ridsdale 2067*); r. *A. antennifera* (Airy Shaw) Airy Shaw(*De Wilde & De Wilde-Duyfjes 15619*); s. *A. prainiana* King ex Gage (*KEP 99137*); t. *A. symplocoides* (Hook.f.) Gage (*King's collector 4288*); u. *A. sarawakensis* Schot (*S 14730*); v. *A. frutescens* Blume (*Maxwell 82-191*); w. *A. brassii* Mansfield (*Hartley 10739*); x. *A. misimana* Airy Shaw ex Schot (*Brass 27800*); y. *A. nigropunctata* Pax & K. Hoffm. (*Ledermann 9698)*; z. *A. carrii* Schot (*Carr 13285*). All specimens from L.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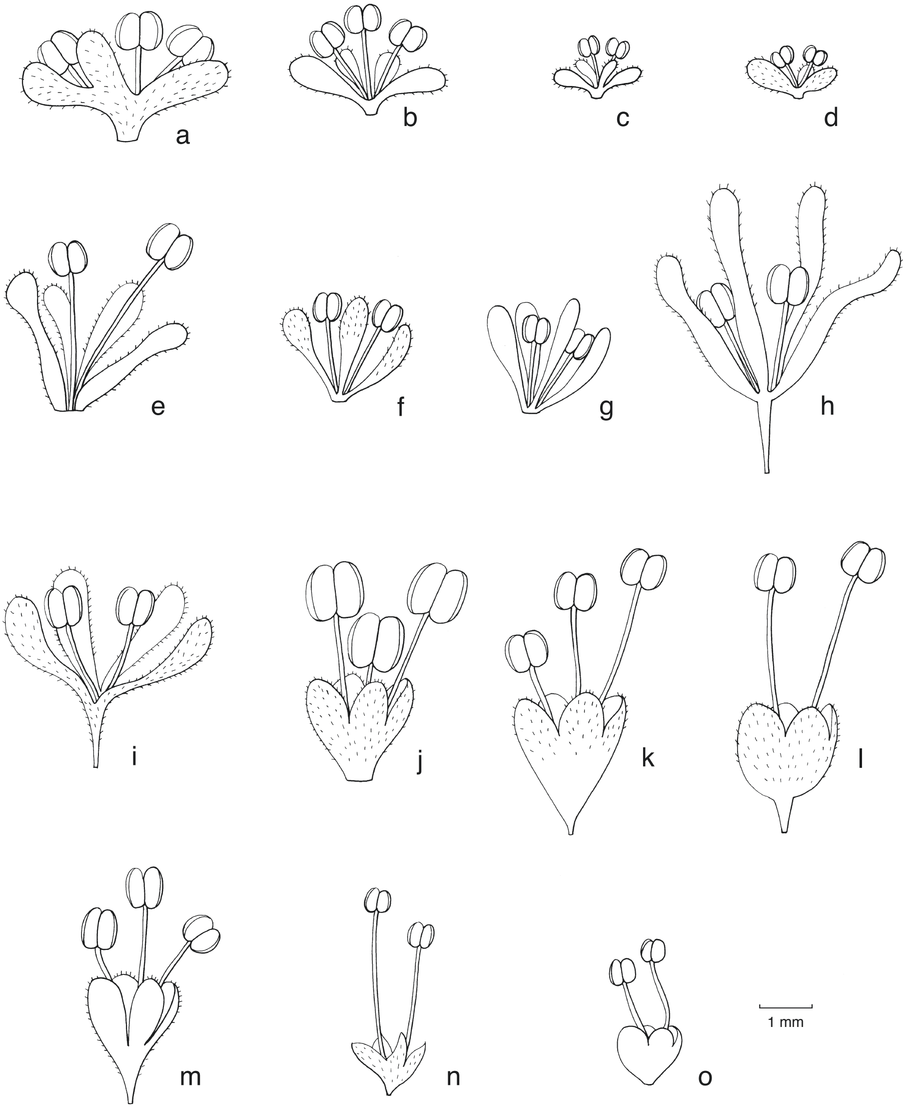

Fig. 3.7. Variation in the staminate flower. Note the differences in connection of the sepals and exertion of the stamens. — a. *Aporosa nervosa* Hook.f.; b. *A. grandistipula* Merr.; c. *A. frutescens* Blume; d. *A. elmeri* Merr.; e. *A. yunnanensis* (Pax & K. Hoffm.) F.P. Metcalf; f. *A. serrata* Gagnep.; g. *A. lanceolata* (Tul.) Thwaites; h. *A. macrophylla* (Tul.) Müll.Arg.; i. *A. ficifolia* Baill.; j. *A. sphaeridiophora* Merr.; k. *A. vagans* Schot; l. *A. papuana* Pax & K. Hoffm.; m. *A. ledermanniana* Pax & K. Hoffm.; n. *A. benthamiana* Hook.f.; o. *A. leptochrysandra* Airy Shaw. All specimens from L.

The sepals also vary in their degree of fusion: they can be free, connate at the base only, or campanulate. These differences form, together with the number of stamens and the relative length of the stamens, particular combinations. They correlate partly with the type of inflorescence. This is very helpful in the difficult task of subgrouping the species within one inflorescence type – especially in those cases where the compactness of the glomerule and indument and size of the rachis overlap, as in the intermediate type c.

The 'sepals connate at base'-condition is the most common one. It is found in part of the species with inflorescence types a, b, and c, and in all species with type d and e. The flowers of these latter types are small – hardly ever longer than 1 mm – and have usually 2 stamens, though every glomerule may harbour one or two flowers with 3 stamens. This extra stamen does not coincide with the presence of the extra sepal. The stamens are approximately of the same length as the sepals, i.e., they are not or slightly exserted.

Free sepals occur only in combination with the continuous inflorescences, type a. They are found in the species around *A. aurea*, where they are often connate to the rachis, which makes it very hard to find the individual flowers. These flowers have almost always two stamens, which are usually not exserted.

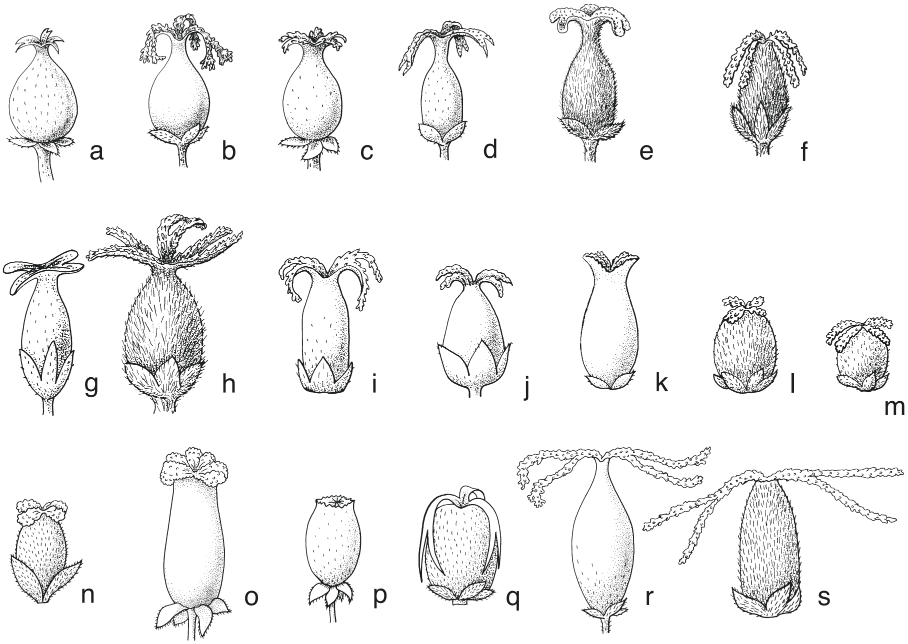

Fig. 3.8. Variation in the pistillate flower. Note the differences in stigma shape, length, and structure. — a. *Aporosa arborea* (Blume) Müll.Arg.; b. *A. dendroidea* Schot; c. *A. whitmorei* Airy Shaw; d. *A. ledermanniana* Pax & K. Hoffm.; e. *A. leytensis* Merr.; f. *A. basilanensis* Merr.; g. *A. brevicaudata* Pax & K. Hoffm.; h. *A. brassii* Mansfield; i. *A. misimana* Airy Shaw ex Schot; j. *A. sphaeridiophora* Merr.; k. *A. planchoniana* Baill. ex Müll.Arg.; l. *A. serrata* Gagnep.; m. *A. elmeri* Merr.; n. *A. penangensis* (Ridl.) Airy Shaw; o. *A. sarawakensis* Schot; p. *A. frutescens* Blume; q. *A. benthamiana* Hook.f.; r. *A. antennifera* (Airy Shaw) Airy Shaw; s. *A. lagenocarpa* Airy Shaw. All specimens from L.

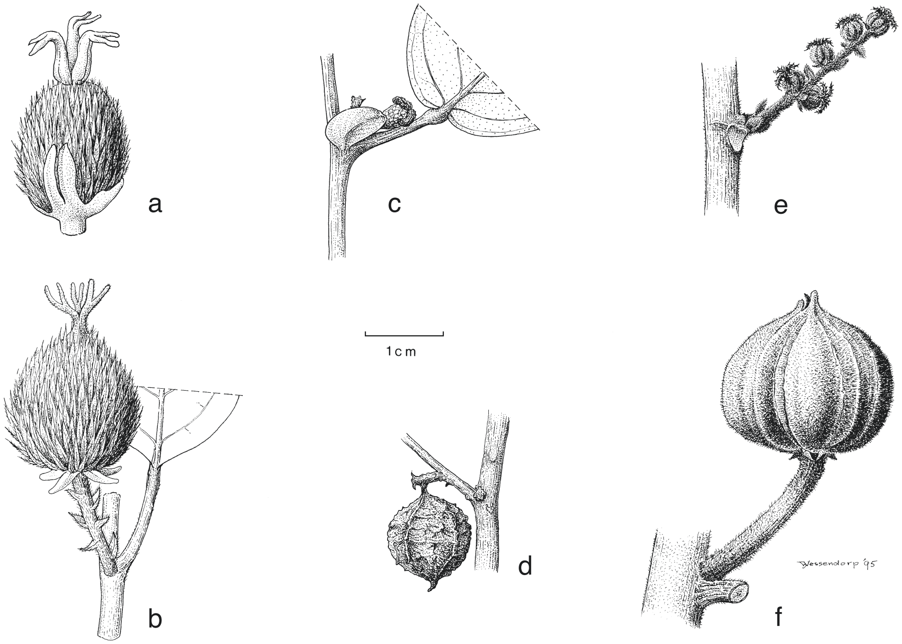

Fig. 3.9. Ornamentation types of the ovary. — a, b. Tuberculate ovary and fruit of *Aporosa bourdillonii* Stapf; c, d. ruminate-verrucate ovary and fruit of *A. selangorica* Pax & K. Hoffm.; e, f. lamellate ovary and fruit of *A. lamellata* Airy Shaw (a, b: after Stapf, 1894; c: *Ridley 13384*; d: *Van Balgooy & Stone 2035*; e: *NGF 42544*; f: *Schodde & Craven 5031*; all L).

The campanulate staminate flowers are the largest flowers in *Aporosa*. They can reach a length of about 3 mm. The 3 or 4 stamens are more or less exserted. They correlate with the larger inflorescences of type b and c. *Aporosa nervosa* and allies, almost all New Guinean species, and the five species of the *A. benthamiana*-group have these campanulate flowers. These latter are very characteristic in their combination of type b and the densely packed flowers with strongly exserted stamens. Together this results in a brush-like appearance of the mature inflorescences (cf. Fig. 3.5c).

Pistillate flower — Pistillate flowers have 3–7 sepals and a pistil. Variation is found in the length of the pedicel, number, direction, thickness, and indumentum of the sepals, indumentum, locularity, and ornamentation of the ovary, and in the structure of the stigma (Fig. 3.8). The correlation of the presence of a pedicel and of the number of carpels with a particular inflorescence type has already been described. Other important variation is discussed here.

The sepals in the mature flower can be ascending, patent, or reflexed. The ascending sepals are often partly connate. The reflexed sepals are in many cases thick and fleshy. These thick, fleshy, reflexed sepals are an exclusive feature of the uniflorous inflorescences (type e).

Sometimes two or three whitish, petal-like structures or staminodes can be found between the sepals and the ovary. They are not always present in all individuals of one species, or in every flower of the same individual. I do not know their origin. Webster (1994a) reports that within the Euphorbiaceae petals are rarely present, and if present, then rather in staminate flowers than in the pistillate flowers. The observed structures might also be homologous with stamens or with disc lobes.

The locularity of the ovary has already been discussed. Another noteworthy feature of the ovary is the unique ornamentation found in *A. bourdillonii*, *A. lamellata*, and *A. selangorica* (Fig. 3.9). These three types of ornamentation represent three of the few autapomorphic features found in *Aporosa* species.

The length and shape of the style – if present – is rather variable. It proved a bit troublesome to describe it in such a manner that the terminology remained comparable between the species. According to Webster (1994a), the styles of the Euphorbiaceae are commonly connate at the base and free and bifid apically. In *Aporosa* both the connection at the base and the free arms can independently be more or less reduced. The basic problem in describing the style is to define where the ovary ends and the style begins. Morphologically there is no difference. To solve this for *Aporosa* I decided not to describe a style, but differentiate between the base and apex of the style as respectively 'ovary not/slightly/distinctly tapering at the apex' and 'style remnant absent/present beneath'. So, the West Malesian small-leaved species around *A. maingayi* are characterized by not tapering ovaries and stigmas without style remnant. The more typical Euphorbiaceous stigmas, such as found in *A. arborea* and relatives and most of the New Guinean species, are described as having a tapering ovary and stigmas with a style remnant beneath.

The stigmas are bifid to bipartite, and variable in direction, length, shape, and structure. The direction can be upwards, patent, or curving down to the sides of the ovary, the length varies between 0.5 and 6 mm, and the shape between narrow, which is more than 10 times as long as broad, to broad, which is approximately as long as broad. The structure of the stigmatic tissue can be anything from almost smooth to densely laciniate (cf. Fig. 3.6). The epidermis of the lower side is smooth to slightly papillate. The combination of these character states is very species specific.

Hermaphroditic flowers — The bisexual flowers are pedicelled and possess sepals, stamens, and a pistil (Fig. 3.10). The sepals and pistil are comparable to those of the pistillate flowers, the stamens to those of the staminate flowers. They are present in *A. hermaphrodita*, *A. heterodoxa*, and occasionally in *A. brevicaudata, A. egregia,* and

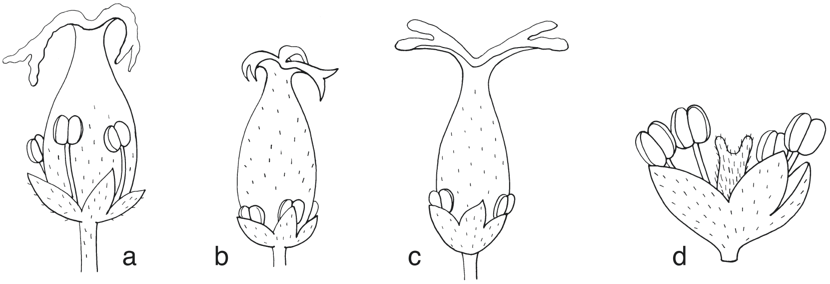

Fig. 3.10. Hermaphrodite flowers. — a. *Aporosa hermaphrodita* Airy Shaw; b. *A. heterodoxa* Airy Shaw; c. *A. egregia* Airy Shaw; d. hermaphroditic form of *A. carrii* Schot. All specimens from L.

A. parvula. *Aporosa hermaphrodita* and *A. heterodoxa* have 4 stamens, *A. brevicaudata, A. egregia*, and *A. parvula* have 2. The pollen is the same as in all other *Aporosa* species. The feature seems to correlate with a higher altitude: all six species are restricted to forests above 1000 m. In addition they appear very locally.

The phenomenon of having hermaphrodite flowers is rare within the Euphorbiaceae. An occasional hermaphrodite has been recorded in *Drypetes*, *Endospermum*, and *Jatropha*, but here they might be regarded as abnormalities. Usually no fruits were found in the hermaphroditic specimens of these three genera. In contrast, the hermaphroditic flowers in *Aporosa* have all aspects of full functionality: no strictly staminate specimens have been found, and the hermaphrodites develop normal fruits. Selfing might occur, but that does not change the fact that the flowers are functionally hermaphrodite.

If the two fully hermaphroditic species are compared with each other, then a parallel development of the hermaphrodite state is possible. For example, *A. hermaphrodita* has a 2-locular ellipsoid or ovoid fruit, *A. heterodoxa* a 3-locular globose one; *A. hermaphrodita* is sparsely puberulous, *A. heterodoxa* is subglabrous. There is also a geographical separation.

The subhermaphroditic form of *A. carrii* near Wau is different. This form has staminate flowers that have large ‘pistillodes’, which can occasionally develop into fruits (Fig. 3.10d).

Fruit and seed

The fruit of *Aporosa* is a typical euphorbiaceous dry and dehiscent capsule (Fig. 3.11). When ripe, the fruit splits along the sutures and the centres of the locules (loculicidal and septicidal), leaving the 1–3(–4) bright red seeds dangling free from the persistent central column. The wall can split either from the top downward or from the bottom upward, but this is variable within a species and has no taxonomical value. Some species, e.g., *A. nitida* and relatives or the Sri Lankanese *A. latifolia*, have capsules with a fleshy pericarp that is only tardily dehiscent. Most fruits are small, 8–15 mm long, globose, ovoid, or ellipsoid. *Aporosa fusiformis*, *A. egregia*, *A. lagenocarpa*, and sometimes *A. antennifera* have fusiform fruits. The fleshy fruits reach a diameter of 25 mm in the herbarium, but have been recorded to be more than 30 mm across when fresh. Sometimes the fruit is stiped or beaked, depending on the tapering of the ovary.

The fruits are yellow when young and turn red with maturity. Whitmore (1973) notes a difference in the colour of splitting and non-splitting fruits. Field studies on *Aporosa* at Pasoh Forest, however, indicate that the fruits may take a rather long time to develop, but eventually all turn red and dehisce. The sepals and stigmas are persistent. The globose fruits of *A. frutescens*, *A. confusa*, *A. quadrilocularis*, and *A. nitida* attract attention in this respect: their fruit is very characteristic because of the sunken stigmas (Fig. 3.11l).

The pericarp is mostly 0.5–1.5 mm thick, but can reach about 6 mm in the mature fruit of, e.g., *A. banahaensis*. The other fleshy fruits have slightly thinner pericarps. The endocarp is horny, glabrous, and splits like the pericarp, but separately. In *A. prainiana*, *A. stellifera*, and *A. sarawakensis* the apex of the endocarp is elongated; it runs through the slightly fleshy pericarp to the stigmas.

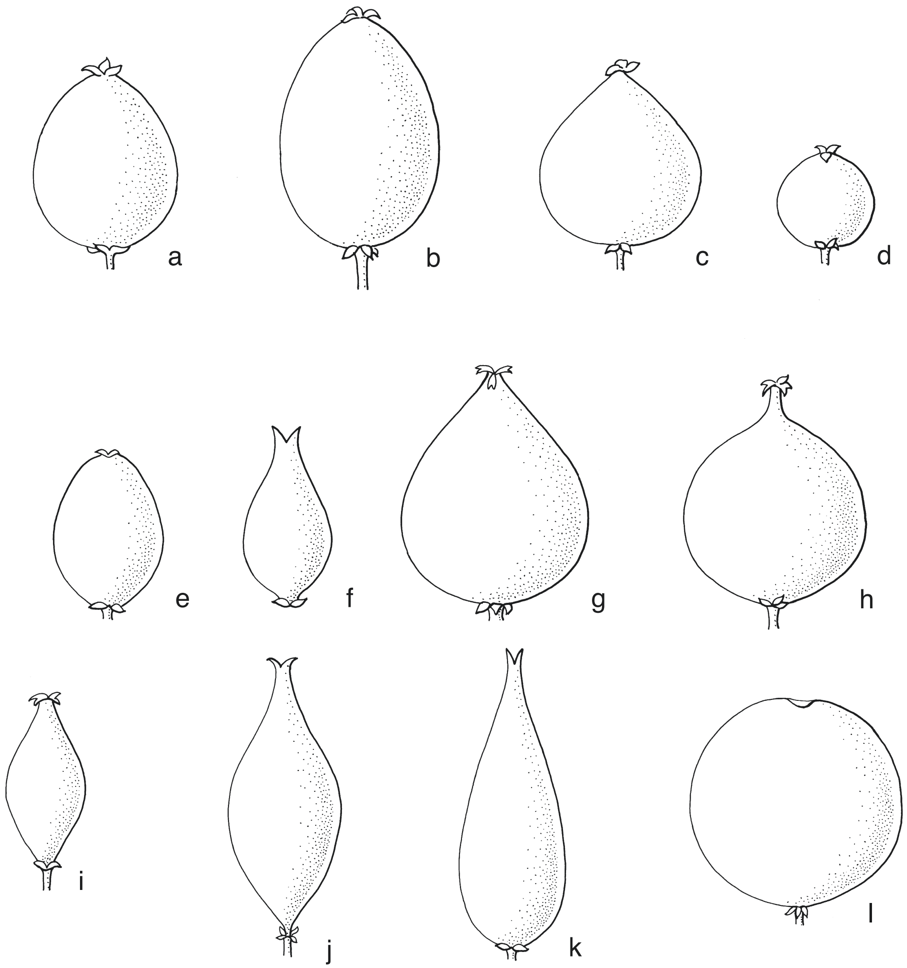

Fig. 3.11. Variation in outline of the fruit. — a. *Aporosa nervosa* Hook.f.; b. *A. arborea* (Blume) Müll.Arg.; c. *A. cardiosperma* (Gaertn.) Merr.; d. *A. lanceolata* (Tul.) Thwaites; e. *A. elmeri* Merr.; f. *A. planchoniana* Baill. ex Müll.Arg.; g. *A. benthamiana* Hook.f.; h. *A. dendroidea* Schot; i. *A. antennifera* (Airy Shaw) Airy Shaw; j. *A. brevicaudata* Pax & K. Hoffm.; k. *A. lagenocarpa* Airy Shaw; l. *A. frutescens* Blume. All specimens from L.

The *A. octandra*-group is unique because of the puberulous septae and column, though I have observed that they can be glabrescent in *A. globifera* and *A. lucida* var. *trilocularis*. This character is shared by no other species. The hairy ring at the base of the column in *A. annulata* is possibly not homologous.

Usually only one of the ovules per locule develops into a bright red seed; in some species even only one seed per fruit develops. The red colour is caused by a thin, fleshy, and sour arilloid. Immature seeds are still yellow. The seed coat is horny, hard, whitish-yellow, and often ribbed – at least in the herbarium.

Chapter 4

MICROMORPHOLOGY

4.1 – **General**

During this study only a limited number of *Aporosa* species were studied for several micromorphological features. These were: a) leaf surface studies of samples from 30 species – with transverse sections taken from six of them; b) pollen from 12 species; c) pistillate flowers from 9 species; and d) aluminium testing on four species. The material examined and the methods used are described in the appropriate paragraphs. To add to my own observations, literature was scanned for extra information.

None of the micromorphological characters were incorporated in the phylogenetic analysis. Some, however, will be used for comparison with the patterns of the cladogram based on macromorphological characters.

4.2 – **Leaf anatomy**

Material examined: *A. alia*: *Mogea 4443*; *A. antennifera*: *SAN 47642*; *A. arborea*: *KEP 108989*; *A. basilanensis*: *S 22504*; *A. brevicaudata*: *LAE 73416*; *A. cardiosperma*: *Kostermans 24403*; *A. carrii*: *Carr 13073*; *A. dendroidea*: *Van Balgooy 4598*; *A. elmeri*: *S 22999*; *A. globifera*: *Maxwell 81-62*; *A. falcifera*: *Kostermans 4993*; *A. hermaphrodita*: *Schodde (& Craven) 4989*; *A. laxiflora*: *Darbyshire 870*; *A. ledermanniana*: *NGF 35127*; *A. leytensis*: *Wenzel 587*; *A. lucida*: *Maxwell 82-84*; *A. maingayi*: *KEP-FRI 11351*; *A. misimana*: *NGF 27028*; *A. nervosa*: *Endert 139.E3.P817*; *A. nigricans*: *SAN 39290*; *A. octandra* var. *malesiana*: *Cuming 1724*; *A. papuana*: *Kanis 1388*; *A. praegrandifolia*: *Clemens 972*; *A. prainiana*: *Forbes 2958*; *A. quadrilocularis*: *De Wilde & De Wilde-Duyfjes 20761*; *A. sarawakensis*: *S 20985*; *A. subcaudata*: *KEP 104361*; *A. tetrapleura*: *Pierre 2858*; *A. vagans*: *NGF 15410*; *A. wallichii*: *Koelz 32622*.

Methods: For surface studies leaves were rehydrated by boiling and subsequently stored in alcohol 70%. Small portions were cut and cleared by soaking in 5% KOH at 45 °C for 2–5 days. Even after this prolonged period part of the species still showed a remarkable persistence of brown substances. These had to be bleached with chlorine. Transverse sections were also made of selected parts of leaves of *A. elmeri*, *A. falcifera, A. globifera, A. nervosa, A. ledermanniana, A. prainiana*, and *A. wallichii*. In addition, a transverse section of *A. chondroneura*, *Nooteboom 1480*, was taken to investigate the nature of the white granules. Leaves of *A. elmeri*, *A. falcifera, A. nervosa*, and *A. ledermanniana* were mounted unstained to score for the presence of brown substances. Leaves of *A. globifera, A. prainiana*, and *A. wallichii* were stained for 15 minutes in a 1% alcoholic Alcian Blue solution to test for mucilage containing cells. Some species were also sampled for scanning electron microscopy. Small parts were taken and rinsed in acetone to clean and expose the surface structure for SEM.

Surface view

The upper epidermis of *Aporosa* has mostly more or less sinuous anticlinal cell walls. The cell wall undulation is usually stronger on the lower side. The epidermal cells over the nerves are about rectangular. A striking feature is the distinctly radiating pattern that the upper epidermis cells form around the mucilage containing cells (Fig. 4.1a). I tested for the presence of mucilage in *A. globifera, A. prainiana*, and *A. wallichii*. All

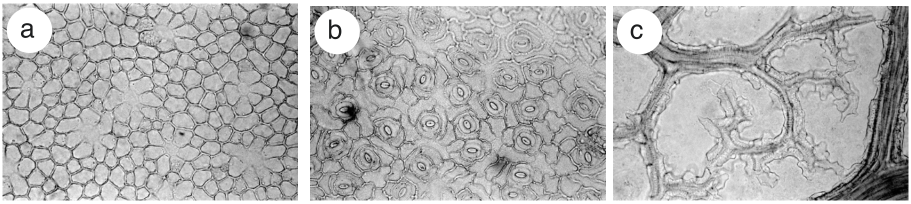

Fig. 4.1. Surface view of the leaves (× 70). a. Upper epidermis of *A. tetrapleura* Hance; b. anisocytic stomata on the lower epidermis of *A. tetrapleura* Hance; c. reticulate venation with free ending veins in *A. arborea* (Blume) Müll.Arg.

three scored positive and I assume that also other species with the distinctive radiating pattern possess them: *A. brevicaudata, A. cardiosperma, A. carrii, A. globifera, A. hermaphrodita, A. lucida, A. maingayi* (few and small)*, A. misimana, A. nigricans, A. octandra* var. *malesiana, A. papuana, A. praegrandifolia, A. prainiana, A. quadrilocularis* (one indistinct one seen), *A. subcaudata* (here the radiating pattern was less clear, but the mucilage cells shone through the epidermis)*, A. tetrapleura, A. vagans*, and *A. wallichii*. Levin (1986) also notes this pattern for *A. symplocifolia*, but attributes them to tanniniferous cells. In *A. alia, A. antennifera, A. arborea, A. basilanensis, A. dendroidea, A. elmeri, A. falcifera, A. laxiflora, A. ledermanniana, A. leytensis, A. nervosa,* and *A. sarawakensis* the radiating pattern was not distinct, but I have not been able to check whether this means that the mucilage cells are absent. They might just be smaller. Transverse sections should be made to positively score for their presence. The transverse section of *A. prainiana* also showed mucilage cells in the lower epidermis, which were not noted in surface view. The radiating pattern around the basal cells of trichomes can sometimes be quite similar, which makes mistakes easy.

The stomata are anisocytic with three neighbouring cells of unequal size and scattered over the entire lower surface with no particular orientation (Fig. 4.1b). On the upper side sometimes anisocytic stomata may occur around the midrib and nerves in a couple of species. Rothdauscher (1896) saw them in *A. frutescens* – but not in *A. cardiosperma, A. lanceolata, A. macrophylla, A. microstachya,* and *A. octandra*. I have found them also in *A. antennifera, A. basilanensis, A. grandistipula, A. sarawakensis,* and *A. subcaudata*.

No variation was found in the type of nervation. All had a reticulate venation with the ends of the veins ending freely in the areoles (Fig. 4.1c). According to Levin (1986) the terminal tracheids are normal, rarely swollen.

Transverse sections

The lamina is bifacial, with compact one- or two-layered palisade parenchyma, of which the second layer has distinctly shorter cells, and loose spongy parenchyma (Fig. 4.2).

The vascular bundles of the veins are collateral, vertically transcurrent by parenchymatous bundle sheath extensions or only connected to the lower epidermis or free from the epidermis on either side; the minor veins are collateral, more or less embedded in the mesophyll.

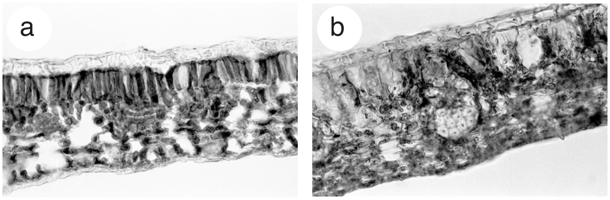

Fig. 4.2. Transverse section of the leaf. a. *Aporosa nervosa* Hook.f. (× 70); b. *A. chondroneura* (Airy Shaw) Schot (× 110).

Foliar glands

Various types of foliar glands are found on the margin and on the lower epidermis. In surface view they resemble small disc-like, slightly sunken areas in the epidermis or on the leaf margin. They are usually connected with the minor veins (Fig. 4.3a). Transverse sections show an identical structure of elongated epidermal cells for both types of glands (Fig. 4.3b, c). Such an anatomical structure is typical for extra-floral nectaries. The fact that on many leaves of *Aporosa* small insects such as lice or ants are found, supports the idea that the disc-like glands in *Aporosa* are extrafloral nectaries. The basal glands also show this same anatomical structure.

The marginal glands occur in almost all species of *Aporosa*. The fact that I did not find them in the anatomical samples of *A. arborea, A. cardiosperma, A. falcifera, A. misimana, A. quadrilocularis*, and *A. tetrapleura* is an artefact due to sampling of only a small part of the lamina. It indicates that the frequency of the glands in these species is low.

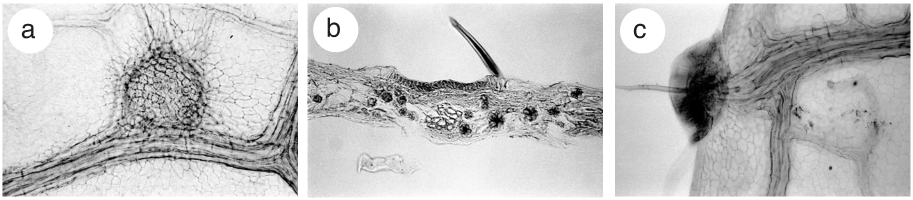

Fig. 4.3. Foliar glands (× 70): a. Disc-like gland in surface view (*A. maingayi* Hook.f.); b. disc-like gland in transverse view (*A. globifera* Hook.f.); c. marginal gland (*A. maingayi* Hook.f.); note the similar structure.

Idioblasts

Mucilage cells — Inflated cells containing mucilage occur in the upper epidermis of many species (Fig. 4.4; cf. also Fig. 4.2 and 4.5c). In surface view they can be identified by a conspicuous radiating pattern of the epidermis cells (see above, Fig. 4.1a). In the lower epidermis of *A. prainiana* I observed smaller mucilage cells. It is possible that also other species have them here, but a complete study has not been carried out. Rothdauscher (1896) reported mucilage cells from the upper epidermis of *A. cardiosperma, A. frutescens, A. lanceolata, A. macrophylla, A. microstachya*, and *A. octandra* and from the lower epidermis of *A. lanceolata*.

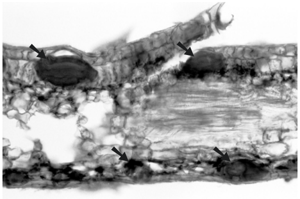

Fig. 4.4. Mucilage cells (arrows) in the upper and lower epidermis of *Aporosa prainiana* King ex Gage.

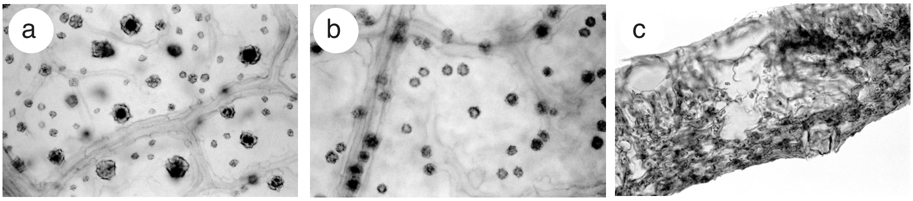

Fig. 4.5. Druses in the mesophyll. — a. *Aporosa sarawakensis* Schot (× 70); b. *A. basilanensis* Merr. (× 70); c. druses lowered and protruding through the lower epidermis of *A. chondroneura* (Airy Shaw) Schot (× 110).

Tanniniferous cells — Tannins are common throughout in the Euphorbiaceae (Metcalfe & Chalk, 1957). Rothdauscher (1896) recorded them from the palisade layers of *A. cardiosperma, A. macrophylla,* and *A. octandra*, from the mesophyll of *A. cardiosperma, A. lanceolata*, and only near the nerves in *A. frutescens*, and from the epidermis of *A. lanceolata*. I have not tested for tannins in *Aporosa*, but I saw brown substances in the palisade and mesophyll layers of *A. nervosa* and *A. ledermanniana* (cf. Fig. 4.2). *Aporosa elmeri* and *A. falcifera* had brown substances in the palisade layer only; the transverse sections of *A. chondroneura* lacked any brownish colour (cf. Fig. 4.5c).

Crystals — Rothdauscher (1896) recorded druses as the only crystal type found in *Aporosa*. I can confirm the presence of many druses of various sizes scattered in the mesophyll of *A. cardiosperma, A. globifera, A. nigricans, A. octandra* var. *malesiana, A. prainiana, A. sarawakensis, A. vagans*, and *A. wallichii* (Fig. 4.5a, b). In addition, *A. alia, A. antennifera, A. arborea, A. dendroidea, A. falcifera, A. lucida, A. praegrandifolia, A. quadrilocularis, A. subcaudata*, and *A. tetrapleura* have them, but less frequently and irregularly. *Aporosa basilanensis, A. brevicaudata, A. carrii, A. ledermanniana*, and *A. leytensis* have them only near the vascular bundles.

In *A. chondroneura*, and possibly also in the other species around *A. frutescens* that have small white granules in their leaves, these druses in the mesophyll cause elevations in the epidermis in dried condition (Fig. 4.5c). This may cause the appearance of the small white granules on the lower side of the leaf of *A. chondroneura*.

Indumentum

Hairs are present in various species. All hairs are unicellular and unbranched. The basis is slightly thickened and darkly coloured (cf. Fig. 4.3b). A study with scanning electron microscopy of the staminate flowers (not mentioned further) showed a low striate-pustulate sculpture on the trichomes of the sepals of *A. chondroneura*, *A. penangensis*, and *A. selangorica*, but in other species and in the studies of the leaf the trichome cuticle appeared to be smooth.

All in all the leaf anatomy of *Aporosa* is strikingly similar to that of *Baccaurea*, and probably also to other genera in the subtribe *Scepinae*, as documented by Bodegom et al. (2001).

4.3 – **Pollen**

Material examined: *A. antennifera*: *De Wilde & De Wilde-Duyfjes 15478*; *A. arborea*: *KL 1843*; *A. aurea*: *Phusomsaeng 114*; *A. benthamiana*: *KEP 76176*; *A. confusa*: *S 22906*; *A. elmeri*: *SAN 29685*; *A. frutescens*: *Maxwell 82-35*; *A. lagenocarpa*: *Jacobs 5102*; *A. maingayi*: *KEP 105044*; *A. papuana*: *BSIP 16372*; *A. prainiana*: *Jaheri 345*; *A. wallichii*: *Maxwell 88-134*.

Method: About 5 mm long parts of complete staminate inflorescences were acetolyzed and processed for light and scanning electron microscopy according to the techniques described in Van der Ham (1990).

Description

The description based on the twelve species studied is as follows (Fig. 4.6): Pollen grains tricolporate. Size (P × E) 15–24.2 by 12.5–22 μm; shape (sub)prolate (P/E 1.1–1.5). Ectoaperture long narrow colpi (apocolpia small); endoapertures lalongate colpi, 3.5–6

Table 4.1. Measurements of the pollen grains of the 12 species studied; P = length of the polar axis; E = length of the equatorial axis.

a. measurements by light microscopy

species	P in μm	E in μm	P/E	endocolpus in μm
A. antennifera	18.4–19.5	17.3–18.5	c. 1.1	
A. arborea	20.7–24.1	16–18.4	1.1–1.5	3.5–5.8
A. aurea	15–17.3	12.7–15	1.1–1.4	3.5–4.6
A. benthamiana	17.3–20.7	16–17.3	1.1–1.4	3.5–4.6
A. confusa	19.5–21.9	15–18.4	1.2–1.3	4.6–5.8
A. elmeri	15–16	12.7–13.8	1.1–1.2	3.5–4.6
A. frutescens	16–20.7	15–17.3	1.1–1.2	4.6–5.8
A. lagenocarpa	17.3–18.4	15–17.3	1.1–1.3	4.6–5.8
A. maingayi	16–18.4	12.7–15	1.1–1.2	3.5–5.8
A. papuana	18.4–19.5	16–18.4	1.1–1.2	3.5–5.8
A. prainiana	18.4–20.7	15–16	1.1–1.3	c. 4.6
A. wallichii	20.7–24.2	18.4–21.9	1.1–1.3	5.8–6.9

b. measurements by scanning electron microscopy

species	exine in μm	nexine in μm	infratectum in μm	tectum in μm
A. antennifera	0.9–1.1	0.4–0.5	0.3	0.6–0.9
A. aurea	1.4–1.8	0.4–0.5	0.3–0.4	0.9
A. confusa	0.6–0.9			
A. maingayi	1–1.1	0.2–0.4	0.3	0.4–0.6
A. papuana	1.1–1.4	0.4–0.5	0.2–0.3	0.5–0.8

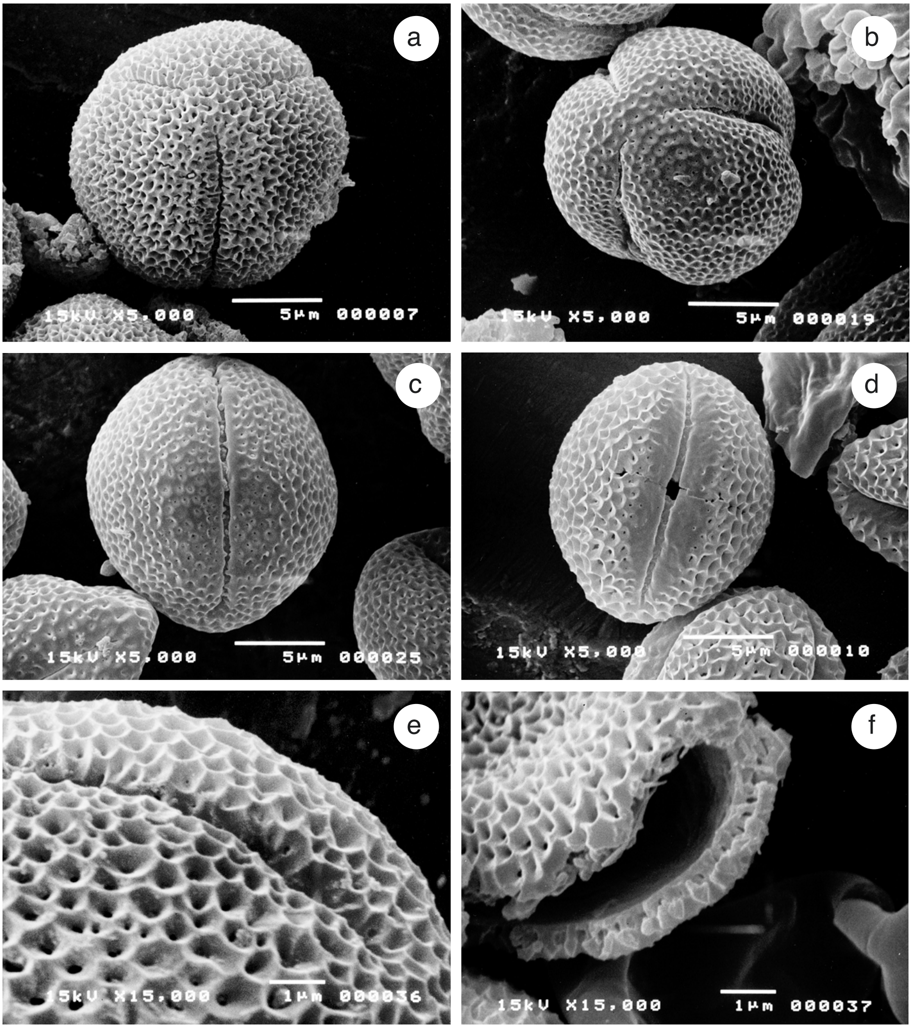

Fig. 4.6. Pollen. — a. *Aporosa antennifera* (Airy Shaw) Airy Shaw, polar view; b. *A. confusa* Gage, polar view; note that the ornamentation is less pronounced, especially near the colpi; c. *A. frutescens* Blume, equatorial view; d. *A. aurea* Hook.f., equatorial view; note the approximately smooth colpus marginalis; e. *A. papuana* Pax & K. Hoffm., detail of the ornamentation; f. *A. papuana* Pax & K. Hoffm., cross section showing the exine.

µm wide, provided with costae transversales. Exine 0.6–1.8 µm thick; nexine 0.2–0.5 µm thick, thickened near the colpi; infratectal layer 0.2–0.4 µm, columellate; tectum 0.4–0.9 µm. Ornamentation microreticulate, sometimes less pronounced to smooth along the colpi (*A. arborea*, *A. aurea*, *A. maingayi*, *A. wallichii*); lumina more or less funnel-shaped, up to 1.2 µm in diameter, with a variably shaped perforation at the bottom; muri more or less triangular in cross section.

The measurements of the individual species are listed in Table 4.1.

Aporosa pollen was studied earlier by Punt (1962), Köhler (1965), Khan (1968), Rao & Lee (1970), and Simpson & Levin (1994). Their results are not essentially different from the above description. Simpson & Levin (1994), who used also transmission electron microscopy, reported for *A. falcifera* a nexine consisting of a thin homogeneous foot layer of 0.17 µm and a moderately thick endexine that is strongly thickened at the apertures, and a 2-layered intine in the apertural areas.

It appears that the species studied by me and those mentioned in the literature all have the same pollen type. No notable differences have been found in grain size, shape, wall structure, or ornamentation. Even the pollen of the hermaphroditic species of New Guinea does not deviate in any perceptible way (Airy Shaw, 1971).

Punt (1962) included the pollen of *Aporosa* in the *Baccaurea* subtype of the *Antidesma* type, which is according to him a relatively primitive subtype. Köhler (1965) classified the *Aporosa* pollen in the *Maesobotrya*-type.

4.4 – **Pistillate flower**

Material examined: *A. antennifera*: *Clemens 40437*; *A. arborea*: *KEP 108989*; *A. benthamiana*: *Kostermans 13642*; *A. elmeri*: *S 36957*; *A. frutescens*: *Maxwell 82-191*; *A. lucida*: *Korthals s.n.*; *A. maingayi*: *KEP 105120*; *A. papuana*: *BSIP 16963*; *A. wallichii*: *Maxwell 88-167*.

Method: The pistillate flowers of the 9 species were rehydrated by boiling, soaked in alcohol, critical point dried, and studied with scanning electron microscopy.

Two noteworthy features were seen when scanning the pistillate flowers: the presence of stomata on the ovary and the highly diverse stigmatic structure.

I saw stomata on the ovary of *A. frutescens* and *A. wallichii* (Fig. 4.7a). It is possible that they are present in the other species as well, since I could not ascertain this for those with puberulous ovaries, such as *A. elmeri*, *A. maingayi*, and *A. papuana*. I can add that in a (failed) attempt to study the staminate flowers by scanning microscopy, stomata were also observed on the outside of the sepals of the staminate flower of *A. nitida*.

The stigmatic tissue of *Aporosa* is highly variable, and probably also highly species specific, although the sample size was too small to really study its specificity. The structure of the stigmata as seen in macromorphological studies varied from smooth to densely laciniate. Scanning microscopic study confirms this (Fig. 4.7b, c):

Fig. 4.7. Scanning electron microscopic features of the pistillate flower. — a. Stomata arrows on the ovary of *Aporosa frutescens* Blume; b. smooth stigmas of *A. benthamiana* Hook.f.; c. laciniate structure of the stigmas of *A. elmeri* Merr.

A. benthamiana has almost smooth stigmas, *A. frutescens* slightly papillate ones, and *A. elmeri* laciniate ones. The stigmas of *A. frutescens* also possessed some kind of exudate, possibly a polysaccharide for pollen capture. Ecological studies in Pasoh (Peninsular Malaysia) showed that the actual flowering period of the pistillate flower is very short.

It might be worth looking closer into the anatomy and functioning of the pistillate flower and especially the stigmas. However, I recommend that such a study is carried out with freshly collected or liquid-preserved material, since the rehydration process does not fully restore the microstructure of the stigmas of dried specimens.

A comparable study in which the staminate flowers were scanned failed because of the insufficient restoration of the original cell shape and size.

4.5 – **Wood anatomy**

I did not study the wood anatomy, but to complete the description of the micromorphology of *Aporosa*, a wood anatomical description compiled from various sources (Metcalfe & Chalk, 1957; Mennega, 1987; Ella, 1998) is presented here:

Growth ring boundaries indistinct or absent. Vessels diffuse, perforation plates mixed scalariform and simple, intervessel pits medium-sized and alternate, vessel-ray pits with strongly reduced borders and elongate, vessel elements 1000–2000 µm long. Faint helical thickenings rarely present in vessel element tails. Tyloses sometimes present. Fibres non-septate, very thick-walled, with simple to minutely bordered pits. Parenchyma typically diffuse-in-aggregates, more rarely in irregular narrow bands, in 3–8-celled strands. Rays uniseriate and multiseriate; the multiseriates 6 (3–17) cells wide, markedly heterocellular, with procumbent body cells and often more than 10 rows of upright marginal cells; sheath cells and perforated ray cells often present.

This type of wood structure has been designated as the *Aporosa* type by Metcalfe & Chalk (1957) and is shared with the genera *Baccaurea*, *Dicoelia*, *Maesobotrya*, *Protomegabaria*, and *Richeria*.

4.6 – **Phytochemistry**

Material examined: *A. grandistipula*: *De Vogel 1742a*; *A. microstachya*: *Zainuddin 2685*; *A. sarawakensis*: *Argent, Kamariah, Pendry & Mitchell 9161*; *A. subcaudata*: *SAN 124788*.

Method: Aluminium content was tested by applying one or two drops of a Chrome-Azurol-S solution on freshly exposed surfaces of the smaller branchlets and leaf bases, as described by Kukachka & Miller (1980). The relative time needed for the reagent to turn blue is a rough indicator for the amount of aluminium. To study more precisely which parts contained the aluminium, slices of branchlets were scored under binoculars to see which part coloured, which fast, and which slow.

Very little is known of the chemotaxonomy of *Aporosa*. Though the genus is common, few known properties have tempted chemists to search for particular compounds.

One is the accumulation of aluminium. Many species of *Aporosa* show a distinct yellowish or greenish colour of their dried leaves. This is usually an indicator for aluminium. Chenery (1948) found a storage of more than 10,000 mg aluminium per kg dried leaves in all of the 24 tested *Aporosa* species. Webb (1957) tested for aluminium in a New Guinean species of *Aporosa* and found a positive reaction of the leaves and a negative one of the bark. Wood samples were tested by Kukachka & Miller (1980) and they also found positive result. Hegnauer (1966) listed a content of 2.06% of aluminium in leaves of *A. sphaeridiophora*. Personally, I tested for presence of aluminium in leaves and branchlets of the green-drying *A. sarawakensis* and the blackish-drying *A. microstachya*. Using Chrome-Azurol-S as reagent the leaf of the former coloured blue within a few minutes, while the latter took several hours. Both thus contain aluminium, but in different quantities. When the branchlet was tested, it was the other way round: *A. sarawakensis* contained less aluminium in the bark than *A. microstachya*.

For a phytochemical survey of Ulu Kinchin, Malaysia, Said et al. (1989) tested *A. stellifera* and *A. prainiana* for the presence of alkaloids, saponins, and steroids/triterpenes, and found both species to be negative. In a later identical test on *A. arborea* and *A. symplocoides* (Said et al., 1995), leaves of *A. arborea* reacted positively for saponine. *Aporosa symplocoides* leaves were found to contain both alkaloids and saponin. This is unexpected considering the close relationship between *A. prainiana* and *A. symplocoides* and may be caused by an unreliable screening method. Several species of *Baccaurea* were also screened and showed the same diversity (Said et al., 1995).

Hemalatha & Radhakrishnaiah (1994) studied the distribution of phenolic acids in the Phyllantheae (sensu Bentham & Hooker). They found that *A. acuminata* contained caffeic acid, o-coumaric acid, p-coumaric acid, ferulic acid, p-OH benzoic acid, p-me benzoic acid, ellagic acid, gallic acid, proto-catechuic acid, and resorsilic acid. Of these, only the ferulic acid and the resorsilic acid are uncommon within the tribe and of taxonomic value. It should be noted, that the greenish drying leaf shows *A. acuminata* to be one of the stronger aluminium accumulating species.

4.7 – **Chromosome number**

The only record of a chromosome number in *Aporosa* is by Hans (1973). He reports as basic number $x = 26$ in *A. octandra*. Compared to the $x = 13$ of Phyllanthoideae and $x = 13$ of *Baccaurea sapida*, this seems to indicate a tetraploid level.

Chapter 5

ECOLOGY

5.1 – **Habitat**

Aporosa is common in the tropical rain forests of Southeast Asia. It is found in both primary as well as secondary evergreen forest. Most *Aporosa* species grow in the lowland rain forest on flatland or low hills and ridges. *Aporosa fulvovittata* (Kinabalu, Sabah), *A. pseudoficifolia* (Perak, Malaysia), *A. fusiformis* (Adam's Peak, Sri Lanka), and many of the New Guinean species are (sub)montane: they are restricted to altitudes above 1000 m. *Aporosa fulvovittata* occurs from 1000 m up to 1500 m altitude on Mt Kinabalu and its surroundings; the species in the central mountain range of New Guinea reach altitudes up to 2200 m.

Many *Aporosa* species are found regularly along rivers or in periodically inundated areas; *A. stenostachys* is restricted to alluvial habitats. The New Guinean *A. ledermanniana* is a tree of swampy areas, as is the only known specimen of *A. spec. F.*

Some specimens of *A. octandra* and *A. villosa* from Thailand are deciduous, indicating that they may prefer a seasonal climate. The same may be true for *A. macrophylla*, which is also said to be deciduous. The patchy distribution of *A. octandra* var. *malesiana* suggests that the species is also seasonal in its Malesian range. No evidence has been found that other species of *Aporosa* are tied to a seasonal climate.

As far as known, all species of *Aporosa* are aluminium accumulators. Because of this they require free Al^+ ions and are restricted to acidic soils, a condition prevailing in rain forest soils. They cannot grow on alkaline soils. From the specimen labels it appears that *Aporosa* grows on all kinds of soil texture: sandy, loamy, and clayey.

In a permanent plot at Pasoh Forest Reserve, Malaysia, *Aporosa* was found to be the second most abundant genus of trees. It was exceeded only by *Shorea* (Dipterocarpaceae). The ecology of the 14 species found in this plot was studied in the course of establishing the plot. I will reproduce here the general ecological notes made by J.V. LaFrankie, assuming that in other West Malesian forests the situation may be comparable. Specific ecological notes on the species found in Pasoh are included in the species descriptions in the Revision (third part of this study). These and further ecological information on *Aporosa* recorded from Pasoh were taken from the same source.

APOROSA AT PASOH FOREST RESERVE, MALAYSIA

(J.V. LaFrankie[1] & A.M. Schot)

Pasoh Forest Reserve is located on the Malay Peninsula at 2° 59' N and 102° 18' E, about 140 km south-east of Kuala Lumpur. The research area comprises 650 ha of primary lowland forest situated between 75–150 m a.s.l., 1000 ha of primary hill forest

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[1] CTFS, Singapore.

rising to 500 m a.s.l., and a surrounding buffer zone of 1000 ha of selectively logged and regenerating forest. The 30-year mean annual rainfall for the nearby town Kuala Pilah is 1850 mm, well distributed throughout the year, and with peaks in April and November. The monthly mean temperature is 24.7 °C.

The more conspicuous emergent species of Pasoh Forest are *Dipterocarpus* spp. and some *Shorea* spp. The forest supports about 510 trees over 10 cm dbh per hectare; in species it is highly diverse without ecological dominants. *Aporosa* comprises about 5% of the trees in the plot. They are chiefly small trees of the understorey. Only *Shorea* has more individuals in the plot. However, the species of *Shorea* do usually not reproduce before reaching 30 cm dbh. If we restrict the calculation of abundance to those individuals that are potentially reproductive, then we can claim confidently that *Aporosa* is the most abundant genus of woody plants in this Malaysian forest.

A total of 14 species of *Aporosa* were found within the plot, viz., *A. aurea, A. confusa, A. falcifera, A. globifera, A. lucida, A. lunata, A. maingayi, A. microstachya, A. nervosa, A. nigricans, A. penangensis, A. prainiana, A. subcaudata, A. symplocoides*. Additionally, *A. benthamiana* is found along the ridges near the Research Station, and *A. arborea* was seen in several places north of the plot. Very often as many as a dozen species are living more or less proximately.

Most of the *Aporosa* species showed marked spatial segregation over the plot. The most obvious aspects of pattern correspond closely to either the course of streams and swampy ground, or to small difference in topography, specifically the small hill that rises to 24 m in the centre of the plot.

Aporosa prainiana and *A. subcaudata* are especially abundant on the slopes of the hill, while *A. microstachya* is largely restricted to the hill top. *Aporosa globifera, A. lucida*, and *A. lunata* are generally most numerous in wet ground, although *A. globifera* is also abundant in the north-western corner of the plot, which is dryer. *Aporosa aurea* and *A. symplocoides* are generally distributed throughout the plot as is the very abundant *A. maingayi*, which appears to avoid only the very wettest spots. The response of close relatives is interesting with regard to potential niche partitioning: of the pair *A. aurea* and *A. lucida*, the first is generally distributed and the second is more abundant in wet ground; and of the pair *A. symplocoides* and *A. prainiana*, the first is generally distributed and the second is most abundant on the hill slopes.

The reproductive biology of *Aporosa* is generally clear in outline, but only a few species have been studied in detail. All species of *Aporosa* are strictly dioecious. The two sexes were rather well mixed spatially. Staminate plants were about one and a half to two times more numerous than pistillate plants. Staminate plants were also found to be more frequently flowering and more variable in size than pistillate individuals (Thomas & LaFrankie, 1993).

The phenology of reproduction follows a pattern that is evident among many genera of Malaysian trees. The species flower between March and May, or, less commonly, between September and November. However, they do not flower every year, at least not to a very obvious extent. When they do flower, each species comes into bloom with very nearly complete synchrony in regard to members of its own species, and yet with a slight asynchrony in regard to other species. The order of blooming for the common species noted at Pasoh was: *A. globifera, A. prainiana, A. maingayi, A. aurea, A. microstachya, A. symplocoides, A. subcaudata*. Evolutionary, it is interesting to note that the closely related species *A. prainiana* and *A. symplocoides* were well separated in phenology. Unfortunately, a complete account is not available for the other proximate pair, *A. aurea* and *A. lucida*.

The abundance and start of the flowering can differ between good and bad years, but the sequence of flowering does not. Since it has been observed that in other areas, e.g., in Singapore, the reproductive phenology can be quite different, the structure of this phenomenon is probably strictly defined on specific circumstances in one particular area.

5.2 – **Interactions with animals**

Pollinators — Pollinators are unknown for *Aporosa*, but wind pollination in the deciduous seasonal species *A. octandra*, *A. villosa*, and, possibly, *A. macrophylla* might be assumed. Wind in the tropical lowland rain forest is too limited to have much influence. Anyway, the notion is refuted by the shortening of the axis of the pistillate inflorescences: wind pollination requires good exposure. Possibly only some species of higher elevation might be abiotically pollinated.

Bawa & Opler (1975) have hypothesized that a correlation exists for dioecious species in tropical forests to have relatively small flowers of white to yellow or pale green colour. Such flowers are thought to attract, because of their unspecialized morphologies, a wide variety of relatively small insects, primarily small bees (see also Bawa, 1994). The dioecious short, small flowers of *Aporosa*, which bear no special features, certainly seem to point to this type of pollinators. Webster (1994a) gives as probable pollinator for the unspecialized Euphorbiaceae "small, general wasps and flies" and S. Thomas told me he had seen only Trigonid bees (*Trigona*) on *Aporosa* at Pasoh Forest, which is in contrast to, e.g., *Diospyros,* which was visited by a host of different insects.

Dispersers — The orange-red colour of the fruits and the seeds with the thin red aril would suggest that the fruits of *Aporosa* are attractive for birds.

In Pasoh, several curious field characters that are probably related to dispersal by birds were noted. The fruits reach their full size within a few weeks after blooming, and may develop their mature colour equally fast, but the development of the seed and seed jacket requires an additional several months. When these are fully ripe, the fruit wall splits, displaying the brightly jacketed seed(s). In *A. maingayi* the single seed is suspended from the column, and dangles just below the recurved and blackened fruit walls. The effect of the display is further heightened by the deep purple colouring of the column. Most of the other species at Pasoh bear fruits with two or more seeds, and a white column.

The more tardily dehiscing, more fleshy structured fruits may also be eaten by small mammals, who collect the fallen fruits and seeds from the ground.

Specimen labels of *A. benthamiana* record that the fruit is eaten by monkeys. *Aporosa frutescens* or *A. stenostachys* fruits are noted to be apparently eaten by squirrels. Orang Utans in Sumatra eat the fruits of *A. whitmorei*. The seed of *A. dendroidea* is said to be eaten by birds.

In a study on the feeding ecology and behaviour of Hanuman langurs (*Presbytis entellus*) in the subtropical Ramnagar forest of Nepal, *A. octandra* was observed to be on the menu (Chalise, 1995). These primates eat young leafy parts and inflorescences, but no fruits. They probably play no role in dispersal.

Ants — I have found hairy nests on leaves of specimens of *A. elmeri*, *A. lunata, A. nigricans, A. subcaudata,* and *A. symplocoides*. This is strange in the latter species, for J. Moog has told me these are formed by species of the ant genus *Monomorium* (subfamily Myrmicinae). They make their nests by cutting the hairs of the plant and gluing them together with spit. *Aporosa symplocoides* is, however, glabrous.

One specimen of *A. subcaudata* from Sabah had thickened end-branchlets with ant holes in it.

Galls — Several forms of galls are found on specimens of *Aporosa*. The most common are the bulbous galls formed on twigs. I have seen these in specimens of *A. antennifera, A. chondroneura, A. frutescens, A. lucida, A. nitida, A. octandra, A. planchoniana, A. prainiana, A. symplocoides, A. tetrapleura,* and *A. villosa*. The same type of small bulbous forms of gall can also be found on the leaves of *A. arborea, A. frutescens, A. subcaudata,* and *A. symplocoides*. Pax & Hoffmann (1922) list for *A. octandra* (*A. dioica* in their monograph) three insect species that form galls on leaf or twig, viz., *Dolcrothrips tryboni*, *Acerocecidium*, and *Eriophyes aporosae*. Galls that cause malformation of the leaves I found once in *A. aurea*. Galled fruits or pistillate flowers occur in *A. aurea, A. caloneura, A. frutescens*, and the New Guinean *A. vagans*.

A more spectacular form of gall are the large bushy structures formed by galled inflorescences. I have seen this regularly in specimens of *A. subcaudata*, and incidentally in *A. antennifera* and *A. elmeri*.

In the variable *A. subcaudata*, some staminate specimens classified under its synonym *A. bracteosa* have strange sterile tubular structures within its glomerules. This has caused the difference in glomerule shape and relative size of the bract, which is the reason why Pax & Hoffmann (1922) described it as a species. I do not know what causes these structures, but galls are not uncommon for this species and these might represent just another sort of gall. I have seen similar structures once in a staminate specimen of *A. elmeri*.

Chapter 6

USES

Few *Aporosa* species are known to have economical uses. They are too small to supply any timber of importance, and possess very little useful chemical elements. A couple of the more common species are mentioned in literature on economical botany, mainly the PROSEA-volumes (Jongkind, 1991; Siemonsma & Piluek, 1993; Ella, 1998), Watt (1889), Heyne (1927), Burkill (1935), Perry (1980), and Ambasta (1986). Below follows a summary of this information. I have added additional information from specimen labels.

6.1 – **Wood**

Aporosa species are not among the major timber suppliers. Their small size makes the timber second-class and useful only for smaller objects. The wood quality is often reported as hard and durable.

The best wood is found in the larger species *A. benthamiana, A. latifolia*, *A. nervosa,* and *A. stellifera*. They provide reasonably hard, durable timber (Burkill, 1935). *Aporosa nervosa* timber is dull white, coarse grained, and does not split on drying (Burkill, 1935). *Aporosa arborea, A. nigricans, A. octandra* var. *malesiana, A. prainiana*, and *A. sphaeridiophora* var. *campanulata* have dark brown, rather hard wood that is suited for planks in houses, beams, or for furniture (Heyne, 1927). The wood of *A. symplocoides* is close-grained, light fawn with distinct rays, hard and compact, and used for houses (Burkill, 1935). The wood of the Indian *A. octandra* ("kokra" according to Lindley, 1836, or "Coco wood" according to Watt, 1889, and Ambasta, 1986) is said to be durable, (very) hard and close-grained. It is used for various purposes such as construction, house posts, rafters, rice-pounders, or even for furniture (Burkill, 1935). The wood of *A. cardiosperma* is also suited for rafters (Ambasta, 1986). *Aporosa globifera* also supplies good and useful wood (Burkill, 1935).

Softer, less durable wood is found in *A. frutescens* (Ella, 1998). It is sometimes used for building houses and making tools. The wood of *A. aurea* is heavy, but variously durable, and can be used for house posts (Ambasta, 1986) or traditional houses (Burkill, 1935). The wood of *A. maingayi* is heavy but not durable and used for houses. *Aporosa nigricans* has hard but flexible wood, fairly good for rafters (Burkill, 1935). According to Ambasta (1986) wood of *A. acuminata* is suitable for match-boxes.

Specimen labels mention further the following uses for various *Aporosa* species: *A. nigropunctata, A. octandra, A. papuana*, and *A. vagans* provide firewood. *Aporosa confusa, A. nigropunctata, A. octandra, A. papuana*, and *A. villosa* are also used in constructing houses.

6.2 – **Chemical contents**

The high concentration of aluminium in certain species makes them suitable as mordant. Jongkind (1991) describes how the bark of *A. frutescens*, called ‘sasah’, was formerly used in the batik industry in Java as a mordant, similarly to *Symplocos*. Sometimes the leaves were used for the same purpose.

Aporosa aurea leaves yield a yellow dye (Ambasta, 1986); those of *A. octandra* can be used in an infusion to make a black dye (Ambasta, 1986; also seen mentioned on a specimen label). The bark of *A. frutescens* can also be used to get a black dye (Jongkind, 1991). The bark of *A. villosa* gives a red dye (Ambasta, 1986).

Medicinal purposes are listed for *A. arborea*: a mixture of mashed bark, twigs, and leaves is said to help cleaning the body when weak or with painful joints (Heyne, 1927). The root of ‘sebasah’ in an infusion is a draught for fever (Burkill, 1935). This might not be *Aporosa*, since the vernacular name ‘sebasah’ is also used for other plants, e.g., *Cleistanthus*. However, Perry (1980) lists a similar use for *A. ficifolia*: water from grating the root is said to be effective against fever. Perry (1980) mentions unspecified medicinal purposes for the fruit of *A. octandra* var. *chinensis*.

6.3 – **Food**

According to Ambasta (1986) both *A. octandra* and *A. cardiosperma* have edible fruits. Burkill (1935) notes that fruits of *A. prainiana* are eaten by the Sakai in North Pahang. Burkill (1935) and Siemonsma & Piluek (1993) mention that the leaves of *A. maingayi* are eaten as vegetable.

Various specimen labels add to the list of edible fruits: *A. nitida* – edible, but sour; *A. selangorica* – edible; *A. villosa* – edible, but not so good; *A. lucida* var. *trilocularis* – edible and sweet. As this last one is the only reference that the fruit is actually nice to eat, I am not sure if it is correct.

PART II

PHYLOGENY

Chapter 7

SETTING THE PHYLOGENETIC PREMISES FOR APOROSA

7.1 – **Introduction**

Two main aims were set for this study: making the first complete revision of *Aporosa* since Pax & Hoffmann (1922) and producing a phylogenetic reconstruction of the genus. The cladogram is the basis for a classification of the 82 species. Additionally, cladograms can indicate hypotheses for evolutionary pathways of characters and species, and, as a special application, be the base for a cladistic biogeographical analysis of the areas where the species occur. The next chapters, Chapter 8 and 9, are devoted to my efforts to produce a reliable phylogenetic pattern for *Aporosa*. Chapter 8 treats the analysis itself; Chapter 9 some theoretical issues and applications of the phylogenetic pattern.

Ever since Hennig's introduction of the parsimony method (Hennig, 1966) the practice of building cladograms is getting more and more common. In theory it sounds simple. A monophyletic group – often a genus – is studied and its characters coded into states. With the aid of the parsimony principle, the addition of a sistergroup for character polarisation (and a computer program because the data set is large) a cladogram is produced (see, e.g., Wiley, 1981; Forey et al., 1992, for detailed explanations of the method).

However, not all cases are as straightforward. Problems arise when the assumptions of the method are not met, e.g., parallel or convergent evolution, or reversals. Reticulating patterns due to hybridization account for even more trouble. Hybrids may or may not destroy the phylogenetic pattern (McDade, 1992). All such events may lead to destabilized patterns, which result in multiple numbers of equally parsimonious solutions. It is then often necessary to choose, if arguments exist, among the different patterns.

A criterion often used to choose among multiple patterns is differential weighting of the characters (e.g., Carpenter, 1988). 'Good' characters (those with a high rescaled consistency index) are designated higher weight factors than 'bad' characters (those with low indices), and patterns preferred by the 'good' characters are preferred over those indicated by the 'bad' characters.

It will be clear that the larger the group analysed, the higher the chance to find multiple patterns. Groups with more taxa show more homoplasies. Furthermore, data sets for speciose genera have relatively fewer characters than sets for small genera. According to Lamboy (1994), this results in less accurate and less stable phylogenies when using parsimony to calculate the cladograms. Kellog & Watson (1993) advise to analyse large groups by stages: first analyse only representatives of the monophyletic parts of the complete group, e.g., genera of one subfamily or sections of one genus. In a second stage, analyse the various genera or sections separately with a newly defined character set and the outgroup which was indicated in the first analysis.

This protocol a priori assumes that the groups to be analysed separately are known and monophyletic. However, the sections of *Aporosa* as defined by Pax & Hoffmann (1922) are probably not natural and monophyletic (e.g., Airy Shaw, 1974, 1980b), and cannot be used. Others, also struggling with multiple patterns and low consistency indices for their cladograms (e.g., Van Welzen, 1989; Adema, 1991), have opted for analysing the complete set first, and cutting it afterwards, based on a monophyly of subsets of taxa demonstrated by this first analysis. This last pathway is the one followed for the phylogenetic reconstruction of *Aporosa*.

A high number of taxa is not the only factor that may entangle the patterns in a phylogenetic reconstruction. Other factors may have the same influence. Wilkinson (1995) discusses how partially known taxa usually cause an increase in the number of species that are placed ambiguously. Extinct, and thus not included species, may also affect the outcome. Especially in older groups this may lead to inaccurate estimations of the basal relationships (Doyle & Donoghue, 1992). Young species may not have enough delimiting characters, which results in an ambiguous position. Considering the patterns found in the macromorphological characters, it is possible that each of these types of disruptive data exist in *Aporosa*.

In an ideal situation one might consider excluding such taxa that are expected to bring only ambiguity into the phylogeny. But it is not always possible to omit these taxa a priori. Firstly, it is hard to argue which are the disruptive taxa; and secondly, theoretically possible disruptive taxa do not necessarily need to cause trouble in practice. Furthermore, to study the effect of disruptive taxa on the phylogeny an analysis with the taxa as well as one without them has to be conducted.

Therefore, the phylogenetic reconstruction of *Aporosa* is conducted in three steps. The complete data set is analysed first. The purpose of this preliminary analysis is twofold. First, it may be used to indicate the monophyletic groups. These can then be analysed separately in a secondary analysis. The second purpose is to determine the taxa that possibly disrupt the pattern. These are then excluded from further analysis. In the last phase the general pattern of the preliminary analysis is combined with the more detailed relationships found in the secondary analyses. These steps in the analysis are described in the various paragraphs of Chapter 8.

But before running the analysis the premises are set in this chapter. These are a statement of the monophyly of the group studied (paragraph 7.2), the computer algorithm chosen (paragraph 7.3), the selection and coding of the character set (paragraph 7.4, Table 7.1, 7.2), the choice of an outgroup (paragraph 7.5) and the description of the ingroup (paragraph 7.6).

7.2 – **Monophyly of Aporosa**

One of the first requirements of a phylogenetic analysis is the monophyly of the group under study. In floras and family treatments, *Aporosa* is distinguished from its closest relatives by short racemose inflorescences and staminate flowers without a pistillode. In practice, the fruits with persistent sepals and stigmas and detached endocarp are also characteristic, though not unique, as well as the glomerulate staminate inflorescences. But are these characters truly unique for *Aporosa* and are they synapomorphies?

When surveying the Euphorbiaceae, we find minute staminate flowers lacking a pistillode in, e.g., *Phyllanthus* and *Glochidion*. *Mallotus* and *Macaranga* have spikes such as *Aporosa*, while *Austrobuxus* and *Claoxylon* have capsules with persistent sepals and stigmas and detached endocarp. Examining the closer relatives in the subfamily Phyllanthoideae, tribe Antidesmeae, subtribe Scepineae, one finds that some species in *Baccaurea* or *Maesobotrya* share part of these characters with *Aporosa*. *Baccaurea racemosa* has racemose inflorescences and *B. obtusa* has fruits with persistent sepals. Nevertheless, the combination of characteristics shown by *Aporosa* is unique within the subtribe.

However, *Aporosa* itself is variable in these characters: the species around *A. benthamiana* have, for instance, distinct cylindric pistillodes. *Aporosa arborea* and *A. symplocoides* have long inflorescences. The staminate inflorescences of *A. lagenocarpa* and *A. leptochrysandra* bear glomerules with the flowers set so laxly that they can almost be interpreted as not clustered. *Aporosa banahaensis* and *A. nitida* have thick fleshy indehiscent fruits. Notwithstanding this high variability, there is usually at most one exceptional character in a species. Therefore, all *Aporosa* species are recognizable as *Aporosa*.

Because of this, the monophyly of *Aporosa* is plausible, being defined by a polythetic set of characters. A global analysis on the larger genera of the Scepinae by Haegens (2000) placed *Aporosa* monophyletic at the base of three other genera. Thus a monophyletic origin of *Aporosa* may be assumed. When more detailed knowledge becomes available on the relationships between the species of *Aporosa* and between those of the related genera this assumption might yet prove to be incorrect.

7.3 – **Selection of cladograms**

All cladograms were calculated with the parsimony criterium as implemented in the computer program HENNIG86 (Farris, 1988). Other workers have shown the pros and cons of other criteria as character compatibility or maximum likelihood methods (see, e.g., Farris, 1983 for a discussion or Forey et al., 1992 for an overview). The parsimony criterium remains the best usable for analysis of multistate macromorphological characters. Alternatively, PAUP 3.1.1 (Swofford, 1991) may be used, but of these two programs HENNIG86 is the fastest.

In view of the large number of taxa the initial tree building command 'mh*' followed by the branch breaker 'bb*' was preferred above implicitly searching all trees with the option 'ie*', so there is a chance that suboptimal trees are obtained. Additionally, it was found that sometimes this combination does not find all possible equally parsimonious trees (e.g., Turner, 1995). This is probably because the 'mh*' takes too few passes through the taxa and is not random enough, which may allow several different islands of most parsimonious trees to be missed (Maddison, 1991). Following Turner's (1995) suggestion NONA 1.0 (Goloboff, 1993b) with 'mu* 50' was tried instead of HENNIG86s 'mh*'. This did not always prove successful due to computational limits. The number of equally parsimonious cladograms found when running the complete data matrix renders more cladograms then can be kept in memory. When all the cladograms calculated by NONAs 'mu* 50' are imported for swapping by HENNIG86s 'bb*', the overflow of memory occurs even earlier. This results in an earlier termination of the search and the possibility exists that suboptimal cladograms are retained. Using only one of NONAs trees does not help in finding the different islands of equally parsimonious cladograms overlooked by 'mh*'. Only when analysing subsets of the matrix, this method performed satisfactory. As an alternative to finding different islands of trees, the program JOYRIDE[1] by Siddall (1994) was also used on the subsets.

Cladograms obtained by HENNIG86 were imported in PAUP 3.1.1 (Swofford, 1991) for calculating options not covered by HENNIG86, such as Adams consensus trees and lists of character state changes. Character transformation series were analysed with MacClade 3.04 (Maddison & Maddison, 1992)

7.4 – **The characters**

7.4.1 – ***Introduction***

Selecting, defining, and coding the characters and character states for the data matrix is the step that primarily determines the outcome of a phylogenetic reconstruction. During the survey of the taxa a preliminary set of features with potential for delimiting and grouping was selected. Subsequently, this set was evaluated for the phylogenetic analysis according to two criteria. First, which characters are fit for cladistics; second, how to define them in terms of independent characters and non-overlapping character states.

These two aspects of building the character set are described in paragraphs 7.4.2 and 7.4.3, respectively. Each paragraph starts with an overview of the theoretical background, followed by the choices made in selecting and coding characters for *Aporosa*.

There are different kinds of characters. To prevent any misunderstanding, I think it will be good to state my use of terminology for these various types. Usually, one differentiates between discrete or qualitative and continuous or quantitative data. Discrete or qualitative characters are characters in which the states are distinct, such as a red or a yellow flower, absence or presence of foliar glands, or a number like a 2- or 5-locular ovary. In continuous or quantitative data the distinction of states is usually problematic due to overlap, very few continuous characters show distinct gaps. Such characters are, e.g., number of sepals 3–5 or leaf shape narrowly ovate to narrowly elliptic (Thiele, 1993).

It will be clear that the difference between qualitative and quantitative is not a property of the characters (see also Stevens, 1991). Discrete characters may become quantitative or continuous when one taxon shows various states, e.g., when some individuals of one species have red flowers and others yellow, or some have foliar glands and others not. To differentiate between these two actually identical types, I speak of *non-overlapping* characters when no overlap of states occurs, and of *overlapping* characters where the states are free to overlap.

A special kind of continuous data is represented by *morphometric* characters. Morphometric characters are ranges, like a statement such as '1–5 cm' or 'up to 25 mm', where there is no obvious distinction into character states.

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1) The package 'Random Cladistics', of which the JOYRIDE.EXE is part, can be freely downloaded from http::/www.vims.edu/~mes/hennig/software.html

7.4.2 – ***Selecting characters***

7.4.2.1 – *Theoretical background*

Not all characters are equally suitable for phylogenetic analysis. Opinions differ over what are 'good' characters and how to code them. Pimentel & Riggins (1987) were among the first to describe the basic rules for selecting and coding characters. They argue that only characters that can be "evaluated as a variable with two or more mutually exclusive and ordered states" are useful. Discrete or qualitative characters are to be preferred over continuous or quantitative ones with morphometric characters as the worse, since dividing ranges is subjective and without theoretical basis. Therefore, such characters should not be used. Another directive is to use mutually independent characters. Then each synapomorphy in the matrix counts as a separate piece of evidence for the proposed relationships of that clade. Dependent characters might emphasize an otherwise not-so-strongly supported clade.

Later authors have commented on some of these recommendations. The more characters, the better the accuracy and stability of the tree (Kim & Burgman, 1988; Rohlf et al., 1990). Selecting only qualitative characters may exclude more information than bargained for. As Stevens (1991) has shown, when looking really closely, apparently discrete characters, such as 'leaf shape ovate or elliptic', turn out to be principally continuous. Strict adherence to the rule to use only non-overlapping qualitative characters would mean discarding both the really continuous numerical ones and all those based on semantic differences. In some cases this will lead to too few characters for a reliable analysis. Therefore, many allow quantitative data if a gap is present.

Furthermore, quantitative characters might be phylogenetically informative and then deserve to be included in the analysis (Thiele, 1993), even if a gap is not evident. These characters should also be considered when the qualitative characters available are limited (Chappill, 1989). Thiele (1993) argues that a character can only be excluded from analysis if it has no information content. This should be deduced in relation to the phylogeny itself, not a priori. He formulates the first criterion to select characters as "… that cladistic characters and states apply to taxa and that they change [in frequency distribution] during cladogenesis". If continuous characters are excluded, it is because the methods cannot handle such data, not because they contain no phylogenetic signal.

In *Aporosa* size differences delimit often closely related species. Furthermore, the generic delimitation of *Aporosa* from *Baccaurea* is also primarily a size difference. A phylogenetic signal is thus possibly present in length characters and they are included into the analysis, also since the qualitative characters in *Aporosa* are really very few.

7.4.2.2 – *Selecting the characters*

The criterion of Thiele (1993) is followed to select the characters that differ among the species. These are the characters used in the synoptical key (see Part III: Revision). But not all of these available 109 characters are informative. Obvious autapomorphies, such as the bullate leaves of *A. bullatissima* or the ramiflory of *A. benthamiana*, have no value for building the cladogram and are not included. On the other hand, autapomorphic states, such as the ornamented ovaries of *A. bourdillonii*, *A. lamellata*, and

A. selangorica or the granular leaf of *A. chondroneura*, have been included as separate states because the other states of these multistate characters do contain information.

Other uninformative characters are those that show too much variability, like leaf shape, curving of the marginal arches, size of the glomerules, or the amount of reticulation of the venation. One could decide to code two states, 'normal' and 'extreme', in which the 'normal' state is given to all species except the aberrant ones – e.g., the cordate leaf shape of *A. macrophylla*. This would then be an autapomorphy again. The same applies to the scalariform venation of *A. subcaudata*. Such characters were also discarded.

Characters that might be informative, but are known in insufficient detail, such as bark characters, growth form, or ecological preference are also not included. The delineation of these characters into states has no reliable basis. The same holds for the micromorphological and chemical characters. Pollen, leaf- or wood-anatomy, chromosomes, isozymes, or other chemical data have shown their uses in various phylogenetic reconstructions, but neither time nor material sufficed to include them in the present analysis.

According to Pimentel & Riggins (1987) independent characters are better than dependent ones. But independence can be hard to stick to in all cases. Often many characters are partly dependent. For example, the larger the leaf, the longer often the petiole and the higher the number of nerves. Tomentose branchlets never bear completely glabrous leaves. A change in the number of sepals is usually accompanied by a change in the number of stamens or carpels. Staminate and pistillate plants have similar features. Fruit shape and indumentum are usually related to ovary shape and indumentum. Should only one character be coded for every complex?

The answer to this question lies in the type of the relation. Sometimes the combination is not strict. Typically, large leaves have many nerves and long petioles. But in a couple of species the combinations are different. *Aporosa longicaudata* has small leaves with many nerves; *Aporosa arborea*, *A. macrophylla*, and *A. praegrandifolia* have relatively long petioles. In such cases of incompletely dependent characters, more than one is defined – but only if they result in combinations that are synapomorphic. Examples are the indumentum of branchlets and leaves, the length of petiole and leaf, indumentum of staminate or pistillate bracts and sepals, the consistency of the glomerules, and the structure of the stigma. On the other hand, some characters appear in all cases in the same combination. In these cases only one of the characters in the complex is coded. Examples are indumentum of branchlets and petiole, indumentum of staminate and pistillate inflorescences, length of the staminate or pistillate bracts, pistillate flower and ovary length, indumentum of the ovary and fruit, length of flowering and fruiting pedicel. Different combinations of these characters – if present – turned out to be mostly autapomorphic.

Sometimes I have chosen to incorporate the different aspects into one character, such as the frequency and consistency of the foliar glands and dots – characters 8, 10, and 17 (see Table 7.1). Defining separate characters for the presence and consistency would introduce unknown data into the matrix for consistency of the glands in aglandular species. There is no phylogenetic information in missing data: it only increases

(*Text continued on page 70*)

Table 7.1. The characters and character states defined for *Aporosa*.

(0. Leaves arranged
   1. evenly
   2. contracted)

1. Branchlets indumentum
   1. completely glabrous
   2. sparsely puberulous/ hirsute
   3. (densely) tomentose
2. Stipules
   1. caducous
   2. present in young leaves
   3. persistent
3. Stipule shape
   1. (narrowly) triangular, symmetric
   2. (narrowly) ovate, symmetric
   3. narrowly ovate, slightly oblique
   4. narrowly ovate, strongly oblique
   5. falcate
4. Maximum length of petiole
   1. up to 5 mm
   2. up to 30 mm
   3. up to 40 mm
   4. up to 100 mm
5. Pulvini
   1. upper one very large
   2. both distinct, upper one not extremely so
   3. lower one indistinct
   4. both indistinct
   5. petiole entirely pulvinate
6. Maximum leaf length
   1. up to 10 cm
   2. up to 22 cm
   3. up to 30 cm
   4. up to 50 cm
7. Leaf base
   1. (slightly) cordate
   2. rounded to cuneate
   3. (slightly) attenuate
   4. emarginate-truncate
8. Basal glands
   1. absent
   2. small, often indistinct
   3. distinct
   4. hairy
9. Margin
   1. (lowly) undulate to (sub)entire
   2. (lowly) undulate to glandular-crenate, -serrate, or -dentate
   3. (lowly) glandular-crenate or -serrate
   4. (lowly) glandular-serrate or -dentate
10. Marginal glands
    1. few, greyish, brownish, or blackish
    2. regular to many, greyish, brownish, or blackish
    3. regular to many, hairy in young leaves
    4. regular to many, all hairy
11. Marginal glands
    1. at end of distinctly thickened veinlets
    2. in margin, veinlets not thickened
12. Leaf apex
    1. acute or acuminate (never cuspidate)
    2. acuminate to cuspidate
    3. (sometimes) caudate
13. Leaf texture
    1. thin(nish)
    2. thick(ish)
14. Leaf surface granular
    1. not
    2. young leaves (lowly) granular
    3. (strongly) granular
15. Leaf colour when dry
    1. yellowish or greenish on both sides
    2. greenish, brownish, or bluish above, brownish beneath
16. Older leaves blackening
    1. no
    2. yes
17. Dots on upper surface dried leaf
    1. absent
    2. irregularly set
    3. laxly set, fine, greyish
    4. densely set, fine, greyish
    5. densely set, large, blackish
18. Disc-like glands
    1. absent
    2. occasionally few along the margin
    3. regularly along the margin
    4. occasionally few at base
    5. scattered within marginal arches
    6. scattered within marginal arches and along margin
    (7. several large ones at both sides along the midrib)
19. Leaf indumentum
    1. completely glabrous
    2. hairs only present beneath on midrib and nerves
    3. hairs beneath present
    4. hairs present beneath and above on midrib
    5. hairs present above and beneath
20. Pairs of nerves
    1. 5–8 (10)
    2. (9) 11–23
21. Marginal arches
    1. distinct
    2. fading
22. Nervation above
    1. indistinct
    2. distinct or fading, slightly prominent to flat
    3. distinct, (slightly) sunken

Table 7.1 (*continued*)

23. Nervation beneath
    1. almost flat
    2. (slightly) prominent
24. Inflorescence indumentum
    1. (sub)glabrous
    2. (sparsely) puberulous
    3. (sparsely to densely) tomentose or sericeous
25. Staminate inflorescences clustered
    1. up to 6 (7) together
    2. up to 20 together
26. Staminate inflorescences length
    1. (mean) < 20 mm
    2. (mean) > 20 mm
    3. (mean) > 80 mm
27. Staminate inflorescences diameter
    1. 0.2–0.5 mm
    2. (mean) < 1.9 mm
    3. (mean) > 1.9 mm
    4. 5–9 mm
28. Peduncle length
    1. 0–3 mm
    2. 3–24 mm
29. Distribution of glomerules
    1. continuous, to base
    2. continuous, peduncled
    3. only at base (slightly) spaced
    4. spaced distinctly at base, more continuous apically
    5. distinctly spaced throughout
30. Glomerules massed apically
    1. no
    2. yes
31. Glomerule shape
    1. ellipsoid
    2. (sub)globose
32. Glomerule flowers set
    1. densely
    2. laxly
33. Maximum number of flowers in glomerule
    1. up to 5
    2. up to 10
    3. up to 15
    4. more than 15
34. Bract relative conspicuousness
    1. conspicuous, longer than glomerule
    2. indistinct, smaller or as long as glomerule
35. Bract indumentum outside
    1. glabrous
    2. sparsely pubescent
    3. (densely) tomentose/sericeous
36. Staminate flower pedicel
    1. absent
    2. minute, < 0.3 mm long
    3. distinct, 0.3–1 mm long
37. Maximum length of staminate flower
    1. up to 1 mm
    2. up to 2 mm
    3. up to 3.5 mm
38. Staminate sepals
    1. free
    2. connate at base only
    3. connate to c. halfway
39. Staminate sepals indumentum outside
    1. glabrous
    2. sparsely pubescent
    3. tomentose/sericeous/ puberulous
40. Number of stamens
    1. always 2
    2. 2 or 3
    3. 2 or 3, but regularly also 4
    4. regularly more than 4
41. Stamens exsertion
    1. not to slightly, stamens c. 0.75–1.25x the sepals
    2. distinctly, stamens c. twice as long as the sepals
    3. strongly, stamens c. thrice as long as the sepals
42. Stamens length
    1. 0.2–1.4 mm (mean < 1.1 mm)
    2. 0.8–4 mm (mean > 1.1 mm)
43. Anthers length
    1. 0.1–0.2 mm long
    2. 0.2–0.4 mm long
    3. > 0.4 mm long
44. Connective
    1. glabrous
    2. sparsely hirsute
45. Pistillode
    1. absent
    2. minute
    3. a hairy tuft
    4. lumpy, resembling undeveloped stamen
    5. cylindric
46. Pistillate inflorescences length
    1. 1.5–14 mm (mean < 11 mm)
    2. 5–78 mm (mean > 11 mm)
47. Pistillate inflorescences diameter
    1. 0.3–1.2 mm (mean < 1.1 mm)
    2. 1–2.5 mm (mean > 1.1 mm)
    3. 2.8–4 mm
48. Number of pistillate flowers per inflorescence
    1. 1–11
    2. more than 11
49. Setting of pistillate flowers
    1. densely set
    2. rather densely set
    3. laxly set

Table 7.1 (*continued*)

50. Distribution of pistillate flowers
    1. throughout the rhachis
    2. few at base, most apically
    3. only apically
    4. one singly apically
51. Bract indumentum outside
    1. glabrous
    2. sparsely pubescent
    3. (densely) tomentose/ sericeous
52. Bracteole length
    1. 0.1–0.5 mm
    2. 0.5–1.4 mm
    3. 1.5–2.5 mm
53. Pedicel length
    1. absent, 0 mm
    2. minute, < 0.3 mm
    3. distinct, > 0.5 mm
54. Pistillate sepals number
    1. 3 or 4
    2. 4 to 5, or more
55. Pistillate sepals degree of opening during flowering
    1. ascending
    2. perpendicular
    3. reflexed
56. Pistillate sepals indumentum outside
    1. glabrous
    2. (very) sparsely pubescent
    3. (densely) tomentose/sericeous
57. Pistillate sepals texture
    1. scarious
    2. fleshy at base
    3. fleshy throughout
58. Petal-like structures
    1. occasionally present
    2. absent
59. Locule number
    1. always 2 or 2 and 3
    2. 3, seldom 2, or 3, seldom 4
    3. 3 and 4 or more
60. Ovary length
    1. up to 1.5 mm
    2. up to 3 mm
    3. up to 5 mm
61. Ovary indumentum
    1. glabrous
    2. sparsely puberulous at base, glabrescent towards apex
    3. (sparsely) puberulous throughout
    4. (densely) tomentose/ sericeous throughout
62. Ovary-stigma transition
    1. direct
    2. ovary slightly tapering
    3. ovary distinctly tapering
63. Stigma shape
    1. broad (index c. 1)
    2. narrow (index >1.5)
64. Stigma direction from ovary
    1. ascending
    2. perpendicular
65. Stigma curving at apex
    1. (rather) straight
    2. recurved
    3. flattened to the sides of the ovary
66. Stigma incision
    1. lobed
    2. up to c. halfway
    3. to near base
    4. divided
67. Stigma length
    1. 0.3–1.5 mm (mean < 1.45 mm)
    2. 1–4 mm (mean > 1.45 mm)
    3. up to more than 4 mm
68. Stigma sculpture above
    1. completely smooth or only ribbed
    2. only at margins papillate or laciniate
    3. papillate to laxly laciniate
    4. densely laciniate/feathered
69. Style remnant below
    1. absent
    2. present along margins
    3. present on complete stigma
70. Stigma structure below
    1. smooth
    2. ribbed
    3. lowly papillate
71. Fruit shape
    1. always globose
    2. (broadly or narrowly) ellipsoid to globose
    3. (broadly or narrowly) ovoid to globose
72. Fruit stipe
    1. absent
    2. present (sometimes only in immature fruits)
73. Fruit beak
    1. absent
    2. small (sometimes in immature fruits only)
    3. distinct
74. Fruit length
    1. up to 13 mm (mean < 11.6 mm)
    2. 10–20 mm (mean > 11.9 mm)
    3. up to > 20 mm
75. Fruit index
    1. c. 1 (0.6–1.2)
    2. c. 1.5 (1–1.9)
    3. c. 2 (1.9–2.5)
76. Fruit sculpture
    1. smooth, somewhat punctulate
    2. punct(ul)ate
    3. (lowly) granular
    4. striate
    5. ruminate-verrucate
    6. tuberculate

Table 7.1 (*continued*)

77. Fruit sutures
    1. smooth
    2. ridged
    3. lobed
    4. lamellate
78. Fruit colour when dry
    1. brownish or blackish
    2. orangish or yellowish
79. Fruit pericarp thickness
    1. 0.2–1 mm (mean < 0.9 mm)
    2. 0.8–3 mm (mean > 0.9 mm)
    3. 3–7 mm
80. Fruit endocarp: shape of apex
    1. acute
    2. caudate
81. Fruit septae and column
    1. glabrous
    2. pubescent
    3. hairy ring at base of column
82. Number of seeds developing
    1. usually 1
    2. often 1 per locule

the number of equally parsimonious solutions. Defined in this way the synapomorphy of the simple presence of glands is lost. But considering their anatomy, there is no sound reason to assume that, say, disc-like glands near the margin were developed in the same ancestor as disc-like glands scattered near the base.

In cases where such coding might destroy evidence of relationship, two characters were retained. For example, the massing of glomerules in an apical head is kept separate from the distribution of the glomerules (characters 29 and 30 in Table 7.1). In this way the clavate-shaped inflorescence is interpreted as a special case of 'glomerules slightly spaced at the base', and the relation of the species with massed glomerules to species with continuous glomerules is not lost. The same is true for the two characters referring to the leaf colour of dried specimens (characters 15 and 16).

7.4.3 – ***Coding characters***

7.4.3.1 – *Theoretical background*

The coding of characters into states is the next step. The advise of Pimentel & Riggins (1987) is to use additive binary or ordered multistate characters for related states. Non-additive binary coding of related states is unable to express the relationships of the states and should be avoided; ordered characters have a higher information content than unordered ones. Not ordering the characters can cause loss of observed similarity between the states.

The preference for ordered states is questionable. Ordering means arranging the states of a multistate character along a linear or branching transformation series according to a preconceived idea about the evolutionary pathway of that character. This idea can be based on ontogeny (e.g., Nelson, 1985) or on similarity or congruence (e.g., Libscomb, 1992). Branching patterns can be coded additively to retain the information. The thus proposed transformation series can then be tested for concordance with other characters in the cladogram found (Mickevich, 1982; Mickevich & Lipscomb, 1991). The advantage of ordering states is that it reduces the number of possible evolutionary pathways for that character. Non-additive coding of the characters considers all solutions, and the final cladogram determines which is the best. Additive coding considers only the putatively best solution, and the final cladogram proves or disproves it.

However, the disadvantage is that a priori ordering may be erroneous. Let us take as example four species with 3, 4, 5, and 6 sepals. Arranging them along a similarity axis gives a linear pattern from 3 to 6. But 6 sepals might just as easily be derived from 3 by a duplication, as from a linear pathway. Another possibility is that no logical evolutionary pathway can be argued, such as in flowers with red, yellow, or white petals. To a priori design one pathway where others are equally well possible has no scientific basis. Ordering assumes nested homology, but homology of characters is a hypothesis to be tested a posteriori in the selected tree. With unordered characters one often finds more cladograms, but the wrong assumptions might veil the overall most parsimonious tree. Also ordering might land the analysis in an inappropriate island and will never find the most parsimonious cladogram.

Apart from such theoretical disadvantages there is a practical reason for objecting against ordered characters. Checking the transformation series in the many thousands of parsimonious trees found for the complete data matrix of *Aporosa* would be very laborious. Thus all characters in the analyses are unordered. Supposed transformation series were later applied as a test to selections of the patterns found.

Pimentel & Riggins' (1987) last suggestion concerns polymorphism, i.e., the occurrence of more than one state in the same taxon. They consider it best to code polymorphism as unknown or solved by splitting the taxon artificially per morph. Other options have also been proposed. They include the use of a plesiomorphic, apomorphic, or separate -intermediate- state for the polymorphic taxon. These various solutions were computed by Kornet & Turner (1999) and most were found to have flaws. Coding the plesiomorphic state assumes knowledge beforehand about the local plesiomorphic state for a node in the cladogram. Coding polymorphism as a separate state does not correctly describe the nature of the polymorphism. According to Kornet & Turner (1999) the best method is still to code the polymorphic taxon as 'unknown' for that state, or, an option found in the newer computer programs, as polymorphic. Afterwards, the transformation series of polymorphic characters should be checked closely in the resulting trees. Not all given solutions need to be equally parsimonious when relating the unknown state back to a polymorphic one.

Polymorphism in *Aporosa* often takes the form of continuous variation and is coded as such. In those cases where the polymorphism corresponded to varieties, the species were simply divided.

Coding morphometric data may also be problematic. Various methods have been suggested. The simplest is simple gap-coding (Mickevich & Johnson, 1976). Here state boundaries are defined at points were the values show enough separation. However, this only works if gaps are present. Size in *Aporosa* is often a continuous morphometric character without gaps (Fig. 3.2 and 3.4) and the states cannot easily be divided. Archie (1985) proposes generalised gap-coding. He calculates a predefined value on the basis of the within-group standard deviation. A state boundary is present when the means of the values of the taxa differ more then this predefined value. Chappill (1989) discusses segment-coding. Here the same within-group standard deviation is used to calculate the lengths of the range-states. In this way the number of states is relative to the variability of the character.

However, I do not consider a standard deviation a good representative of the morphometric data scored in *Aporosa*: the standard deviation uses individuals and population sizes. But here we are dealing with species data. Common practice in taxonomy is that only minimum and maximum values of small samples of the species are scored. The true standard deviation of leaf size for a species is thus not known. Furthermore, even if there was time to measure all collected specimens, the question remains whether this is useful. The specimens that find their way into the herbarium or museum need not be representative for the real variation found in a species. Especially, the sizes of vegetative parts in plants are notably variable due to environmental factors. It is well-known that leaves growing in the shade are larger then those growing in the sun. There is also a difference between the leaves in the fertile and the sterile part of the plant. In the herbarium mostly the smaller leaves of the fertile parts are found. Sterile parts of the tree are seldom collected, and these usually have larger leaves. The standard deviation, if known, will in these cases not be representative. For this reason botanists have often used maximum values only. This has given good results (e.g., Van Welzen, 1989; Sosef, 1994).

But using maximum values in *Aporosa* still poses the same problem. Gaps are not evident. Thiele (1993) proposes "gap weighting" for assigning states to morphometric data. But when applying his formula to *Aporosa* the states defined show autapomorphic higher states and an – to the eye – arbitrary division. The autapomorphic states are not that bad if, as advised by Thiele (1993), the character is entered ordered. However, for reasons already explained, I do not wish to order my characters a priori. To maintain the information in an unordered character, some states would have to be merged. This would be an arbitrary decision, and the advantage of having calculated the states by an objective formula would be undone.

As none of the formulas published seem to work in *Aporosa*, the states are divided based on graphical representation and strict mean values, as explained below.

7.4.3.2 – *Coding the characters*

The following paragraphs briefly highlight how I coded my choice of characters. The characters and their coding are listed in Table 7.1. Table 7.2 summarizes the types of the characters and the arguments according to which they were coded.

Of the available informative characters for *Aporosa*, only a few are qualitative, and even these are not always non-overlapping. Actually, only characters 11 (position of the marginal glands), 23 (protrusion of nervation above), 32 (flower setting of the glomerules), 38 (union of the staminate sepals), 45 (type of pistillode), 55, 57 (direction and texture of the pistillate sepals), 63, 66, 69 (shape, incision, and attachment of the stigma), 80 (apex of the endocarp), and 81 (indumentum of the septae and columella) show in the synoptical key no variability within a species or coded taxon and can be coded directly.

In some other characters the variation within a species shows some exceptions. These characters can be coded into states by discarding the unusual forms. Thus, characters 1 (indumentum of the branchlets), 13 (leaf texture), and 14 (leaf granularity) can be added to the list of discrete characters. More characters become discrete when the states used in the synoptical key are combined or split. These include characters, which are either always non-overlapping or non-overlapping in the majority of cases: 8, 10 (basal and marginal glands), 15, 16 (leaf drying colour), 22 (conspicuousness of the

Table 7.2. Summary of types of characters and the criterion used to code the states. For an explanation of the types see text.

char.	type	states coded by	char.	type	states coded by
1	discrete	majority	42	morphometric	range & mean
2	polymorphic	extremes	43	morphometric	max. value
3	polymorphic	extremes	44	polymorphic	extremes
4	morphometric	max. value	45	discrete	–
5	polymorphic	extremes	46	morphometric	range & mean
6	morphometric	max. value	47	morphometric	range & mean
7	overlapping	overlap	48	overlapping	max. value
8	discrete	combination	49	discrete	combination
9	overlapping	overlap	50	discrete	combination
10	discrete	combination	51	discrete	combination
11	discrete	–	52	morphometric	range & mean
12	overlapping	overlap	53	morphometric	max. value
13	discrete	majority	54	overlapping	max. value
14	discrete	majority	55	discrete	–
15	discrete	combination	56	polymorphic	extremes
16	discrete	combination	57	discrete	–
17	polymorphic	extremes	58	polymorphic	extremes
18	polymorphic	extremes	59	overlapping	max. value
19	polymorphic	extremes	60	morphometric	max. value
20	morphometric	range & mean	61	polymorphic	extremes
21	polymorphic	extremes	62	polymorphic	extremes
22	discrete	combination	63	discrete	–
23	discrete	–	64	polymorphic	extremes
24	polymorphic	extremes	65	discrete	combination
25	overlapping	max. value	66	discrete	–
26	morphometric	range & mean	67	morphometric	range & mean
27	morphometric	range & mean	68	discrete	combination
28	morphometric	range & mean	69	discrete	–
29	discrete	combination	70	discrete	combination
30	discrete	combination	71	overlapping	overlap
31	polymorphic	extremes	72	discrete	combination
32	discrete	–	73	discrete	combination
33	overlapping	max. value	74	morphometric	range & mean
34	polymorphic	extremes	75	morphometric	range & mean
35	polymorphic	extremes	76	overlapping	overlap
36	morphometric	max. value	77	discrete	combination
37	morphometric	max. value	78	discrete	combination
38	discrete	–	79	morphometric	range & mean
39	polymorphic	extremes	80	discrete	–
40	overlapping	max. value	81	discrete	–
41	polymorphic	extremes	82	overlapping	max. value

nervation above), 29, 30, 49, 50 (distribution of the glomerules and pistillate flowers), 51 (indumentum of the bract), 65, 68, 70 (curving and sculpture of the stigma), 72, 73, 77 (presence of stipe, beak, or conspicuous sutures in the fruit), and 78 (fruit drying colour).

The states defined for these 32 characters listed above match the descriptions of the species and the synoptic key. They are the only ones that are taken directly from the taxonomic descriptions. Together they need minimally 63 steps to be reconstructed on a cladogram. Since the analysis deals with 103 taxa of *Aporosa*, more characters are needed. Therefore, the more continuous characters available also have to be included.

Several types of continuous data can be distinguished. These are: a) discrete characters that become continuous because of polymorphic taxa; b) overlapping discrete characters, such as shapes and numbers, where the states overlap; c) continuous morphometric data, such as size ranges. The following paragraphs deal with the various methods employed for their coding.

Dealing with simple polymorphism — Kornet & Turner (1999) showed that, among other solutions, polymorphism is best coded as unknown. However, in a large matrix like *Aporosa*, where unknown data are already abundant, it is not advisable to do this. Therefore, I tried to assign as few question marks as possible. Some polymorphic taxa were split, such as *A. subcaudata* or *A. illustris*. In other cases, the presence of an extreme or maximum value, such as a stronger indumentum, was considered to be decisive. For example, *A. confusa* is scored for strongly oblique stipules, *A. tetrapleura* for two distinct pulvini, *A. maingayi* for irregularly set dots, *A. vagans* for disc-like glands scattered within the marginal arches, *A. arborea* for a puberulous venation above, *A. yunnanensis* for distinct marginal arches, *A. aurea* for tomentose rhachises, *A. nigricans* for a slightly contracted ovary, and *A. lanceolata* for ascending stigmas.

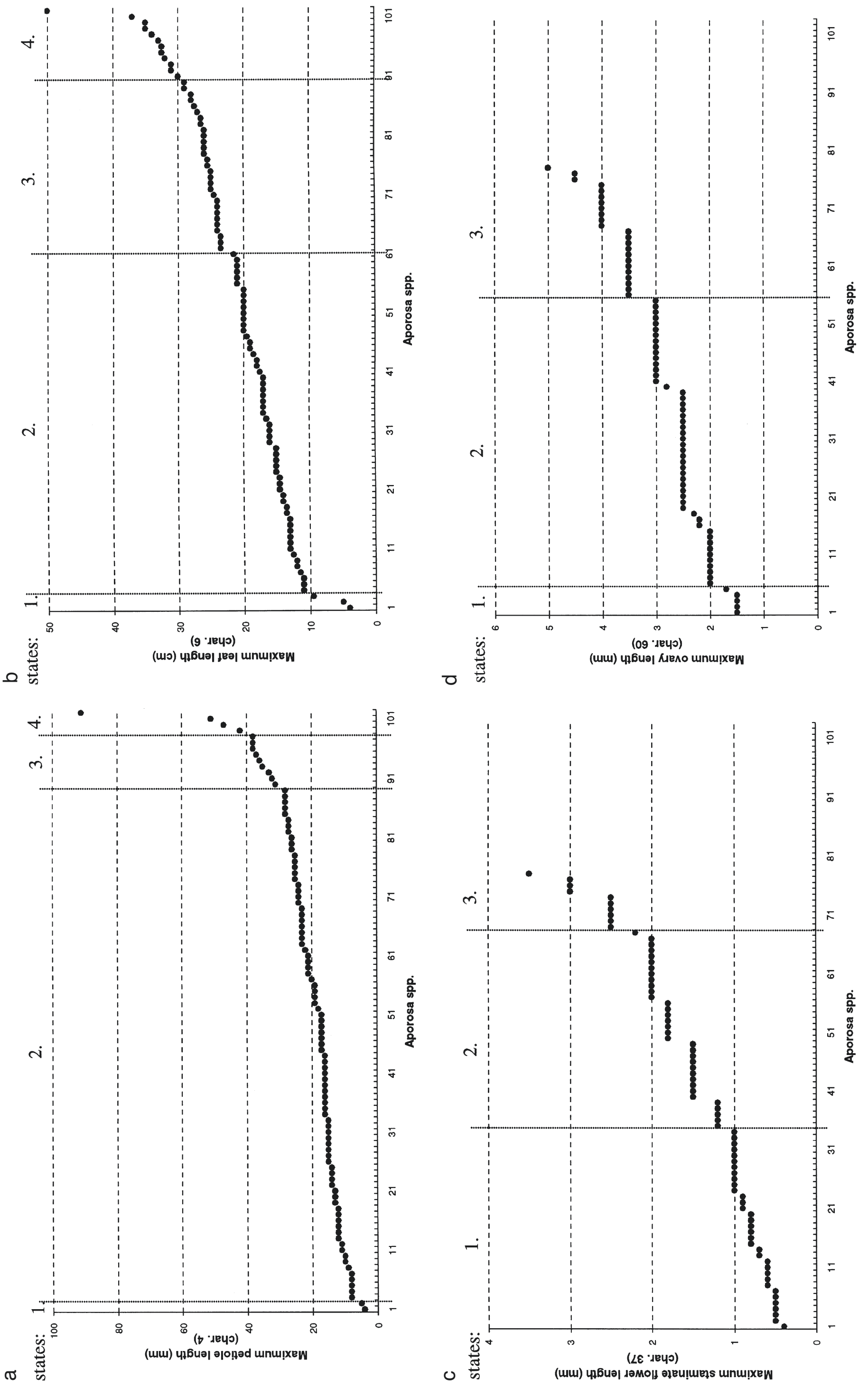
In this way, the list of discrete characters is extended with characters 2, 3 (stipule presence and shape), 5 (pulvinus sizes), 17 (leaf dots), 18 (disc-like glands), 19 (leaf indumentum), 21 (distinctness of marginal arches), 24 (indumentum of inflorescences), 31 (glomerule shapes), 34 (bract conspicuousness), 35, 39 (indumentum of staminate bracts and sepals), 41 (exertion of the stamens), 44, 56 (indumentum of connective and pistillate sepals), 58 (presence of petal-like structures), 61 (ovary indumentum), 62 (ovary contraction), and 64 (stigma direction).

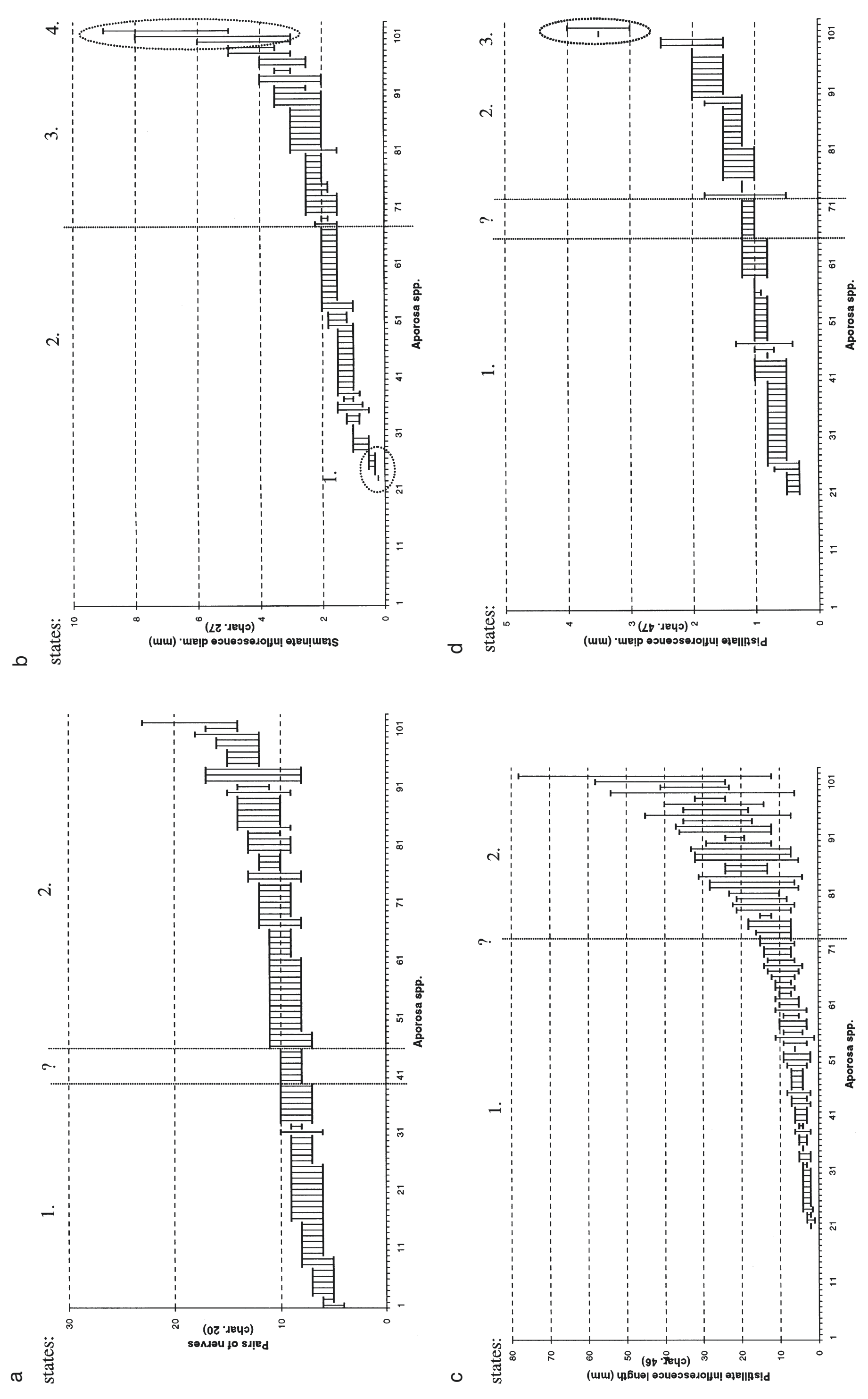
Coding continuous characters — Shape characters and numbers are the continuous data in *Aporosa*, which are more difficult to handle. Many species vary between all possible states, while others show only the extreme ones.

There is no simple way to code such characters. They are arbitrarily divided into at least three – overlapping – states: two or more for the extremes, and one for all intermediates. Examples are the shape of the leaf base or apex, characters 7 and 12: the 'real' states are the extremes, these are the important ones. A cuneate base or cuspidate apex is of no value, for almost all species have this. The important fact is whether they ever have other states as well. If coding of negative characters would not have been so tricky, it might be better to state for the intermediates 'never cordate or never attenuate'

→

Fig. 7.1. Examples of how states were assigned to maximum values for continuous morphometric characters. — a. Maximum petiole length, character 4; b. maximum leaf length, character 6; c. maximum length of the staminate flower, character 37; d. maximum length of the ovary, character 60. The X-axis plots the taxa of *Aporosa* sorted by increasing size, the Y-axis shows the maximum size values. The state boundaries are drawn between turning points in the charts, where the curve changes direction or is disrupted. These points are indicated by lines, and the states, thus defined, are given in between.


a
states:
1.
2.
3.
4.
Maximum petiole length (mm)
(char. 4)
0
20
40
60
80
100
1
11
21
31
41
51
61
71
81
91
101
Aporosa spp.
b
states:
1.
2.
3.
4.
Maximum leaf length (cm)
(char. 6)
0
10
20
30
40
50
Aporosa spp.
c
states:
1.
2.
3.
Maximum staminate flower length (mm)
(char. 37)
0
1
2
3
4
Aporosa spp.
d
states:
1.
2.
3.
Maximum ovary length (mm)
(char. 60)
0
1
2
3
4
5
6
Aporosa spp.


a
states:
1.
?
2.
Pairs of nerves (char. 20)
0
10
20
30
Aporosa spp.
1
11
21
31
41
51
61
71
81
91
101
b
states:
1.
2.
3.
4.
Staminate inflorescence diam. (mm) (char. 27)
0
2
4
6
8
10
Aporosa spp.
c
states:
1.
?
2.
Pistillate inflorescence length (mm) (char. 46)
0
10
20
30
40
50
60
70
80
Aporosa spp.
d
states:
1.
?
2.
3.
Pistillate inflorescence diam. (mm) (char. 47)
0
1
2
3
4
5
Aporosa spp.

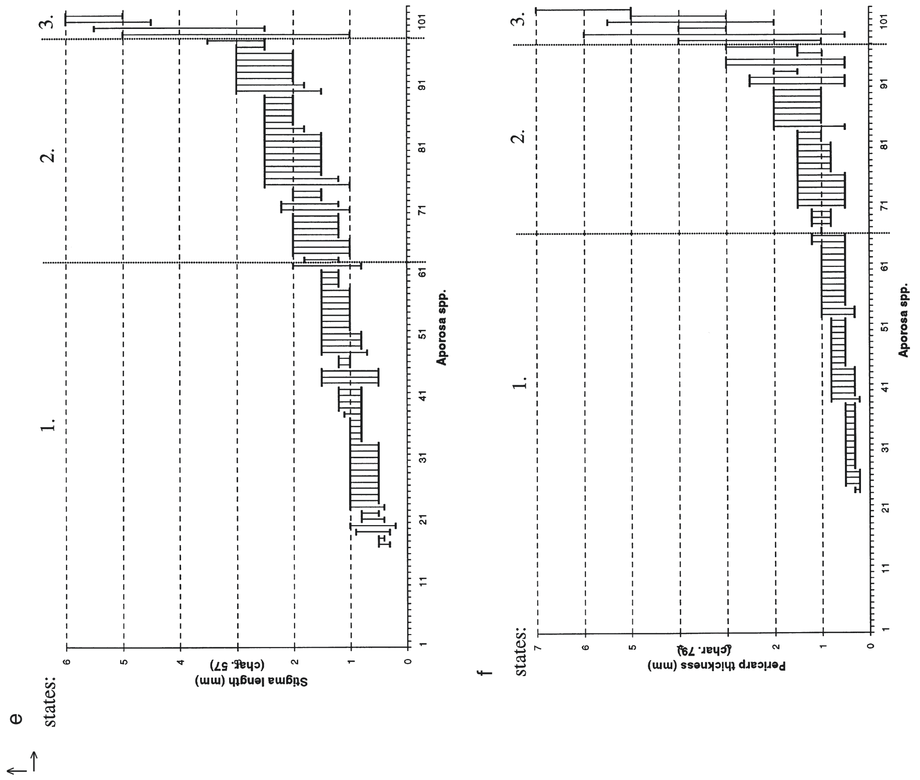


Fig. 7.2. Six examples of how states were assigned for ranges of continuous morphometric characters. — a. Pairs of nerves, character 20; b. diameter of the staminate inflorescence, character 27; c. length of the pistillate inflorescence, character 46; d. diameter of the pistillate inflorescence, character 47; e. stigma length, character 67; f. thickness of the pericarp, character 79. The X-axis plots the taxa of *Aporosa* sorted by increasing mean size, the Y-axis plots the range values. The state boundaries are drawn by first separating the extreme ranges, and then dividing the remnant arbitrarily at the mean value of the remaining ranges. a and c have no extremes; b shows two extremes; and d, e, and f have one extreme. The state boundaries are indicated by lines and the states are given in between.

or ‘never acute or never caudate’, respectively. Other characters in this category are 9 (leaf margin), 71 and 76 (fruit shape and sculpture).

The numbers of various organs can be divided according to the same principle. There is a common state that most taxa have, and one or more extreme ones that only few taxa have. The difference lies in the fact that the common state is not necessarily intermediate. An example is character 25, the number of staminate inflorescences in one cluster; most taxa have only one to five, others may have often up to 20. Here, the common state is not intermediate. The other characters belonging in this category are 33 (number of flowers per glomerule), 40 (number of stamens), 48 (number of pistillate flowers per inflorescence), 54 (number of pistillate sepals), 59 (number of locules), and 82 (number of seeds developing).

Together with the non-overlapping discrete characters this sums up to a total of 63 characters, which need at least 134 steps in the cladogram. Even more characters are desirable to solve the relationships of the 103 taxa, thus morphometric characters were included.

Coding morphometric data — To produce at least a partly objective definition of the states, I plotted the ranges by increasing values in a chart (cf. Fig. 3.2 & 3.4). Two types of data ranges were considered: maximum values for organs that are expected to be best represented by their largest score, i.e., characters 4 (petiole length), 6 (leaf length), 36 (staminate pedicel length), 37 (staminate flower length), 43 (anthers length), 53 (pistillate pedicel length), and 60 (ovary length). Ranges and their means were depicted for parts of which the herbarium specimens are possibly a proper sample of the actual situation, viz., characters 20 (number of nerves), 26, 27 (staminate inflorescence length and diameter), 28 (peduncle length), 42 (stamen length), 46, 47 (pistillate inflorescence length and diameter), 52 (bracteole length), 67 (stigma length), 74 (fruit length), 75 (fruit index), and 79 (pericarp thickness). Ten of the charts of Chapter 3 showing variation in sizes are reproduced in Fig. 7.1 and 7.2.

For coding the maximum lengths into states the chart was checked for the occurrence of gaps or so-called turning points, where the line of the dots in the chart changes direction. For example, in the chart of the maximum leaf length, Fig. 7.1b, gaps are present at 5 cm, 10 cm, 15.5 cm, 20.5 cm, 22 cm, 28 cm, 29 cm, and beyond at almost every cm. There would be too many autapomorphies when all of them are taken as state boundaries. Therefore, some of the groups were united. Four states remained: up to 10 cm, up to 22 cm, up to 30 cm, and beyond (Fig. 7.1b: indicated between the lines). This classification seemed to me the most natural one and the one that contained the highest information content. Theoretically it is a kind of partial ordering, but without the constraints of true ordering. The same reasoning applies for the coding of the other states of characters of maximum sizes. Three further examples for coding of maximum values are given in Fig. 7.1a, c, d, viz., maximum petiole length (character 4), maximum length of the staminate flower (character 37), and maximum length of the ovary (character 60). The state boundaries are drawn between gaps or at turning points (Fig. 7.1: lines). Choosing gaps or turning points as state boundaries and not accepting autapomorphies, i.e., uniting the larger taxa into one state, results in the codings of Table 7.1 for the characters 4, 6, 37, and 60, respectively. The states for the other continuous maximum values were defined with the same method (characters 36, 43, and 53, not shown, but cf. Fig. 3.2).

The state boundaries of the continuous range values were also defined using a graphical representation. Figure 7.2 shows six examples. First, species that were distinctly different in the plots, were taken out. They were given their own state, e.g., the species with staminate inflorescences up to 0.5 mm in diameter (character 27, Fig. 7.2b), the species with pistillate inflorescences more than 2.8 mm in diameter (character 47, Fig. 7.2d), the species with stigmas longer than 4 mm (character 67, Fig. 7.2e), or the species with a pericarp of more than 3 mm thick (character 79, Fig. 7.2f). Next, the mean of all minimum and maximum values of the remaining species was calculated. This was taken as the separator of the states. Species with means lower were given one state, those with a higher mean got another. Species with exactly the mean value were interpreted as polymorphic, and coded with a '?'. Examples of the resulting states of this calculating method are given in Fig. 7.2. The state boundaries are indicated by lines.

Table 7.3. Character codings for *Aporosa* and its outgroup.

character	**0**	**1–5**	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**	**31–35**	**36–40**	**41–45**	**46–50**	**51–55**	**56–60**	**61–65**	**66–70**	**71–75**	**76–80**	**81, 82**
hyp. bacc.	2	21142	22121	11212	12232	12221	22241	22112	32224	11115	21222	22312	21222	32221	31321	?1122	21121	12
bacc. sumat.	2	21122	23221	12222	21721	11221	12241	22112	32224	11115	21222	21312	21212	22221	31331	21112	21111	11
bacc. dulcis	2	11132	23122	11212	11311	22211	12241	22111	32214	11112	21223	12312	13222	11121	4111?	?1122	21121	12
bacc. minor	2	21132	22221	12112	23721	11221	22241	22212	32224	11112	21231	21212	21222	31221	31131	11111	11111	12
bacc. javan.	2	21122	23121	12212	22121	11211	21251	22122	31214	11215	21131	11312	21212	32221	31331	22112	21111	12
bacc. racem.	2	21132	22122	12111	12221	11211	22251	21122	31224	11115	21131	21312	21222	33221	31331	31221	11121	12
bacc. odora.	2	21142	23121	12111	12221	12221	22241	21122	31224	11114	21132	21312	21212	31221	31321	22111	21111	12
acuminata	1	21124	22421	12111	13551	12231	12111	22222	23121	11211	12111	22112	21212	22211	41331	12111	21111	21
alia	1	21323	22123	13111	13121	12221	12131	22222	11221	11111	11112	21122	21111	31221	31331	32122	31111	12
annulata	1	32422	22111	12112	11541	22231	12141	21223	32323	22215	11121	32311	21212	43222	22331	21212	21111	31
antennifera	1	21?23	22123	12112	23121	22221	12141	22222	12221	22211	11131	21312	21213	23222	23332	22312	11111	11
arborea	1	21542	42122	12112	14242	12231	22141	11422	21221	11214	21131	21322	21223	32222	21331	21222	11121	12
aurea	1	11232	3231?	12211	12512	22231	12111	11211	11111	11211	12111	21221	11212	11221	31321	11111	11111	22
banahaensis	1	21422	22122	12121	11222	12211	12141	21321	21212	11112	11134	12323	13222	11121	2131?	31331	12231	12
basilanensis	1	31?23	22121	11112	14232	12231	2?241	11323	21221	11214	21131	32312	31212	32222	32232	31122	21122	12
benthamiana	1	23521	41112	22212	12322	12222	23221	11323	22322	32115	12213	32222	31223	21223	33131	31121	11121	12
bourdillonii	1	31?22	22122	13112	22541	11231	13221	22312	12222	11213	21122	23212	2122?	43221	23321	31321	61111	22
brassii	1	32524	31122	12212	24452	13231	23241	11412	13323	22215	22221	32311	31233	42221	32421	31321	11121	12
brevicaudata	1	22425	13121	11212	25241	11211	13231	22111	12321	12323	11112	12311	21212	22221	32121	21323	21111	12
bullatissima	1	32522	22112	22212	12342	13221	13221	1132?	22331	3211?	11113	3?322	31122	21223	32131	311??	??1?1	1?
caloneura	1	21?33	22122	11212	15221	12221	13241	22222	12221	22215	2?131	12312	21212	13222	32232	?2232	11121	12
cardiosperm	1	11122	22421	11212	15511	21231	22111	12222	12121	22211	1?121	22312	21222	22222	21321	32311	11111	22
carrii	1	22422	21122	12212	12421	12231	22241	22322	23322	22315	21131	22312	21113	43222	22331	31222	11111	12
car. shortped	1	22422	21122	12212	12421	12231	22241	22322	23324	22315	21131	22221	22113	43222	22321	31?22	11111	12
chondron.	1	11432	42122	12131	1321?	12211	21152	21221	22212	11212	21131	11313	13222	12222	21321	?1112	22221	12
confusa	1	32422	32122	12121	11252	12231	24231	11322	11221	11111	12134	31323	3123?	31121	4131?	11131	11231	12
decipiens	1	33524	21143	12112	23142	13231	131?1	?1???	??32?	?????	12111	32112	31222	42221	32421	31112	21121	12
dendroidea	1	21?22	22121	12112	15511	12221	????1	?????	?????	?????	11122	22312	21222	23222	22321	31311	21111	12
duthieana	1	21?23	22121	11212	25221	21231	????1	?2???	???2?	?????	21122	21212	2121?	32222	22332	21212	21111	11
egregia	1	22423	22121	11212	24221	12211	13141	22221	11321	11321	21112	2?311	21212	22221	32321	21123	21121	11
elmeri	1	32224	34121	12112	2415?	12222	21151	21223	21221	11114	21231	31222	21211	41223	41431	21112	21111	11
falcifera	1	22522	32112	11212	12322	12221	13221	11323	22323	32112	?1113	21322	21222	31223	32131	31111	11111	12
ficifolia	1	31224	32424	11212	24551	13231	23111	21213	32122	12214	13111	32122	31213	41211	21321	11121	11121	22
flexuosa	1	21322	22121	12112	12321	12211	???41	?1???	????1	?????	11131	11321	11222	12222	11321	??1??	??1??	1?
frutescens	1	22423	22122	12121	11251	12221	13142	11221	11211	11111	12134	21323	23222	31121	1131?	11121	11221	12
fulvovittata	1	21422	22122	11121	14231	12211	12151	21221	11214	11211	21134	12323	1212?	12221	32321	31111	21221	12
fusiformis	1	11122	22342	11212	15611	12231	13111	22211	13121	12311	12111	12312	21213	12221	32321	22323	21111	22

Table 7.3 (*continued*)

character	**0**	**1–5**	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**	**31–35**	**36–40**	**41–45**	**46–50**	**51–55**	**56–60**	**61–65**	**66–70**	**71–75**	**76–80**	**81, 82**
globifera	1	31?22	22124	11111	1254?	12231	12111	21122	11231	11111	12111	31122	3122?	42211	21321	31121	21121	22
grandistipula	1	23542	44132	12112	14222	12211	11151	21321	21212	11214	21131	11322	11222	12222	31332	31122	21111	12
granularis	1	22323	23121	13112	13141	12221	12131	21121	21221	11112	11112	2?112	21212	21223	32331	21112	31111	11
hermaphrod.	1	21?22	22121	12212	14131	12221	????1	?????	????3	1232?	21131	22322	21213	23222	12231	?1211	21111	12
heterodoxa	1	21?22	22121	12212	15221	12221	????1	?????	????1	1131?	21222	22311	21212	22222	21321	11221	21111	12
illustris	1	32532	32123	12212	14232	12231	22251	21322	21223	11213	21131	21312	21223	22223	32332	31122	11131	12
ill. forma	1	23532	32123	12212	14232	12231	22251	21322	21223	11213	21131	21312	21223	22223	32332	31122	11121	12
lagenocarpa	1	32424	2211?	12112	24151	12231	12221	?2123	12321	22211	1?112	31112	31213	41221	33331	31233	11111	11
lamellata	1	33532	42122	12112	14132	12231	????1	11???	??32?	?????	21221	32222	31232	42221	32421	21121	44121	12
lanceolata	1	21122	22322	13111	14512	12221	12111	21121	12111	11211	1?111	11111	11212	11211	31221	11111	21111	21
latifolia	1	11122	22322	11212	15611	11231	13111	222?1	??121	1?211	12111	2?122	33222	12222	12321	31132	11131	22
laxiflora	1	22522	32122	11212	11322	22221	22151	21322	22223	22214	21131	21312	21223	33222	22321	31121	21111	12
ledermann.	1	22424	22122	12112	13522	21231	12241	21322	22312	22211	11122	21312	21212	32222	22321	21112	21111	12
leptochrys.	1	11?22	23111	12112	15211	12211	12111	?2121	12311	22211	?????	?????	?????	?????	?????	?????	?????	??
leytensis	1	33522	32123	12112	12552	12231	23241	11322	22223	22214	22121	22312	21222	43222	21321	31221	11121	12
leyt. sulaw.	1	23522	32123	12112	12522	12231	23241	11322	22223	22214	22121	22312	21222	33222	21321	31221	11121	12
longicaudata	1	22422	22121	13112	25222	12231	12121	21221	11221	11211	11122	22212	21222	22222	21332	31111	11111	12
lucida	1	21?22	33222	12111	2351?	12222	12111	11321	21121	11214	1?111	11222	22112	12211	41221	31211	21111	22
luc. ellips.	1	21?22	33222	12111	2351?	12222	12111	11321	21121	11214	1?111	11222	22112	12211	41221	21212	21111	21
luc. pubes.	1	21?22	33222	12111	2351?	12222	12111	11321	21121	11214	1?111	11222	22112	32211	41221	31211	21111	22
luc. triloc.	1	21?22	33222	12111	2351?	12222	12111	11321	21121	11214	1?111	11222	22122	12211	41221	31211	31111	22
lunata	1	33522	44122	21212	12352	13221	23221	1132?	23322	32115	2?113	31222	21122	41223	22131	31122	11111	12
macrophylla	1	11143	41111	11212	12511	12231	23111	22211	32211	11211	13111	33112	31213	41221	21231	111?1	??1?1	22
maingayi	1	21322	23111	13112	12241	12221	12121	21222	11231	11111	12112	31122	21212	41123	31431	21112	21111	11
microstach.	1	21122	22122	13112	12241	12221	12121	21222	11231	11111	12112	31212	31212	32223	32431	31212	21111	11
misimana	1	22422	21111	12112	15221	12221	12111	?2222	12321	22211	11122	31221	21213	22222	22321	31311	21111	12
nervosa	1	21422	23122	12212	15141	12221	22241	22222	22323	22224	11122	22312	21212	21222	31221	21132	11121	12
nigricans	1	21?32	32223	12112	2413?	12231	13111	11422	21221	11114	12111	22212	32113	42211	41321	31111	11121	22
nigropunct.	1	21122	22111	13112	15221	12221	12251	21222	22322	11215	11131	21312	21222	33222	32231	31311	23121	12
nitida	1	11?32	42122	12221	13612	12211	24232	11321	21221	11111	11134	11323	11232	11121	4111?	11131	11231	12
octandra	1	21222	32222	12112	1355?	12221	22111	22212	11121	11212	12111	22111	22112	22222	31321	?2212	21111	21
oct. chinens.	1	21222	23232	12111	1255?	12221	22111	22212	11121	11212	12111	22111	22112	22222	31321	22212	21111	21
oct. malesia.	1	21222	32222	12112	1255?	12221	22111	22212	11121	11212	12111	22111	22112	32222	31321	22212	21111	21
oct. yunnan.	1	31222	32222	12112	1355?	12221	22111	22212	11121	11212	12111	22111	22112	42222	31321	?2212	21111	21
papuana	1	33522	42122	12112	13252	22231	23131	11413	23322	32211	21221	32312	31223	43222	32421	31321	13121	12
parvula	1	21215	12121	11212	15221	12231	12131	22121	12321	22321	??112	11311	1121?	32222	31221	21112	21111	12
penangensis	1	21?22	22121	12112	14121	22231	13141	22221	21222	11214	11121	22212	31212	31123	31321	22122	11111	11

Table 7.3 (*continued*)

character	**0**	**1–5**	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**	**31–35**	**36–40**	**41–45**	**46–50**	**51–55**	**56–60**	**61–65**	**66–70**	**71–75**	**76–80**	**81, 82**
planchoniana	1	21122	22221	12111	15512	12231	22111	11221	11111	11212	11111	11111	12113	12211	21321	?2112	21111	21
praegrandif.	1	13542	42122	11212	13222	22231	23151	11413	23324	32225	12111	3?121	31222	41221	31331	11121	21121	12
prainiana	1	11323	23222	12121	14611	22211	22151	21221	12211	11111	21131	11312	23222	12222	31321	31122	22212	12
pseudoficif.	1	31?24	22134	11212	12542	13231	23111	22213	12121	11211	12111	31112	31122	41221	21331	11112	21111	22
quadriloc.	1	11422	22121	12121	11211	12211	14232	11321	21221	11111	11134	21323	23232	11121	3111?	11131	11231	12
reticulata	1	31?23	22122	11112	11551	22231	12141	22222	1?323	??214	??121	32322	31212	42222	32332	31212	21121	12
rhacostyla	1	32224	22111	12112	21151	12221	11151	21222	21221	11111	21231	21212	21211	41213	31231	21112	21121	11
sarawakens.	1	11322	22222	12121	13212	12212	22241	22221	11211	11112	11134	1?323	13123	11123	1231?	?1132	12222	12
sclerophylla	1	32415	12121	12212	25321	12221	12131	22121	12321	1?311	11122	21322	21211	32222	21221	?1112	21111	11
selangorica	1	22422	34122	12112	23142	12231	12121	22222	11211	11114	11112	22112	21213	32223	32331	31121	51121	12
serrata	1	31223	22444	11212	12551	13231	13111	21312	22122	11213	12111	22122	31212	41221	41321	?11??	??1??	2?
sphaeridio.	1	21?22	23122	12212	15221	12221	22241	22211	13323	22311	2?222	21312	23212	11222	41221	11111	21111	12
spha. camp.	1	21?22	23122	12212	15221	11221	22241	22211	23322	22321	???31	2?312	2121?	1122?	41221	21111	21121	12
stellifera	1	11332	42122	12211	12212	12212	23141	11321	21211	11111	11122	22323	13122	11121	4131?	21132	21222	12
stenostachys	1	21322	22122	13121	11622	12222	22251	11223	21221	11111	11134	2?322	23123	31121	2231?	31111	21211	12
subcaudata	1	32322	34122	13112	24142	12231	12241	22213	21231	11114	12212	31112	31212	41223	41431	?1112	21111	11
subc. andal.	1	32322	34122	13112	24142	12231	12241	22223	21231	11114	12112	31112	31212	41223	41431	21112	21111	11
subc. glob.	1	32322	34122	13112	24142	12231	12241	22223	21231	11114	12112	31112	31212	41223	41431	11121	21121	12
sylvestri	1	32522	32121	22212	12342	13221	???21	11?2?	??3??	3??1?	12113	21222	31122	41223	32131	311??	??1?1	1?
symplocifolia	1	11122	22221	12211	14511	12121	1?111	22212	12111	11211	12111	11111	12212	12211	31321	?1112	21111	22
symplocoid.	1	11322	22221	12121	13211	12212	22151	21222	21211	11112	21131	12312	13212	12221	11121	?1112	11211	12
sym. chalar.	1	11322	22221	12121	13211	12212	22151	21222	21211	11112	21131	12312	13212	12221	11121	22223	11211	12
tetrapleura	1	11122	22311	11211	15511	12131	23111	22211	12111	11211	??111	1?111	1221?	12211	31321	?1222	22121	22
vagans	1	21522	32122	12112	15552	13231	13241	21322	13322	22215	22121	22322	21223	43222	32321	31121	21121	12
vag. lowland	1	21522	32122	12112	15552	13231	13241	21322	13322	22215	22121	22322	21223	33222	32321	31121	21121	12
villosa	1	31224	31232	11212	1255?	12231	23111	22212	12122	12311	12111	32112	22213	42221	31321	?1112	21111	21
wallichii	1	21222	22222	12111	13511	12221	23111	22212	12121	12325	12111	22111	21212	13222	22321	32312	21111	22
whitmorei	1	21323	22122	12121	13142	12211	11151	21221	21212	11211	21131	11322	21222	12222	21321	?1122	11221	12
yunnanensis	1	11122	22222	12112	13511	12231	23111	22211	12111	22212	12111	12111	11113	13222	32321	?1312	31111	22
speca	1	21?23	22121	12112	11521	12221	????1	?????	?????	?????	21131	22322	21222	33222	21321	111??	111?1	1?
specb	1	21?23	22111	11112	11311	12222	22241	11322	12321	22215	?????	?????	?????	?????	?????	?????	?????	??
specc	1	31?23	22111	22212	13142	12231	23211	?2123	13321	22211	?????	?????	?????	?????	?????	?????	?????	??
specd	1	32522	32111	12212	23452	13231	23251	22222	12324	22313	22121	22322	21222	41221	22331	?????	?????	12
spece	1	11?22	32121	12121	11212	12211	12141	11221	11211	11114	??134	1?322	1322?	11121	3131?	31122	22221	12
specf	1	32323	34121	12112	13242	12231	12241	11222	21221	11214	12112	32112	31212	41121	31331	?????	?????	1?
specg	1	21?23	22122	12212	12121	22231	23141	22322	33223	22315	22231	22322	21123	23221	32332	?????	?????	12

When no distinctly separate values were spotted, such as for the number of nerves or the length of the pistillate inflorescence (characters 10 and 46, Fig. 7.2a and c, respectively), all species were used to calculate the mean value. Infraspecific taxa and outgroup taxa did not count. The state boundaries for the other continuous range values where defined accordingly (characters 20, 26, 28, 42, 52, 74, and 75, not shown, but cf. Fig. 3.4). With all these morphometric characters included there are now 82 multistate characters with a minimum of 171 steps available for the phylogenetic reconstruction.

7.5 – **The outgroup**

A further requirement in phylogenetic computer programs as PAUP or HENNIG86 is the designation of an outgroup. Often the nearest related genus is chosen. Maddison et al. (1984) suggest the sistergroup as most suited, a view that is also advocated by Wiley (1981) and Brooks & McLennan (1991). This idea has been on the wane the last years, as pointed out by Nixon & Carpenter (1993). Similarity is more important, since the more similar, the better comparable the outgroup taxa and the ingroup taxa. Outgroups do not need to be 'primitive'. Polarising characters is a problem to be solved by the analysis, not by preconceived ideas of the analyser.

For *Aporosa* the most appropriate candidate regarding both relationship and overall similarity – at least partly – is *Baccaurea*. Other candidates like *Ashtonia,* similar in its leaves, or *Antidesma,* similar in its spiky inflorescences, could compete. But *Baccaurea* shares a higher number of features with *Aporosa* than any of them. The African genus *Maesobotrya* might also be suitable, but was discarded because its cauliflorous inflorescences are more reminiscent of *Baccaurea* than of *Aporosa*.

Baccaurea consists of 43 species (Haegens, 2000). They are rather variable. A quick survey was made to select those species that are most similar to *Aporosa*. Thus species were selected that bear their inflorescences axillary or just below the leaves, carry dry dehiscent fruits, and have only simple hairs. Furthermore, only fully known species were considered, since it is not practical to have an outgroup with much unknown data. The species meeting these criteria were *B. dulcis*, *B. javanica, B. minor*, *B. odoratissima*, *B. racemosa*, and *B. sumatrana*. In addition, a hypothetical *Baccaurea* was constructed combining those common features of *Baccaurea* that were not present in the species chosen. The species were scored for the characters listed in Table 7.1 from descriptions by Haegens (2000). States that occur only in the outgroup are given between brackets. An extra character 0, leaves contracted along short branches (candalibriform growth habit), was added to represent the generic differences between the outgroup and the ingroup. The codings for the species are given in Table 7.3.

According to Nixon & Carpenter (1993) the best method is first treating all outgroup terminals as equal to the ingroup taxa. With the command 'out = 0.6' all seven *Baccaurea* species were given equal status. HENNIG86 then chooses for the most parsimonious outgroup from among these. In a second phase the tree may be rerooted between the outgroup and ingroup. The character states shown at this node are scored as an hypothetical ancestor. This ancestor can then be used for the subanalyses.

7.6 – **The ingroup**

The complete ingroup consists of 82 species, 8 varieties, 6 forms, and 7 insufficiently known species of *Aporosa*. Varieties and forms were included to partly meet the problem of polymorphism. The character codings are listed in Table 7.3. Some raise objections against including taxa below the species level because of possible reticulations. But hybrids have been found also between species, and even between species of different genera. Anyway, allowing infraspecific taxa in the analysis is one of the most elegant solutions for polymorphism. Furthermore, assuming we are trying to reconstruct the evolution, it is more logical to use the distinct varieties as units of speciation than the complete species themselves. This is especially true when the species shows geographical variability, such as *A. octandra*, *A. sphaeridiophora*, or *A. vagans*, or has small aberrant populations, such as *A. carrii* or *A. subcaudata*.

In later analyses monophyletic groups were represented by their basal species only. Various other analyses were run with subsets of taxa, chosen on the basis of the results of the analyses with all taxa. The taxa included as ingroup for these various subanalyses and their local outgroups are indicated when these subanalyses are described.

Chapter 8

RESULTS OF THE PHYLOGENETIC ANALYSIS OF APOROSA

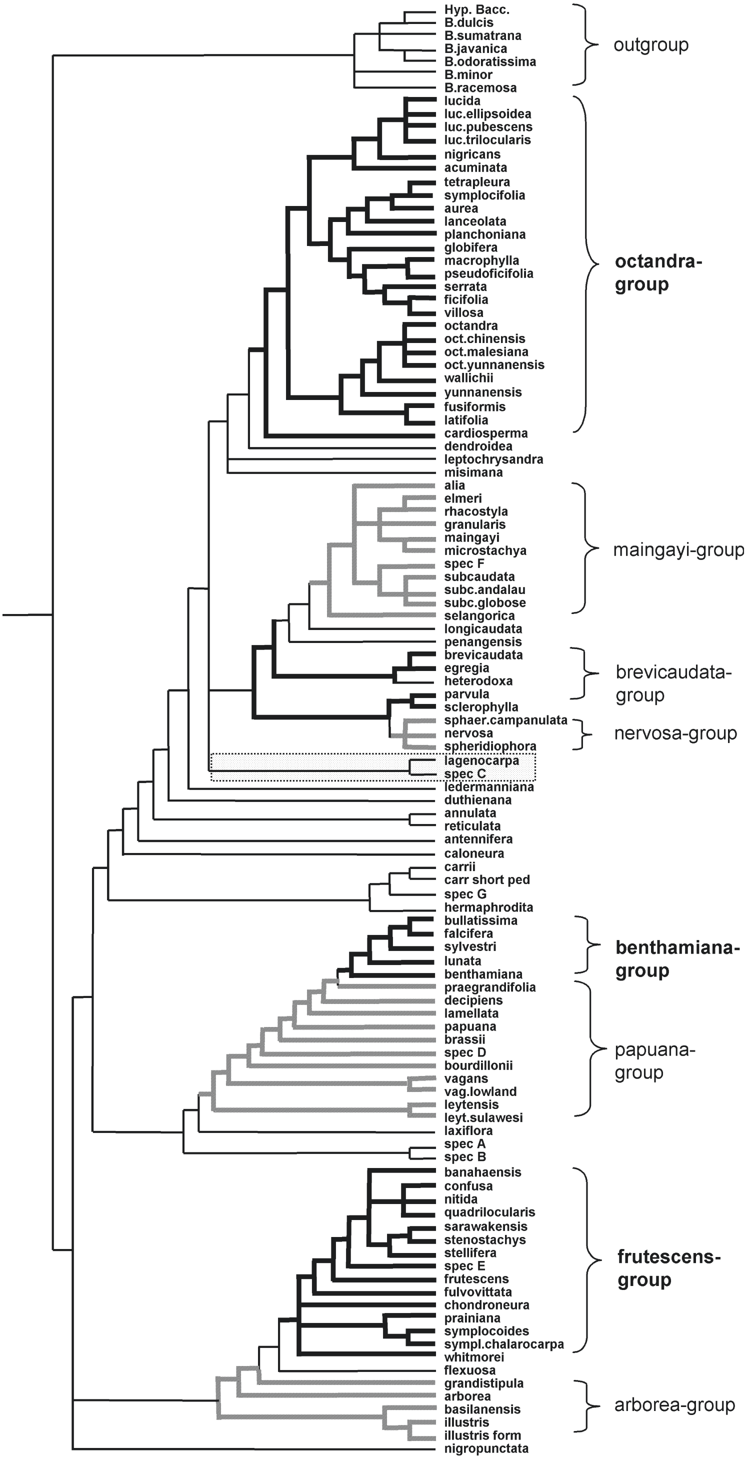
The stage has been set. The phylogenetic reconstruction of the 110 taxa of *Aporosa* with the 82 unordered multistate characters (Table 7.3) is conducted in several steps. Paragraph 8.1 describes how all data are used without assumptions in HENNIG86, resulting in multiple equally parsimonious patterns with much homoplasy. Paragraph 8.2 continues with character weighting to reduce the number of patterns. However, character weighting produced no satisfactory results, and a third step is needed before the subsets are defined for the subanalyses: establishing the stability of the clades found. Paragraphs 8.3 and 8.4 explore the patterns in the consensus tree by manipulating characters and taxa, respectively. Next, the subsets found are analysed anew with redefined character sets and outgroups (paragraph 8.5). The final phase in the phylogenetic reconstruction consists of building a consensus pattern by combining the results of the complete analysis and the subanalyses (paragraph 8.6).

8.1 – **Analysis 1: the complete data set with all characters given equal weight**

A first analysis of the complete matrix with the taxa entered in alphabetical order and with ‘mh*’ and ‘bb*’ caused an overflow of memory at 875 equally parsimonious trees, length 1432, CI 0.11, and RI 0.57. Because HENNIG86 stops searching for more trees once the memory is full, the ones found need not be the most parsimonious ones. This was proven by a subsequent analysis, in which the branch breaker ‘bb*’ was given one of NONAs ‘mult* 50’ trees as starting point. Again, a memory overflow was reported, but the 875 trees retained had length 1430, CI 0.11, and RI 0.57. Incidentally, this shows that Farris’ idea that a shorter initial cladogram gives the best results (Farris, 1988) not always holds, because the ‘mh*’ initial tree had 1433 steps and NONAs initial tree 1436.

Since HENNIG86 gave an overflow message, these cladograms also need not be the most parsimonious ones. A third analysis, using a random one of the 875 as starting cladogram for ‘bb*’, gave no other trees than the ones already found. This is logical, for when all trees are representatives of the same island, the same trees will be found each time one of them is used as starter for branch swapping. A fourth analysis was run with the command ‘hennig*’ as initial tree builder. This analysis did not render better results (> 875 trees length 1434). Analysis with the taxa in a different order was also not helpful: an overflow occurred at 875 trees with length 1432. Because these trees were not better than those in former analyses, the taxa were again entered alphabetically in all subsequent analyses for practical reasons.

When weighting the characters with RI (see below), I stumbled on even shorter cladograms. Feeding one of these, length 1429, to the ‘bb*’ resulted in an overflow of 875 trees length 1428, CI 0.11, RI 0.57. The search for more trees with the complete


Hyp. Bacc.
B.dulcis
B.sumatrana
B.javanica
B.odoratissima
B.minor
B.racemosa
outgroup
lucida
luc.ellipsoidea
luc.pubescens
luc.trilocularis
nigricans
acuminata
tetrapleura
symplocifolia
aurea
lanceolata
planchoniana
globifera
macrophylla
pseudoficifolia
serrata
ficifolia
villosa
octandra
oct.chinensis
oct.malesiana
oct.yunnanensis
wallichii
yunnanensis
fusiformis
latifolia
cardiosperma
octandra-group
dendroidea
leptochrysandra
misimana
alia
elmeri
rhacostyla
granularis
maingayi
microstachya
spec F
subcaudata
subc.andalau
subc.globose
maingayi-group
selangorica
longicaudata
penangensis
brevicaudata
egregia
heterodoxa
parvula
sclerophylla
brevicaudata-group
sphaer.campanulata
nervosa
spheridiophora
nervosa-group
lagenocarpa
spec C
ledermanniana
duthienana
annulata
reticulata
antennifera
caloneura
carrii
carr short ped
spec G
hermaphrodita
bullatissima
falcifera
sylvestri
lunata
benthamiana
benthamiana-group
praegrandifolia
decipiens
lamellata
papuana
brassii
spec D
bourdillonii
vagans
vag.lowland
leytensis
leyt.sulawesi
papuana-group
laxiflora
spec A
spec B
banahaensis
confusa
nitida
quadrilocularis
sarawakensis
stenostachys
stellifera
spec E
frutescens
fulvovittata
chondroneura
prainiana
symplocoides
sympl.chalarocarpa
whitmorei
frutescens-group
flexuosa
grandistipula
arborea
basilanensis
illustris
illustris form
arborea-group
nigropunctata

data matrix and all characters equal was abandoned at this point. Note, however, that there might still be more parsimonious trees.

The Adams consensus tree (Adams, 1972) of the last analysis is given in Fig. 8.1. I have chosen to depict this rather then the strict consensus tree, because it gives a better impression of the general pattern among all analyses and within the last one. The position of the *A. lagenocarpa-A. spec. C* clade is ambiguous in the fifth analysis (boxed in the figure). It can be positioned either at the top of the *A. aurea* branch or near *A. maingayi*, causing both clades to collapse in a strict consensus. As the low consistency index indicates, not too much confidence should be given to the precise patterns in these trees. The general shape of the cladogram is more relevant at this stage of the analysis.

The consensus patterns of the four other analyses do not differ much from this one. The same species form constant groups or have controversial placements. The clades, which are present in the strict consensus trees of all five analyses, are indicated in black in Fig. 8.1. These are the 15 taxa around *A. frutescens* (Fig. 8.1: '*frutescens*-group'), the 5 species around *A. benthamiana* with its paraphyletic tail consisting of the 8 species with affinity to *A. papuana* (Fig. 8.1: '*papuana*/*benthamiana*-group'), and part of the subsets of the 25 taxa around the variable *A. octandra* (Fig. 8.1: '*octandra*-group'). Other groups also exist, but not in all strict consensus patterns. Those that are present in all Adams consensus patterns are indicated by the accolades in Fig. 8.1. Other groups are often paraphyletic (Fig. 8.1: shaded). *Aporosa maingayi* is often placed with 6 to 9 other species (Fig. 8.1: '*maingayi*-group'), and occasionally even 11 other species. *Aporosa nervosa* and its allies, *A. arborea* and its allies, and the four species with affinity to the New Guinean *A. brevicaudata* form three smaller groups of taxa that are often placed in close relationship. *Aporosa antennifera, A. bourdillonii, A. cardiosperma, A. duthieana, A. longicaudata*, *A. nigropunctata*, and all New Guinean species with intermediate character combinations (Fig. 8.1: in grey) are controversial: they have no settled place in the five analyses.

In the next paragraph, I will investigate whether there is any possibility to reduce the number of solutions.

8.2 – **Analysis 2: the complete data set with weighted characters**

There are several ways to choose among large numbers of most parsimonious trees (MPTs). The most widely advocated and used method is character weighting (e.g., Carpenter, 1988). HENNIG86 has a built-in automatic iterative character weighting method, options 'xs w' followed by a new 'mh*' and 'bb*' (mh* was added due to memory problems). In this way, the characters are assigned different weights, which are calculated using the scaled product of the CI and RI – the 'rescaled consistency index RC'. A new tree is built corresponding to these weight factors. The weighting is repeated until the weighting factors and the cladograms no longer change (Farris, 1969).

←

Fig. 8.1. Adams consensus tree of 875 cladograms (length 1428) of the fifth analysis, which included all taxa and with the characters unweighted. Eight groups are present in the various analyses, three of them monophyletic (bold) and five paraphyletic (shaded). The ambiguous clade *Aporosa lagenocarpa – A. spec. C* is boxed.

Table 8.1. Character statistics of the characters in the fifth analysis of analysis 1 (875 trees length 1428, CI 0.11, RI = 0.57) and the weight factors assigned to them in the various weighted analyses. *CI* = best consistency index of the character in the 875 trees; *RI* = best retention index; *RC* = rescaled consistency index, RIxCI; *I* = weight assigned to the characters by HENNIG86s 'xs w', RCx10; *W* = weight assigned on base of the RI; *f3* = fit of characters according to Goloboff (1993) at K = 3; *f6* = fit of characters at K = 6; *F3* = weight factor assigned to the characters based on f3; *F6* = weight factor assigned to the characters based on f6.

char.	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
CI	1.00	0.08	0.10	0.28	0.17	0.16	0.12	0.13	0.23	0.15	0.10	0.33	0.08	0.05
RI	1.00	0.54	0.48	0.83	0.17	0.25	0.48	0.36	0.61	0.20	0.46	0.50	0.37	0.59
RC	1.00	0.05	0.05	0.24	0.03	0.04	0.06	0.05	0.14	0.03	0.05	0.17	0.03	0.03
I	10	0	0	2	0	0	0	0	1	0	0	1	0	0
W	10	5	5	8	2	3	5	4	6	2	5	5	4	6
f3	1.00	0.12	0.14	0.23	0.18	0.13	0.13	0.14	0.23	0.16	0.10	0.60	0.13	0.15
F3	10	1	1	2	2	1	1	1	2	2	1	6	1	2
f6	1.00	0.21	0.25	0.38	0.30	0.22	0.22	0.24	0.38	0.27	0.18	0.75	0.22	0.26
F6	10	2	3	4	3	2	2	2	4	3	2	8	2	3

char.	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**
CI	0.50	0.11	0.06	0.09	0.19	0.10	0.06	0.09	0.11	1.00	0.08	0.16	0.04	0.16
RI	0.84	0.73	0.40	0.53	0.63	0.54	0.65	0.23	0.20	1.00	0.65	0.54	0.58	0.61
RC	0.42	0.08	0.03	0.05	0.12	0.06	0.04	0.02	0.02	1.00	0.06	0.09	0.06	0.10
I	4	0	0	0	1	0	0	0	0	10	0	0	0	1
W	8	7	4	5	6	5	7	2	2	10	7	5	6	6
f3	0.60	0.27	0.17	0.08	0.11	0.08	0.18	0.23	0.16	1.00	0.13	0.38	0.14	0.17
F3	6	3	2	1	1	1	2	2	2	10	1	4	1	2
f6	0.75	0.43	0.29	0.14	0.19	0.15	0.30	0.38	0.27	1.00	0.22	0.55	0.24	0.29
F6	8	4	3	1	2	2	3	4	3	10	2	6	2	3

char.	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**
CI	0.08	0.17	0.33	0.07	0.06	0.14	0.09	0.08	0.09	0.10	0.16	0.13	0.13	0.22
RI	0.73	0.69	0.33	0.58	0.67	0.60	0.61	0.56	0.64	0.64	0.80	0.55	0.48	0.76
RC	0.06	0.12	0.11	0.05	0.04	0.09	0.06	0.05	0.06	0.06	0.13	0.07	0.06	0.17
I	0	1	1	0	0	0	0	0	0	0	1	0	0	1
W	7	7	3	6	7	6	6	6	6	6	8	6	5	8
f3	0.21	0.14	0.60	0.20	0.17	0.14	0.23	0.13	0.14	0.14	0.23	0.19	0.13	0.30
F3	2	1	6	2	2	1	2	1	1	1	2	2	1	3
f6	0.35	0.24	0.75	0.33	0.29	0.25	0.38	0.22	0.24	0.25	0.38	0.32	0.23	0.46
F6	4	2	8	3	3	3	4	2	2	3	4	3	2	5

char.	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**
CI	0.12	0.11	0.16	0.12	0.09	0.16	0.10	0.18	0.25	0.07	0.10	0.11	0.04	0.14
RI	0.80	0.68	0.28	0.50	0.75	0.71	0.30	0.85	0.76	0.52	0.61	0.68	0.52	0.57
RC	0.10	0.08	0.05	0.06	0.07	0.12	0.03	0.15	0.19	0.04	0.06	0.08	0.02	0.08
I	1	0	0	0	0	1	0	1	1	0	0	0	0	0
W	8	7	3	5	8	7	3	9	8	5	6	7	5	6
f3	0.30	0.17	0.38	0.09	0.23	0.23	0.25	0.25	0.25	0.11	0.14	0.17	0.13	0.20
F3	3	2	4	1	2	2	3	3	3	1	1	2	1	2
f6	0.46	0.29	0.55	0.17	0.38	0.38	0.40	0.40	0.40	0.20	0.25	0.29	0.23	0.33
F6	5	3	6	2	4	4	4	4	4	2	3	3	2	3

Table 8.1 (*continued*)

char.	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**
CI	0.08	0.16	0.09	0.13	0.09	0.08	0.09	0.20	0.20	0.12	0.09	0.10	0.15	0.15
RI	0.50	0.62	0.54	0.72	0.32	0.57	0.64	0.66	0.66	0.75	0.43	0.58	0.54	0.77
RC	0.04	0.10	0.05	0.10	0.03	0.05	0.06	0.13	0.13	0.09	0.04	0.06	0.09	0.12
I	0	1	0	1	0	0	0	1	1	0	0	0	0	1
W	5	6	5	7	3	6	6	7	7	8	4	6	5	8
f3	0.13	0.23	0.23	0.19	0.14	0.09	0.13	0.43	0.43	0.18	0.09	0.15	0.16	0.21
F3	1	2	2	2	1	1	1	4	4	2	1	2	2	2
f6	0.22	0.38	0.38	0.32	0.24	0.16	0.23	0.60	0.60	0.30	0.17	0.26	0.27	0.35
F6	2	4	4	3	2	2	2	6	6	3	2	3	3	4

char.	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**
CI	0.14	0.08	0.09	0.09	0.08	0.07	0.17	0.37	1.00	0.08	0.25	0.66	0.06
RI	0.33	0.42	0.33	0.44	0.52	0.47	0.35	0.16	1.00	0.47	0	0.96	0.39
RC	0.11	0.03	0.03	0.06	0.07	0.06	0.06	0.06	1.00	0.04	0	0.64	0.03
I	1	0	0	0	0	0	0	0	10	0	0	6	0
W	4	4	3	5	5	5	4	2	10	5	0	10	4
f3	0.38	0.12	0.23	0.14	0.13	0.12	0.11	0.38	1.00	0.13	0.50	0.75	0.18
F3	4	1	2	1	1	1	1	4	10	1	5	8	2
f6	0.55	0.21	0.38	0.25	0.22	0.21	0.20	0.55	1.00	0.22	0.67	0.86	0.30
F6	6	2	4	3	2	2	2	6	10	2	7	9	3

This method does not work for *Aporosa*. Table 8.1 shows why: the CI and therefore the RC value of most characters is very low, and as a consequence the weighting factor calculated by HENNIG86 (Table 8.1: I) assigns a value '0' to 61 characters out of the 83. It is impossible to calculate a satisfactory cladogram of 110 taxa with only 22 characters.

The low CI is a direct consequence of the high number of taxa (e.g., Sanderson & Donoghue, 1989). The more taxa, the more frequent the occurrence of a particular state. This leads automatically to a lower CI in analyses with many taxa. The effect is strongest in binary characters, where one extra step weighs more heavily on the amount of homoplasy: in a 3-state character one extra step reduces the CI to 66%, in a binary character to 50%.

On the other hand, the retention index, RI, looks at the synapomorphous value of a character (Farris, 1989). The RI does not suffer from dependence on the number of taxa or favouring of multistate characters (see also comments by Turner, 1995). Looking at the RIs of the characters in *Aporosa* as given in Table 8.1, we see that they are rather high. Naylor & Kraus (1995) demonstrate how the RI is inflated for multistate characters in which one state is autapomorphic or shared by only two taxa. They further conclude that this variance in RI is more influential in analyses with few taxa. But for *Aporosa* neither of these facts has to be negative: unique states are so rare that giving them extra weight might actually be preferable. Moreover, the 110 taxa might be a sufficient counterbalance. Therefore, the RI was taken of the best fits and used for the calculation of weighting factors W.

Rerunning the matrix in the first instance with the W-factors found for the 875 trees of length 1430, 48 trees were produced with length 7619. These trees are length 1429 if the characters are unweighted. This is even shorter than the 1430 steps of the second unweighted analysis. Using one of these trees of length 1429 for an unweighted analysis with ‘bb*’ gave the 875 trees of length 1428, which are the basis for a new round of weighting (Table 8.1). Analysis with these new weight factors rendered 4 trees of length 7640. Unweighted, these cladograms have length 1431. This illustrates one of the disadvantages of character weighting: the cladograms found with weighted characters need not be among the set of most parsimonious ones in an unweighted analysis.

This disadvantage might be tackled by recalculating the lengths of the trees of the original set of most parsimonious trees with the weighted characters. If one or more among them are shorter with the weighted set of characters then these may be preferred above the longer ones.

Thus I determined the length of the 875 trees of length 1428 with the weighted character set. Surprisingly, some of these are shorter than the 7640 steps of the most parsimonious trees found when running the weighted analysis: 7631 steps (other island). Even worse, 14 of the 48 trees of the first weighted analysis had a recalculated length of 7627 with this second weighted character set. This shows that the ‘mh*’ and ‘bb*’ sometimes indeed can miss the most parsimonious trees (cf. Farris, 1988). Because shorter trees were possible, one cladogram of the 14 with length 7627 was taken for the branch breaker ‘bb*’ in a new analysis. Only twelve of the above 14 trees were rediscovered. The combination of NONAs ‘mult* 50’ with HENNIG86’ ‘bb*’ was not helpful in this case: though ‘mult* 50’ finds trees from different islands of trees better than ‘mhennig*’, the branch breaker ‘bb*’ cannot escape the island it starts from. It seems that with such highly weighted characters the gap to go from one island to another is too large to be taken by ‘bb*’. The analysis will thus strand with trees from the same island. Goloboff (1993b) has discerned this problem, and implemented the command ‘jump N’ to deal with it. He is, however, unsure of its effects in finding trees of different islands in NONA. Due to these imperfections in finding the shortest weighted trees, iterative weighting was not performed.

Goloboff (1993a) has proposed another method for character weighting. The ‘fit’ of every character is determined during analysis. This fit F is calculated by $F = K/(ES + K)$, where ES is the number of observed extra steps and K – the concavity – a measure of the concaveness of the function. Higher values of K weigh more strongly against characters with high homoplasy levels. This function is not dependent on the number of taxa and the different treatment of binary and multistate characters. Goloboff implemented this weighting method in his program Pee-Wee (Goloboff, 1993b). The trees obtained are those that maximize the fit of the characters, rather then shortest trees.

Turner & Zandee (1995) have shown that the maximum fit for the complete tree sometimes behaves erratically. However, the formula for calculating the fit of the individual characters is straightforward. Thus, I calculated only the fits for the characters and entered them as weight factors in HENNIG86, instead of using Goloboff’s program Pee-Wee. Two K values were chosen arbitrarily: 3 and 6. The weighted analysis for $K = 3$ resulted in 180 trees of length 2203 (corresponding length with unweighted characters 1442–1445), and for $K = 6$ in 24 trees of length 3884 (corresponding to length 1434–1435 with unweighted characters).

The Adams consensus tree of all 256 trees found during the various weighting sessions is shown in Fig. 8.2. The various groups found before in the unweighted analysis

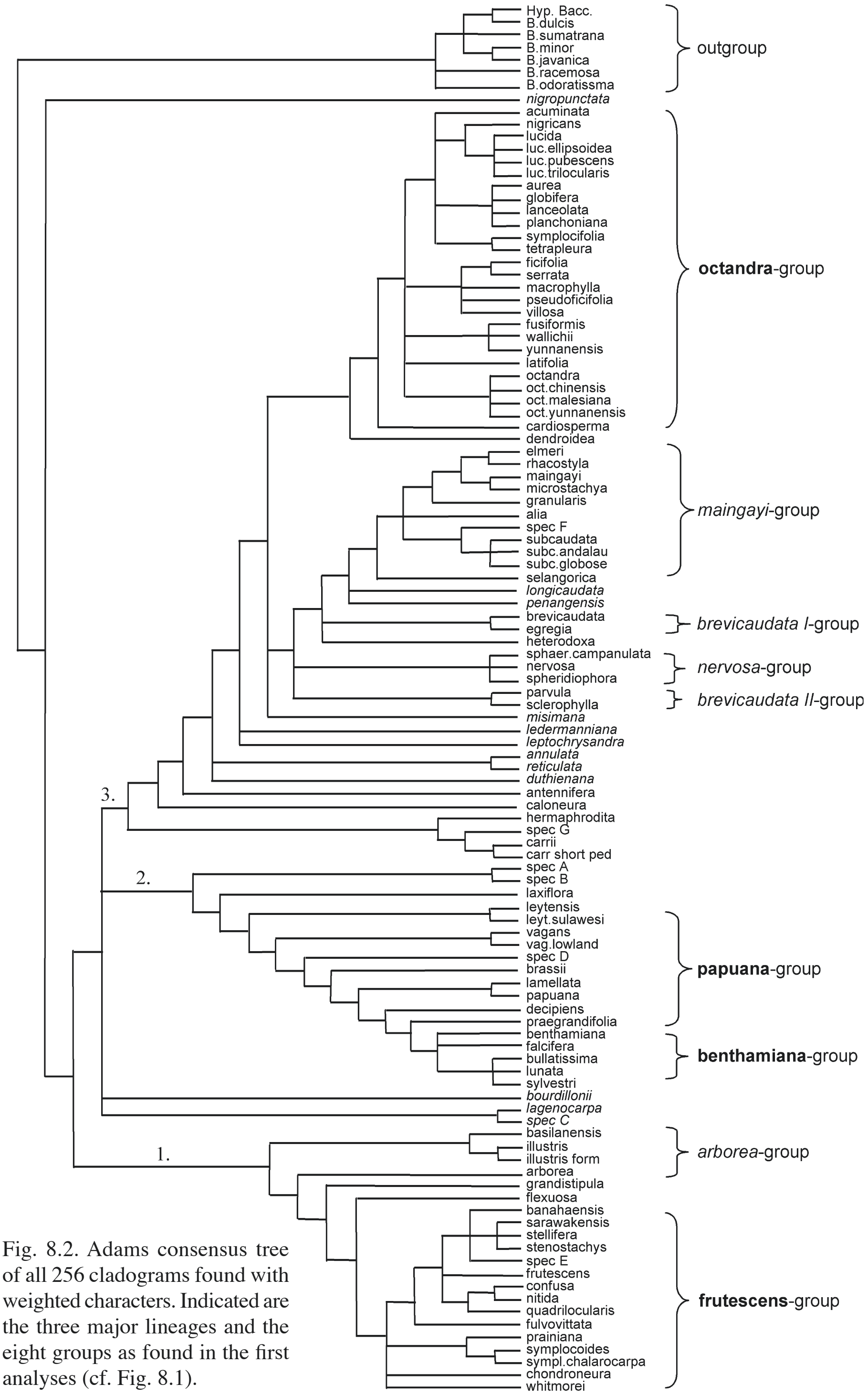


Fig. 8.2. Adams consensus tree of all 256 cladograms found with weighted characters. Indicated are the three major lineages and the eight groups as found in the first analyses (cf. Fig. 8.1).

(Fig. 8.1) are indicated. Groups, that are also present in the strict consensus pattern of all four weighted analyses, are indicated bold; groups that showed up in three of the four strict consensus patterns are in italics. From the new consensus it might seem that a grouping with three major clades is preferred (Fig. 8.2: 1, 2, 3). The first split is for the *frutescens*-clade, with at its base the paraphyletic *arborea*-group. The second lineage consists of the combined *papuana*- and *benthamiana*-groups, of which the latter is monophyletic. The last clade consists of the paraphyletic tail of the *maingayi*-, *nervosa*-, *brevicaudata*-groups with at the top the monophyletic *octandra*-clade. Four taxa have no preferred placement in any of the analyses (Fig. 8.2: italics). *Aporosa nigropunctata* is shown at the basis of all. *Aporosa bourdillonii* and the *A. lagenocarpa*/*A. spec. C*-clade are switching among the clades. Furthermore, a couple of other taxa within the third lineage also have an ambiguous placement (Fig. 8.2: italics).

The next logical step in the analysis would be to take the three lineages and analyse them as subsets in three different runs with a local outgroup. However, with the present data – unweighted, and especially with the weighted data – the possibility that shorter trees are present is high. The problem of multiple islands, increased with weighted characters, might have clouded the search. Thus I cannot be sure that the unweighted 875 trees of 1428 steps or the 14 weighted trees of length 7627 are really the shortest and whether or not all shortest cladograms are included. Knowing this, I would not dare to accept at this point the general pattern chosen by the weighted analysis. Therefore, an extra testing of the three lineages was carried out.

8.3 – **Analysis 3: testing by varying the characters**

8.3.1 – ***General***

Testing the pattern found can be done by manipulating the data matrix or relaxing the parsimony criterium. Phylogeneticists are divided about the point of these tests (e.g., Carpenter, 1992; Trueman, 1993; Davis, 1993; Bremer, 1994). Randomly changing the data can never be used to find a more parsimonious tree. However, it serves to indicate the stability of the patterns and the conclusions drawn from them. Thus in the case of *Aporosa*, such exercises may give more confidence in the pattern found. In the next paragraph, 8.3.2, I will therefore investigate if the clades keep turning up after manipulation of the characters.

Bremer's support index is a different kind of test: it tests the presence of a particular group under relaxation of parsimony. Strict consensus cladograms of groups of longer and longer trees are examined until a strict consensus cladogram is found in which a clade does not exist anymore. The extra number of steps indicates the stability of the clade (Bremer, 1994). However, at the time that the *Aporosa* analyses were performed (1995) the computational problems were still too large to perform this test.

A third method of testing for monophyly was developed by Siddall (1995). He investigated the stability of groups by studying the effects of removing taxa from the matrix. According to his results, removal of some taxa substantially increased the number of solutions, while removal of others reduced it. This is an interesting line of investigation to follow for *Aporosa*. The influence of excluding taxa is studied in paragraph 8.4.

In the weighted data set of *Aporosa* three major lineages are present, consisting of a monophyletic group at the top, i.e., the *frutescens*-, *benthamiana*-, and *octandra*-groups, each with a paraphyletic group at its tail, i.e., the *arborea*-, *papuana*-, and combined *nervosa*/*brevicaudata*/*maingayi*-groups, respectively (Fig. 8.2). The tests performed here on the matrix of *Aporosa* are primarily intended to measure the stability of the three monophyletic groups mentioned. The position of the *arborea*-, *papuana*-, and combined *nervosa*/*brevicaudata*/*maingayi*-groups as paraphyletic tail to the three monophyletic groups respectively was only tested as an aside. They are ambiguous and testing may or may not give their relationships more confidence. The taxa of uncertain position, shown in polytomies, bear no influence on the outcome of the tests since they possess no constant position that can be tested anyway.

8.3.2 – ***Revisiting characters***

Two basically different tests to re-estimate the characters can be conducted: testing for information content, and testing for monophyly or non-monophyly. The first is aimed to demonstrate whether the given data matrix has the power to solve relationships, the second how stable particular groups are when changing the data. Methods such as tree-length distribution skewness (Huelsenbeck, 1991), permutation tail probabilities (PTP: Archie, 1989; Faith & Cranston, 1991), and data decisiveness (Goloboff, 1991) fall under the first type. Källersjö et al. (1992) found fault with both skewness and PTP and developed a total support index. All these various measurements indicate the possible non-randomness of a cladogram.

Tests of the second type are designed to measure the strength of a monophyletic clade within the cladogram. They estimate the support for individual branches. The best known is the bootstrap (Felsenstein, 1985). An alternative is the jackknife. Sanderson (1989) described how to calculate a monophyly index, Faith (1991) adapted the PTP test into the T-PTP test for monophyletic groups. Davis (1993) developed the sequential character removal (SCR). However, all these methods suffer from computational difficulties or unreliable results when analysing large data sets. Thus, none were possible or meaningful to conduct for *Aporosa*.

However, to have at least some indication how the characters interact, I reran the data set with 12 chosen sets of characters inactivated. The sets were: 1) Indumentum characters – since they are considered to be more important for species delimitation than for phylogenetic reconstruction. 2) Morphometric characters – for their rather arbitrary way of coding might have a negative influence on the phylogenetic structure. Two runs were made: a) without the overlapping characters; and b) without the morphometric characters. Inactivating all characters in the same run would leave too few characters for a reliable analysis. 3a–c) The reproductive characters – to check if evolutionary patterns for the various ecological requirements for staminate or pistillate flowers or fruits would disagree. Vegetative characters had to be included also, otherwise too few characters were left. The reproductive characters were enhanced by giving them weight two. 4a–e) Five random sequences of 11 characters. 5) Synapomorphies of the three groups – to test for the unity of the species without their synapomorphies.

I will not discuss the results of these analyses in detail. Most analyses suffered from a memory overflow, except for the analysis with the first set of random characters inactivated. The strict consensus pattern of this was comparable to those of the weighted analyses, so possibly the island factor is effecting the low number of cladograms. The result of the analysis with the morphometric characters inactivated was peculiar, because the command 'bb*' was unable to swap on the initial tree; this may point to the fact that the information, which these characters possess, cannot be missed in the total analysis.

The strict consensus patterns of the various analyses show, in regard to the three monophyletic groups, mostly the same general pattern as before. The *frutescens*-, *benthamiana*-, and *octandra*-groups are always present, except for the three analyses of set 3. But in these cases very few characters were left. Here the outgroup also became polyphyletic. It is also interesting to note that even without the synapomorphies the three groups remained intact, though became paraphyletic. The paraphyletic tails of the three monophyletic groups were more often disrupted. The *papuana*-group was in 9 out of the 12 runs coupled to the *benthamiana*-group; the *arborea*-group ended 6 times in the outgroup position of the *frutescens*-group; the paraphyletic tail of the *octandra*-group was never completely intact, only partly. The complete *nervosa*-, *maingayi*-, and *brevicaudata*-groups were present only in four cases near the *octandra*-group, though supplemented with other taxa. Throughout the analyses, individual taxa were 'jumping'.

The cladograms found strengthen the arguments for the existence of the three monophyletic groups. Of the three lineages they formed in the weighted analysis, only the *papuana*/*benthamiana*-lineage can be found in a majority of cases and is assumed stable. Regarding the *arborea*/*frutescens*-lineage the connection of the *arborea*-group to the *frutescens*-group is not particularly strong. However, with or without *A. arborea*, the *frutescens*-group represents in itself one lineage. The third lineage is more problematic, it consists at least of the monophyletic *octandra*-group and part of the *maingayi*-group with supposedly other taxa. Which taxa exactly cannot be said with certainty.

8.4 – **Analysis 4: testing by excluding taxa**

A different method to study the stability of monophyletic clades was advocated by Siddall (1995). In contrast to the methods mentioned above, he manipulates the taxa. Based on the jackknife procedure he developed a Jackknife Monophyly Index (JMI) in which he tested the effect of taxon removal on the stability of the groups they belonged to. The clades that persist in at least 95% of the analyses with one taxon removed he calls stable.

His method suffers from the same negative point as other tests mentioned in the foregoing paragraph: when the number of taxa increases, so does the number of the analyses to be conducted. To test the three monophyletic groups indicated for *Aporosa* would require 54 runs with every taxon removed once; if several taxa out of each group and out of the paraphyletic tail are deleted, even more runs are required. This would be much too time consuming.

Sidall (1995) also pointed out that some taxa substantially increased the number of solutions, while others reduced it. If it could be shown for *Aporosa* that some taxa cause most of the ambiguity, analysis without them might reveal new stable relationships. Thus the next step in testing the phylogenetic pattern of *Aporosa* is excluding various categories of ambiguous taxa. But first, to facilitate these analyses, the monophyletic groups are reduced to their basal taxa.

8.4.1 – ***Reducing the monophyletic subsets***

The most logical step to reduce the number of taxa in the monophyletic groups is to replace them by their respective ancestors, coded from the states shown on the basal node. The problem with *Aporosa* is, however, that many of the characters on the basal nodes of the monophyletic groups have ambivalent states, and because polymorphism cannot be coded in HENNIG86, one state should be chosen when coding the hypothetical ancestor. When I tried to do so, the resulting cladograms showed shifting positions for the ancestors within the phylogenetic trees. Since the purpose of defining the temporary subset is to get a smaller data set, that has a consensus tree comparable to that of the full set of taxa, this is, at this stage of the phylogenetic reconstruction, an unwanted effect. The next option is to reduce the monophyletic groups to their basal species.

Which are the basal species? Of the 15 taxa of the *frutescens*-group, *A. chondroneura* and *A. whitmorei* are nearly always the basal ones and were at first selected as representatives of the complete clade. The *benthamiana*-group was represented by two of the five taxa, *A. falcifera* and *A. lunata*. The *octandra*-group was less easy reduced. The basal relationships of the 26 taxa are depicted in a polytomy and thus not known. However, the more derived taxa are evidently the three varieties of both *A. lucida* and *A. octandra*. The glabrous species with the yellow drying leaves with distinct basal glands, viz., *A. aurea, A. lanceolata, A. planchoniana, A. symplocifolia*, and *A. tetrapleura*, are also terminal in all analyses. These can be excluded. A further reduction is deleting one of two sister-species. Three constant species pairs are present. Of the pairs *A. ficifolia – A. serrata* and *A. yunnanensis – A. wallichii*, *A. serrata* and *A. yunnanensis* were excluded, respectively. The pair *A. lucida – A. nigricans* was left as it was, for in some analyses this pair was disrupted. This leaves 13 of the more basal taxa within the *octandra*-group. Excluding all 28 taxa mentioned from the ingroup of 103 leaves 74 taxa.

However, re-analysis with only the mentioned representatives for the three monophyletic clades unexpectedly produced major shifts in the topology. Obtaining a pattern comparable to the complete analysis (paragraph 8.1) required the re-addition of two members of the *frutescens*-group, of which one with slightly interrupted staminate inflorescences, e.g., *A. banahaensis* and *A. prainiana*, and inclusion of all five taxa of the *benthamiana*-group. In addition, the sheer number of taxa within the *octandra*-clade s.l. had to be kept above a certain minimum to undo some of the major shifts of its direct outgroup-taxa. However, this is almost impossible because the point of the next analysis is investigating the effects of excluding taxa.

In a next step, I also tried deleting one taxon in some closely related species pairs. However, it seems that the deletion effects the optimisation of the characters. This causes a different placement for the retained taxon in comparison with analyses where both of them are included. This effect was especially bad for the group of the four forms of *A. subcaudata*. The monophyly of this group seemingly rests on the number of taxa in it: less taxa probably shifts the balance of one or more characters into a more parsimonious solution when shown as parallel than if four taxa would have to show this parallel.

When the forms of *A. subcaudata* are excluded, *A. subcaudata* appears closer to the root of the *maingayi*-group, disrupting the relationships with *A. spec. F*, *A. selangorica*, and *A. elmeri*. This shows that the relations within the *maingayi*-group and other subsets of the paraphyletic tail are not stable. Only omitting the almost identical form of *A. illustris* seemed to have no influence on the tree topology. So, of all the closely related species pairs only this form was excluded.

The ingroup now consists of 78 taxa. Before conducting the analysis, the outgroup needs re-evaluation. According to Nixon & Carpenter (1993) the cladogram found in a preliminary analysis should be rerooted between the in- and outgroup and the states on this branch taken as ancestral to the complete ingroup. However, there is no single cladogram for *Aporosa*. Consequently, there are different ways to code for the ancestor: characters 3, 17, 26, 29, 33, 37, 46, 62, 67, 69, 71, 74, 76, and 79 vary between the several analyses. As none can be chosen above another, an artificial ancestral *Aporosa* could not be coded. However, in all strict consensus trees of the analyses with the full set of characters and in many consensus trees of the analyses with variously omitted characters the same 3 of the 7 *Baccaurea* species are closest to the ingroup, viz., *B. membranacea, B. minor*, and *B. racemosa*. These three acted as outgroup in further analyses.

With the selected three *Baccaurea* and 78 *Aporosa* species the matrix of Table 7.3 was run again. HENNIG86 returned a memory overflow at 1181 trees, length 1128, CI 0.14, and RI 0.53. Because of the overflow more parsimonious trees are theoretically possible, though they can be found by chance alone. The Adams consensus pattern of this analysis (not shown) is similar to that of the complete analysis (cf. Fig. 8.1) except for some minor shifts in the positions of taxa within the monophyletic groups and *A. bourdillonii*. The resemblance with the complete analysis goes even further because shorter trees were found as well. Using JOYRIDE and 'he*' chance recovered 690 trees of length 1126, CI 0.14, and RI 0.53. I have not reproduced the strict consensus pattern here, for there is no way to recalculate it. The initial sequence of taxa needed to find a tree this short is unknown. All in all it shows that the presently selected 78 taxa can be used to investigate the effect on the number of MPTs when particular categories of taxa are excluded.

The most likely candidate taxa to exclude first are those that were ambiguously placed by the earlier analyses. They can be found by comparing the Adams consensus trees of the unweighted analysis (paragraph 8.1; Fig. 8.1) with the Adams consensus tree of the weighted analyses (paragraph 8.2; Fig. 8.2). Both trees have three lineages, but not quite similar. Taxa that are placed differently or ambiguously are *A. annulata*, *A. duthieana*, *A. heterodoxa*, *A. lagenocarpa*, *A. leptochrysandra*, *A. longicaudata, A. misimana*, *A. nigropunctata*, *A. penangensis*, *A. reticulata*, and *A. spec. C*. Furthermore, the placement of the *nervosa*-group and the *brevicaudata*-group also varies. By checking the 'jumping' species among the analyses with part of the characters inactivated (paragraph 8.3), this list can be further extended. Taxa which switch strongly in position between these analyses are, in addition to the above, *A. antennifera*, *A. caloneura*, *A. cardiosperma*, *A. flexuosa*, *A. hermaphrodita*, *A. ledermanniana*, *A. selangorica*, *A. spec. A*, *B*, *D*, *F*, and *G*. Furthermore, the subhermaphroditic form of *A. carrii* was also found to greatly influence the outcome of the analysis. Different or ambiguous placements within the three accepted monophyletic lineages, the *frutescens*-group, the *papuana-benthamiana*-group, and the *octandra*-group, are not considered here.

The above list of taxa can be divided on macromorphological grounds in three categories: 1) incompletely known taxa. *Aporosa duthieana*, *A. flexuosa*, *A. leptochrysandra*, *A. spec. A–G* are taxa that are only known from pistillate or staminate specimens; 2) often rare, local species, possessing unique characters, which are not found in other taxa of *Aporosa*. These are *A. antennifera*, *A. bourdillonii*, *A. caloneura*, again *A. duthieana*, *A. lagenocarpa*, *A. longicaudata*, *A. nigropunctata*, *A. penangensis*, and *A. selangorica*; and 3) the New Guinean species that formed the range of taxa intermediate between the large-leaved species around *A. papuana* and the small-leaved species around *A. brevicaudata*. *Aporosa annulata*, *A. flexuosa*, *A. hermaphrodita*, *A. heterodoxa*, *A. ledermanniana*, *A. leptochrysandra*, *A. misimana*, *A. reticulata*, *A. spec. A, B, C, D*, and the subhermaphroditic form of *A. carrii* are representatives of this group.

Each category is in the next paragraphs excluded to investigate its effect on the number of MPTs. The categories were supplemented by taxa that theoretically belong to them, even if they did not show an ambiguous placement in the analyses. As starting point the truncated matrix is used with 78 *Aporosa* and 3 *Baccaurea* to avoid memory and CI problems as much as possible.

8.4.2 – ***Excluding incompletely known taxa***

It is widely recognized that poorly known taxa may increase the number of most parsimonious solutions and reduce the resolution of the consensus tree (e.g., Wilkinson, 1995). The many missing entries of such taxa introduce uncertainty into the data set and may thus obscure the relationships. The accuracy dwindles, affecting the reliability of the pattern. Several phylogeneticists have therefore opted for excluding such taxa.

Little known species are also present in *Aporosa*. In coding the characters, I tried to avoid inapplicable data as much as possible. There is, however, one unavoidable origin of question marks in the data set: *Aporosa* is dioecious. Some species are only known from staminate, pistillate, or fruiting specimens. One third or two thirds of the characters of such species are thus simply unknown.

Besides the mentioned 10 incompletely known species, there are 12 others that are partly known. Of these 22 taxa, three are of no importance here because they are already excluded from the temporary subset: *A. serrata*, *A. tetrapleura*, and *A. spec. E*. The remaining 19 incompletely known taxa, viz. *A. bullatissima, A. decipiens, A. dendroidea, A. duthieana, A. flexuosa, A. hermaphrodita, A. heterodoxa, A. lamellata, A. leptochrysandra, A. macrophylla, A. reticulata, A. sphaeridiophora* var. *campanulata, A. sylvestri, A. spec. A, B, C, D, F,* and *G*, and their category of missing data are listed in Table 8.2.

From Table 8.2 it follows that not all taxa are equally likely to effect the tree topology. The more unknown data, the more influence is supposed. Therefore, runs were made in which taxa with several categories of missing data were excluded. These were:

a) the 10 taxa with staminate inflorescences partly or completely unknown, viz., *A. decipiens*, *A. dendroidea*, *A. duthieana*, *A. flexuosa*, *A. hermaphrodita*, *A. heterodoxa*, *A. lamellata*, *A. reticulata*, *A. sylvestri*, and *A. spec. A*;
b) the 4 taxa with pistillate inflorescences partly or completely unknown, viz., *A. leptochrysandra*, *A. sphaeridiophora* var. *campanulata*, *A. spec. B*, and *C*;

c) the 11 taxa with fruits partly or completely unknown, viz., *A. bullatissima*, *A. flexuosa, A. leptochrysandra*, *A. macrophylla*, *A. serrata*, A. *sylvestri, A. spec. B, C, D, F*, and *G*;
d) the 8 taxa with more than one of the above categories unknown, viz., *A. dendroidea*, *A. duthieana*, *A. flexuosa*, *A. leptochrysandra*, *A. sylvestri*, *A. spec. A, B,* and *C*;
e) the 11 taxa with only one category of characters unknown, viz., *A. bullatissima, A. decipiens, A. hermaphrodita, A. heterodoxa, A. lamellata, A. macrophylla, A. reticulata, A. sphaeridiophora* var. *campanulata, A. spec. D, F,* and *G*; and
f) all 19 incompletely known taxa.

In studying the results of these six analyses, the main interest focuses on the effect on the number of MPTs and on the solution of the strict consensus pattern. Additionally, it is relevant to see how the three lineages found with the weighted analysis behave.

In general, the influence of excluding various sets of incompletely known taxa has reduced the number of MPTs: they range from 18 in analysis f to 810 in analysis e. This is what was expected. In detail, however, the ambiguity, expressed by polytomies in the strict consensus, has not decreased. The basal part is still ambiguous; the stabilizing influence is restricted to the top and middle part of the cladogram. Furthermore, comparing the sequence of splitting among the strict consensus patterns over all six analysis, the stability of the middle part is deceptive. Each analysis shows a different sequence. The first and second lineages, i.e., the *frutescens*-group with the *arborea*-agglomeration at its base and the combined *papuana*/*benthamiana*-groups, are always present. Sometimes

Table 8.2. The 19 incompletely known taxa in *Aporosa* and the category of characters that is missing (staminate, pistillate or fruiting), and in how far: + = completely known; ± = incompletely known; partly filled in with the aid of immature inflorescenses (for staminate characters), fruits (for pistillate characters) or pistillate characters (for fruits); – completely unknown.

taxon	staminate	pistillate	fruiting
A. bullatissima	±	+	±
A. decipiens	–	+	+
A. dendroidea	–	+	+
A. duthieana	–	+	+
A. flexuosa	–	+	-
A. hermaphrodita	–	+	+
A. heterodoxa	–	+	+
A. lamellata	–	+	+
A. leptochrysandra	+	–	–
A. macrophylla	+	+	±
A. reticulata	±	+	+
A. sphaeridiophora var. *campanulata*	+	±	+
A. sylvestri	–	+	±
A. spec. A	–	+	±
A. spec. B	+	–	–
A. spec. C	+	–	–
A. spec. D	+	+	–
A. spec. F	+	+	–
A. spec. G	+	+	–

they are apart, sometimes together; sometimes the *papuana*-group is paraphyletic at the base of the *benthamiana*-group, and sometimes the two are monophyletic sistergroups (when excluding the incompletely known species from the *benthamiana*-group!). The third lineage, consisting of the *octandra*-, *maingayi*-, *brevicaudata*-, *nervosa*-groups and various remaining species, is, depending on the position of the first two lineages, sometimes monophyletic, sometimes paraphyletic, and once even polyphyletic. It should be noted, however, that the *octandra*-group is always monophyletic; only the other species of the third lineage are ambiguous.

In conclusion, the role of the incompletely known taxa in reconstructing the phylogeny of *Aporosa* lies mainly in increasing and destabilizing patterns that are ambiguous already in other ways. Excluding them does not unveil other patterns.

8.4.3 – ***Excluding West Malesian species***

The second category of taxa with instable positions consists of local, rare, or nondescript taxa, many of them characterized by a unique character. These are *A. antennifera*, *A. bourdillonii*, *A. caloneura*, *A. duthieana*, *A. lagenocarpa*, *A. longicaudata*, *A. nigropunctata*, *A. penangensis*, *A. selangorica*, and *A. spec. G*.

The circumscription of this group on rareness, localness, or possession of a unique feature includes *A. duthieana* and *A. spec G*, though they have already been investigated in the last paragraph. Also, when interpreting ambiguously placed groups as one taxon, the complete *arborea*-, *benthamiana*-, and *nervosa*-groups can be added to this category of taxa.

The taxa are divided into several subcategories. *Aporosa bourdillonii*, *A. lagenocarpa*, and *A. selangorica* possess autapomorphic traits and are switching positions in the topmost part of the cladogram. A similar situation exists for the complete *benthamiana*-group. *Aporosa antennifera*, *A. caloneura*, *A. duthieana*, *A. longicaudata*, *A. nigropunctata*, *A. penangensis*, and *A. spec. G* have patchy distributions and have an ambiguous position because they combine primitive characters with some derived ones. They are jumping around at the basal portion of the cladograms. The *arborea*- and *nervosa*-groups can also be reckoned to this category.

I conducted six analyses with a selection of these taxa excluded. These were:

a) without *A. bourdillonii*, *A. lagenocarpa*, and *A. selangorica*;
b) without *A. antennifera*, *A. caloneura*, *A. duthieana*, *A. longicaudata*, *A. nigropunctata*, *A. penangensis*, and *A. spec. G*;
c) without the *benthamiana*-group;
d) without the *nervosa*-group; and
e) without the *arborea*-group.

The exclusion of these subsets of taxa shows both decreases and increases in the number of MPTs. However, when the MPTs decrease, the resolution of the strict consensus tree decreases also. This means that, even though the basic number of solutions is less, the ambiguity shown by them is increased. This ambiguity is the result of a large shift in the position of various clades, and not of the number of MPTs found.

Looking at the composition of the three lineages, a rather surprising result is seen: the basal species of one lineage apparently influence the solution at the base of the

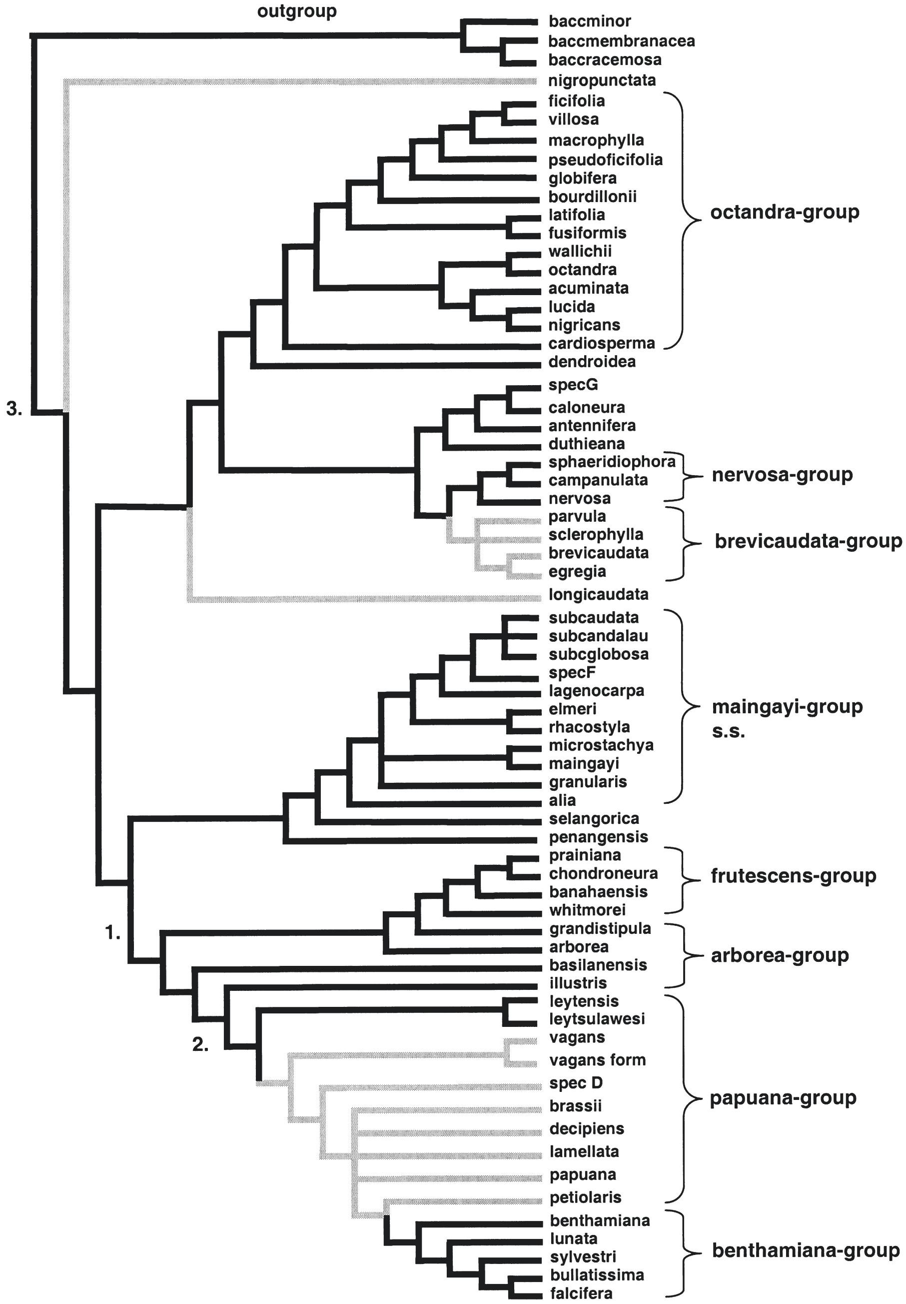


Fig. 8.3. Strict consensus tree of 24 cladograms (length 977, CI 0.17, RI 0.53) after analysis of *Aporosa* with 14 intermediate New Guinean taxa excluded. The remaining New Guinean taxa (in grey) cluster in two groups; the three lineages (1 and 3 paraphyletic) and the 8 groups are also indicated.

other lineage, than of the one they theoretically belong in. So, excluding the taxa of the third lineage, *A. antennifera* and companions (analysis b), induces the loss of resolution at the root of the two first lineages. On the other hand, excluding the *arborea*-group (analysis e), which was switching among the roots of the first and second lineages alternately, increases the ambiguity of the topology of the *maingayi*-group in the third lineage. The effect of omitting *A. bourdillonii*, *A. lagenocarpa*, and *A. selangorica* (at upper part third lineage; analysis a) is not so distinct. They seem to affect the pattern in all three lineages, though slightly more so in their own.

It can thus be concluded that exclusion of this category has neither brought insight into possible underlying patterns.

8.4.4 – ***Excluding New Guinean taxa***

In the various analyses, 14 of the New Guinean taxa wander in position among the various cladograms. These are *A. annulata*, *A. carrii*, the subhermaphroditic form of *A. carrii*, *A. flexuosa*, *A. hermaphrodita*, *A. heterodoxa*, *A. laxiflora*, *A. ledermanniana*, *A. leptochrysandra*, *A. misimana*, *A. reticulata*, *A. spec. A, B*, and *C*.

Excluding these 14 intermediate New Guinean taxa is the next step in the testing phase. In addition, to investigate whether the other New Guinean taxa have the same influence or whether the 14 intermediate taxa show exceptional behaviour, I also conducted some analyses excluding the non-switching New Guinean taxa. Six analysis were run:

a) without the 14 mentioned ones;
b) without these 14 and the also jumping – but similar to the West Malesian taxa – *A. nigropunctata* and *A. longicaudata*;
c) without the four taxa of the *brevicaudata*-group;
d) without these four and *A. nigropunctata* and *A. longicaudata*;
e) without the 10 taxa of the *papuana*-group; and
f) without all 28 New Guinean taxa.

The first immediately noticeable effect in all these analyses is the low number of MPTs found, with its minimum of 12 cladograms for analysis f and analysis a as second best with only 24 MPTs. Furthermore, the ambiguity has also decreased; the various analyses show the three lineages in identical configurations, though differences in the basal splitting sequence are still present. The strict consensus cladogram of the 24 trees of the analysis without the 14 switching New Guinean taxa (analysis a, length 977, CI 0.17, RI 0.53) is depicted in Fig. 8.3. The figure shows, in grey, how the remaining New Guinean taxa cluster in two groups. Excluding the intermediate New Guinean taxa from the analysis has finally produced the desired effect: a decrease of MPTs coupled to an increase in the resolution of the – strict – consensus tree. Clearly, part of the New Guinean taxa are the main cause for the ambiguity in the phylogenetic reconstruction of *Aporosa*.

With the results of this subanalysis I can state with some confidence which subgroups can be analysed separately. The eight groups of the analysis with the complete data set (Fig. 8.1), and the three lineages indicated at first by analysis 2 with weighted characters (Fig. 8.2), are shown to be stable by the analyses with characters or taxa excluded in the following compositions:

1) the *frutescens*-group. Its paraphyletic tail consisting of the *arborea*-group had no stable position and is excluded;
2) the *benthamiana*- and *papuana*-group, starting from *A. leytensis* onwards. Other taxa in this lineage were swapping;
3) the *octandra*-, *maingayi*-, *nervosa*-, and *brevicaudata*-groups with *A. antennifera*, *A. bourdillonii*, *A. caloneura*, *A. dendroidea*, *A. duthieana*, *A. lagenocarpa*, *A. longicaudata*, *A. nigropunctata*, *A. penangensis*, and *A. selangorica*. These species are always close together, though their internal relationships are still obscure. The question whether this lineage is truly monophyletic is also open.

These three lineages are analysed separately in the following paragraph. All taxa omitted in paragraph 8.4.1 are included again in their respective lineages. The 14 intermediate New Guinean taxa are discarded.

8.5 – **Analysis 5: phylogenetic analysis of the found subsets**

8.5.1 – ***The subsets and their local outgroups***

The first lineage consists of the 15 taxa of the *frutescens*-group. The outgroup position of the 5 paraphyletic taxa of the *arborea*-group is stable only insofar as the position of *A. grandistipula* is considered. The conclusion for the exact composition of this subset is thus easy: the 15 taxa with affinity to *A. frutescens* and as outgroup *A. grandistipula*.

The second lineage consists of the *papuana*/*benthamiana*-clade. *Aporosa laxiflora*, *A. spec. A*, and *B* are excluded and the position of *A. bourdillonii* in this clade was shown to be erroneous. The candidate for the local outgroup is also quickly found: in most analyses this lineage was depicted near the first with as direct sister the basal taxa of the *arborea*-group, viz., *A. basilanensis* and *A. illustris* (and form). These two species can act as local outgroup. This conclusion is supported by the pattern shown in the analyses where the *arborea*-group was separated from the *frutescens*-group: it then invariably turned up at the root of the *papuana*/*benthamiana*-clade.

The third and last lineage contains the rest of the species, united in the *octandra*-, *maingayi*-, *nervosa*-, and *brevicaudata*-groups with the jumping species that do not belong in the category of the intermediate New Guinean taxa, viz., *A. antennifera*, *A. bourdillonii*, *A. caloneura*, *A. dendroidea*, *A. duthieana*, *A. lagenocarpa*, *A. longicaudata*, *A. nigropunctata*, and *A. spec. G*. It is not certain that this clade is monophyletic – it could be alternately depicted as a monophyletic sistergroup to the other two lineages or as a paraphyletic clade parental to them. However, this should be no reason to decide a priori that analysis of this subset should not be attempted. Many paraphyletic groups were analysed before. Even the monophyly of the genus itself is still a question. This cannot be helped. It only means that one should proceed with more care when interpreting the results.

The candidates for the local outgroup of this remnant, if accepting a sistergroup position to the other two lineages, should be sought near the base of these two. The most basal species for both lineages is the pair *A. basilanensis*/*A. illustris* (and form). These two species can be depicted at the base of either of them. Another possibility, when choosing to depict the complete *arborea*-group at the base of the *frutescens*-group, is taking the basal species of the *papuana*-group. This would be *A. leytensis* and form. Both candidates were tried.

8.5.2 – *Selecting characters for the subsets*

After determining the subsets, the character matrix should be re-appraised for each subset. Some characters are informative and should be included in the matrix, while others have no information content any more, i.e., they will have 0 steps in the tree, while still others, such as the morphometric characters might need recoding. The data matrix for each of the three subgroups was scanned and uninformative characters pruned. Some of the morphometric characters, of which the states are calculated on the basis of the mean value, had to be recoded. They are coded according to the new means and ranges shown by the subsets in the same way as explained in paragraph 7.4. However, this was not always necessary: since relatively more characters per taxon are available, doubtful codings, such as the number of pairs of nerves, could simply be left out. Yet, size characters were retained as much as possible because of their proven importance in shaping the cladogram. The changes in characters and the codings for the three subsets are listed in Table 8.3a–c. For the *frutescens*-group some characters were ordered according to their transformation series in the complete data set. The results of the three subanalyses are discussed separately.

8.5.3 – *Analysis of the subsets*

a. The *frutescens*-group

There are 15 taxa and 56 characters in the ingroup (Table 8.3a). Because of the low number of taxa, the analysis could be carried out with the option ‘ie*’, which calculates all possible trees. Two runs were made: one containing all taxa and one without the incompletely known *A. spec. E.* The first gave 6 trees, length 188, CI 0.45, and RI 0.51, the second 3 trees length 179, CI 0.47, and RI 0.53. The Adams consensus tree of the first analysis is given in Fig. 8.4. In the strict consensus tree, the resolution is much reduced because of an ambiguous placement of *A. spec. E.* In comparison, the strict consensus of the second analysis lacks only the basal node, indicated by a dashed line in Fig. 8.4. Two species with unstable positions cause the multiple patterns. These are *A. chondroneura* (in both analyses) and *A. spec. E* (in the first analysis).

To test for the effect of a different rooting both analyses were rerun with *A. arborea* as outgroup. This resulted in 2 trees length 195, CI 0.43, RI 0.50, and 5 trees length 186, CI 0.45, RI 0.51, respectively. Relative to the Adams consensus tree in Fig. 8.4 no new patterns are present. The strict consensus tree of the first analysis is almost identical, except that *A. spec. E* is now firmly placed as sister to *A. banahaensis*. In the second analysis one of the cladograms has a deviating position for *A. stenostachys*; *A. chondroneura* causes the other ambiguity.

Because the influence of the changed outgroup and the inclusion or exclusion of *A. spec. E* is so small, I will accept the pattern depicted in Fig. 8.4. Two trichotomies

(*Text continued on page 108*)

Table 8.3. The recoded data sets for the three clades of the subanalyses of analysis 5. **a**) The *frutescens*-group; **b**) the *papuana*/*benthamiana*-clade; and **c**) the *octandra*/*maingayi*/*nervosa*/*brevicaudata*-clades and remnant. The various local outgroups are also included in the three data sets. The firsts rows indicate the corresponding old character numbers in the complete analysis, as listed in Table 7.1 and the type of recoding, if any: – = no change; r = recoded, (r) made ordered and states adapted only if necessary.

Table 8.3**a**. Character recodings, renumbering and data matrix for the subanalysis with the *frutescens*-group (56 characters, 15 ingroup taxa, 2 outgroup taxa).

char. (old) + rec. type	1: –	2: – 3: – 4: r 5: – 6 : r –	8: – 10: – 13: – 14: (r) 15: –	17: – 18: (r) 19: – 20: r 24: –	25: – 27: r 28: – 29: – 30: –	31: – 33: – 35: – 36: – 37: –	39: – 40: – 43: – 45: – 46: r	50: (r) 51: – 52: – 54: – 55: –	56: – 57: – 58: – 59: – 60: – –	61: – 62: – 63: – 65: – 66: –	68: – 69: (r) 71: – 74: r 75: –	76: – 77: – 78: – 79: – 80: –
character	**0**	**1–5**	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**	**31–35**	**36–40**	**41–45**	**46–50**	**51–55**
grandistip.	2	35322	12112	42221	11151	23121	12242	11122	11222	12223	33312	21111
arborea	2	15322	12112	42423	11141	14221	21242	12122	21223	32222	33222	11121
banahaens.	2	14221	12121	122?1	11141	23121	12121	21223	13222	11112	31331	12231
chondron.	1	14322	12131	32111	11151	22122	12222	11113	13222	12222	32?12	22221
confusa	3	24122	12121	12523	12232	13211	21111	23123	3323?	31114	31121	11231
frutescens	2	24131	12121	12512	12142	12111	11111	22123	23222	31111	31111	11221
fulvovittata	2	14121	12121	42311	11151	22111	14212	21223	1212?	12213	32311	21221
nitida	1	1?322	12221	33121	12232	13121	21111	21123	13232	11114	11131	11231
prainiana	1	13131	22121	43111	11151	22112	11112	11112	23222	12223	32312	22212
quadriloc.	1	14221	11121	12111	12232	13121	21111	22123	23232	11113	11121	11231
sarawak.	1	13121	22121	32121	21241	22111	1112?	21?23	13123	11131	31?22	12222
stellifera	1	13322	12211	22121	2?141	13121	11111	32223	13122	11114	31222	21222
stenostach.	2	13121	12121	13222	21251	12321	21112	22?22	23123	31112	31311	21211
symploc.	1	13221	21121	32111	21151	22221	11122	11212	13212	12211	12?12	11211
symp. chal.	1	13221	21121	32111	21151	22221	11122	11212	13212	12211	12223	11211
whitmorei	2	13131	12121	31421	11151	22121	12212	11122	21222	12222	32?12	11221
spec e	1	1?222	11121	121?1	11141	12111	1114?	21?22	1322?	11113	31312	22221

Table 8.3**b**. Character recodings, renumbering, and data matrix for the subanalysis with the papuana/benthamiana-clade (53 characters, 18 taxa).

char. (old) + rec. type	1: –	2: – 4: r 5: – 6: r 7 : – –	9: – 10: – 11: – 12: – 13: –	16: – 17: – 18: – 19: – 21: –	22: – 24: – 28: – 29: – 31: –	33: – 34: – 35: – 36: – 37: –	38: – 40: – 41: – 43: – 45: –	48: – 49: – 50: – 51: – 52: –	53: – 54: – 55: – 56: – 58: – –	59: – 60: – 61: – 62: – 65: –	66: – 68: – 69: – 70: – 73: –	75: – 76: –
character	**0**	**1–5**	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**	**31–35**	**36–40**	**41–45**	**46–50**	**51, 52**
basilanens.	3	11322	21111	14231	23241	32321	21124	13132	31232	12322	32321	22
bentham.	2	32131	12222	12321	22221	32322	32315	21332	22232	23213	31311	11
brassii	3	21421	22122	24451	33241	41213	33225	22132	31132	33421	34213	11
bullatissima	3	21212	12222	12341	32221	32?22	3131?	1133?	32231	22213	31311	??
decipiens	3	31411	43121	23141	331??	?????	3????	11132	11232	22421	34211	22
falcifera	2	21222	12112	12321	22221	32322	33312	11321	32222	22313	31311	11
illustris	3	23232	23122	14231	23252	32221	23123	13121	31222	23223	33321	21
ill. forma	2	33232	23122	14231	23252	32221	23123	13121	31222	23223	33321	21
lamellata	3	33232	22121	14131	23??1	?????	3????	22132	22232	32421	34211	14
leytensis	3	31232	23121	12551	23241	32222	23224	12122	31222	22432	23212	11
leyt. sulaw.	2	31232	23121	12521	23241	32222	23224	12122	31222	22332	23212	11
lunata	3	31234	22212	12351	32221	32?23	32315	11331	22221	22413	21311	21
papuana	3	32232	22121	13252	23131	41323	32321	22132	31232	23432	34213	11
praegrand.	1	33232	22112	13222	23151	41323	34325	1113?	12132	22411	33311	12
sylvestri	3	21232	21222	12341	32?21	?2???	3?3??	11321	22231	22413	31311	??
vagans	2	12222	22121	15551	33242	32213	32225	12122	32222	23432	33211	12
vag. lowl	2	12222	22121	15551	33242	32213	32225	12122	32222	23332	33211	12
spec d	3	22222	11122	23451	33252	22212	34233	12122	32222	22411	2331?	??

Table 8.3**c**. Character recodings, renumbering, and data matrix for the subanalysis with the *octandra*/*maingayi*/*nervosa*/*brevicaudata*-clades and remnant (75 characters, 59 taxa).

	1: –	2: –	7: –	13: –	19: –	24: –	31: –	36: –	41: –	46: r	51: –	56: –	61: –	66: –	71	76: –
		3: –	8: –	15: –	20: r	26: r	32: –	37: –	42: –	47: r	52: –	57: –	62: –	67: r	72: –	79: –
		4: r	9: –	16: –	21: –	27: r	33: –	38: –	43: –	48: –	53: –	58: –	63: –	68: –	73: –	81: –
		5: –	10: –	17: –	22: –	28: –	34: –	39: –	44: –	49: –	54: –	59: –	64: –	69: –	74: r	82: –
		6: r	12: –	18: –	23: –	29: –	35: –	40: –	45: –	50: –	55: –	60: r	65: –	70: –	75: –	
character	**0**	**1–5**	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**	**31–35**	**36–40**	**41–45**	**46–50**	**51–55**	**56–60**	**61–65**	**66–70**	**71–74**
acuminata	2	11242	24212	11135	5?122	31211	22222	23121	11211	12111	22112	21212	22211	41331	12111	2121
alia	2	13333	21233	11131	21122	22113	22222	11221	11111	21112	21122	21111	31221	31331	32122	3112
antennifera	2	1?232	21232	12231	21222	22214	22222	12221	22211	21131	21312	21212	23222	23332	22312	1111
aurea	1	12424	231?2	21125	12222	32211	11211	11111	11211	12111	21221	11211	11221	31321	11111	1122
basilanensis	3	1?333	21211	12142	32122	33224	11323	21221	11214	31131	32312	31211	32222	32232	31132	2212
bourdillonii	3	1?322	21223	12225	4?112	32322	22312	12222	11213	2?122	23212	2122?	43221	23321	31331	6122
brevicaud.	2	24251	31211	22252	41112	12323	22111	12321	12323	21112	12311	21211	22221	3?121	21333	2112
caloneura	2	1?433	21221	22152	2?122	22324	22222	12221	22215	32131	12312	21212	13222	32232	?2232	1212
cardiosp.	1	11322	24211	22155	11212	33211	12222	12121	22211	12121	22312	21221	22222	21321	32321	1122
dendroidea	2	1?222	21212	12155	11122	2????	?????	?????	?????	21122	22312	21222	23222	22321	31321	2112
duthieana	2	1?332	21211	22252	21212	3????	?2???	???2?	?????	21122	21212	2121?	32222	22332	21222	2111
egregia	2	24332	21211	22242	21122	12314	22221	11321	11321	3?112	2?311	21211	22221	32321	21133	2211
elmeri	3	22344	41212	12241	52122	23115	21223	21221	11114	31231	31222	21211	41223	41431	21112	2111
ficifolia	3	12344	24241	22245	5?132	32311	21213	32122	12214	13111	32122	31213	41211	21321	11121	1222
fusiformis	1	11322	23421	22156	11122	32311	22211	13121	12311	12111	12312	21212	12221	32321	22333	2122
globifera	3	1?323	21241	11125	42122	32211	21122	11231	11111	12111	31122	3122?	42211	21321	31121	2222
granularis	2	23232	31213	12131	41122	21213	21121	21221	11112	11112	2?112	21211	21223	3?331	21112	3111
illustris	3	25424	21232	22142	32122	33225	21322	21223	11213	31131	21312	21223	22223	32332	31132	1312
illforma	2	35424	21232	22142	32122	33225	21322	21223	11213	31131	21312	21223	22223	32332	31132	1212
lagenocarpa	3	24342	211?2	12241	51122	32222	?2123	12321	22211	12112	31112	31213	41221	33331	31233	1111
lanceolata	2	11222	23223	11145	12122	22211	21121	12111	11211	12111	11111	11211	11211	31221	11111	2121
latifolia	1	11322	23221	22156	11112	32311	222?1	??121	1?211	12111	2?122	33222	12222	12321	31132	1322
leytensis	3	35324	21232	12125	52122	33324	11322	22223	22214	32121	22312	21222	43222	21321	31221	1212
leyt. sulaw.	2	35324	21232	12125	22122	33324	11322	22223	22214	32121	22312	21222	33222	21321	31221	1212
longicaud.	2	24222	21213	12252	22122	31212	21221	11221	11211	?1122	22212	21222	22222	21332	31111	1112
lucida	2	1?324	32222	11235	12122	22211	11321	21121	11214	12111	11222	22111	12211	41221	31211	2122
luc. ellips.	2	1?324	32222	11235	12122	22211	11321	21121	11214	12111	11222	22111	12211	41221	21212	2121

Table 8.3**c** (*continued*)

character	**0**	**1–5**	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**	**31–35**	**36–40**	**41–45**	**46–50**	**51–55**	**56–60**	**61–65**	**66–70**	**71–74**
luc. pubes.	2	1?324	32222	11235	12122	22211	11321	21121	11214	12111	11222	22111	32211	41221	31211	2122
luc. triloc.	2	1?324	32222	11235	12122	22211	11321	21121	11214	12111	11222	22121	12211	41221	31211	3122
macrophylla	1	11434	11111	22125	1?122	33311	22211	32211	11211	13111	33112	31213	41221	21231	111?1	??22
maingayi	2	13222	31113	12122	41122	21212	21222	11231	11111	12112	31122	21211	41123	31431	21112	2111
microstachya	2	11222	21223	12122	41122	23212	21222	11231	11111	12112	31212	31211	32223	32431	31212	2111
nervosa	2	14323	31222	22151	41122	23224	22222	22323	22224	2?122	22312	21211	21222	31221	21132	1212
nigricans	2	1?424	22232	12241	32122	32311	11422	21221	11114	12111	22212	32112	42211	41321	31121	1222
nigropunct.	2	11222	21113	12152	21122	22225	21222	22322	11215	21131	21312	21221	33222	32231	31311	2212
octandra	2	12324	22222	12135	52122	23211	22212	11121	11212	22111	22111	22111	22222	31321	?2222	2121
oct. chinens.	2	12322	32322	11125	52122	23211	22212	11121	11212	22111	22111	22111	22222	31321	22222	2121
oct. males.	2	12324	22222	12125	52122	23211	22212	11121	11212	22111	22111	22111	32222	31321	22222	2121
oct. yunnan.	3	12324	22222	12135	52122	23211	22212	11121	11212	22111	22111	22111	42222	31321	?2222	2121
parvula	2	12151	21211	22152	21122	31213	22121	12321	22321	??112	11311	1121?	32222	31221	21112	2112
penangensis	2	1?223	21212	12141	21222	32?14	22221	21222	11214	2?121	22212	31211	31123	31321	22122	1111
planchoniana	2	11222	22212	11155	12122	33211	11221	11111	11212	1?111	11111	12112	12211	21321	?2112	2121
pseudoficif.	3	1?343	21341	22125	42132	33311	22213	12121	11211	12111	31112	31122	41221	21331	11122	2122
rhacostyla	3	22242	21112	12211	51122	22115	21222	21221	11111	31231	21212	21211	41213	31231	21122	2211
sclerophylla	3	24151	21212	22253	21122	22?13	22121	12321	1?311	21122	21322	21211	32222	21221	?1112	2111
selangorica	2	24224	41222	12231	42122	32212	22222	11211	11114	2?112	22112	21213	32223	32331	31121	5212
serrata	3	12333	24441	22125	51132	32311	21312	22122	11213	12111	22122	31211	41221	41321	?11??	??2?
sphaeridio.	2	1?322	31222	22152	21122	23224	22211	13323	22311	22222	21312	23212	11222	41221	11121	2112
spha. camp.	2	1?322	31222	22152	21112	23224	22211	23322	22321	???31	2?312	2121?	1122?	41221	21121	2212
subcaudata	3	23324	41223	12241	42122	32224	22213	21231	11114	12212	31112	31211	41223	41431	?1112	2111
subc. andal.	3	23322	41223	12241	42122	32224	22223	21231	11114	12112	31112	31211	41223	41431	21112	2111
subc. globo.	3	23324	41223	12241	42122	32224	22223	21231	11114	12112	31112	31211	41223	41431	11121	2212
symplocifolia	1	11322	22212	21145	11121	22211	22212	12111	11211	22111	11111	12212	12211	31321	?1112	2122
tetrapleura	1	11322	23111	21155	11121	33311	22211	12111	11211	??111	1?111	1221?	12211	31321	?1222	2222
villosa	3	12344	12321	22125	52122	33311	22212	12122	12311	12111	32112	22212	42221	31321	?1112	2121
wallichii	2	12322	22222	11135	1?122	23311	22212	12121	12325	?2111	22111	21212	13222	22321	32312	2122
yunnanensis	1	11322	22222	12135	11122	33311	22211	12111	22212	12111	12111	11113	13222	32321	?1322	3122
spec f	3	23234	41212	12132	42122	32224	11222	21221	11214	22112	32112	31212	41121	31331	?????	??1?
spec g	2	1?333	21222	22121	21222	33314	22322	33223	22315	32231	22322	21122	23221	32332	?????	??12

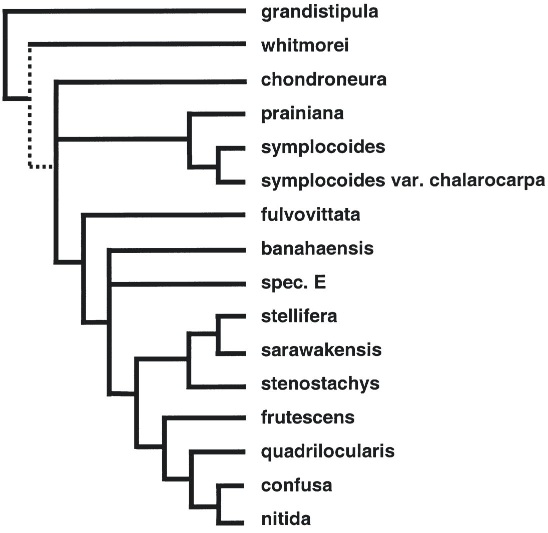


Fig. 8.4. Adams consensus tree of six cladograms resulting from the analysis of the *frutescens*-group (length 188, CI 0.45, RI 0.51). The dashed line indicates the node that collapsed when excluding *A. spec. E.*

are left: one at the base and a second for the unresolved position of *A. spec. E.* The many synapomorphies of the *frutescens*-group in comparison with its outgroup might indicate that at some time in history there may have been intermediate taxa. Without knowledge of such taxa the root may probably not be solved unambiguously (Donoghue et al., 1989). The second polytomy is caused by the switching position of *A. spec. E*, and that can only be resolved when this species is better known.

Compared with the analyses of the complete data set, the position of *A. frutescens* has undergone the largest shift (cf. Fig. 8.1). However, according to theory the current solution with the highest character/taxon ratio is the most accurate one (Lamboy, 1994). This is strengthened by the small effect of deleting a taxon or changing the outgroup.

b. The *papuana/benthamiana*-group

This group consists of 18 taxa and 53 characters, and was also analysed with the option 'ie*'. Initial analysis with all taxa gave 24 trees of 193 steps, CI 0.46, and RI 0.59. These trees are so widely different that a strict consensus gives no solution at all. Therefore, analogous to paragraphs 8.4.3 and 8.4.4, two further analyses were carried out: one without the autapomorphic *A. praegrandifolia*, and one without *A. praegrandifolia* and the intermediates *A. spec. D* and *A. vagans*. These analyses gave 6 trees of length 178, CI 0.50, RI 0.61 and 1 tree of length 148, CI 0.57, and RI 0.63, respectively. This last cladogram is depicted in Fig. 8.5.

It is interesting to note how exclusion of the taxa with confusing character combinations again reduces the number of solutions. On the other hand, exclusion of the incompletely known taxa *A. decipiens, A. lamellata*, and *A. sylvestri*, did not give better results: 23 trees were found with length 170, CI 0.51, and RI 0.59.

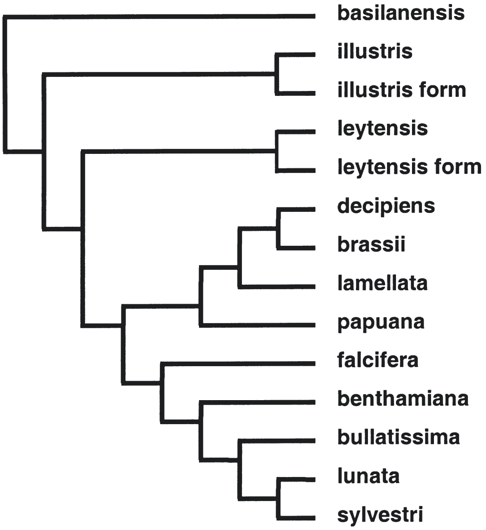


Fig. 8.5. Cladogram for the analysis with the *benthamiana-/papuana*-groups, excluding *Aporosa praegrandifolia* (S. Moore) Schot, *A. vagans* Schot, and *A. spec. D* (length 148, CI 0.57, RI 0.63).

To test the influence of the outgroup, two further analyses were run with only *A. basilanensis* as outgroup and either all 15 taxa or the selected 12 taxa. In both cases one cladogram was found, of which the cladogram of the complete set differed from Fig. 8.5 in placing the *leytensis*/form-pair with *A. vagans* and *A. spec. D* as sister to the *papuana*-group, but with *A. praegrandifolia* at the base of the *benthamiana*-group. The second analysis gave exactly the same cladogram of Fig. 8.5 – with the exclusion of *A. illustris* of course. This shows that this last pattern is rather stable and I will accept it in the configuration shown in Fig. 8.5.

In respect to former analyses, the largest difference is the shift of the *benthamiana*-group to the base of the *papuana*-group. This is the more logical solution. However, because the relationships of *A. papuana* to the other New Guinean taxa cannot be solved this way, the *papuana*-group may be paraphyletic. Its descendants should have to be included, but since the delimitation of them is gradually shifting to the truly intermediate New Guinean species, the *papuana*-group cannot be delimited on any macromorphological or phylogenetic ground.

c. The *octandra-maingayi-nervosa-brevicaudata* group

There are 59 taxa left in this group and 75 characters. The 59 taxa were too much for ‘ie*’, so ‘mh*’ and ‘bb*’ were again invoked. Analysis with *A. basilanensis* and *A. illustris* (and form) as outgroup produced 24 trees with length 775, CI 0.19, and RI 0.55. The same data set, but with the outgroup taxa in reversed positions produced 36 different trees of the same length, CI, and RI. By calling on JOYRIDE with this second configuration an additional 270 equally parsimonious trees were found. Analysis with

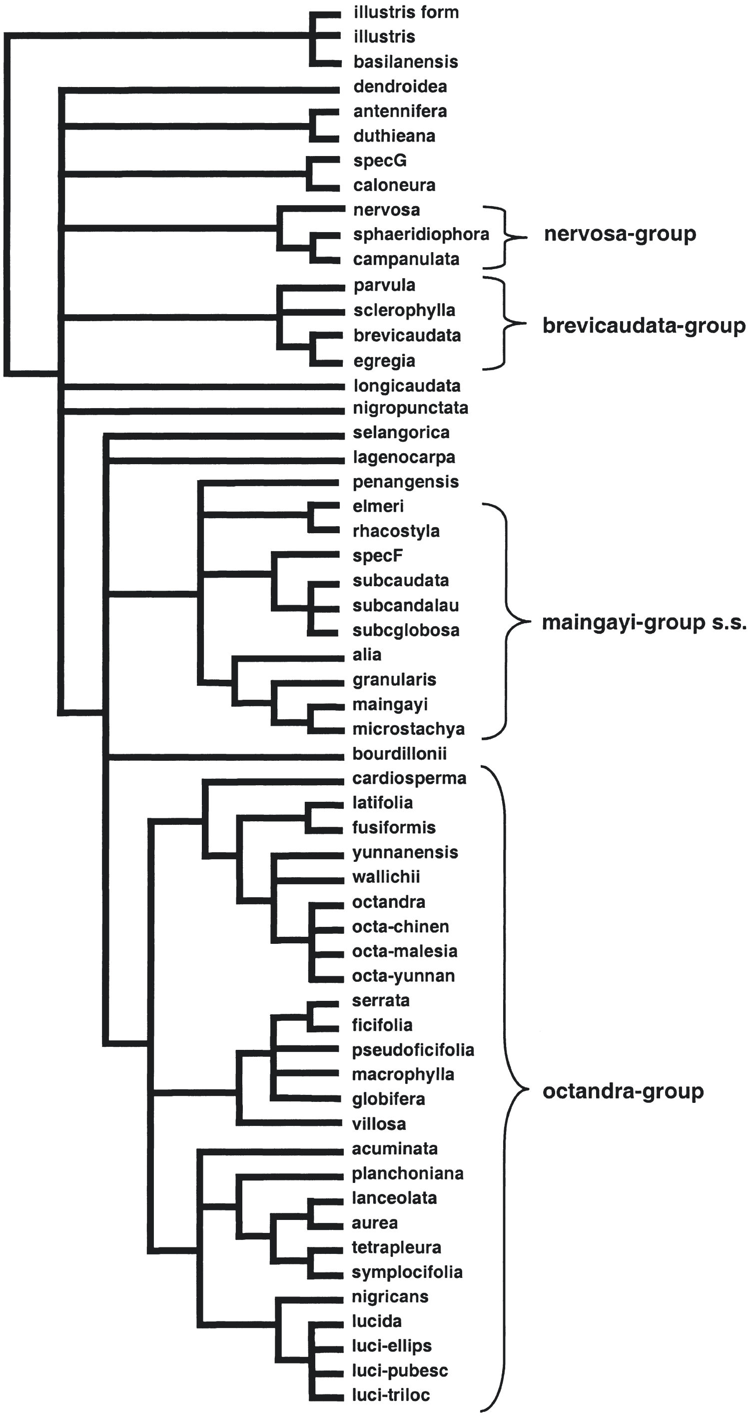


Fig. 8.6. Compiled phylogenetic reconstruction for the analysis of the third lineage.

NONAs 'mult*' was not successful in finding more than these 270 extra cladograms. A third analysis with *A. leytensis* (and form) as outgroup gave 18 trees of length 758, CI 0.19, and RI 0.56. These 18 had in their turn a different configuration from the first two.

The fact that three analyses run with exactly the same data set produced different results illustrates how the problem with multiple islands of trees is still in effect. It also diminishes my confidence in the pattern found. I still cannot be sure whether all MPTs have been found. The swapping of the positions of some taxa when using a different outgroup points to a further instability of the pattern found. Tests are called for.

Analogous to the analyses with the complete matrix, the stability of the relationships of this clade can be investigated by manipulating characters and excluding particular species. The same type of characters can be excluded as in paragraph 8.3.2 or the same categories of possibly destabilizing taxa as in paragraphs 8.4.2 and 8.4.3. However, just as in the analyses with the complete data set, such exercises only increased the ambiguity for the basal and middle taxa. Only the various subsets of the *octandra*-group and the subsets of the *maingayi*-group were present in most tests.

It is thus evident that there is much controversy. I could still think of more combinations of taxa to be excluded, or try other outgroups. But this would not be a useful exercise, since probably even more patterns would show up. Adding this to the island problem I can only conclude that the problem lies with the data themselves. It certainly seems that the characters for this third lineage are not suitable to solve the detailed phylogenetic relationships between the various taxa.

I have composed a general consensus pattern for the third lineage in Fig. 8.6. This pattern is mainly based on the Adams consensus tree of the 330 trees found with *A. basilanensis* and *A. illustris* as outgroup, but collapsed on nodes that were shown to be instable by the various tests. Thus I have brought both the *nervosa*- and *brevicaudata*-clades to the basal polytomy, where they appear together with the unspecialized or autapomorphic or incompletely known *A. antennifera, A. caloneura, A. dendroidea, A. duthieana, A. longicaudata, A. nigropunctata,* and *A. spec. G*. The position of these species and the two groups within the various analyses is so ambiguous that a polytomy is the best option.

The clade with the *maingayi*- and *octandra*-groups but excluding the above mentioned species is strong. However, their basal relationships remain ambiguous, which is illustrated by a polytomy formed by the ambiguous *A. selangorica*, *A. lagenocarpa*, *A. bourdillonii* and the *maingayi*- and *octandra*-groups. The *octandra*-group in this configuration is always monophyletic; the *maingayi*-group is not. However, it is always present, though sometimes in a paraphyletic configuration. Since the composed consensus pattern is based on an Adams consensus tree I have retained the monophyletic depiction.

The configuration of the *maingayi*-clade is largely as it was in the analysis, except that *A. lagenocarpa* has been moved out of it and *A. spec. F* in, according to what was found in a majority of the tests. The relationships between the few subgroups indicated, i.e., the species around *A. maingayi*, the taxa around *A. subcaudata*, the *A. elmeri*–*A. rhacostyla* pair, and *A. penangensis*, are unstable and they are depicted in a polytomy.

Within the *octandra*-clade the relations of the various subgroups could not be solved beyond doubt and the group is depicted at the base as a polytomy of the 3 subgroups indicated to be stable by the various analyses. These subgroups are:

a) the eight species around *A. aurea* with glabrous, yellowish drying leaves;
b) the six tomentose species around *A. globifera*; and
c) the remaining six species.

The splitting sequence of the taxa in these three subgroups is a combination of the complete analyses and the test runs: when taxa were established to be switching in the test runs, they were placed in a basal polytomy, according to the rules of making Adams consensus patterns. Thus, the pair *A. nigricans*–*A. lucida* (and its varieties), which can either be shown at the top of the *aurea*-group or at the base with *A. acuminata*, is moved to the base of this subgroup. *Aporosa cardiosperma*, that invariably ends up in the subgroup (c) near the *A. latifolia*–*A. fusiformis* pair when excluding the incompletely known *A. dendroidea*, is moved to this subgroup. The group includes also *A. octandra*, since it is always near, whether in a monophyletic or paraphyletic configuration. In a consensus pattern based on Adams techniques such a relationship may be depicted monophyletically.

I will leave this analysis with its unsolved root and accept the composed consensus pattern of Fig. 8.6 with all its polytomies as the best to be obtained. The detailed relationships within this lineage cannot be solved with the present data and methods (see paragraph 9.3.3 for further discussion).

8.6 – **The consensus pattern for Aporosa**

8.6.1 – ***Combining the patterns***

The various analyses with the data set for *Aporosa* have revealed a general pattern for three lineages. The configuration of these lineages is only stable when excluding the 14 intermediate New Guinean taxa. Then each lineage consists of a stable monophyletic group, which is accompanied by a paraphyletic tail. Of these paraphyletic tails two were consistent; the third, the *arborea*-group, sometimes switched from the first to the second lineage.

Combining these two patterns results in a bifurcation at the base of the consensus tree (Fig. 8.7). The first branch contains a polytomy of the first and second lineages together with the *arborea*-group; in the second branch the complete third lineage is placed. This is the general configuration to compose a consensus pattern for *Aporosa*. Next the patterns found in the subanalyses are filled in for the three lineages.

The accepted relationships of the first lineage, the *frutescens*-group, were shown in Fig. 8.4. This same configuration can be directly depicted into the consensus pattern. The second lineage, the *papuana*/*benthamiana*-clade, was accepted in the configuration of Fig. 8.5, i.e., excluding a further 4 New Guinean taxa. No stable pattern could be found for these four taxa and, therefore, they cannot be placed in the consensus pattern. Last, the accepted relations for the third lineage as shown in Fig. 8.6, are pasted to produce the final composed consensus pattern for *Aporosa*.

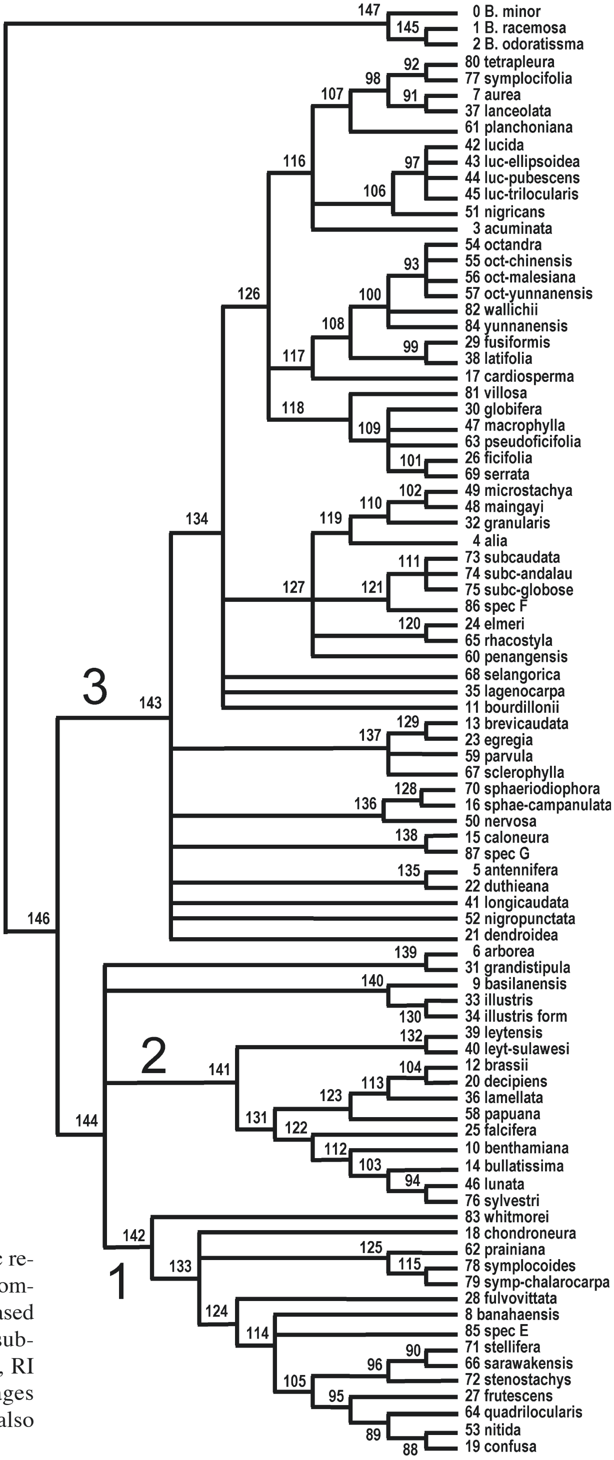


Fig. 8.7. Accepted phylogenetic reconstruction for *Aporosa*. The composed consensus diagram is based on the various analyses and subanalyses (length 1265, CI 0.13, RI 0.53). Three recognized lineages are indicated. The nodes are also numbered

The pattern described above is given in Fig. 8.7. As outgroup only the three species of *Baccaurea* selected before are included. The composed consensus pattern has length 1265, CI 0.13, and RI 0.53. I will accept this reconstruction as the best phylogenetic model of the relationships for the species of *Aporosa* to be obtained with the data available now.

8.6.2 – ***Some general notes on consensus trees***

The question arises in how far the choice for a reconstructed consensus pattern influences its use. Is it still possible to obtain a classification for the 82 species, or outline the hypotheses for character transformation series and evolutionary pathways for species? In my opinion these goals can be reached even with the selected consensus pattern.

Consensus techniques are mostly used to compare and summarize patterns between analyses of different data sets or multiple patterns within the same data set. An example of the first use is comparison between the results of analyses with, e.g., molecular data and morphological characters. This type and the problems it raises, though more in the picture now in view of the increase in molecular studies, is not what I am concerned with and is not elaborated upon. Here the problems with consensus patterns are of the second type: depicting and using the ambiguous solutions found within one data set.

Two parties have been formed: those against (e.g., Miyamoto, 1985; Carpenter, 1988; Muona, 1995) and those in favour of the use of consensus (e.g., Kluge, 1989; Wilkinson, 1996). The central issue seems to be why one chooses to depict the ambiguous data in a consensus tree. Phylogenetic reconstruction aims to find the historical relationships between the taxa analysed. This aim is reached by analysing the characters, finding the pattern that optimizes the congruence among the characters, and depicting this pattern in a cladogram. It is the incongruence of data that causes ambiguous solutions and one method proposed to deal with the ambiguity is the use of consensus techniques.

The two sides argue mainly on whether this is the best option. Consensus trees are less parsimonious and cannot summarize the data as well as true cladograms (Miyamoto, 1985). They have lower explanatory power and less possibilities to hypothesize models. Consensus trees can therefore not be used to formulate evolutionary hypotheses (Muona, 1995). Part of the information present in the original cladograms is lost and it is much better to choose among the original multiple solutions by, e.g., weighting (Carpenter, 1988). But using consensus techniques has it advantages. When the incongruence among the characters is very large it can be quite bothersome to find the similarities. Consensus trees are an efficient way to summarize alternative hypotheses (Kluge, 1989). When different consensus techniques result in the same consensus pattern it means that the character support for that part of the pattern is high. The evolutionary pathways shown by such cladograms are as useful as those of a single cladogram, since it is the congruence of the characters that is needed to formulate the hypothesis.

Which of these points counts most for *Aporosa*? As expected, the length of the consensus tree is longer than in any of the fundamental cladograms. The length is increased because many relationships are shown in polytomies, which is less parsimonious than in a dichotomous depiction. Another fact influencing the number of steps is that the consensus tree for *Aporosa* is formed by pasting various subtrees into one big pattern. This is the advised method for handling large data sets (e.g., Kellog & Watson, 1993), but it is known that this may increase the length of the final cladogram (Van Welzen, 1989). However, the CI of the characters in the various subtrees is much better when working with smaller data sets. Additionally, in subsets the value of some characters may be better, since one character can be a good synapomorphy in one clade, but show many parallels in another clade. Such differences in overall optimisation of characters are also responsible for differences in relationships between a tree based on all data and subtrees. In my view, both aspects caused by pasting subtrees represent more efficient uses of the information content of the characters. Therefore, they make up to the slight gain in overall length. Furthermore, since many of the subsets within, e.g., the *frutescens*-group, are in their strict consensus tree fully dichotomous, I do not think that the relationships shown here have suffered any loss of information and are thus just as well suited for modelling evolutionary hypotheses. This is especially true for the configuration of the *benthamiana*/*papuana*-clade, which does not even originate from a consensus pattern.

The patterns depicted by the lower nodes of Fig. 8.7 are a different case. When interpreting these it must be taken into account that they originate from an Adams consensus pattern. Adams consensus trees are excellently suited to pinpoint the taxa which are responsible for the incongruence (Barrett et al., 1991). However, they may depict components that are not present in any of the fundamental trees (Barrett et al., 1991). A good example of this is, e.g., the bifurcation at the base. None of the cladograms found in the true analyses had these two lineages. However, the closer connection between the first and the second lineage than of either of them with the third lineage was shown in other ways. Other examples are the monophyletic representation of the *maingayi*-, *brevicaudata*-, and *nervosa*-groups or of some the subgroups of the *octandra*-group. In many of the fundamental analyses they were paraphyletic. But is it really unrealistic to depict them monophyletically?

Baum & Estabrook (1996) showed how groups of taxa with long phyletic lines analysed together may cause the more primitive of the groups to be dissolved into a pectinate topology at the base of the more derived group. Though I cannot view their example without some criticism, a pattern similar to what they found may be present here in *Aporosa*. The three monophyletic groups are characterized by synapomorphies, i.e., they have many character changes on their root. However, speciation within the group has introduced reversals. In the meantime, the relative outgroups to the monophyletic groups have themselves speciated. Because of the present parallels and reversals with their sistergroup, the algorithm will depict them along a pectinate cladogram rather than in a monophyletic representation, in which each group is represented by synapomorphies. This phenomenon may hold true for the *benthamiana*/*papuana*-group-pair, the *frutescens*/*arborea*-group-pair, or the *octandra*/*maingayi*-group-pair. This in its turn might point to a possible monophyly of the *papuana*-, *arborea*-, and *maingayi*-groups, despite their paraphyletic representation. This view is supported at least for the *papuana*-group in its subanalysis with the *benthamiana*-group: here the *papuana*-group turns monophyletic (see paragraph 8.5.2). Therefore, I do not think it so unrealistic to maintain the monophyletic depiction of the discussed groups in the composed consensus pattern. Figure 8.7 is the best graphical summary of the possible relationships; the interpretation of the relationships differs for groups, monophyletic by the Adams consensus technique, and the ‘truly’ monophyletic groups.

Accepting the composed consensus pattern for *Aporosa* is also a practical solution. The second analysis with weighted characters has shown that weighting was impossible (paragraph 8.2). It could in no way be ascertained that the cladograms found were all the most parsimonious trees or even if they were the shortest ones. The problem with multiple islands, especially when weighting the characters, was also considerable. Choosing among the multiple solutions found, or use of, e.g., Sharkey's (1993) exact indices, which are designed to choose with weighted characters among a set of most parsimonious trees generated with unweighted characters, is thus meaningless. Still other ways to choose among MPTs exist. Many are based on the CI, but the low CI of the cladograms in *Aporosa* points to a large amount of homoplasy and thus incongruency in the matrix. This makes the use of the CI or any CI related index for choosing or comparing senseless. It is true that correction factors exist for reducing the influence of number of taxa on the CI, but these formulas cannot be implemented here. For example, Sanderson & Donoghue's (1989) regression line is not fitted for more than 60 taxa. It raises the question whether any phylogenetic analysis with so many taxa is in principle unreliable.

But why choose? If the only reason is to produce a tree with a higher resolution, I do not consider it valid. A better resolved tree makes hypothesizing character evolution easier, but it does not make the pattern chosen more accurate (Wilkinson, 1996). The fact that multiple and instable patterns are present in the data set indicates uncertainties. There is no scientific value in speculating about evolutionary patterns one already suspects to be unreliable. The main pattern in the phylogenetic reconstruction of *Aporosa* is the shown incongruence and ambiguity among the taxa. This is thus the pattern that should be accepted.

A last negative point of the consensus pattern shown is that not all taxa are included. This means that the phylogeny is one of a paraphyletic group. And one of the rules of phylogenetic inference is still that only monophyletic groups may be analysed correctly. The main problem seems to be the classification, or how one should classify the excluded taxa. But the alternative, including the ambiguous taxa, destroys the few patterns there are, and without reliable patterns classification makes no sense. In depicting a consensus pattern for a selection of taxa of *Aporosa* I have depicted the stable part of the relationships. The choice for the consensus is a choice between a phylogenetic reconstruction without useful relationships or one with at least part of the species depicted in a useful configuration.

An issue that should always be kept in mind in a discussion like the one above about resolution and stability of cladistic patterns is what the cladogram and data really are. A cladogram is nothing more than the, most parsimonious, summary of the characters (Bryant, 1989). Building cladograms may help to discover evolutionary models. They provide hypotheses of three-taxon relationships. With these hypotheses, models for the evolution of characters and species can be formulated. The cladogram itself is not the model, but merely the building block on which to base the evolutionary hypotheses (Nixon, 1996). Considering this, neither parsimony nor complete resolution are really necessary in a cladogram. Consensus trees hypothesize the unambiguous relationships just as well as fundamental cladograms, and in addition show evidence of controversy in the data with unresolved branches.

Chapter 9

PATTERNS AND RELATIONSHIPS IN APOROSA

9.1 – **Introduction**

Now that I have argued that the composed consensus pattern given is the best solution to depict the phylogenetic patterns in *Aporosa* and that at least part of the shown relationships are suited to reconstruct evolutionary pathways, the next step is to model them. Two kinds of evolutionary models can be developed: those for hypothesizing character evolution and those for hypothesizing species evolution. Paragraph 9.2 investigates some of the character transformation series; paragraph 9.3 deals with speciation.

Reconstructing the historical biogeography of *Aporosa* is almost impossible with a consensus pattern, i.e., a pattern containing polytomies. This is a problem caused by a limited methodology; the historical biogeography seeks to explain distribution patterns on the basis of the phylogenies of taxa inhabiting the area. The cladogram is used to infer the historical relationships of the areas by substituting the taxa in the cladogram for their areas of distributions (Zandee & Roos, 1987; Page, 1988; Wiley, 1988; Brooks, 1990). Substituting species by areas in a polytomy renders no information about the relationships of the areas and is thus useless. Still, some biogeographical information is present in the consensus tree for *Aporosa*, but a cladistic method is not suited to deal with it. The next best method available is the one that was used before phylogeny was invented: comparing proposed relationships, distribution patterns, and the geological history of the area. Therefore, when dealing with the speciation patterns in paragraph 9.3, comparisons with distribution patterns and historical data of the area, when available, are included. A cladistic biogeographical analysis is not attempted.

After studying the evolutionary models, the last of the aims of the phylogenetic analysis, set at the start of this study, can be carried out: proposing an infrageneric classification for *Aporosa*. When defining sections on phylogenetic results, the question whether or not the cladogram is fully resolved is not relevant. A section classification should be stable, users do not like a classification that changes with every discovery of some new taxon, character, method, or point of view. For practising taxonomists, morphological recognizability and stability of the infrageneric groups are important (cf. also Siddall, 1994). The proposed sections, defined by the cladistic analysis, and described in paragraph 9.4 are both: they are based on the stable results of the phylogenetic analyses, i.e., the three monophyletic groups, and on morphological criteria.

9.2 – **Evolutionary patterns of the characters**

9.2.1 – ***General notes***

Tracing character transformation series in the cladogram is one of the first applications after the phylogenetic reconstruction. Evolution is recognized by a change in characters. Describing these changes is a way to find out more about how evolution occurred

(Baum & Donoghue, 1995). If these patterns are acceptable to modern biological and evolutionary understanding, then the confidence in the relationships shown grows.

This last point is desirable when in a next step speciation patterns are proposed. Though I did argue that it is not impossible to use consensus patterns to trace evolution, the situation is not optimal. Working with strict and Adams consensus patterns was necessary because of the high level of ambiguity. It was discovered that part of the ambiguity was caused by some of the New Guinean taxa, which were thereupon excluded. However, taxa are represented by character codings, which means that basically the disruption is caused by the characters.

In retrospect, considering the characters and how their codings were effected, the ambiguity is not unexpected. The species are minimally distinct and often defined on various combinations of (polymorph) character states, and there are many taxa. More taxa increase the amount of homoplasy and lower the CI-values of both the cladogram and the characters (Sanderson & Donoghue, 1989). Furthermore, the circumscription of the character states was in some cases subjective and the ratio of the characters in comparison to the number of taxa is low. The total number of characters, calculated as binary characters, is 171. This gives a character/taxa ratio of 171/103 = 1.66 (or 173/110 = 1.57 when including the outgroup) in the analysis with all taxa. Part of the characters, however, are not informative as autapomorphic states are present. The effective ratio will thus be even lower. As a ratio of more than 2 is recommended (Lamboy, 1994), one can only expect a very inaccurate and unstable cladogram.

However, it does not follow automatically that the transformation series are useless. Even homoplasious patterns can indicate evolution. In the view of Kornet (1993) a character change is sufficient to define a species. However, in her composite species concept the individuals in the starter internodon may still be polymorphic for the character. At a later evolutionary stage the same character state may get fixed in several taxa. This process is called parafixation by Kornet & Turner (1999). In evolutionary terms it means that the presence of a particular state can also indicate a closer relationship of the taxa within one group, even if they are not sister species. The character is homoplasious and its CI is low, but it still has power to indicate relationships.

Another point that increases the value of the characters despite their low CIs, is that part of the patterns in the composed consensus pattern of Fig. 8.7 was arrived at by analysis of subsets. In especially the analysis of the *frutescens*-group and the *benthamiana*/*papuana*-group there was less ambiguity (3 and 1 cladogram, respectively) and a higher character/taxon ratio (85 minimum steps/15 taxa = 5.67 for the *frutescens*-group and 91 minimum steps/18 taxa = 5.06 for the *benthamiana*/*papuana*-group). Character transformation series from these subsets may thus give acceptable evolutionary models. The analysis of the third subset, the *octandra*/*maingayi*/*brevicaudata*/*nervosa*-groups and some other taxa, gave 330 different trees and had a character/taxon ratio 2.53 (149 minimum steps and 59 taxa) and is less useful.

Below follows the discussion of changes in characters, taking into account the limitations mentioned above. Two types of characters are discussed: coded ones and non coded ones. Changes in the coded ones are traced on in the consensus pattern of Fig. 8.7 and commented on; possible changes in non coded characters are discussed as independent support for the hypothesized relationships.

9.2.2 – ***Character evolution in coded characters***

The consensus pattern of Fig. 8.7 has 1263 steps. Most characters have a very low CI (cf. Table 9.1) and it would be of little use to discuss all changes individually. Therefore, the discussion following is divided into three categories of characters, viz., vegetative characters, staminate characters, and pistillate characters including fruiting characters. For each category only the changes in the least ambiguous characters are considered. Some of the transformation series discussed are depicted using MacClade 3.04 (Maddison & Maddison, 1992).

Table 9.1. Character statistics for *Aporosa*. Steps, CI, RI: for the consensus pattern; steps-f, CI-f, RI-f for the analysis with *frutescens*-group; steps-bp, CI-bp, RI-bp for the analysis with *benthamiana/papuana*-group; and steps-2, CI-2, RI-2 for the analysis with the second lineage. Characters marked * were recoded for one or more of the subanalyses and may not be directly comparable in the statistics.

char.	**0**	**1**	**2**	**3**	**4***	**5**	**6***	**7**	**8**	**9**	**10**	**11**	**12**	**13**
steps	1	24	18	17	14	20	26	17	11	16	25	1	19	15
CI	1.00	0.08	0.11	0.23	0.21	0.20	0.11	0.17	0.27	0.18	0.12	1.00	0.10	0.06
RI	1.00	0.46	0.40	0.74	0.21	0.30	0.36	0.39	0.68	0.07	0.40	1.00	0.41	0.53
steps-f	–	6	2	3	7	3	4	–	2	–	3	–	–	2
CI-f	–	0.33	0.50	0.33	0.28	0.33	0.24	–	0.50	–	0.33	–	–	0.50
RI-f	–	0	0	0.60	0.16	0	0.25	–	0.66	–	0.33		–	0
steps-bp	–	3	4	–	3	2	4	3	–	3	3	1	2	2
CI-bp	–	0.33	0.25	–	0.66	1.00	0.50	0.66	–	0.66	0.66	1.00	0.50	0.50
RI-bp	–	0	0	–	0	1.00	0	0.50	–	0.50	0.50	1.00	0	0.75
steps-2	–	13	8	11	19	14	18	11	8	12	15	–	14	10
CI-2	–	0.15	0.12	0.27	0.15	0.21	0.16	0.27	0.37	0.25	0.20	–	0.14	0.10
RI-2	–	0.47	0.41	0.65	0.11	0.35	0.40	0.50	0.75	0	0.50	–	0.50	0.55

char.	**14***	**15**	**16**	**17**	**18***	**19**	**20***	**21**	**22**	**23**	**24**	**25**	**26***	**27***
steps	3	8	13	35	21	31	11	7	12	1	21	5	19	18
CI	0.66	0.12	0.07	0.11	0.28	0.12	0.09	0.14	0.16	1.00	0.09	0.20	0.05	0.16
RI	0.91	0.76	0.45	0.49	0.70	0.54	0.69	0.14	0.28	1.00	0.60	0.60	0.53	0.54
steps-f	2	0	–	6	4	6	3	–	–	–	3	2	–	1
CI-f	1.00	1.00	–	0.50	0.50	0.66	0.33	–	–	–	0.66	0.50	–	1.00
RI-f	1.00	1.00	–	0.50	0	0	0.60	–	–	–	0	0.75	–	1.00
steps-bp	–	–	1	3	4	6	–	1	2	–	–	–	–	–
CI-bp	–	–	1.00	0.66	1.00	0.50	–	1.00	0.50	–	–	–	–	–
RI-bp	–	–	1.00	0.50	1.00	0.25	–	1.00	0.75	–	–	–	–	–
steps-2	–	6	11	21	12	16	9	5	8	1	13	–	15	11
CI-2	–	0.16	0.09	0.19	0.33	0.25	0.11	0.20	0.25	1.00	0.15	–	0.13	0.18
RI-2	–	0.61	0.47	0.50	0.68	0.64	0.61	0.20	0.14	1.00	0.56	–	0.38	0.47

char.	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**
steps	15	19	1	11	13	19	11	24	21	20	9	12	19	10
CI	0.06	0.21	1.00	0.09	0.07	0.15	0.09	0.08	0.09	0.10	0.22	0.16	0.15	0.20
RI	0.51	0.72	1.00	0.62	0.65	0.50	0.54	0.48	0.53	0.47	0.82	0.60	0.33	0.52
steps-f	3	3	1	3	–	3	–	3	6	2	–	2	4	–
CI-f	0.33	0.66	1.00	0.33	–	0.33	–	0.66	0.16	0.50	–	0.50	0.50	–
RI-f	0.50	0.83	1.00	0.66	–	0.50	–	0.50	0	0	–	0.66	0	–
steps-bp	2	2	–	0	–	1	1	2	1	2	1	–	3	2
CI-bp	0.50	1.00	–	1.00	–	1.00	1.00	0.50	1.00	0.50	1.00	–	0.66	0.50
RI-bp	0	1.00	–	1.00	–	1.00	1.00	0.50	1.00	0.50	1.00	–	0.50	0.50
steps-2	7	10	–	5	10	11	9	16	12	13	8	7	8	7
CI-2	0.14	0.40	–	0.20	0.10	0.27	0.11	0.12	0.16	0.15	0.25	0.28	0.25	0.14
RI-2	0.45	0.72	–	0.50	0.50	0.33	0.57	0.46	0.47	0.52	0.77	0.58	0.25	0.33

Table 9.1 (*continued*)

char.	**42**	**43**	**44**	**45**	**46***	**47***	**48**	**49**	**50***	**51**	**52**	**53**	**54**	**55**
steps	11	16	5	29	11	13	8	16	12	24	22	16	15	9
CI	0.09	0.12	0.20	0.13	0.09	0.15	0.12	0.12	0.25	0.08	0.09	0.12	0.06	0.22
RI	0.54	0.64	0.20	0.43	0.62	0.64	0.22	0.66	0.72	0.50	0.42	0.68	0.56	0.68
steps-f	–	2	–	5	2	–	–	–	2	4	3	–	2	4
CI-f	–	0.50	–	0.40	0.50	–	–	–	1.00	0.50	0.33	–	0.50	0.25
RI-f	–	0.50	–	0.25	0.80	–	–	–	1.00	0.33	0.50	–	0.66	0.40
steps-bp	–	1	–	3	–	–	3	2	1	3	2	4	2	1
CI-bp	–	1.00	–	1.00	–	–	0.33	0.50	1.00	0.33	0.50	0.50	0.50	1.00
RI-bp	–	1.00	–	1.00	–	–	0.33	0.75	1.00	0.33	0.50	0.33	0.75	1.00
steps-2	9	12	5	16	9	8	4	11	7	14	15	11	10	4
CI-2	0.11	0.16	0.20	0.25	0.22	0.25	0.25	0.18	0.14	0.14	0.13	0.18	0.10	0.25
RI-2	0.42	0.50	0.20	0.50	0.66	0.45	0.25	0.35	0.68	0.50	0.40	0.64	0.30	0.76

char.	**56**	**57**	**58**	**59**	**60***	**61**	**62**	**63**	**64**	**65**	**66**	**67***	**68**	**69***
steps	21	9	10	17	21	32	20	4	5	16	28	19	20	14
CI	0.09	0.20	0.10	0.11	0.09	0.09	0.10	0.25	0.20	0.12	0.10	0.10	0.15	0.14
RI	0.50	0.68	0.55	0.60	0.09	0.49	0.60	0.72	0.66	0.67	0.35	0.43	0.48	0.70
steps-f	6	2	2	2	2	3	1	1	–	3	9	–	3	1
CI-f	0.33	1.00	0.50	1.00	0.50	0.33	1.00	1.00	–	0.66	0.33	–	0.33	1.00
RI-f	0	1.00	0.66	1.00	0	0	1.00	1.00	–	0.50	0.25	–	0.33	1.00
steps-bp	3	–	1	2	3	4	2	–	–	2	2	–	2	1
CI-bp	0.33	–	1.00	0.20	0.33	0.50	1.00	–	–	1.00	0.50	–	1.00	1.00
RI-bp	0.33	–	1.00	0	0	0	1.00	–	–	1.00	0.50	–	1.00	1.00
steps-2	10	7	7	10	15	21	14	3	5	9	16	12	13	9
CI-2	0.20	0.28	0.14	0.10	0.13	0.14	0.14	0.33	0.20	0.22	0.18	0.16	0.23	0.11
RI-2	0.57	0.61	0.53	0	0.31	0.47	0.53	0	0.66	0.73	0.45	0.23	0.44	0.60

char.	**70**	**71**	**72**	**73**	**74***	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**
steps	5	22	11	21	25	23	28	9	1	23	3	2	13
CI	0.20	0.09	0.09	0.09	0.08	0.08	0.17	0.33	1.00	0.08	0.33	0.50	0.07
RI	0.50	0.39	0.28	0.32	0.37	0.46	0.32	0.00	1.00	0.38	0.33	0.96	0.42
steps-f	–	3	–	–	5	4	5	5	0	4	2	–	–
CI-f	–	0.66	–	–	0.40	0.50	0.20	0.20	1.00	0.50	0.50	–	–
RI-f	–	0.75	–	–	0.40	0.66	0.20	0	1.00	0.66	0.50	–	–
steps-bp	0	–	–	3	–	2	2	–	–	–	–	–	–
CI-bp	1.00	–	–	0.66	–	0.50	1.00	–	–	–	–	–	–
RI-bp	1.00	–	–	0.50	–	0	1.00	–	–	–	–	–	–
steps-2	3	15	9	14	19	15	17	–	–	13	–	2	13
CI-2	0.33	0.13	0.11	0.14	0.10	0.13	0.23	–	–	0.15	–	0.50	0.07
RI-2	0.50	0.40	0.33	0.40	0.34	0.38	0	–	–	0	–	0.96	0.42

9.2.2.1 – *Vegetative characters*

The characters 1 to 23 are the coded vegetative characters (Table 7.1). Most of these play no important role in establishing the relationships. Exceptions are the stipule shape, character 3, and some types of foliar glands (8, 10, 11, 18). In addition, the colour of the dried leaf, character 15, was an important delimiting factor for species recognition and the presence of dots, character 17, is often used to delimit *Aporosa* from *Baccaurea*. Both deserve some notice, as does the size in general. These five aspects of the vegetative parts will be discussed in this paragraph.

Stipule shape (character 3; Fig. 9.1)

Large falcate stipules (character 3, state 5; node 146) are a synapomorphy for *Aporosa*. They developed in the ancestral *Aporosa* species and might have been one of the first

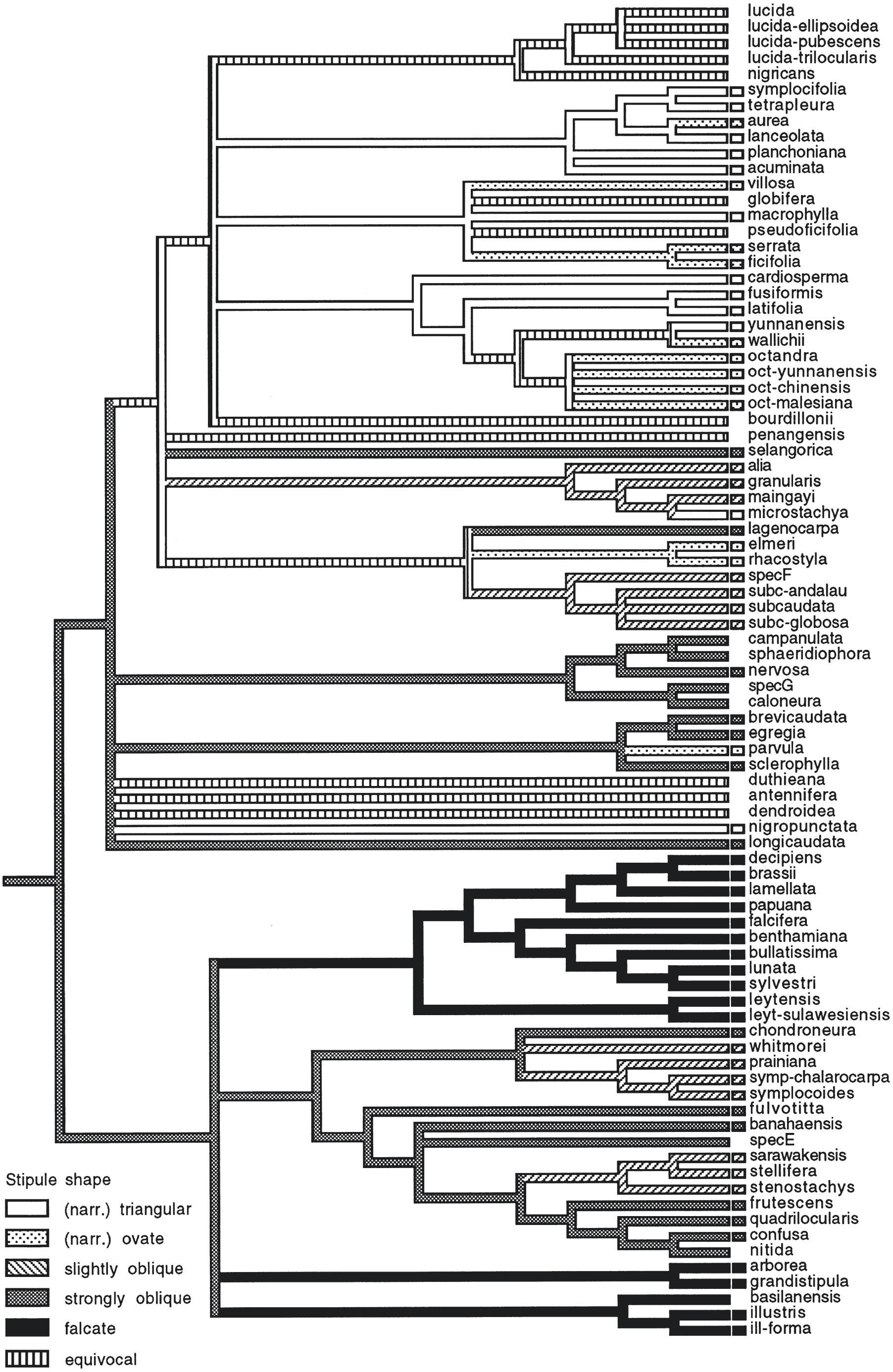


Fig. 9.1. Character transformation series for the shape of the stipules (character 3).

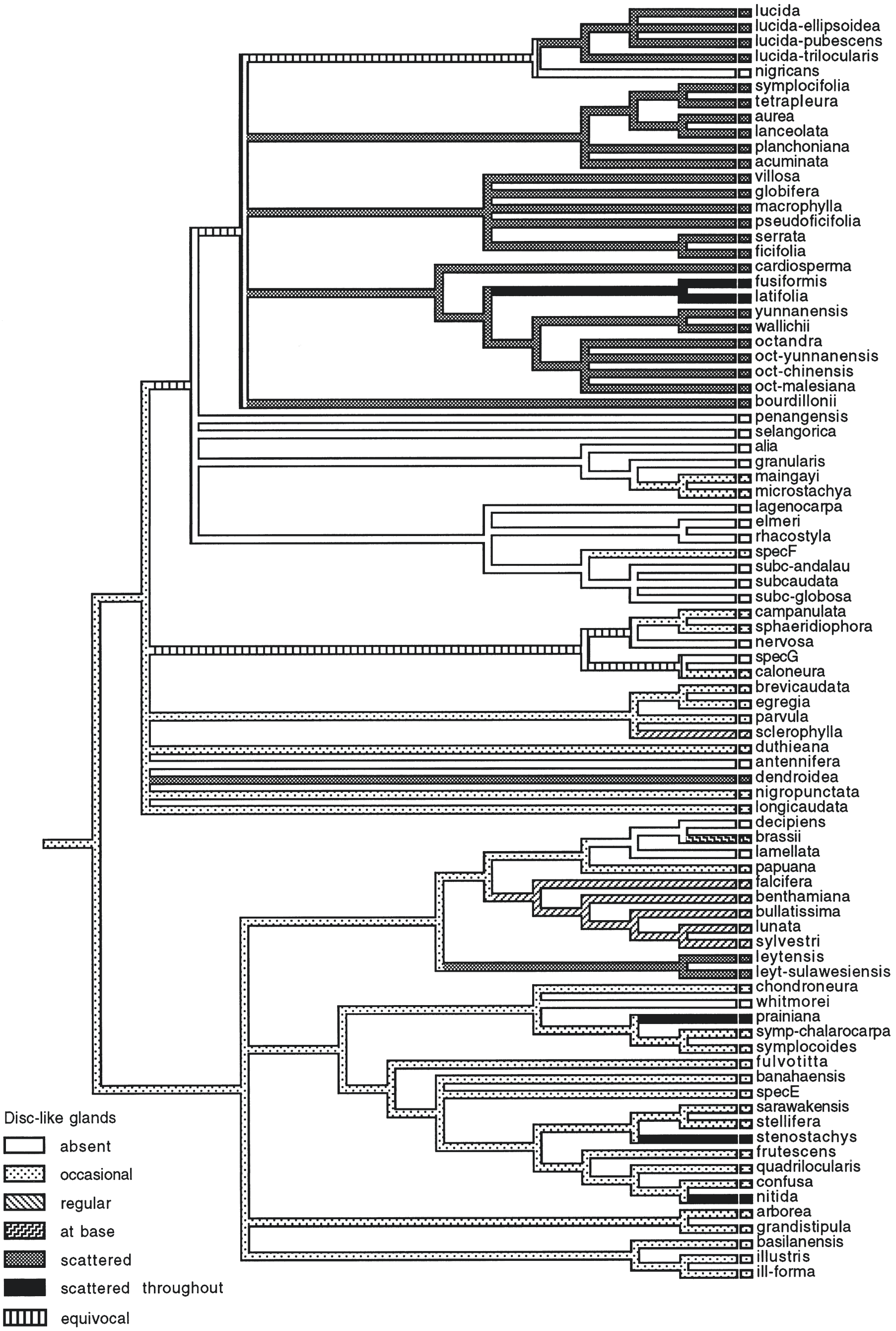


Fig. 9.2. Character transformation series for the foliar disc-like glands (character 18).

characters to differentiate it. Nowadays, only the species in the *benthamiana/papuana*-clade retain the large stipules, in both the second clade and the *frutescens*-group the stipules have become smaller (state 4; nodes 143 and 142), a trend that continued in the *maingayi*-group and some of the members of the *frutescens*-group (state 3; nodes 127, 125, 96, *A. whitmorei*). Still later, in most species of the *octandra*-group, the complete reversal to symmetric stipules was completed (state 1; node 126).

If the falcate stipules are a good synapomorphy for *Aporosa*, it might be used to separate *Aporosa* from its outgroup *Baccaurea*, where falcate stipules are unknown. The fact that it is not used for this purpose, can be explained by the subsequent evolution of the stipules: the more derived – and more common – *Aporosa* do not have falcate stipules. It is a pity that the function of large stipules is unknown, this might give an indication of how this first separation of *Aporosa* was initiated. In a later stage, the importance of large stipules became less important and the character reversed.

It is interesting to note that the persistence of the stipules (character 2), which is not completely independent from its shape (paragraph 3.2), is not important in the phylogenetic reconstruction.

Foliar glands (characters 8, 10, 11, and 18; character 18 in Fig. 9.2)

The ancestral *Aporosa* probably possessed few marginal glands and few disc-like glands along the margin (characters 8 and 10 state 1; character 18, state 2). In the *octandra*-group and two members of the *frutescens*-group, the ancestor of *A. prainiana–A. symplocoides* and *A. sarawakensis*, glands also developed at the base of the leaf (character 8, state 2). These basal glands were lost again in the *globifera*-subgroup (node 109, state 1) and modified for *A. tetrapleura* and the ancestors of *A. fusiformis–A. latifolia* and *A. aurea–A. lanceolata* (state 3) and *A. acuminata*, *A. cardiosperma*, and the ancestor of *A. ficifolia–A. serrata* (state 4).

Meanwhile, the number of marginal glands, character 10, increased in the first lineage (node 144, state 2, but with three reversals) and individual members of the second lineage (nodes 138, 136, 111, 108, 97, and five further species). Three species of both lineages developed hairy glands in young leaves (state 3: *A. illustris, A. leytensis*, and *A. decipiens* in the first lineage and *A. alia*, *A. antennifera*, and *A. nigricans* in the second lineage). Only in the *globifera*-subgroup the hairy glands were retained in the older leaves (node 109, state 4, but with a reversal for *A. macrophylla*).

The disc-like glands, character 18, remained few during some period of time, and were occasionally even lost completely (state 1, nodes 134, 113, and three further species), but returned on two occasions (node 102 and *A. spec. F*). This repeated switching might be the result of incomplete fixation of the character state or genes that are switched on and off. In later times the character became fixed in other configurations, like the many glands of the *benthamiana*-group (node 122, state 3, with a curious parallel in *A. sclerophylla*). The *octandra*-group developed its scattered disc-like glands (node 126, state 5, parallel with *A. dendroidea*, *A. leytensis*, and *A. bourdillonii*). Three species of the *frutescens*-group (*A. nitida*, *A. prainiana*, and *A. stenostachys*) and the ancestor of *A. fusiformis–A. latifolia* developed glands along the margin as well as scattered. The type with only disc-like glands at the base, state 4, was present in some of the excluded New Guinean species and now appears only as an autapomorphy for *A. brassii*.

Leaf drying colour (character 15)

The greenish-yellow colour of the dried leaf is a synapomorphy for the *frutescens*-group (character 15, state 2, node 142). However, a parallel is present for one of the three subgroups of the *octandra*-group, the *aurea*-group (node 116, with one reversal) and four individual species, of which three from other subgroups of the *octandra*-group. If this drying colour is connected with the amount of aluminium accumulated in the leaf, it is worth noting that two of the more derived groups possess the typical colouring. This does not agree with a hypothesis that a high aluminium accumulation, indicated by more yellowish dried leaves, is primitive (Chenery, 1948). Possibly the accumulation itself is primitive, since it probably occurs in all species of *Aporosa*, but the amount of it and its manifestation in the leaf is not.

Dots on the upper surface of the leaf (character 17)

The dots that adorn the upper surface of the leaf (character 17) are in the configuration with dense and large dots a synapomorphy for *Aporosa* (node 146, state 5). However, this character is immediately reduced again in the first lineage and subbasally in the second lineage (nodes 144 and 134, state 4, with reversals for *A. tetrapleura, A. planchoniana*, and the three species from Sri Lanka in the *octandra*-subgroup, node 117, reversed in node 100). Thus only most of the more basal species of the second clade have the distinct dots that are used to recognize the genus *Aporosa*. However, the intermediate states 3 and 4 with finer dots appear more often, so the character has still some value to separate *Aporosa* and *Baccaurea*. Only some more derived species in the *frutescens*-group lack the dots completely (node 114, state 1, but reversals for *A. stellifera*, *A. sarawakensis*, and *A. nitida* and a parallel loss for *A. rhacostyla*). This last feature coincides with the presence of the granules, character 14, which were only present in some members of the *frutescens*-group.

Size in general (characters 4, 6, 26, 27, 37, 46, 47, and 74)

Though none of the characters coding for size ranges have a high enough CI or RI to play a role in reconstructing phylogeny, some trends are present.

In general, the species with large leaves and long inflorescences are the basal species. The more derived ones often have smaller leaves and shorter inflorescences. Flowers are getting smaller. A reduction of all parts in *Aporosa* was also one of the generic delimitating features. This indicates how an evolutionary pathway, which was initiated at the origin of the genus, is a continuing process. The process, however, is not irreversible, as shown by the many exceptions.

Yet, the many reversals and parallels are responsible for the low CI values of the various size characters. However, though very homoplasious, the size characters cannot be omitted from the analysis as is shown by the analysis without the morphometric characters: this matrix lacked probably any general trend and swapping of the initial tree found by the ‘mh*’ command ended only in a mess.

9.2.2.2 – *Staminate characters*

Of the characters representing the staminate inflorescence, characters 25–33, and those representing the staminate flower, characters 34–45, only the distribution of

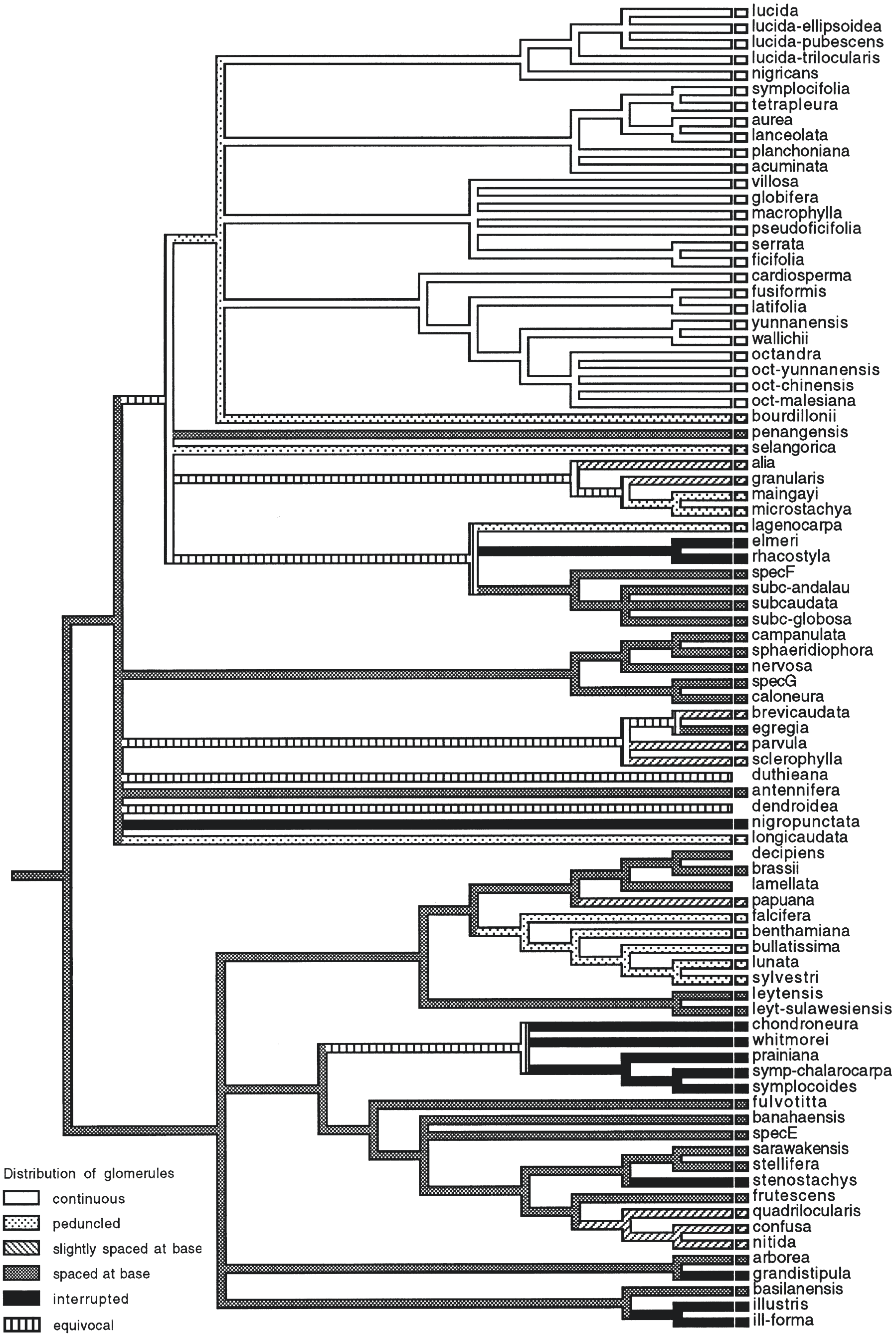


Fig. 9.3. Character transformation series for the distribution of the glomerules in the staminate inflorescences (character 29).

the glomerules (character 29 and 30), the fusion of the sepals (character 38), and the exsertion of the stamens (character 41) are discussed. These characters were, macromorphologically speaking, the basis to describe five different types of inflorescence (see Chapter 3). Not unexpected, they are also rather important in the complete analysis and in one or more of the subanalyses. The transformation series for the distribution of the glomerules, character 29, is illustrated in Fig. 9.3.

Staminate inflorescence (characters 29 and 30; character 29 in Fig. 9.3)

State 5, the distinctly spaced glomerules, is a synapomorphy for the basal species of the *frutescens*-group, with parallels for *A. nigropunctata*, the pair *A. elmeri–A. rhacostyla*, *A. illustris*, and *A. grandistipula*. These last two need not be real parallels, but may be caused by the polytomy in the first lineage. State 1, the continuously set glomerules, is unique for the *octandra*-group without *A. bourdillonii*, and state 2, the continuously set glomerules with a peduncle appear in the *benthamiana*-group with parallels for *A. papuana*, *A. longicaudata*, the pair *A. microstachya–A. maingayi*, and the three species in the polytomy at node 134. Considering that, though the distribution of the glomerules in these taxa are the same, the type of staminate flower is not (see below), it might mean that the various manifestations of state 2 are truly convergent, and not products of parafixation or caused by the depiction in a consensus tree. The remainder of the taxa alternate between state 3 and 4, indicating that these two states might, genetically speaking, not represent a real difference.

The other important character of the staminate inflorescence is character 30. State 2, the apically massed glomerules, are only present in the four species around *A. frutescens*, node 95. It is one of the few unique characters in *Aporosa*.

Of the further characters in the staminate inflorescence, 25–35, one other aspect attracts notice: most staminate characters are of good quality in the subanalysis with the *benthamiana*- and *papuana*-groups; four characters are even maximally resolved (Table 9.1). These synapomorphies were not strong enough to keep the *papuana*-group united when analysing all species, but in an analysis with less species they are robust. However, it should also be noted that the staminate characters of two of the four species of the *papuana*-group are incompletely known.

Staminate flower (characters 38 and 41)

The free sepals, character 38 state 1, are a synapomorphy for the *octandra*-group, with reversals for *A. nigricans*, *A. macrophylla*, and *A. globifera* and the connate sepals, state 3, form five parallels for the *brevicaudata*-group, the *nervosa*-group, the *benthamiana-papuana* clade, *A. nigropunctata*, and *A. lagenocarpa*. These latter five are supposedly more primitive taxa.

The stamens are distinctly exserted, character 41 state 2, in the *benthamiana/papuana*-clade, but this time including *A. leytensis*, and the *nervosa*-group. Furthermore, this state is found in *A. antennifera, A. caloneura*, *A. cardiosperma*, *A. lagenocarpa*, *A. parvula*, *A. yunnanensis*, and *A. spec. G*. The *benthamiana*-group and *A. papuana* have developed strongly exserted stamens, state 3. In comparison with character 38 it seems that exserted stamens occur with more or less fused sepals, except in *A. cardiosperma*, which is also deviating in its pedicelled pistillate flowers.

Another striking point is that neither of the above characters plays any role in the *frutescens*-group; this is in contrast with the characters of the staminate inflorescence. Of all characters of the staminate flower, only 39, the indumentum of the sepals, and 43, the length of the anthers, count in reconstructing relationships within this clade. These are rather unexpected categories of characters to be of importance. Of the others occurring in the *frutescens*-group, characters 36, 37, and 40, all have an RI of zero (Table 9.1). Comparing this with the fact that in the *benthamiana*/*papuana*-clade all (!) flower characters play a role, it might indicate that, though all species co-occur in the Malesian Archipelago, different ecological factors, such as pollination, has led the evolution of the staminate flower into different directions.

9.2.2.3 – *Pistillate characters*

Characters 46–50 treat the pistillate inflorescence, characters 51–70 the pistillate flower, and characters 71–82 the fruit. Of these, character 50, the distribution of the pistillate flowers on the rachis, is the most important and is discussed. It was also the basis for the division of the inflorescence types as described in Chapter 3. Of the characters coding for the pistillate flower and fruit many are important in one of the subanalyses, but only few in the complete analysis. They are described generally. The transformation series for the number of locules, character 59, is shown in Fig. 9.4.

Pistillate inflorescence (character 50)

The second clade, node 143, is characterized by flowers set mostly apically on the rachis (character 50, state 1). This feature is reversed seven times to flowers set regularly along the rachis: for the pair *A. caloneura*/*A. spec. G*, the pair *A. elmeri*/*A. rhacostyla*, *A. penangensis*, *A. nigropunctata*, *A. sphaeridiophora* var. *campanulata*, *A. antennifera*, and the *octandra*-group s.s. The *benthamiana*-group is characterized by flowers distributed only apically (state 3) and the upper part of the *frutescens*-group by the uniflorous inflorescences (state 4), which is reversed for *A. stellifera*. The importance of these last two synapomorphies is reflected by the maximum value of the CI and RI in the subanalyses with these last two groups (Table 9.1).

Pistillate flower (characters 51–70; character 59 in Fig. 9.4)

Five pistillate flower characters have a high CI and RI (Table 9.1). Of these five, three code for the stigma, characters 63, 64, and 70; character 55 shows the degree of opening of the sepals during flowering and character 57 the texture of the sepals. In addition, character 59, the number of locules, which was an important delimiting factor, is also discussed.

The reflexed sepals seem correlated with the uniflorous inflorescence (character 55, state 3, node 124), though the relation is not strict; there is a parallel for *A. chondroneura* and a reversal for *A. stenostachys*. The ascending sepals are found in the five species around *A. aurea* (node 107), in the three species around *A. octandra* (node 100), and in the New Guinean *A. brassii, A. brevicaudata*, *A. egregia*, and *A. parvula*. This is a rather polymorphic group. It may be that the ascending sepals of the New Guinean species originated differently from those in the *octandra*-group as a logical consequence of the fusion of the sepals.

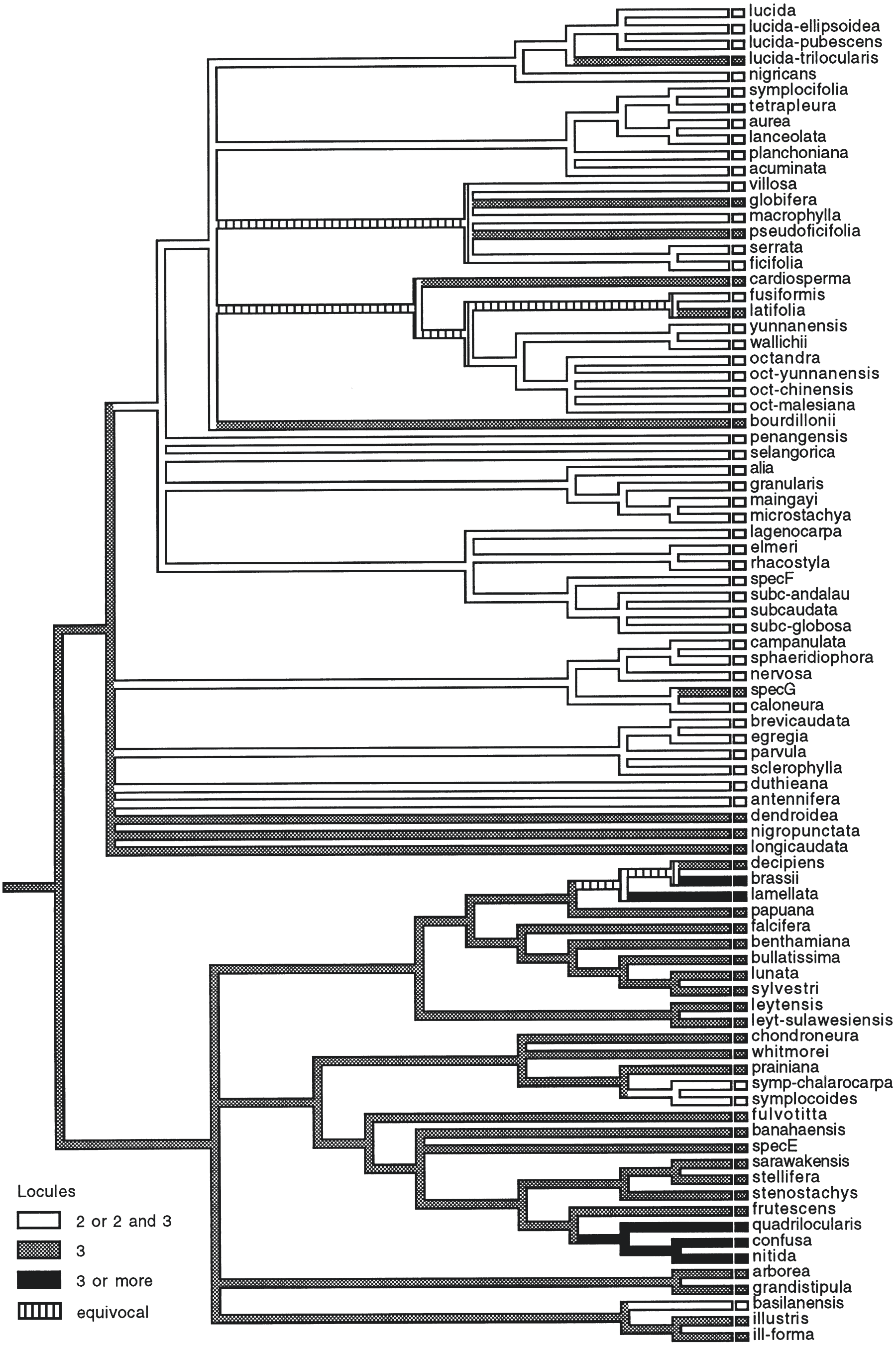


Fig. 9.4. Character transformation series for the number of locules (character 59).

The texture of the sepals, character 57, follows a comparable pattern; the fleshy sepals, state 3, occur mostly in the *frutescens*-group, with a half reversal for *A. fulvo-vittata* (state 2) and two parallels for *A. sphaeridiophora* and *A. latifolia*. The partly fleshy state, state 2, is also present in scattered members of the *octandra*-group. There seems to be some connection with the direction of the sepals, but whether this is real and in how far cannot be said based on this analysis.

Though character 59, the number of locules (see also Fig. 9.4), does not seem important in the analysis, the 2-locular pistil, state 1, is a strong synapomorphy for the second clade (node 143). There are only parallels for *A. symplocoides* and *A. basilanensis*. Its low CI and RI are caused by the ten reversals that occur due to the 3-locular state. If the development from 3- to 2-locular occurred as early in the evolution as the origin of the second clade, then the chance to develop reversals is high. This does not diminish the use of the feature in delimiting groups, it only lowers the CI in a phylogenetic analysis. A further point in favour of an early differentiation between the number of locules in the two lineages is the fact that state 3, 4- or more-locular, occurs only in the upper part of the first clade.

That the stigma plays an important role in determining the relationships is expected. There was much differentiation in stigma structure among the species. Of the characters describing the stigma, 62–70, only 67, the length of the stigma, has no influence in any of the subanalyses. It might be that the length is dependent on the maturity of the flower. Character 66, the incision of the stigma, is neither really informative and may be more a feature of age rather than of relationship. Character 62, state 1, a direct transition between the ovary and the stigma, is synapomorphous for the *benthamiana*-group (node 122) and the uniflorous members of the *frutescens*-group (node 114). In the *frutescens*-group the direct transition is coupled to a broad stigma, character 63 state 1. Character 64, the direction of the stigmas, in its turn is only important in the subanalysis of the second clade; the ascending stigmas, state 1, occur in part of the *octandra*-group and *A. rhacostyla*. Character 65 codes for the curving of the stigmas. The stigmas flattening to the sides of the ovary, state 3, is a synapomorphy for the *benthamiana*-group, node 122, and the *maingayi*-group s.s. including *A. selangorica* and excluding *A. alia*. It is rather surprising that there is some information in this character; I would have expected it to be correlated with the length of the stigma. Character 68, the sculpture of the stigma is only important in the subanalysis of the *benthamiana*/*papuana*-clade. The densely laciniate stigmas, state 4, are a synapomorphy for the *papuana*-group and the smooth stigmas, state 1, a synapomorphy for the *benthamiana*-group. In the complete analysis much switching occurs between the intermediate states, state 2 and 3. The difference between these states is probably small and early *Aporosa* might have been polymorphic for it. Later, two evolutionary directions developed, one leading to the laciniate stigmas and another to smooth stigmas.

Character 69, the presence of a style remnant on the lower side of the stigma, shows an analogous development; states 2 and 3 are intermediate, with many parafixations in the basal members of both lineages and three reversals in more derived species. Only the uniflorous members of the *frutescens*-group, node 114, have developed a unique character state, state 1. The last of the characters coding for the stigma, character 70, consists of five parallels, all found in the more basal taxa.

In summary, the stigma is one of the more important features. Most parallels occur in the basal species in both lineages, while reversals are rare. The more derived groups are often characterized by synapomorphies of the stigmatic characters. The *benthamiana*-group and the uniflorous taxa of the *frutescens*-group are very well represented. This might indicate that most of the variation present in the stigma was already present in early *Aporosa* and got variously fixed.

In comparison with the staminate flower, it is striking that a different evolutionary scenario is supposed. Whereas the features of the staminate flower varied only little among the more primitive taxa, all states of the pistillate flower are supposed to have evolved early in the evolution of the genus. The fact that *Aporosa* is delimited from *Baccaurea* on the staminate flowers is thus logical; the pistillate flowers are more variable and may share more features with other genera than the staminate flowers and are thus less fit for generic delimitation.

Fruit (characters 71–82)

The fruit plays only a minor role in the phylogenetic reconstruction. Of the 12 characters two are important; both are a synapomorphy: character 78 state 2, yellowish drying fruits, for the *frutescens*-group and character 81 state 2, pubescent septae and column, for the *octandra*-group including *A. bourdillonii*.

9.2.3 – ***Non coded characters***

Another type of tracing character evolution concerns characters that were not used in the phylogenetic analysis. Such characters can yield independent support for the patterns found. Agreement among the evolutionary pathways hypothesized by a cladogram and those of different data are a support for the relationships found (Miyamoto & Fitch, 1995).

In *Aporosa* the characters that could not be included for various reasons might provide such additional support for the phylogenetic pattern. Excluded characters were incompletely known ones, such as the tree height and stature, or ecological and distributional data (see paragraph 7.4.2). In this paragraph the growth form and the presence of galls are mapped on the consensus pattern and discussed.

Growth form

One of the first features to check is the height of the tree. If *Aporosa* is supposedly getting smaller, it would be expected that the more basal species are larger trees and the more derived ones small shrubs, taking into account individual exceptions caused by different habitats. The tree heights of the species of *Aporosa* are listed in the synoptical key. The excluded New Guinean taxa can be ignored. From this list it can be seen that the above hypothesis is generally supported. The larger trees, reaching a height of 30 m, are mostly species placed in the basal polytomies: e.g., *A. arborea*, *A. nervosa*, or the *benthamiana*-group. Under the smallest trees, up to 10.5 m, fall many taxa of the *frutescens*- and *octandra*-group, some of the species in the *A. maingayi*-group, and the New Guinean *A. nigropunctata* and *A. longicaudata*. This list is in concordance with the general trend.

A further noteworthy non-coded feature is the appearance of ramiflorous taxa. This might be a good example of parafixation. Ramiflory is found in *A. arborea*, *A. benthamiana, A. grandistipula*, *A. lunata*, and some New Guinean taxa. All these species are basal taxa of the first lineage. None of the taxa in the second lineage is ever ramiflorous.

Ecological features

A possible ecological feature that might show evidence of phylogenetic relationships is the presence of galls. Galls originate by a manipulation of the genetic development of the plant by a gall forming insect; similar galls are thus more likely to be found in related species. The typical bush-like galled inflorescences found in *A. elmeri*, *A. subcaudata*, and sometimes *A. antennifera* are an example. *Aporosa subcaudata* and *A. elmeri* were shown to be closely related.

The bulbous galls formed on twigs and leaves, on the other hand, are almost exclusively found on members of the *frutescens*- and *octandra*-group, two of the supposedly more derived groups within *Aporosa*. This might indicate that the insects forming these galls have only recently become associated with *Aporosa*.

9.3 – **Speciation patterns**

9.3.1 – ***Interpretation of relationships***

The next issue in reconstructing phylogenetic relationships is modelling speciation patterns. A cladogram represents relationships of taxa based on the most parsimonious summary of the characters. These relationships can be used as starting point to hypothesize evolutionary processes. However, their interpretation as speciation models is not one to one. Wiley (1981) gives five modes of additive speciation: allopatric, allo-parapatric, parapatric, stasipatric, and sympatric speciation. He predicts that the first three are simply represented in a dichotomous cladogram, because there is a linear relationship from ancestor to descendant, which can be indicated by plesiomorphic and apomorphic characters. The fourth mode, stasipatric speciation, and the peripheral isolates model may give polytomies in the cladogram. The fifth speciation mode mentioned by Wiley, sympatric speciation, under which fall hybridization and ecological segregation of sister species, has no particular way to show up in the cladogram. Data about distributions may be more useful to formulate the evolutionary patterns here (Wiley, 1981).

However, though allopatric and parapatric speciation may give dichotomous patterns, it does not mean that each dichotomy represents an allopatric or parapatric speciation event. Furthermore, polytomies caused by an ambiguous optimisation of the characters, resulting from, e.g., parallel development, reversal of characters or incomplete sampling of the group, should not be confused with polytomies that result from the mode of speciation. To make matters worse, if the ambiguity is not balanced, i.e., if one of the alternative solutions is better supported, it is only more parsimonious to depict it dichotomously, though in theory it should be a polytomy. In conclusion, both dichotomies and polytomies in a cladogram may or may not show any of the first four speciation models. It is the character support that indicates in how far the relationship depicted can be used as basis for an evolutionary pathway. Once it is established that the relationship shown is probable, a speciation model may be hypothesized. Distribution patterns can then be used to amplify the model.

When modelling speciation and distribution processes, the geological and climatological history of the area should be taken into account. From a geological point of view the history of the Malay Archipelago is an intricate one. The region lies at the collision zone of six tectonic plates, the Eurasian, the Australian, the Indian, the Indian Ocean, the Pacific, and the Philippine plate (Hamilton, 1979). Because of this, many different geological processes are active in the Indo-Malay area. Volcanic activity results in the forming of land. At the borders of the plates small slivers of land are chafed off and accreted elsewhere. Island arcs are being formed. Subsequent tectonic movements repositioned these islands and island arcs and fragmented continental slivers. The combination of all these processes has produced the configuration of the present day Malay Archipelago.

Others have extensively treated these geological events. For example, Ridder-Numan (1996) gives an excellent summary of the various literature on the sequence of fragmentation of the various terrains from Gondwana and their accumulation onto the margin of Asia. De Boer (1995) describes the forming of the Tertiary Island Arc system and its incorporation into Central Malesia. Burrett et al. (1991) treat the opening of a land connection along the Sunda Arc. Pigram & Davies (1987), Veevers (1991), and Vermeulen (1993) treat various aspects of the forming of New Guinea. Hall (1996, 1998), Daly et al. (1991), and Rangin et al. (1990) provide geological reconstructions for the development of Indonesia through time. These authors and the literature they cite are referred to for a detailed and complete overview of the geological history of Southeast Asia.

The geological history is not the only important event which influences the distributions of the modern biota. The climate now and in the past has to be considered as well. Nowadays, the SE Asian tropical rain forest consists of two core areas, Sunda and Sahul, with a zone containing a mixture of patches with a more and lesser seasonal climate in between, Wallacea. This has not always been the case. The Tertiary and, more notably, the Pleistocene are known for their periodical changes in climate.

The fluctuating climates resulted in a succession of different vegetations in Indo-Malaya. Tropical everwet conditions were alternated with drier, more monsoonal, ones. During such drier and cooler periods the tropical forest declined in area and at the borders the monsoonal forests and savannahs increased, giving plants which were adapted to such conditions possibilities to spread from Asia into Malesia and Australia, and vice versa.

The periods with high and low mean temperature were accompanied by high and low sea level, respectively, causing land areas to be flooded or to fall dry. A detailed account of the fluctuating sea level and an overview of references can be found in Ridder-Numan (1996); Rangin et al. (1990) and Hall (1998) provide maps of the configuration of the land masses at various times.

Little is known about how much dry land the various islands arcs contained during such periods of high or low sea level. Tectonic activity causes varying upheaval and submerging of the slivers of land, which makes it almost impossible to find the influence of the sea level changes directly. However, the fact that many dispersal patterns of biota exist showing similar pathways between the mainland of Asia and Australia (see, e.g., Van Steenis, 1979) suggests that enough dry land must have been present to allow colonization.

A last point to be considered is the relative age of *Aporosa*. Though geological processes and changing climates have been shaping the biota on the land masses of the Earth for hundreds of millions of years, the majority of these events took place probably before Euphorbiaceae or *Aporosa* existed. Known fossil remnants of the Euphorbiaceae contain pollen records from the Miocene in Southeast Asia and from a slightly earlier period, the late Palaeocene and early Eocene from Australia (Muller, 1981). Awasthi & Srivastava (1991) record the find of an Euphorbiaceous fruit from the middle Miocene in Kerala.

Such finds indicate that the Euphorbiaceae were well established in Malesia somewhere in the Miocene (10–25 Ma). According to geological theory, in the middle Miocene Southeast Asia consisted of the mainland of Asia, the Malay Peninsula, Sumatra, Java, southwest Borneo, and west Sulawesi. The opening of the South China Sea and the rotation of Sundaland was initiated. Australia was nearing with the Sepik terrain and the East Papuan block already accreted onto the margin. The first fragments of the Philippines and Sulawesi were near their present positions (Rangin et al., 1990; Hall, 1998).

The climate in the middle Miocene was humid, but becoming increasingly drier and cooler, increasing the amount of available dry land. This changing climate might have been the initiator of the spreading of early *Aporosa*. This process may have taken place in several steps corresponding with the various stages of the fluctuating climates.

Any outline of a history hypothesized for *Aporosa* may feel less speculative if biogeographic patterns in unrelated groups occurring in Malesia show similarities. Thus the pathways hypothesized for *Aporosa* are also compared with those already found by monographers who worked with Southeast Asian taxa unrelated to *Aporosa*. For example, Van Steenis (1979) explored the pathways and seasonal influences of a number of Malesian taxa. Later, with the advent of various applications for phylogenetic reconstruction, the area became an interesting study object for historical biogeography (e.g., Duffels, 1986; Van Welzen, 1989; Duffels & De Boer, 1990; Vermeulen, 1993; De Boer, 1995; Turner, 1995; Ridder-Numan, 1996; Haegens, 2000). These authors have each studied a different group of species and its relations between distribution and the history of the Malay Archipelago. If analogous patterns are found in such non-related groups, they may strengthen the support of the supposed evolutionary incidences. However, it is possible that similar patterns originated in different times or that one group of species reacts in a different way to the same event as another group. When comparing biogeographic patterns among unrelated genera, it is thus not necessary that the complete speciation history coincides. Small similarities here and there may already be adequate.

9.3.2 – ***Evolutionary patterns for selected subsets***

The phylogenetic analysis of *Aporosa* ended in the acceptance of the compiled consensus pattern of Fig. 8.7. The major characteristic of the phylogenetic reconstruction was the ambiguity, which showed in the high number of MPTs. It is evident that ambiguous relationships cannot be treated the same way as the unambiguous ones. Thus only the possible evolutionary models to be derived from the unambiguous relationships are discussed in this paragraph. Speculations on what might have caused the ambiguity in the phylogenetic reconstruction are found in paragraph 9.3.3.

Unambiguous groups in the phylogeny are the three monophyletic clades. Next to these, some smaller stable subgroups were present in the three monophyletic groups and in the basal polytomy, e.g., the uniflorous species of the *frutescens*-group, the species with yellow drying leaves and distinct basal glands around *A. aurea*, or part of the *maingayi*-group. As explained in paragraph 9.3.1, the dichotomous branching patterns in these stable subsets may indicate diverging sister taxa, but only if the support for the dichotomy is adequate. The reliability of a dichotomy, and therewith the pattern it presents, is not directly dependant on the number of changes, but more on the quality of the changes. This is dependant not only on the CI of the character in question, but also on the changing frequency of the particular state. Synapomorphies with many reversals, the presence of many parallels for a particular state or reversals that might also be optimized as parallels reduce the reliability of the shown relationship; linear character evolution or the presence of unique synapomorphous states may, on the other hand, increase the reliability.

In this paragraph the support for the stable clades is reviewed, and, if considered reasonable, evolutionary pathways are proposed for the depicted relationships with the aid of distribution patterns, possible geological or climatological processes, and considering biogeographical patterns found in other taxa. If allo- or parapatric speciation has taken place, the sister species should be vicariant, i.e., occur in neighbouring or only slightly overlapping areas of distribution. In sympatric speciation the sister species are found in substantially overlapping areas (Wiley, 1981). Additionally, in case the first mode of allopatric speciation has occurred, recent or historical geological or climatological barriers should mark the boundaries. The distributions of all taxa can be found in the revision. Map 9.1 to 9.3 show the distributions in some of the discussed groups.

Patterns in the frutescens-group

Within the first monophyletic group discussed, the *frutescens*-group, the taxa show a seemingly linear ancestor-descendant pattern. Four subgroups are present. The first, the set formed by *A. prainiana* and *A. symplocoides* and its variety, is characterized by glabrous branchlets, slightly oblique stipules, small basal glands, few nerves, small anthers, and a thin pericarp. It is the sistergroup to the characteristic group with uniflorous pistillate inflorescences (Fig. 8.7, node 124). This character state has no parallel in *Aporosa* and is reversed only in *A. stellifera*. The development is accompanied by some other character changes, but none of these is really unique; reversals and parallels exist. From this group, *A. fulvovittata* splits, and the others develop the interruptedly set glomerules that become more continuous apically. This is accompanied by a broadening and shortening stigma that becomes attached to the top of the ovary. The broad stigma is unique; the state sessile stigma has only three parallel origins.

In a next stage this lineage diversifies into the two other stable subsets; those around *A. frutescens* (node 95) develop the clavate staminate inflorescence and characteristic globose fruits with thick pericarp and sunken stigma and the sistergroup, node 96, gets longer and more staminate inflorescences and occasionally present petaloids. Among the above-mentioned characters are many with relative high CI, that were already discussed in paragraph 9.2, e.g., stipule shape, type of staminate and pistillate inflorescence, and stigma attachment. So, both the group itself as well as the relationships among the taxa seem reliable.

However, the dichotomous relationships in the *frutescens*-group are not amplified by the distributions of the species: many are widespread on Sundaland. Species with more local distributions are: *A. chondroneura*, *A. sarawakensis*, and *A. nitida* widespread on Borneo; *A. fulvovittata* only above 1000 m altitude on Mt Kinabalu and its surroundings; *A. stenostachys* only along rivers in Sarawak; and *A. banahaensis* in the Philippines. *Aporosa quadrilocularis*, *A. stellifera*, and *A. whitmorei* are restricted to the Malay Peninsula and Sumatra.

With such distributions it can only be concluded that if there has been allo- or parapatric speciation, the original vicariant pattern has been obscured by later dispersal events: a dispersal at the base from Malay Peninsula/Sumatra (*A. whitmorei*) to Borneo (*A. chondroneura*) and widespread (*A. prainiana* and *A. symplocoides*, possibly in sympatry), which is repeated in the more derived groups, i.e., the four species with the clavate inflorescences and the sistergroup of this latter. This makes it impossible to design an argued evolutionary pathway for the complete group or any one of its subsets. The only possible conclusion is that the basis for this group has most likely been on Sundaland.

Patterns in the benthamiana-group

The *benthamiana*-group, node 122, is the most characteristic group within *Aporosa* with the disc-like glands regularly set along the margin, the peduncled brush-like staminate inflorescence, the pistillate flowers that are set only apically and have long, smooth, directly connected, stigmas flattened to the ovary. All these are synapomorphies with high CI and RI and without reversals in the group. The apical setting of the pistillate flowers is even unique within *Aporosa*. The conclusion may be drawn that the support for this group is strong.

However, when looking at the support for the relationships within the group, all three subnodes within the *benthamiana*-group, nodes 112, 103, and 94, have much fewer character changes, viz., four each. These relationships are thus not so robust as the group itself. *Aporosa benthamiana*, *A. falcifera*, and *A. lunata* are widespread in Sundaland. *Aporosa bullatissima* and *A. sylvestri* occur in Sarawak. This part of Borneo is known to have a high percentage endemic species and a complex geological history (Ridder-Numan, 1996). Thus both may have descended independently from local populations of *A. lunata*. This should have yielded a polytomy in the cladogram. But since the support for the pair *A. lunata*–*A. sylvestri* is of low quality it may be interpreted that these two evolved by multiple speciation.

Since the splitting sequence of the three other species, *A. benthamiana*, *A. falcifera*, and *A. lunata*, is not very reliable, it is tricky to hypothesize any evolutionary model for them or for the origin of the group. All three are widespread among the greater Sunda Islands. It is, however, noteworthy that each of the three widespread species reaches a different geographic outskirt: *A. benthamiana* into the South Philippines, *A. falcifera* into North Sulawesi, and *A. lunata* into West Java. Its possible sistergroup, the *papuana*-group, occurs on New Guinea. The Tertiary Arc System (De Boer, 1995) is one of the supposed pathways for dispersal from Malesia to New Guinea, and runs from the Philippines, over North and East Sulawesi to North New Guinea.

If the splitting sequence in the cladogram for the *benthamiana*-group is accurate, *A. falcifera* is the oldest and *A. lunata* the youngest. This might indicate an origin for the group on the northern part of this arc system, represented nowadays by the Minahassa Peninsula of Sulawesi and the South Philippines. From here they spread into Malesia. Its sistergroup was present on the southern part of the arc system and spread into New Guinea.

Patterns in the octandra-group

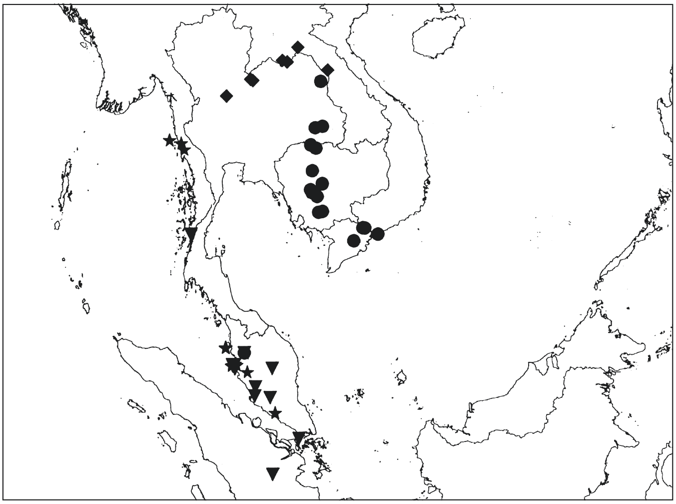
The last monophyletic group, the *octandra*-group, node 126, is supported by 9 changes, of which 6 have a high CI and RI in both the complete analysis as well as in the subanalysis of the second clade (Table 9.1). The continuous staminate inflorescence is unique among *Aporosa* and has no reversals; the free staminate sepals are also unique but have three reversals within the group; the pubescent septae and columella is unique if *A. bourdillonii* is placed within the *octandra*-group. These three characters support together with the not unique and not always present symmetric stipules, small basal glands, and scattered disc-like glands the *octandra*-group.

Within the *octandra*-group, four subsets were stable in most of the phylogenetic analyses: the five species around *A. aurea*, the set formed by *A. nigricans* and the four varieties of *A. lucida*, the subgroup around *A. octandra*, and the subgroup around *A. globifera*. Of these four, the last three, viz. the pair *A. lucida–A. nigricans*, the subset formed by *A. fusiformis*, *A. latifolia*, *A. yunnanensis*, *A. wallichii*, and *A. octandra*, and the group around *A. globifera* are supported by characters of low CI and it can be said that the support for these groups is not adequate. However, the group around *A. globifera* without *A. villosa*, node 109, is supported by three characters with high CI and RI; one of them is the regular occurrence of hairy marginal glands, which is a unique character within *Aporosa*.

The group formed by *A. planchoniana*, *A. lanceolata*, *A. aurea*, *A. tetrapleura*, and *A. symplocifolia*, node 107, is also supported by three 'good' characters, viz., the glabrous staminate sepals and the glabrous, ascending pistillate sepals. The striking yellowish drying glabrous leaves of this group are shared at a lower level, i.e., including *A. lucida* and *A. acuminata*. The distinct basal glands are not really distinct in *A. symplocifolia*, which results in a parallel of distinct basal glands for *A. tetrapleura* and the pair *A. aurea–A. lanceolata*. This is, of course, a result of using delayed transformation for optimizing the character transformation series. Choosing distinct basal glands as support for node 98 would have been just as parsimonious.

Concluding it can be said that of the four subsets mentioned, only the five species around *A. globifera* and the five species around *A. aurea* form well-supported groups. Only for these two subsets the modelling of speciation patterns may be attempted.

The distribution of the first subset, *A. globifera*, *A. pseudoficifolia*, *A. macrophylla*, *A. serrata*, and *A. ficifolia*, is given in Map 9.1. There is no overlap in the distributions; even though *A. globifera* and *A. pseudoficifolia* occur both in the West Malay Peninsula, they are ecologically separated: *A. pseudoficifolia* keeps to higher altitudes than *A. globifera*. It seems possible that a classical case of vicariance is represented: iso-

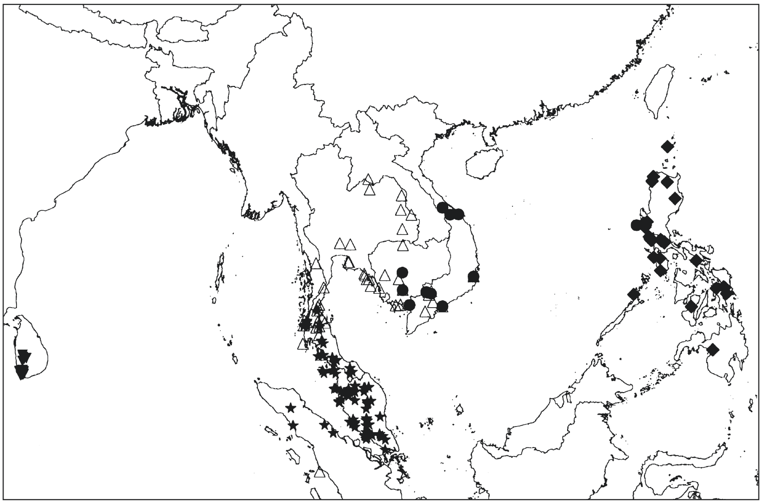


Map 9.1. Vicariant distribution patterns for *Aporosa ficifolia* Baill. (●), *A. globifera* Hook.f. (▼), *A. pseudoficifolia* Pax & K. Hoffm. (★), and *A. serrata* Gagnep. (◆).

lation of a widespread ancestor and allopatric speciation of its decendants in time through geological or climatological barriers. The first split is the separation into a western and eastern group: the ancestor of *A. globifera*, *A. pseudoficifolia*, and possibly *A. macrophylla*, and the ancestor of *A. ficifolia* and *A. serrata,* respectively. The presence of the polytomy does not influence the support for this separation: *A. ficifolia* and *A. serrata* share in all scenarios the most recent ancestor. It is difficult to pinpoint a cause for the separation: it may be that the initiation of a dry monsoon was buffered by the rivers. The ancestor of *A. ficifolia*/*A. serrata* was restricted to the Mekong valley; the ancestor of *A. globifera*/*A. pseudoficifolia*/*A. macrophylla* occurred in the area near the Indian Ocean. The species slowly retracted from the mountains in North Thailand. Later, with the monsoonal climate driving the rain forest southward, the separation between on the one side *A. ficifolia* and *A. serrata* and on the other side *A. pseudoficifolia* and *A. globifera* took place.

The place of *A. macrophylla* does not fit into this vicariancy scenario. Its position in the phylogenetic reconstruction is ambiguous, as is any timing for its isolation from the rest of the *globifera*-subset. *Aporosa macrophylla* is endemic to the Rangoon delta and may have been formed in the periphery of the distribution of the ancestor of *A. ficifolia*/*A. serrata*. A long isolation may account for the autapomorphic features.

The group with the five species around *A. aurea* shows another good example of a possibly vicariant speciation pattern (Map 9.2). The first to split is *A. planchoniana*, which occurs widely in Indochina and Thailand. This is the central distribution of the group. The other four species occur in the peripheries of the distribution areas of this species: two groups are present, the *A. symplocifolia*/*A. tetrapleura* ancestor that lived east of the central *A. planchoniana*, and the *A. aurea*/*A. lanceolata* ancestor west of *A. planchoniana*. In a later vicariant event the north-south distinction became evident: *A. tetrapleura* speciated in South Indochina. This might correspond with the vicari-



Map 9.2. Vicariant distribution patterns for *Aporosa aurea* Hook.f. (★), *A. lanceolata* (Tul.) Thwaites (▼), *A. planchoniana* Baill. ex Müll.Arg. (△), *A. symplocifolia* Merr. (◆), and *A. tetrapleura* Hance (●).

ance event that separated *A. ficifolia*. Meanwhile, *A. symplocifolia* developed in the northern Philippines. This indicates a connection between Indochina and the northern Philippines. *Aporosa symplocifolia* could have reached the Philippines over Taiwan to Luzon, of which its presence in the Bataan province might be supportive. Another possibility is by way of Palawan, where *A. symplocifolia* is also found, when it was drifting south along with the opening of the South China Sea.

The western species, the ancestor of *A. aurea–A. lanceolata* shows a similar pattern. It speciated in isolation from its *planchoniana*-like parent. It is possible that this ancestor had a larger distribution, maybe reaching over all of the mainland. Later, one line dispersed southward to Malesia and another spread to Sri Lanka, possibly via the Sumatra–Andaman–Nicobar pathway or from Sumatra directly to Sri Lanka when the Indian plate drifted by (see also Ridder-Numan, 1996).

With the biogeography of the subsets of the *octandra*-group described, the origin and spread of the group itself remains to be investigated. Judging from the distributions of its hypothesized sistergroup, the *maingayi*-group, it is probable that the ancestor to both groups originated somewhere on the Malay Peninsula. When a land connection established from here to Thailand, e.g., when the Isthmus of Kra became again passable in a cooler era, the *octandra*-group took possession of Asia, while its sister, the *maingayi*-group, remained in the Malay Peninsula. Along with this conquest of Asia the new species formed in the *octandra*-group. But when and where is impossible to judge from the relationships in the cladogram.

One further point should be mentioned. The four varieties of *A. lucida* as well as of *A. octandra* are characterized by very few changes. *Aporosa lucida* var. *lucida* and *A. octandra* var. *octandra* even have no changes at all. These may be cases of surviving ancestors, resulting in natural polytomies in the cladogram. The choice for describing them as varieties is hereby phylogenetically corroborated.

Subsets in the maingayi-group

The sistergroup of the *octandra*-group, the *maingayi*-group, has three stable subsets, viz., the subset consisting of *A. subcaudata* and *A. spec. F*, node 121, the pair *A. elmeri–A. rhacostyla*, node 120, and the set starting with *A. alia*, node 119.

The subset formed by *A. subcaudata*, its two forms, and *A. spec. F* (node 121) is rather well supported by 10 changes, four with relatively high CI. However, two of these are shared with *A. penangensis* and may be 'false' parallels, and the remaining two, viz., an emarginate-truncate leaf base and rather long stamens, are not the type of character one expects to have any importance in defining relationships. It may indicate that the difference between the four taxa is not above the species level. The fact that there are also very small differences between *A. subcaudata* and its two forms, suggests the same. This leads to a speciation model of one widespread species, with diverging populations at its boundaries. The polytomy is then a natural one. The form of *A. subcaudata* from Andulau (Brunei) with small leaves has no apomorphies at all, suggesting that the character set of this taxon represents the ancestral combination.

The pair *A. elmeri–A. rhacostyla*, node 120, is also present in all analyses. It is supported by 17 character state changes, which makes it the longest and one of the best supported nodes in the cladogram. But how should such a good support be interpreted? *Aporosa rhacostyla* is only slightly different from *A. elmeri*; it has only five apomorphies. Thus it may be that most of the changes result from diversification of a small population of the ancestor of *A. elmeri* in Sabah, where isolation and geological activity or ecological segregation resulted in speciation. *Aporosa rhacostyla* might be interpreted as a recently evolved local form.

The last stable group within the *maingayi*-group is formed by node 119, consisting of *A. alia*, *A. granularis*, *A. maingayi*, and *A. microstachya*. Six changes support this node. Two changes are shared with the *elmeri*/*rhacostyla*-pair and one with *A. penangensis*, leaving only three 'true' apomorphies. One of these, the synapomorphy of character 29 state 3, glomerules spaced only at the base, has few parallels within the genus and can be considered to be adequate.

The distributions of the four species show a biogeographically frequently found pattern. The ancestor inhabited the Sunda Shelf. With the rising sea level, Borneo is separated from the Malay Peninsula and Sumatra. *Aporosa granularis* evolves as a result. Next, a possibly ecologically induced diffusion occurs between the northern and southern specimens on the Malay Peninsula and Peninsular Thailand. This pattern is still in effect to keep the species distinct in overlapping areas: the more northern taxon, *A. microstachya*, keeps to the higher hill tops and ridges, while the southern *A. maingayi* remains abundant in the valleys. There is also a difference in flowering time[1]. This pattern with a basal split for Bornean species, followed by diversification between species on the Malay Peninsula is a very common one (e.g., Schot, 1991; Ridder-Numan, 1996). It is also found in the *benthamiana*-group, and the three topmost subsets of the *frutescens*-group.

The only problem is how to fit in *A. alia*; it does not directly fit this vicariance pattern. But it is possible, as its position in the cladogram suggests, that it split from the

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1) Personal observations in Pasoh and elsewhere of J.V. LaFrankie.

widespread Sundanese ancestor before the isolation of Borneo. Its speciation is then explicable as instigated by the very same changing environment of Borneo, which has resulted in other Bornean endemics (e.g., Van Welzen, 1989).

The nervosa/brevicaudata agglomeration

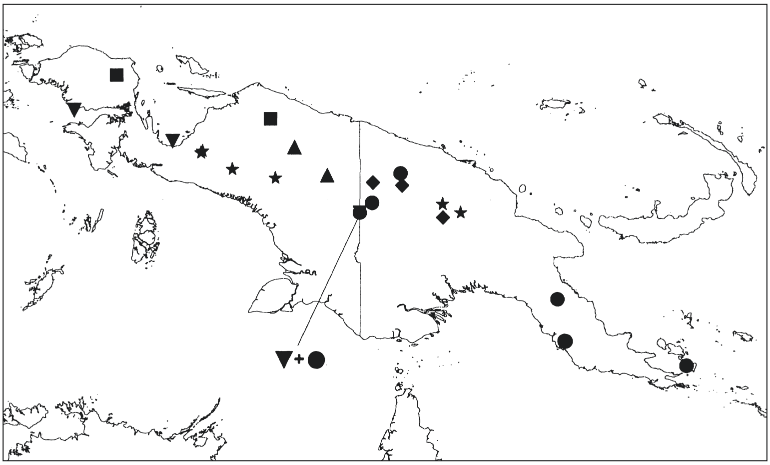
The last subsets of species to be studied are the two stable groups in the polytomy of the second lineage, viz. the *nervosa*-group, node 136, and the *brevicaudata*-group, node 137.

The *nervosa*-group is supported by 12 changes. Of these 12, only one, the staminate flowers with connate sepals, may be counted as 'good' support for the group. This is, considering the position of this group in a polytomy, rather meagre and because no sistergroup relations are to be deduced from the polytomy, no evolutionary model is made for the *nervosa*-group, despite the fact that it was present in most analyses.

The other subset, consisting of the four New Guinean taxa in the *brevicaudata*-group, has 14 changes; two of these represent unique states within *Aporosa*: the entirely pulvinate petiole and the tiny leaves. Both characters are reversed in *A. egregia*.

Two further New Guinean species are present in the polytomy of the second lineage: *A. nigropunctata* and *A. longicaudata*. They share four character changes among each other and respectively one and three character changes with the *brevicaudata*-group. The one character change shared by *A. nigropunctata* and the *brevicaudata*-group is also present in the *nervosa*-group. If this is tentatively taken as indicative, a speciation pattern might be modelled where an ancestral *Aporosa* species, possibly sister to the ancestor of the *nervosa*-group, colonized New Guinea and speciated.

The distribution of the six New Guinean species of the second lineage is given in Map 9.3. *Aporosa nigropunctata* and *A. longicaudata* are lowland species, the species around *A. brevicaudata* are found at altitudes above 1000 m. The scenario for this group could be a dispersal of a lowland species, followed by speciation with the uplifting of



Map 9.3. Vicariant distribution patterns for *Aporosa brevicaudata* Pax & K. Hoffm. (★), *A. egregia* Airy Shaw (■), *A. longicaudata* Kaneh. & Hatus. ex Schot (▼), *A. nigropunctata* Pax & K. Hoffm. (●), *A. parvula* Schot (▲), and *A. sclerophylla* Pax & K. Hoffm. (◆).

the land: the ancestor is represented by the basal species *A. nigropunctata*. It arrived on New Guinea via the Vogelkop and reached into Sepik. When the central mountains formed during the various stages of accretion, the mountainous species evolved. *Aporosa sclerophylla* evolved in the eastern highlands; in the western part *A. egregia* and *A. brevicaudata* diversified. The position of *A. parvula* is ambiguous: it may either have evolved from *A. sclerophylla* or from *A. brevicaudata*. The species that remained in the lowlands evolved into *A. longicaudata* in the east and *A. nigropunctata* in the west.

Comparable speciation patterns were found by Van Welzen (1989) and Vermeulen (1993). In some other cases New Guinea is only seen as a means to disperse from the west to the east (De Boer, 1995) or vice versa (Turner, 1995). It may be that these dispersal events took place in a more recent time than the establishment and speciation in *Aporosa*.

9.3.3 – ***Evolutionary processes as explanation for the ambiguity***

Next to the stable (monophyletic) groups the phylogenetic reconstruction of *Aporosa* yielded much ambiguity. Though speciation models based on phylogenetic relationships are unavailable for these taxa, it is not impossible to contrive evolutionary hypotheses based on other theories.

The question to be considered is what could have caused so much controversy in the data. There are a number of possible hypotheses. One of these is that new species do not yet have enough discriminating characters for phylogenetic analysis. Though this is very much true for *Aporosa*, as evidenced by the low number of characters, this should mainly effect the relationships of the younger taxa, i.e., those at the top end of the cladogram. It explains the ambiguity in, e.g., the *octandra*-complex and among the varieties of *A. lucida*. However, these few top end polytomies have no influence on the basis. Here something different seems to be clouding the outcome of the phylogenetic analysis.

Incompletely known taxa may be another factor causing ambiguity in phylogenetic studies (e.g., Wilkinson, 1995). However, it was shown in paragraph 8.4.2 that excluding these rather increased than decreased the ambiguity. Thus it would not be logical to suggest these as a cause for the controversy.

A third possibility that may entangle the phylogenetic reconstruction is the occurrence of hybrid speciation. The possibility of hybridization as a major factor in plant evolution has been recognized and advocated (Gallez & Gottlieb, 1982; Stebbins, 1985; Potts & Reids, 1988). Hybridization as speciation mode is evolutionarily plausible when new, different habitats need to be colonized. It is speculated that hybridization is adaptationally advantageous in changing habitats. According to Arnold & Hodges (1995) hybrids are not necessarily less fit, but depending on genotypic classes they have a lower, equal or higher fitness relative to their parents. Arnold (1992) suggested a prominent role for natural hybridization in numerous species complexes. He provided examples of plants and animals with apparent reticulate events in their phylogenies. Knobloch (1972) also argued that hybridization can be adaptive, and gave about 40 examples of known hybrids in Euphorbiaceae.

But hybrids have always been a source of trouble in phylogeny and in natural classification schemes. A phylogenetic analysis, which only assumes dichotomous splitting between species, cannot be used to analyse reticulate evolution. Skála & Zrzavý (1994) reviewed the literature on how phylogeneticists recognize and deal with reticulating patterns. They found no consensus. According to Wanntorp (1983), hybrids share the apomorphies of both parents and will be placed near the most derived parent. Funk (1985) described how hybrid taxa are defined mostly by character conflicts or reversals. They may be spotted in a phylogenetic analysis because they swap position between the parental species, causing multiple solutions. In McDade's (1992) experiments, hybrids disrupted the patterns between the parents only if they were hybrids of two distantly related species.

Hybrids are not necessarily intermediate (Wagner, 1983). According to Rieseberg & Ellstrand (1993) the characteristics of hybrids are unpredictable. Rieseberg (1995) described hybrids as a mosaic of parental, intermediate, and novel characters. Character coherence is exceptional. In view of this, an ambiguous pattern is not surprising. Hybrids express characters and phylogenetic patterns in unpredictable ways and no rules can thus be formulated on how to deal with them. I have as yet not found any suitable computer program for calculating hybrid relations. Alroy's (1995) Continuous Track program and Bandelt's networks (1994), as well as the program RETICLAD by Morefield (Rieseberg & Morefield, 1995) all need known parents to start with. Furthermore, none of the programs mentioned allow for unordered multistate characters. The best option is still to exclude them from phylogenetic analysis.

In *Aporosa* the exclusion of the intermediate New Guinean taxa restored much of the phylogenetic pattern; it is these taxa that come to mind when supposing hybrid speciation or introgression. Primitive, exceptional, and intermediate characters are scattered among the intermediate New Guinean taxa without any apparent cohesion in the combinations. Examples of both intermediate and exceptional characters are given in Table 9.2. As listed there, generic, and sometimes even familial characters are breaking down.

New Guinea is geologically active. Drifting fragments are accumulated to the northern edge, accompanied by the forming of mountains and basins (Pigram &

Table 9.2. Examples of exceptional and intermediate characters in some New Guinean species.

species	exceptional character: found further in	intermediate character
A. egregia	fusiform fruits: *A. fusiformis*	
A. annulata	hairy ring at base of column: ?	ovary 2- and 3-locular
A. laxiflora	many large disc-like glands: *A. benthamiana*	glomerules widely spaced, pistillate flowers more densely set
A. brevicaudata	petiole short, completely pulvinate: *Antidesma, Drypetes*	
A. ledermanniana	sometimes branching inflorescences: New Guinean *Antidesma*	ovary 2- and 3-locular
A. carrii, subhermaphroditic form	distinct pistillodes: *Baccaurea, Antidesma*	
A. praegrandifolia	8 stamens: *Baccaurea, Ashtonia*	sessile flowers and long pedicelled fruits
A. hermaphrodita, A. heterodoxa	functionally hermaphrodite flowers: Flacourtiaceae	

Davies, 1987; Vermeulen, 1993). New environments are created and modified constantly. If hybrids are expected to form in unstable environments, New Guinea is a plausible candidate to contain hybrid complexes.

The strict consensus cladogram of the analysis with the intermediate New Guinean taxa excluded showed the remaining New Guinean taxa clustered in two clades (Fig. 8.3), one as sistergroup to the *benthamiana*-clade, the other among the basal polytomy of the second lineage. If this pattern is tentatively taken as a basis for a possible evolutionary pathway, it might be hypothesized that these two clades colonized New Guinea at different times or by different routes and their renewed meeting effected the emergence of the disruptive character combinations. This was already suggested in the forgoing paragraph: the *papuana*-group might have originated somewhere on the Tertiary Arc system, and from there reached the Sepik side of New Guinea. The *brevicaudata*-group might have dispersed over the Sunda Arc, reaching New Guinea via the Vogelkop. As shown in Schot (1998) the distributional patterns of both these supposed parental clades as well as the distributions of the putative hybrid taxa do not disrepute this hypothesis: the *papuana*-group is mostly concentrated in north New Guinea and the species around *A. brevicaudata* are concentrated in the central mountains and the easterly and westerly adjacent lowlands. The distribution of the putative hybrid species ranges from Sepik, the western part of the Central mountain range and the adjacent lowlands, and in the Owen Stanley range of the Papuan Peninsula southwards into the Papuan Islands.

The geological possibility to reach New Guinea from different sides is also present (Schot, 1998). Both the pathway to north New Guinea along the Tertiary Arc system as well as the dispersal route to south New Guinea along the Sundanese Islands have been used by other species (Van Steenis, 1979; De Boer, 1995).

Yet, even if a renewed contact of two separate lineages of *Aporosa* produced the emergence of the particular character combinations of the intermediate New Guinean taxa, another hypothesis is needed as explanation for the ambiguity in the west Malesian taxa. The west Malesian taxa in the polytomies of Fig. 8.7 do not have a mosaic of primitive, derived and exceptional characters. Also, excluding them from the analysis did rather increase the ambiguity than decrease it (paragraph 8.4.3). Evolution has seemingly followed a different path in West Malesia.

If exclusion of taxa increases the ambiguity, it might mean that the information in these taxa is necessary to solve the relationships. However, since even with these taxa the pattern cannot be completely solved, possibly there is too little information contained in them. Thus there may be some information missing, or an incomplete sampling of the data might have occurred.

One possible bias that may produce incomplete data at the base of a phylogenetic cladogram, is analysis of a paraphyletic group, in which more derived descendants have been placed in another taxon and are thus excluded from analysis. Considering the other genera in the *Scepinae*, this hardly seems appropriate for *Aporosa*. A second cause of paraphyly may be the extinction of the basal taxa.

Extinction is a consequence of evolution. Characters change and with it the species alter. A new species descends from its ancestor, which then, by definition, becomes extinct. If this process takes place gradually the extinct ancestors are reconstructed in the phylogenetic analysis. However, it is also possible that evolution proceeds from a relatively quiet time to a rapid emergence of new characters. This process with alternating periods of no change and rapid change is known as punctuated equilibrium (Eldredge & Gould, 1972). In such a quick diversion of new taxa the intermediates at the base leave no offspring and thus too little evidence on which to model phylogenetic hypotheses (Brooks & McLennan, 1991).

Little is known of the effect of rapid changes in combination with extinction without leaving offspring on reconstructing phylogenies. Theoretically the absence of extinct taxa from a phylogenetic analysis might produce an effect similar to the analysis of a paraphyletic group. When analysing paraphyletic groups, it is not possible to arrive at a correct cladogram. The information contained in the excluded taxa is needed to solve the relationships at the root of the tree sufficiently. Donoghue et al. (1989) and Novacek (1992) studied the effect of including fossil taxa into a data set of extant taxa. They showed how in some cases the addition of the 'missing links' brought new combinations and different relations for the root of the extant clade. However, no fossils are known for *Aporosa*, and I cannot include them in the analysis. This is, however, no excuse to assume that no swift periods of evolution have taken place in *Aporosa*. Rapid changes may be induced by changes in the climate followed by shrinkage and re-expansion. Enough fluctuations in the climate and alterations in the configuration of the land in Southeast Asia have occurred through time to argue the possibility of this process.

If there have been rapid changes and extinctions in *Aporosa* somewhere in the past, resulting in paraphyly at the base, some circumstantial evidence might be present. Two patterns have been said to possibly indicate extinction: the presence of taxa with many synapomorphies (Donoghue et al., 1989; Novacek, 1992) or with disjunct distributions (e.g., Van Steenis, 1979). Both are in some measure present in the taxa that form the basal polytomies of Fig. 8.7.

The polytomy at the base of the first clade, node 44, contains the taxa around *A. arborea*, the ancestor of the *frutescens*-group, and the ancestor of the *benthamiana/papuana*-clade, which may be represented by *A. leytensis*. The *frutescens*-group and the *benthamiana*-group are characterized by relatively many synapomorphies (paragraph 9.3.2). In addition, their basal taxa occur respectively on the Malay Peninsula and the Philippines. Borneo is only populated by the more derived taxa. This might point to a hypothetical ancestor once connecting the two clades on Borneo, e.g., a taxon from the group around *A. arborea*. The two monophyletic groups have since that time changed so much that their relationship can now no longer be reconstructed on the character combinations of the remaining species around *A. arborea*.

The polytomy at the base of the second clade, node 43, is formed by *A. antennifera*, *A. caloneura*, *A. dendroidea*, *A. duthieana*, *A. longicaudata*, *A. nigropunctata*, *A. spec. G*, and the ancestors of the *nervosa*-group, the *brevicaudata*-group, and the *maingayi/octandra*-clade. Among these taxa some special features occur, e.g., the long stigmata of *A. antennifera* or the completely pulvinate petiole of the *brevicaudata*-group, but these are not really distinctive. The distributions show, when considering the group as a whole, a rather disjunct pattern: the greater Sunda Islands are well presented (*A. antennifera*, *A. maingayi*, *A. nervosa*), but the farther away, the more patchy the populations (*A. caloneura, A. dendroidea, A. duthieana*, *A. sphaeridiophora* var. *campanulata, A. spec. G*). Furthermore, no species are connecting the New Guinean branch, *A. nigropunctata*, *A. longicaudata*, and the ancestor of the *brevicaudata*-group, with its West Malesian counterpart. A scenario to explain this pattern might be as follows: the ancestor of the second clade may have reached from Thailand to the Philippines and via the Sunda Islands to New Guinea. Within this group a climatic event – possibly drought – arose to split the species and reduce and isolate its representatives in the less inhabitable areas.

The second polytomy of the second lineage, node 134, consists of *A. bourdillonii*, *A. lagenocarpa*, *A. selangorica*, the ancestor of the *maingayi*-group, and the ancestor of the *octandra*-group. The first three species mentioned all have very local distributions and special features: *A. bourdillonii* has a curious ornamentation of the ovary and is endemic to Kerala, *A. lagenocarpa* has typical flask shaped fruits and is found only in Sabah and Sarawak, and *A. selangorica* has also a distinctive but different ornamentation of the ovary and is present only in the western provinces of the Malay Peninsula. The *octandra*-group is also represented by relatively many synapomorphies and is almost the only group to have spread to the mainland of Asia. Only the last, the *maingayi*-group, does not possess any special features. This group might harbour the ancestors to the other four: some conquered Asia and others evolved rapidly in isolated places. However, the differences with these more derived clades have grown now too large to give any clue to how and when.

Considering the complete pattern found in the phylogenetic reconstruction of *Aporosa*, it can be said that many defects are present in the method practised. If hybridization is as common a phenomenon in nature as some advocate, then some of the mentioned irregularities in New Guinea may be caused by a mixing of the species boundaries. And if hybridization is, at least in plants, such a common evolutionary process, cladists should give more attention to the possible presence of hybrids. To quote Rieseberg & Ellstrand (1993): “plant phylogenists must come to grips with the reality of reticulate evolution in many plant groups and the unpredictability of phenotypic characters in terms of inheritance and expression in hybrids”.

If, on the other hand, the assumption that geological activity and fluctuations in the climate in the past have caused unreconstructable patterns due to rapid evolution in combination with extinctions is true, phylogeneticist should also keep in mind the possible bias caused by incomplete sampling. Only analysis of truly monophyletic groups, i.e., groups with all ancestors extant or reconstructable, may result in accurate phylogenetic predictions.

If such processes are really as common as some suppose, the usability of cladistic analysis as we know it now declines. The parsimony algorithm seems only suited to analyse small, recent groups that have evolved along strictly dichotomous evolutionary pathways and where all or most species are known or can be reconstructed. This could mean that the many tests designed not to go beyond 50 taxa have some truth in it: beyond so many taxa too many non-applicable events may have taken place through time to make the characters unsuitable for phylogenetic analysis by the parsimony algorithm. Partition of such a set into subsets, of, say, a maximum of 30 or 40 taxa is needed.

This study shows an example of how a large group can be partitioned into smaller sets using testing and consensus techniques. The shown basal relationships of such a group must then be treated with doubt and paraphyletic tails not immediately to be believed paraphyletic. One should allow ambiguity and polytomies, and accept that only part of the pattern may be accurate. I think that we should learn to live with the fact that not all speciation processes can be found. To strive for fully resolved dichotomous cladograms from the root to the top is utopian.

New algorithms should be developed to incorporate other modes of speciation than the vicariant allopatric speciation model. May this study serve as an example that a vast area of investigation into the origin of species is still unthreaded. We are far from understanding even a tiny piece about the biodiversity of the earth.

With this thought I conclude the discussion of possibly evolutionary pathways to explain the patterns found in the phylogenetic analysis. Next, the last application of the phylogenetic analysis is discussed: an infragenetic classification.

9.4 – **Infrageneric classification of Aporosa**

The last application of the selected cladogram is the provision of a natural infrageneric classification into sections. Natural was equated with monophyletic by Hennig (1966) and since then it has been advocated not to accept paraphyletic and polyphyletic groupings of taxa, but only the monophyletic groups found by a cladistic analysis.

However, in *Aporosa* defining sections purely on the outcome of the phylogenetic analysis meets various difficulties. The most obvious one is that the phylogenetic reconstruction ended with part of the New Guinean taxa excluded. The problem is how to classify these. In theory, a monophyletic group consists of an ancestor and all its known descendants. There are no clues in the phylogenetic analysis to propose an ancestral clade for the excluded New Guinean taxa. Classifying all New Guinean taxa into one section would be practical, but the probability that such a section would be monophyletic is low.

There are two options. The first is not to give an infrageneric classification at all. However, what should be done with the old one? Pax & Hoffmann (1922) distinguished two sections: 1) section *Euaporosa* divided in three subsections: a) subsection *Grandistipulosae*, consisting of species with falcate stipulae; b) subsection *Gymnogynae*, consisting of species with glabrous ovaries; c) subsection *Trichogynae*, consisting of species with hairy ovaries; and 2) section *Appendiculatae*, containing the two species with sculptured ovaries, *A. bourdillonii* and *A. selangorica*.

The macromorphological delimitation of these sections already proved to be problematical (cf. Airy Shaw, 1971). For example, the *Grandistipulosae* originally contained the species with persistent falcate stipules, but not those with rather persistent, oblique stipules. The *Trichogynae* blend gradually into the *Gymnogynae* since species like *A. lucida* or *A. hermaphrodita* have both glabrous and sparsely puberulous ovaries. And Pax & Hoffmann's second section, *Appendiculatae*, is nothing else but an artificial grouping of species with 'special' ovaries, the ruminate-verrucate *A. selangorica* and the tuberculate *A. bourdillonii*. In addition, the phylogenetic reconstruction of *Aporosa* has also shown that this classification is unnatural.

Therefore, this classification cannot be used any longer. To simply reject the old classification without giving a new one is unsatisfactory and unnecessary, because a better classification is possible, at least for part of the taxa: the three monophyletic groups are phylogenetically and morphologically distinct and deserve to be distinguished. Description of distinct monophyletic clades into well-defined entities adds to the predictability and stability of the classification of the genus in question and should at least be attempted.

However, the option of creating an infrageneric classification raises the question what to do with the taxa that do not fit into the three monophyletic clades. According to Wiley (1981) in cases where the phylogenetic analysis yielded distinct monophyletic groups it is possible, as was done in evolutionary taxonomy before cladistics was invented, to form paraphyletic groups at lower levels (see also references in Sosef, 1997). This example will be followed here.

The proposed sectional classification is as follows: the three monophyletic groups, the *frutescens*-, *benthamiana*-, and *octandra*-group can be directly classified as sections. These groups are accepted because of their monophyly. Their main macromorphological characteristics are the different types of staminate and pistillate inflorescences (Fig. 3.5 and 3.6) and the position of the foliar glands (Fig. 3.3).

The paraphyletic tail consists of the two larger paraphyletic components, three smaller paraphyletic components, some small monophyletic groups containing 2 taxa each, all remaining taxa of ambiguous placement, and the excluded New Guinean taxa. Though these components exist as an entity in all analyses, they are not particularly stable or recognizable. Thus there are no morphological characters for further strict division of the paraphyletic remnant. There is, however, a geographical distinction to be made in the remainder: part of the taxa are Sunda Shelf species, others New Guinean. This distinction also solves the question of placing the excluded taxa. As this is the only available character to divide the polymorphic remainder, I have used this as character to delimit the remainder into two, paraphyletic, sections.

This division into a Sundanese and a New Guinean part is rather arbitrary. In the fundamental cladograms with all taxa included, the New Guinean taxa jump around at the base among the Sundanese species. But the division is very convenient. The New Guinean species, as described in paragraph 2.5.2, are deviating. They show different character combinations and have retained more primitive features then the Sundanese species. The main character for the distinction is geographical, but there is also at face value a macromorphological basis, though this basis is hard to describe exactly (see the comments in paragraph 2.5.2).

Using the above criteria, the following sections will be described in paragraph 10.2:

1) section *Aporosa*, containing the taxa in the *frutescens*-group;
2) section *Appendiculatae*, containing the taxa in the *octandra*-group, including *A. bourdillonii*.
3) section *Benthamianae*, containing the five taxa of the *benthamiana*-group;
4) section *Papuanae*, containing all New Guinean taxa and including *A. leytensis*, which was in all analyses placed near the *papuana*-group;
5) section *Sundanenses*, containing the Sundanese taxa of the paraphyletic tail and including the Moluccan *A. dendroidea* because of its morphological likeness; its phylogenetic position near the later excluded New Guinean *A. misimana* and *A. leptochrysandra* is not to be trusted;

PART III

REVISION

Chapter 10

REVISION OF APOROSA

10.1 – **Generic description**

Aporosa Blume

Aporosa Blume, Bijdr. 10 (1825) 514; Fl. Javae 2 (1828) 6; Lindl., Nat. Syst. Bot., ed. 2 (1836) 178; Endl., Gen. Pl. 4 (1837) 282; Baill., Étude Gén. Euphorb. (1858) 643; Miq., Fl. Ind. Bat. 1, 2 (1859) 430; Benth., Fl. Hongk. (1861) 316; Thwaites, Enum. Pl. Zeyl. (1861) 288; Müll.Arg. in DC., Prod. 15, 2 (1866) 469; Kurz, For. Fl. Brit. Burma 2 (1877) 361; Benth. & Hook.f., Gen. Pl. 3 (1883) 282; Fl. Brit. India 5 (1887) 345; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 29; Trimen, Handb. Fl. Ceyl. 4 (1898) 39; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; J.J. Sm., Meded. Dept. Landb. Ned.-Indië (1910) 226; Koord., Exkurs.-Fl. Java 2 (1912) 480; Merr., Enum. Born. Pl. (1921) 330; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 80; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 409; Ridl., Fl. Malay Penins. 3 (1924) 235; S. Moore, J. Bot. Brit. For. 63, Suppl. (1925) 97; Gagnep., Fl. Indo-Chine 5 (1927) 552; Merr., Pl. Elmer. Born. (1929) 141; Pax & K. Hoffm. in Engl. & Prantl, Nat. Pflanzenfam., 2e aufl., 19c (1931) 52; Corner, Wayside Trees Malaya 1 (1940) 235; Worth., Ceylon Trees (1959) 376; Backer & Bakh.f., Fl. Java 1 (1963) 455; Airy Shaw, Kew Bull. 20 (1966) 380; Meijer, Bot. News Bull. Sandakan 7 (1967) 33; Airy Shaw, Kew Bull. 26 (1972) 213; Whitmore, Tree Fl. Malaya 2 (1973) 58; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 30; 8 (1980) 28; Kew Bull. 36 (1981) 252; 37 (1982) 7; Alph. Enum. Euphorb. Philipp. Isl. (1983) 8. — *Aporosa* Blume sect. *Euaporosa* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 81, nom. inval. — *Aporosa* Blume subsect. *Gymnogynae* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 85, nom. inval. — Type: *Aporosa frutescens* Blume.

Leiocarpus Blume, Bijdr. 12 (1825) 581; Fl. Javae 2 (1828) 7; Lindl., Nat. Syst. Bot., ed. 2 (1836) 116; Endl., Gen. Pl. 10 (1839) 1120; Baill., Étude Gén. Euphorb. (1858) 655; Miq., Fl. Ind. Bat. 1, 2 (1859) 362; Fl. Ind. Bat., Suppl. (1860) 178. — Type: *Leiocarpus fruticosus* Blume [= *Aporosa frutescens* Blume].

Scepa Lindl., Nat. Syst. Bot., ed. 2 (1836) 441; Endl., Gen. Pl. 4, 1897 (1837) 288; Tul., Ann. Soc. Nat., Sér. 3, 15 (1851) 254. — Type: *Scepa stipulacea* Lindl. [= *Aporosa octandra* (Buch.-Ham. ex D. Don) Vickery].

Lepidostachys Wall. [Cat. (1832) 6816, nomen] ex Lindl., Nat. Syst. Bot., ed. 2 (1836) 441; Endl., Gen. Pl. 4, 1898 (1837) 288; Tul., Ann. Soc. Nat., Sér. 3, 15 (1851) 253. — Type: *Lepidostachys roxburghii* Wall. ex Lindl. [= *Aporosa octandra* (Buch.-Ham. ex D. Don) Vickery].

Tetractinostigma Hassk., Hort. Bogor. Descr. (1858) 55; Miq., Fl. Ind. Bat., Suppl. (1860) 185. — Type: *Tetractinostigma microcalyx* Hassk. [= *Aporosa octandra* (Buch.-Ham. ex D. Don) Vickery].

Small to medium sized trees, sometimes shrubs, dioecious, no exudate. *Indumentum* of simple, brown hairs only; young branches densely tomentose to glabrous, old ones glabrous; stipules hairy to glabrous; petiole densely tomentose to glabrous; leaf above and beneath densely tomentose to glabrous, beneath often stronger on midrib and nerves. *Branches* terete. *Stipules* just above base of petiole, equal, narrowly triangular to ovate or falcate, persistent or caducous, sometimes lower surface along the margin with hollow or black disc-like glands. *Leaves* alternate, simple; petiole terete or flattened, often slightly grooved or ridged, pulvinate at base and apex (entirely so in *A. brevicaudata* and *A. parvula*), lower pulvinus sometimes indistinct, upper pulvinus larger; blade (narrowly) ovate to (narrowly) obovate; base symmetric, cordate to attenuate, occasionally with two basal, adaxial glands, black to brownish grey spots or hair tufts; margin mostly (lowly) undulate to (lowly) glandular-crenate, sometimes glandular-serrate, glandular-dentate, or (sub)entire, often with distinct glands at ends of thickened venule endings in margin or abaxially submarginally, black to grey or hairy, few to many; apex acuminate to caudate; lamina thick to thin, shiny to dull, sometimes brittle, smooth, sometimes bullate or irregularly lowly granular (regular white granules in *A. chondroneura*), dark to mid-green above, dull or shiny, paler beneath and colouring upon drying greyish, brownish, greenish, bluish, or yellowish (in the aluminium accumulating species) on both sides, or discolorous, in dried condition often (densely) covered with (fine) black to grey dots above, sometimes fading with age, disc-like glands sometimes present beneath, scattered within the marginal arches or at some distance from the margin, brownish or blackish in dry leaves. *Nervation* pinninerved, raised to sunken above, raised to flat beneath; nerves ascending, in species with cordate bases the first pairs at first descending, anastomosing with often distinct arches at some distance from the margin; veins and venation distinct or indistinct, forming a densely or laxly reticulate or (slightly) scalariform pattern. *Inflorescences* simple spikes (seldomly few-branched in *A. ledermanniana*), axillary or just beneath the leaves, sometimes borne on the branches, single to many clustered together; rachis short and thick to long and slender, densely tomentose to subglabrous, usually (light) yellow or greenish (purplish in *A. quadrilocularis*); staminate glomerules and pistillate flowers spirally arranged, either laxly to densely spaced along the rachis, or concentrated or only at apical end and then peduncle present; bracts 1 for each staminate glomerule or pistillate flower, small, often caducous or large, conspicuous and persistent, (broadly) triangular, densely tomentose to glabrous outside, glabrous or only hairy at base inside, margin often ciliate. *Flowers* unisexual (all bisexual in *A. hermaphrodita* and *A. heterodoxa*, and some in *A. brevicaudata* and *A. egregia*), small, slightly fragrant; sepals 3–6, connate at base only to c. halfway, hairy to glabrous; petals absent; disc absent. *Staminate flowers* white, or creamish to yellow or yellowish green, sometimes slightly reddish; few to many together in dense or lax globose or ellipsoid glomerules; pedicel absent or up to 1 mm long; sepals (narrowly) obovate to spathulate; stamens 2–4 (up to 6 in *A. fulvovittata*, up to 8 in *A. praegrandifolia*), episepalous, not to strongly exserted; filaments free, glabrous, white(ish); anthers with 2 thecae, dorsoversatile, ellipsoid to subglobose, latrorsly longitudinally dehiscent, glabrous, whitish to (pale) yellow-(brown), connective sometimes sparsely hairy; pistillode absent or minute, then a hair tuft or cylindrical, often apically lobed. *Pistillate flowers* solitary, white to creamish to pale or bright yellow(-green); bracteoles small, at base of pedicel, triangular to ovate, hairy to glabrous outside, glabrous or hairy at base inside; pedicel present or absent, green (cream or purple to violet in *A. nitida* and *A. quadrilocularis*); sepals (narrowly) ovate; petal-like organs erratically 2 or 3 present; ovary globose, ovoid, or (narrowly) ellipsoid, sometimes flask-shaped, 2- or 3-locular, sometimes 4-locular (5–7-locular in *A. nitida*), densely sericeous to glabrous; ovules two per locule; style absent; stigmas sessile or raised, broad or elongated, apically lobed to completely divided, flattened to the sides of the ovary to ascending, straight to recurved, whitish turning yellow to red(dish) or (dark) purple, almost smooth to densely laciniate above, often also longitudinally ribbed, glabrous smooth, papillate or ribbed beneath, sparsely sericeous to glabrous when free, sometimes completely fused to the ovary or style remnant present. *Infructescences* often longer and thicker than pistillate inflorescences, glabrescent.

Fruit a regma, dehiscent; pedicel often slightly or strongly longer than in flowering stage, green (red to purple in *A. nitida*); capsule broadly ovoid, globose, or (narrowly) ellipsoid (flask-shaped in *A. lagenocarpa* and fusiform in *A. fusiformis* and *A. egregia*), topped by the persistent stigmas, sometimes stiped and/or beaked, sometimes ridged or lobed along the sutures, granular to smooth (ruminate-verrucate in *A. selangorica*, tuberculate in *A. bourdillonii*, laminate in *A. lamellata*), soft or hard, densely sericeous to glabrous, greenish when immature and at maturity turning yellow, pink, orange to (dark) red or violet outside and whitish or orange inside; pericarp splitting from base to apex septicidally and loculicidally, thin papery or thick and sometimes fleshy; endocarp splitting separately from pericarp, as pericarp, slightly later in time, thin horny, sometimes caudate at apex towards the stigmas, glabrous, whitish; septae very thin, hairy or glabrous; column hairy or glabrous, red or purple. *Seeds* only one or one per locule developing, seldom two per locule, hanging apically on column, shape and size dependent on number of seeds developing, mostly (half-)terete, ovoid to ellipsoid, base and apex truncate, covered with a thin, fleshy, juicy, yellow, orange, pink, or red to scarlet aril; testa creamy or green; endosperm fine granular, thin; embryo small, radix quadrangular, cotyledons flat, base cordate to truncate, apex rounded.

Distribution — 82 species, found from Sri Lanka and South India (Kerala), from North India southwards to South China, Burma, Thailand, Laos, Cambodia, and Vietnam; Malesia: Peninsular Malaysia, Singapore, Sumatra, West Java, Borneo, Philippines, Sulawesi, South Moluccas, Papua Barat, Papua New Guinea, and two species in the Western Solomons.

10.2 – **Section classification**

1. Aporosa section **Aporosa**

Stipules narrowly ovate, oblique, mostly caducous. *Leaves*: basal glands mostly absent (small and often indistinct in *A. prainiana*, *A. sarawakensis*, and *A. symplocoides*); blade papery, regularly scattered with small or distinct white granules above and/or beneath, drying greyish green or yellowish green on both sides, disc-like glands along the margin, small, few, irregularly present. *Inflorescences* drying yellow or yellowish; staminate ones with glomerules laxly set throughout the rachis (but massed in an apical head in *A. confusa*, *A. nitida*, *A. quadrilocularis,* and sometimes *A. frutescens*); pistillate ones with flowers laxly set or uniflorous. *Flowers*: staminate flowers with stamens not or slightly exserted; pistillate flowers with papillate stigmas. *Fruits* drying yellowish; septae and column glabrous.

Species — *Aporosa banahaensis, A. chondroneura, A. confusa, A. frutescens, A. fulvovittata, A. nitida, A. prainiana, A. quadrilocularis, A. sarawakensis, A. stellifera, A. stenostachys, A. symplocoides, A. symplocoides* var. *chalarocarpa, A. whitmorei (A. spec. E).*

Distribution — Mainly Peninsular Malaysia, Singapore, Sumatra, Borneo. *Aporosa frutescens* widespread from Peninsular Thailand to West Java, the Philippines, Sulawesi and Seram; *A. banahaensis* in the Philippines.

This section is characterized by the greyish green drying leaves, sometimes with white granules above or beneath, and the yellowish drying fruits and inflorescences. The staminate inflorescences are long, narrow, with interrupted glomerules and often glabrous rachises. The pistillate inflorescences are also long, narrow, often glabrous, and with spaced, pedicelled, mostly 3-locular flowers.

Within the section subgroups are formed on the apically massed glomerules, the uniflorous pistillate inflorescences, and the fleshy fruit: *Aporosa confusa*, *A. nitida*, *A. quadrilocularis,* and to a lesser extent, *A. frutescens* have clavate-shaped inflorescences with the glomerules massed apically. The globose fleshy fruits of these four species are also unique due to their broad, sunken stigmas. *Aporosa banahaensis, A. confusa, A. fulvovittata, A. frutescens, A. nitida, A. quadrilocularis, A. sarawakensis, A. stenostachys*, (and *A. spec. E*) have uniflorous pistillate inflorescences.

The local outgroup to this clade is *A. grandistipula*. It shares the laxly set glomerules and flowers of the staminate and pistillate inflorescences with the *frutescens*-group.

2. **Aporosa** section **Appendiculatae** Pax & K. Hoffm.

Aporosa Blume sect. *Appendiculatae* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 104. — Lectotype (designated here): *Aporosa bourdillonii* Stapf.

Aporosa Blume subsect. *Trichogynae* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 92. — Lectotype (designated here): *Aporosa dioica* (Roxb.) Müll.Arg. [= *Aporosa octandra* (Buch.-Ham. ex D. Don) Vickery].

Stipules narrowly ovate, mostly caducous. *Leaves*: basal glands usually present; blade papery, smooth, drying greenish to brownish above, brownish beneath, or greenish to yellow on both sides, disc-like glands scattered within the marginal vein arches (absent in *A. nigricans*). *Inflorescences* drying (dark) brownish, staminate glomerules or pistillate flowers densely set, completely covering the rachis (peduncled in *A. bourdillonii*). *Flowers*: staminate flowers with stamens not or slightly exserted; pistillate flowers with papillate stigmas. *Fruits* drying brown to black; septae and column sparsely sericeous to sparsely tomentose, seldom glabrescent.

Species — *Aporosa acuminata, A. aurea, A. bourdillonii, A. cardiosperma, A. ficifolia, A. fusiformis, A. globifera, A. lanceolata, A. latifolia, A. lucida, A. macrophylla, A. nigricans, A. octandra, A. planchoniana, A. pseudoficifolia, A. serrata, A. symplocifolia, A. tetrapleura, A. villosa, A. wallichii, A. yunnanensis.*

Distribution — Sri Lanka, South India, North India, Nepal, Bhutan, Burma, Thailand, Laos, Cambodia, Vietnam, South China. *Aporosa aurea, A. globifera* and *A. pseudoficifolia* in Peninsular Malaysia and Singapore, *A. symplocifolia* in the Philippines, and *A. lucida, A. nigricans*, and *A. octandra* widespread in West Malesia.

The synapomorphy of this section – when including all species – is the puberulous inner side of the fruit. Other characteristic items for this section are the short, thick, tomentose inflorescences with compact sessile flowers, and the scattered disc-like glands. These characters, however, are not unique for the group and do not occur in all species: *A. bourdillonii* has peduncled inflorescences, *A. lucida* and *A. nigricans* slightly interrupted ones, *A. cardiosperma* has pedicelled pistillate flowers, and *A. nigricans* lacks the disc-like glands. Moreover, the dense inflorescences and the scattered disc-like glands occur occasionally outside this section.

The inner relationships among the members of this section remain unclear. An outstanding subgroup is formed by six species around *A. aurea*: *A. acuminata*, *A. aurea*, *A. lanceolata*, *A. planchoniana*, *A. symplocifolia*, and *A. tetrapleura* (*A. lucida* may or may not be included). They have glabrous, thick, shiny leaves that turn greenish yellow to lurid yellow with distinct black basal glands when dried. The geographically vicariant and densely tomentose *A. ficifolia*, *A. globifera*, *A. pseudoficifolia*, and *A. serrata* form a slightly less distinct subgroup; phylogenetically the glabrous-leaved *A. macrophylla* is also part of this group. The other taxa are variously placed. *Aporosa bourdillonii* is the most deviating species within section *Appendiculatae*.

The sistergroup of this section is probably found among the taxa in the cluster around *A. maingayi*. Here the compact inflorescences are also found.

3. **Aporosa** section **Benthamianae** Schot, *sect. nov.*

Inflorescentiis staminatis maturitate typice penicillatis, floribus pistillatis stigmatibus longis laevibus curvatis notata. — Typus: *Aporosa benthamiana* Hook.f.

Aporosa Blume subsect. *Grandistipulosae* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 82. — Lectotype (designated here): *Aporosa benthamiana* Hook.f.

Stipules falcate, often persistent. *Leaves*: basal glands absent; blade leathery, smooth, drying greenish to (dark) brownish above, (dark) brownish beneath, disc-like glands many, distinct, along the margin. *Inflorescences* drying brownish; staminate glomerules and pistillate flowers densely set only at apical 2/3. *Flowers*: staminate flowers with minute sepals, stamens strongly exerted, c. thrice as long as the sepals and giving mature inflorescences a typical brush-like appearance; pistillate flowers with smooth stigmas. *Fruits* drying brownish; septae and column glabrous.

Species — *Aporosa benthamiana, A. bullatissima, A. falcifera, A. lunata, A. sylvestri.*

Distribution — Peninsular Malaysia, Singapore, Sumatra, Borneo. *Aporosa falcifera* also found on Sulawesi, *A. lunata* on West Java, and *A. benthamiana* in the southern Philippines.

Note — Though Pax & Hoffmann's name *Grandistipulosae* is available for this section, I do not use it to avoid confusion with *A. grandistipula* (section *Sundanenses*).

The five species of this section are very characteristic because of their typical brush-like staminate inflorescences (Fig. 3.5c). The group shares further the unique long, smooth, downwards curving stigmas. Other synapomorphies, such as the large falcate stipules and the distinct disc-like glands along the margin, also occur outside the section, notably in the species around the New Guinean *A. papuana*. *Aporosa bullatissima*, *A. lunata*, and *A. sylvestri* have (strongly) bullate leaves.

Its closest relatives are the Philippinian *A. leytensis* and the species around *A. papuana* in New Guinea.

4. **Aporosa** section **Papuanae** Schot, *sect. nov.*

Grex specierum in Nova Guinea Insulis Solomonis inveniuntur. — Typus: *Aporosa papuana* Pax & K. Hoffm.

Stipules mostly falcate or oblique, persistent or caducous. *Leaves*: basal glands absent; blade papery or leathery, smooth, drying greenish or brownish above, brownish beneath or greyish green on both sides, disc-like glands scattered only along the margin or only basally or over the complete blade, distinct or small or disc-like glands absent. *Inflo-*

rescences drying yellowish or (dark) brownish; glomerules or pistillate flowers laxly or densely set along the rachis or rachis peduncled or laxly flowered at base and more densely apically. *Flowers* largish; staminate flowers with stamens exserted; pistillate flowers with papillate stigmas. *Fruits* drying yellowish or brownish; septae and column glabrous (column at base hairy in *A. annulata*).

Species — *Aporosa annulata, A. brassii, A. brevicaudata, A. carrii, A. decipiens, A. egregia, A. flexuosa, A. hermaphrodita, A. heterodoxa, A. lamellata, A. laxiflora, A. ledermanniana, A. leptochrysandra, A. leytensis, A. longicaudata, A. misimana, A. nigropunctata, A. papuana, A. parvula, A. praegrandifolia, A. reticulata, A. sclerophylla, A. vagans* (*A. spec. A, A. spec. B, A. spec. C, A. spec. D*).

Distribution — Papua Barat and Papua New Guinea. *Aporosa papuana* reaching the Solomons, *A. brevicaudata* also found on Seram (Moluccas), and *A. leytensis* occurring in Sulawesi and the Philippines.

The New Guinean species are highly variable, and maybe the only feature they have in common – except for their geography – is that they have the more primitive character states within *Aporosa*. The Philippine–Sulawesian *A. leytensis* is also classified in this group; its macromorphology equals that of the *papuana*-group and is in the phylogenetic analyses placed near the *papuana*-group.

Three overlapping subsets may be identified. The species with large leaves around *A. papuana* always form one clade with *A. leytensis* at the base. Via *A. praegrandifolia* and *A. vagans* this group gradually merges into the intermediate taxa. These intermediates, in turn, gradually change into the species with small leaves around *A. brevicaudata*. *Aporosa nigropunctata* and *A. longicaudata* are controversial.

5. **Aporosa** section **Sundanenses** Schot, *sect. nov.*

> Grex intermedius satis primitivus paraphyleticus, sectionem Trichoseptas proximus, ab hac in absentia combinationis plenae proprietatum proprium sectionis huius differt. In insulis sundanensibus maioribus distributus. — Typus: *Aporosa nervosa* Hook.f.

Stipules (narrowly) ovate, oblique or not, usually caducous. *Leaves*: basal glands absent; blade papery or leathery, smooth, drying brownish to greenish or bluish above, brownish beneath; disc-like glands absent or along the margin, small, few, irregularly present (scattered within the marginal vein arches in *A. dendroidea*). *Inflorescences* drying (dark) brown, seldom yellowish; mostly with staminate glomerules or pistillate flowers interruptedly set at the base, more densely set apically (densely set in *A. maingayi*, interrupted throughout in *A. grandistipula* and *A. elmeri*). *Flowers*: staminate flowers with stamens exserted or not; pistillate flowers with ribbed or papillate or laciniate stigmas. *Fruits* usually drying (dark) brown to black; septae and column glabrous.

Species — *Aporosa alia, A. antennifera, A. arborea, A. basilanensis, A. caloneura, A. dendroidea, A. duthieana, A. elmeri, A. grandistipula, A. granularis, A. illustris, A. lagenocarpa, A. maingayi, A. microstachya, A. nervosa, A. penangensis, A. rhacostyla, A. selangorica, A. sphaeridiophora, A. subcaudata* (*A. spec. F, A. spec. G*).

Distribution — Peninsular Thailand, Peninsular Malaysia, Singapore, Sumatra, Borneo. *Aporosa duthieana* found in Thailand, Burma, and Vietnam, *A. sphaeridiophora* in the Philippines and its variety *campanulata* in West Java; *A. dendroidea* in the South Moluccas.

There is no feature within this section that is present in all species; it is a collection of West-Malesian species that do not fit into the sections *Aporosa*, *Appendiculatae*, or *Benthamianae*. Stipules are usually more or less asymmetric, but falcate ones (*A. grandistipula*, *A. illustris*) and (narrowly) ovate ones (*A. elmeri*) are also present. The leaves and inflorescences are intermediate without any particularly notable features, just like the flowers and fruits.

The Moluccan *A. dendroidea* is provisionally included in this group. The pistillate inflorescences are more alike with those of the *nervosa*-species, but in the phylogenetic reconstructions it is mostly united with the New Guinean *A. leptochrysandra* and *A. misimana* at the root of the *octandra*-group. Biogeographically the position of the Moluccas is ambiguous: both the New Guinean *A. brevicaudata* and the Sundanese *A. frutescens* are found there. If the macromorphological features of *A. dendroidea* are considered, then it should be reckoned with the Sunda species. This might change if the staminate inflorescences of *A. dendroidea* are found to be more like those of the New Guinean species, but for the time being *A. dendroidea* is classified with the Sundanese section.

The largest subgroup is the *maingayi*-clade. The 'hard core' of this group contains *A. alia, A. elmeri, A. granularis, A. maingayi, A. microstachya, A. rhacostyla, A. subcaudata*, and *A. spec. F*. In various cases other species are added to this group, viz., *A. lagenocarpa, A. penangensis*, or *A. selangorica*. This shows the impossibility to delimit the 'hard core' on any ground, though they are morphologically and phylogenetically distinctive. Two smaller subgroups are formed by *A. arborea, A. basilanensis*, *A. grandistipula*, and *A. illustris*, and by *A. nervosa* with the two varieties of *A. sphaeridiophora*. But these can neither be strictly defined. Species that cannot be allocated into any subgroup are *A. antennifera*, *A. caloneura*, *A. dendroidea*, *A. duthieana*, and *A. spec. G*.

10.3 – **Identification keys**

10.3.1 – ***Notes and recommendations***

Aporosa consists of c. 80 species. They are mainly separated by a specific combination of characters. This makes it difficult to construct simple dichotomous keys. Because one character identifies different groups of species then another character, it is hard to find reasonable combinations of characters for the same lead.

There are several keys. The dichotomous keys are split according to six areas: South India and Sri Lanka, Mainland Asia, Peninsular Thailand to West Java, Borneo, Central Malesia and the Philippines, and Papua Barat, Papua New Guinea, and the Solomon Islands. For Asia and West and Central Malesia the keys are split into one for staminate material and one for pistillate specimens. The species delimitations are for a major part based on the arrangement of the glomerules or pistillate flowers along the rachis (Fig. 3.5 & 3.6). It is thus not possible to identify sterile specimens with these keys. For these and for specimens of unknown origin one should refer to the synoptic key, which is given at the end.

The New Guinean species have other combinations of characters then the West-Malesian species. It proved to be rather senseless to separate the staminate from the pistillate specimens, thus only one key is provided. Size differences of leaves and inflorescences are the best character to distinguish between the species. But since many intermediate forms are found on New Guinea the key is not always reliable. Deviating forms cannot be determined. For these I also recommend the synoptic key.

Because it is often the combination of characters that defines a species, some leads of the keys are rather long and difficult to read. In order to fit all possibilities many characters seem to overlap at first sight. Yet, when actually identifying the species, only part of the characters overlap, and the species may fit partially into both leads, but only completely into one of them. This is the lead that should be chosen in these cases. But be careful to read the complete set of leads in these cases.

I have noticed that some characters may be differently interpreted. For instance, when I count the number of nerve pairs, I include the basal ones and exclude the apical ones in the proper apex. Completely glabrous means for *Aporosa* really **completely** glabrous; this is best seen in young leaves. If the leaf has only three or four very short hairs at the base of the midrib beneath, it is **not** completely glabrous. For other interpretations of characters the relevant pages on the macromorphology (Chapter 3) should be read. The figures are also found there.

10.3.2 – *Key to the species of Sri Lanka and South India*

Staminate specimens

1a. Staminate inflorescences floriferous to the base, peduncle absent (Fig. 3.5a). Bracts to the glomerules broadly triangular, up to 2 mm long 2
b. Staminate inflorescences peduncled (cf. Fig. 3.5c, g). Bracts to the glomerules elliptic, 2–3 mm long . . . . **17. A. bourdillonii**
2a. Inflorescences 5–13 mm long, 1.5–2 mm diameter. Leaves drying on both sides greyish green or yellowish green, texture papery; blade narrowly ovate to narrowly elliptic; apex cuspidate to caudate 3
b. Inflorescences 10–35 mm long, either 1–1.5 or 2–3 mm diameter. Leaves drying above brownish, greenish brown, or reddish brown, beneath light to dark brown, texture (often) leathery; blade elliptic to obovate, or narrowly ovate to narrowly obovate; apex acute to cuspidate 4
3a. Petioles and leaves sparsely hairy, glabrescent. Leaves drying greenish grey; basal glands indistinct; marginal glands indistinct . . . . **15. A. acuminata**
b. Petioles and leaves glabrous. Leaves drying yellowish green; basal glands distinct, black, marginal glands distinct, blackish to brown . . . . **22. A. lanceolata**
4a. Leaf blades elliptic to obovate; apex acute to acuminate. Inflorescences 2–3 mm diameter 5
b. Leaf blades narrowly ovate to narrowly obovate; apex acuminate to cuspidate. Inflorescences 1–1.5 mm diameter . . . . **18. A. cardiosperma**
5a. Leaf blades 5–13 by 2.5–8 cm. — Altitude 1200–1800 m . . . .**20. A. fusiformis**
b. Leaf blades 8–17 by 5.5–10 cm. — Altitude low to 400 m . . . . . .**23. A. latifolia**

Pistillate specimens

1a. Ovary and fruit punctulate to smooth, sparsely sericeous to glabrous 2
b. Ovary and fruit tuberculate, (sparsely) tomentose (Fig. 3.9a, b) . . . . **17. A. bourdillonii**

2a. Ovary and fruit (mostly) 2-locular 3
b. Ovary and fruit (mostly) 3-locular 5
3a. Fruits ellipsoid to globose, 6–11 mm long (Fig. 3.11a, b, d, e). Leaf narrowly ovate to narrowly elliptic; apex cuspidate to caudate; texture papery; drying on both sides greyish green or yellowish green 4
b. Fruits fusiform, 14–17 mm long (Fig. 3.11j). Leaf elliptic to obovate; apex acute to acuminate; texture leathery; drying above reddish brown, beneath light brown . . . . **20. A. fusiformis**
4a. Petioles and leaves sparsely hairy, glabrescent. Ovary and fruit sparsely sericeous at base; stigmas 0.5–1.5 mm long. Leaves drying greenish grey; basal glands indistinct; marginal glands indistinct . . . . **15. A. acuminata**
b. Petioles and leaves glabrous. Ovary and fruit glabrous; stigmas 0.3–0.5 mm long. Leaves drying yellowish green; basal glands distinct, black; marginal glands distinct, blackish to brown . . . . **22. A. lanceolata**
5a. Flowers and fruits pedicelled. Fruit globose, 10–12 by 10–13 mm, sparsely sericeous at base; pericarp 0.5–1 mm thick. Ovary sparsely sericeous at base; stigmas 0.5–0.8 mm long. Leaves narrowly ovate to narrowly obovate . . . . **18. A. cardiosperma**
b. Flowers and fruits sessile. Fruit ovoid, 20–24 by 17–21 mm, glabrous; pericarp 5–7 mm thick. Ovary glabrous; stigmas 2–2.5 mm long. Leaves elliptic to obovate . . . . **23. A. latifolia**

10.3.3 – *Key to the species of North India, Burma, China, Thailand (excl. Peninsular), Laos, Cambodia, and Vietnam*

Staminate specimens

1a. Petiole 3–25 mm long. Leaves (narrowly) elliptic or narrowly ovate; base rounded to attenuate 2
b. Petiole 43–91 mm long. Leaves ovate; base cordate. — Branchlets, petiole, and leaves completely glabrous. Inflorescences 22–55 mm long, 2–3.5 mm diameter. Burma, Rangoon . . . . **25. A. macrophylla**
2a. Leaf: disc-like glands set abaxially along the margin (Fig. 3.3b, c). Inflorescences more or less interruptedly floriferous at base of rachis, minutely or shortly peduncled (Fig. 3.5d, h, i); glomerules ellipsoid (as far as known), bracts indistinct 3
b. Leaf: disc-like glands scattered abaxially within the vein arches (Fig. 3.3d). Inflorescences more or less continuously floriferous to base (Fig. 3.5a); glomerules subglobose, often divided by (rather) conspicuous bracts 5
3a. Leaves smooth; drying above rather dark greyish or bluish green, beneath brownish; nerves 5–7 pairs. Inflorescences (as far as known) 1–1.5 mm diam., drying (dark) greyish 4
b. Leaves young lowly white granular; drying above and beneath yellowish green; nerves 8–10 pairs. Inflorescences 2–3.5 mm diam., drying yellowish . . . . **4. A. frutescens**
4a. Leaves 7–19.5 cm long, coriaceous, shiny, disc-like glands on lower surface more than 1 mm from margin. Staminate inflorescences 25–50 mm long, glomerules basally spaced up to 5(–11) mm to apically continuous along rachis . . . . **74. A. duthieana**

b. Leaves 6–12 cm long, papery, dull, disc-like glands on lower surface along margin, never more than 1 mm from margin. Staminate inflorescences 6–14 mm long, glomerules indistinct; peduncle 0–0.5 mm long .... **6. A. microstachya**

5a. Branchlets very sparsely puberulous to glabrous. Petioles and leaves completely glabrous. Leaves drying bright yellowish to greenish yellow, often on both sides 6

b. Branchlets, petioles, and leaves sparsely puberulous to densely tomentose, glabrescent. Leaves drying greyish brown to greenish yellow above, (light) brownish or light greenish beneath 9

6a. Leaf: basal glands small, brownish; blade narrowly ovate to (narrowly) elliptic, papery, dull to slightly shiny, not brittle when dry; apex acuminate to cuspidate; nerves 7–11 pairs 7

b. Leaf: basal glands large, black; blade (narrowly) elliptic, leathery, shiny, often rather brittle when dry; apex acute to acuminate; nerves 6–8 pairs .... **32. A. tetrapleura**

7a. Petiole 5–19 mm long. Leaves 7–18 by 2–7 cm; drying brownish, or green to rather light greenish brown; dots irregularly or laxly set, often fading. Inflorescences 18–41 mm long, 1.8–2.5 mm diam.; bracts rather conspicuous; flowers laxly set 8

b. Petiole 3–8 mm long. Leaves 5–13 by 1.5–3.5 cm; drying greenish brown to greenish yellow; dots densely set, distinct. Inflorescences 12–37 mm long, 1.2–1.8 mm diam.; bracts inconspicuous; flowers densely set ... **28. A. planchoniana**

8a. Young branches very sparsely puberulous. Leaves drying yellowish green or greenish, seldom brownish. Bracts (sparsely) puberulous ..... **34. A. wallichii**

b. Young branches glabrous. Leaves drying rather light greenish brown with lighter nervation. Bracts glabrous .... **35. A. yunnanensis**

9a. Leaf: basal glands absent or present and surrounded by hairs; marginal glands surrounded by hairs; nervation often (slightly) sunken above. Bracts (sparsely or densely) tomentose outside 10

b. Leaf: basal glands present, not surrounded by hairs, often indistinct; marginal glands seldom in young leaves surrounded by hairs; nervation not or seldom sunken above. Bracts (sparsely) tomentose or puberulous outside 12

10a. Leaf: midrib and lamina (sparsely) tomentose above; nerves 8–10 pairs. — Thailand, Laos, Cambodia, Vietnam 11

b. Leaf: only midrib (sparsely) hirsute above; nerves 9–12 pairs. — Inflorescences 15–36 mm long, 2–2.5 mm diameter. Burma: Tenasserim ....**29. A. pseudoficifolia**

11a. Leaf: margin (lowly) glandular-crenate; often bullate. Inflorescences 15–24 mm long, 3.5–5 mm diameter ....**19. A. ficifolia**

b. Leaf: margin glandular-dentate; slightly bullate near the margins. Inflorescences 9–18 mm long, 2–3 mm diameter .... **30. A. serrata**

12a. Branchlets usually with few, small scars of fallen leaves. Leaf: (narrowly) ovate to (narrowly) elliptic; margin (lowly) glandular-crenate to (lowly) glandular-serrate; base cuneate to obtuse ....13 (**27. A. octandra**)

b. Branchlets often with thick scars of fallen leaves. Leaf: (broadly) ovate to elliptic; margins lowly glandular-crenate, sometimes lowly glandular-serrate; base often broadly subcordate . . . . **33. A. villosa**

Aporosa villosa and *A. octandra* are only really distinct in the extreme forms of the *A. villosa* leaf. Intermediates occur!

13a. Branchlets and leaves (sparsely) puberulous, leaves texture papery or slightly leathery 14

b. Branchlets and leaves tomentose, leaves texture leathery . . . . **27d. A. octandra** var. **yunnanensis**

14a. Leaf: margin lowly glandular-crenate to lowly glandular-serrate; texture papery; drying above greyish or brownish 15

b. Leaf: margin (at apex) strongly glandular-serrate; texture slightly leathery; drying above greenish . . . . **27b. A. octandra** var. **chinensis**

15a. Branchlets, petiole, and leaves puberulous . . . **27c. A. octandra** var. **malesiana**

b. Branchlets, petiole, and leaves sparsely puberulous, glabrescent . . . . **27a. A. octandra** var. **octandra**

The varieties of *A. octandra* are not always distinct: many forms occur that cannot be placed in any of the varieties and are not identifiable beyond *A. octandra*.

Pistillate specimens

1a. Flowers and fruits subsessile to distinctly pedicelled, singly (Fig. 3.6u) or several more or less densely set mostly at apical part of rachis (cf. Fig. 3.6d, e, l). Fruit: septae and column glabrous. Leaf: disc-like glands abaxially set along the margin (Fig. 3.3b, c), sometimes indistinct 2

b. Flowers and fruits sessile (seldom pedicelled), densely set along the rachis (Fig. 3.6a, c, i, j). Fruit: septae and column sparsely hairy, sometimes glabrescent. Leaf: disc-like glands scattered abaxially within the vein arches (Fig. 3.3d), often distinct 4

2a. Flowers and fruits 2-locular, more than 1 in each inflorescence. Flower: stigmas elongated, 1.5–2.5 mm long, perpendicular to the sides of the ovary, reflexed, or recurved. Fruits ellipsoid to ovoid, stigmas not sunken 3

b. Flowers and fruits 3-locular, only one at apically end of rachis (Fig. 3.6u). Flower: stigmas broad, 0.5–1 mm long, flattened on top of the ovary (Fig. 3.8p). Fruit globose with sunken stigmas (Fig. 3.11l) . . . . **4. A. frutescens**

3a. Leaves 7–19.5 cm long, coriaceous, shiny, disc-like glands on lower surface more than 1 mm from margin. Flowers subsessile; stigmas 2–2.5 mm long, papillate to laciniate. Fruiting pedicel 1–2 mm long . . . . **74. A. duthieana**

b. Leaves 6–12 cm long, papery, dull, disc-like glands on lower surface along margin, never more than 1 mm from margin. Flowers (sub)sessile; stigmas 1.5–2.5 mm long, laciniate. Fruiting pedicel 0.1–0.5 mm long . . . . **81. A. microstachya**

4a. Petiole 3–25 mm long. Leaves (narrowly) elliptic or narrowly ovate; base rounded to attenuate 5

b. Petiole 43–91 mm long. Leaves ovate; base cordate. — Branchlets, petiole, and leaves completely glabrous. Inflorescences 3–4 mm diam.; ovary densely tomentose. Fruit possibly globose, tomentose. Burma: Rangoon . **25. A. macrophylla**

5a. Branchlets (very) sparsely puberulous to glabrous. Petioles and leaves completely glabrous. Leaves drying often on both sides bright yellowish to greenish yellow. Ovary and fruit (sub)glabrous (though stigmas sometimes hairy) 6

b. Branchlets, petioles, and leaves sparsely puberulous to densely tomentose, glabrescent. Leaves drying above greyish brown to greenish yellow, beneath (light) brownish to light greenish. Ovary and fruit densely to sparsely puberulous .. 9

6a. Leaves drying dull greenish brown to greenish yellow or shiny yellow; margin subentire to lowly undulate, marginal glands few, often indistinct; dots densely set, often rather distinct. Stigmas short, 0.5–1.1 mm long, straight (Fig. 3.8k) 7

b. Leaves drying brownish, or green to rather light greenish brown; margin lowly undulate to (lowly) glandular-crenate, marginal glands regular, mostly distinct; dots irregularly or laxly set, often fading. Stigmas long, 1.5–3 mm long, recurved 8

7a. Petiole 3–8 mm long. Leaves narrowly ovate to narrowly elliptic, 1.5–3.5 cm broad, papery; drying greenish brown to greenish yellow; basal glands small, brownish; apex cuspidate; nerves 9–11 pairs. Fruits 7–11 mm long, shortly stiped, beaked, not ridged; pericarp 0.3–0.5 mm thick .... **28. A. planchoniana**

b. Petiole 9–21 mm long. Leaves (narrowly) elliptic, 2.5–6 cm broad, leathery; drying shiny bright yellow-green; basal glands large, black; apex acute to acuminate; nerves 6–8 pairs. Fruits 11–14 mm long, not stiped, only immature ones beaked, ridged at sutures; pericarp 0.5–1.5 mm thick .... **32. A. tetrapleura**

8a. Young branches very sparsely puberulous. Leaves drying yellowish green or greenish, seldom brownish. Flowers up to 11 per inflorescence; stigmas and/or ovary at base sometimes sparsely puberulous. Fruit punctate, drying brownish to black .... **34. A. wallichii**

b. Young branches glabrous. Leaves drying rather light greenish brown with lighter nervation. Flowers up to 5 per inflorescence; stigmas and/or ovary completely glabrous. Fruit punctate to lowly granulate, drying light orange-brownish .... **35. A. yunnanensis**

9a. Fruit globose, not stiped or beaked, (sparsely) tomentose. Flower: ovary ellipsoid, densely tomentose. Leaf: basal glands absent or present and surrounded by hairs; marginal glands surrounded by hairs; nervation often (slightly) sunken above 10

b. Fruit ovoid to ellipsoid, often stiped and/or beaked, sparsely puberulous. Flower: ovary ovoid, densely to sparsely puberulous. Leaf: basal glands present but often indistinct; marginal glands seldom in young leaves surrounded by hairs; nervation not or seldom sunken above 12

10a. Fruit and ovary 2-locular. Leaf: midrib and lamina (sparsely) tomentose above; nerves 8–10 pairs. — Thailand, Laos, Cambodia, Vietnam 11

b. Fruit and ovary 3-locular. Leaf: only midrib (sparsely) hirsute above; nerves 9–12 pairs. — Burma: Tenasserim ....**29. A. pseudoficifolia**

11a. Leaf: margin (lowly) glandular-crenate; nervation often sunken. Inflorescences c. 3.5 mm diameter. Bracts 1.5–1.8 mm long, densely tomentose outside. — Infructescences 8–12 mm long, 2.5–4 mm diam.; fruits globose, densely sericeous .. ..**19. A. ficifolia**

b. Leaf: margin glandular-dentate; nervation slightly sunken near the margins. Inflorescences 1.5–2 mm diameter. Bracts 0.8–1 mm long, sparsely sericeous outside. — Infructescences and fruits unknown .... **30. A. serrata**

12a. Branchlets usually with few, small scars of fallen leaves. Leaves (narrowly) ovate to (narrowly) elliptic; margin (lowly) glandular-crenate to (lowly) glandular-serrate; base cuneate to obtuse . . . . 13 (**27. A. octandra**)

b. Branchlets often with thick scars of fallen leaves. Leaves (broadly) ovate to elliptic; margins lowly glandular-crenate, sometimes lowly glandular-serrate; base often broadly subcordate . . . . **33. A. villosa**

Aporosa villosa and *A. octandra* are only really distinct in the extreme forms of the *A. villosa* leaf. Intermediates occur!

13a. Branchlets and leaves (sparsely) puberulous, leaves papery or slightly leathery. Ovary (sparsely) puberulous 14

b. Branchlets and leaves tomentose, leaves leathery. Ovary tomentose . . . . **27d. A. octandra** var. **yunnanensis**

14a. Leaf: margin lowly glandular-crenate to lowly glandular-serrate; papery; drying above greyish or brownish. Ovary evenly (sparsely) puberulous 15

b. Leaf: margin (at apex) strongly glandular-serrate; slightly leathery; drying above greenish. Ovary (sparsely) puberulous at base, glabrescent towards apex . . . . **27b. A. octandra** var. **chinensis**

15a. Branchlets, petiole, and leaves puberulous . . . **27c. A. octandra** var. **malesiana**

b. Branchlets, petiole, and leaves sparsely puberulous, glabrescent . . . . **27a. A. octandra** var. **octandra**

The varieties of *A. octandra* are not always distinct: many forms occur that cannot be placed in any of the varieties and are not identifiable beyond *A. octandra*.

10.3.4 – *Key to the species of Peninsular Thailand, Peninsular Malaysia, Singapore, Sumatra, and Java*

Staminate specimens

1a. Staminate inflorescences strongly interrupted; all individual glomerules distinct, distinctly spaced throughout the rachis (Fig. 3.5k) 2

b. Staminate inflorescences continuous to more or less interrupted at base; individual glomerules at least at apex of rachis indistinct, not or only slightly spaced (Fig. 3.5a–j) 4

2a. Branchlets and leaves completely glabrous 3

b. Branchlets and leaves (sparsely) tomentose, glabrescent . . . . . **13. A. whitmorei**

3a. Leaf: nerves 5–8 pairs; texture slightly leathery, drying dull greyish green to dark green; dots densely set, fine, greyish . . . . **7. A. prainiana**

b. Leaf: nerves 7–10 pairs; texture papery, drying shiny yellowish green or dark green; dots indistinct . . . . **12. A. symplocoides**

4a. Stipules falcate, mostly persistent. Leaf: margin subentire, marginal glands in margin, small, indistinct; disc-like glands often present, distinct, along the margin (Fig. 3.3c). Inflorescences (when mature) brush-like due to long exserted stamens, glomerules indistinct, densely set at apical 3/4–7/8 of the rachis (Fig. 3.5c); peduncle present. Flowers: stamens strongly exserted, c. thrice as long as the sepals (Fig. 3.7n); anthers 0.1–0.2 mm long 5

b. Stipules narrowly ovate, symmetric to oblique, seldom persistent (almost falcate and rather persistent in *A. selangorica*). Leaf: margin lowly undulate to (lowly) glandular-crenate or (lowly) glandular-serrate, marginal glands near the margin, not particularly small, often distinct, seldom indistinct or absent (*A. aurea*); disc-like glands absent, or small and indistinct along the margin, or distinct and scattered within the marginal vein arches (Fig. 3.3b, d). Inflorescences not brush-like, continuously floriferous to the base (Fig. 3.5a, b), or peduncled, with the glomerules at least at base interrupted, distinct (Fig. 3.5d–h), or peduncled with the glomerules massed in a distinct head (Fig. 3.5i, j). Flowers: stamens not or slightly exserted and anthers up to 0.3 mm long (Fig. 3.7a–g), if stamens c. twice as long as the sepals, then anthers 0.4–0.5 mm long 7

5a. Leaves glabrous or only sparsely hairy beneath; nerves slightly raised to flat above 6

b. Leaves (sparsely) hirsute above and beneath; nerves more or less sunken above .... **39. A. lunata**

6a. Stipules 6–20 by 11–37 mm, often persistent. Petiole: upper pulvinus swollen, 5–11 by 3–6 mm. Leaves 14–47 cm long; base cordate; nerves strongly raised beneath, not fading towards the margin .... **36. A. benthamiana**

b. Stipules 4–8 by 11–18 mm, present in young stages only. Petiole: upper pulvinus distinct, but not extremely so, 2–6 by 1.5–2.5 mm. Leaves 8–25 cm long; base emarginate to rounded; nerves less raised beneath, fading towards the margin .... **38. A. falcifera**

7a. Branchlets glabrous or very sparsely puberulous. Petiole and leaves completely glabrous 8

b. Branchlets sparsely puberulous to tomentose. Petiole and leaves at least sparsely puberulous on midrib beneath 12

8a. Leaf: basal glands present, large or small, black to grey; disc-like glands present, scattered within marginal vein arches (Fig. 3.3d). Inflorescences not peduncled, continuously floriferous to the base (Fig. 3.5a, b) 9

b. Leaf: basal glands absent; disc-like glands occasionally present, along the margin (Fig. 3.3b). Inflorescences peduncled, glomerules more or less interrupted at base (Fig. 3.5d–j) 10

9a. Leaves drying shiny yellowish green to yellow; basal glands large, black, distinct; marginal glands absent. Inflorescences continuous, glomerules indistinct .... **16. A. aurea**

b. Leaves drying slightly shiny yellowish green to green or brownish, often darkening with age; basal glands small, greyish, often indistinct; marginal glands small, greyish. Inflorescences continuous, but glomerules distinct, slightly interrupted .... **24. A. lucida**

10a. Inflorescences cylindric, at apex 1.2–2.5 mm diam., glomerules interrupted below, continuous above, not massed in a head (Fig. 3.5d–h), drying yellowish ... 11

b. Inflorescences clavate, at apex 3–6 mm diam., glomerules massed in a head (Fig. 3.5i, j), drying rather dark brownish .... **8. A. quadrilocularis**

11a. Petiole 18–33 mm long. Leaves 15.5–33 by 6.5–13 cm, rather leathery. Inflorescences 9–44 mm long, 1.5–2.5 mm diameter .... **10. A. stellifera**

b. Petiole 9–23 mm long. Leaves 11–20 by 3.5–7.5 cm, papery. Inflorescences 7–16 mm long, 1.2–1.8 mm diameter .... **14. A. spec. E**

12a. Leaves with 4–17 nerve pairs. Inflorescences cylindric, or slightly clavate-shaped, but at apex not more than 3.5 mm diameter 13

b. Leaves with 10–14 nerve pairs. Inflorescences clavate (Fig. 3.5i, j), apical head 5–9 mm diameter . . . . **3. A. confusa**

13a. Nerves 12–17 pairs 14

b. Nerves 4–11 pairs 17

14a. Branchlets (sparsely) tomentose. Stipules often present, at least in young stages, narrowly ovate, slightly to strongly oblique. Petiole 5–15 mm long. Leaves 7–26 by 2–8.5 cm; above midrib (sparsely) tomentose, beneath (sparsely) tomentose. Inflorescences axillary to just below the leaves; 5–23 mm long, 1–2 mm diameter 15

b. Branchlets sparsely puberulous. Stipules early caducous (falcate). Petiole 14–51 mm long. Leaves 13.5–35 by 4.5–15 cm; above glabrous, beneath only nerves sparsely puberulous. Inflorescences below the leaves or borne on the upper branches; 16–55 mm long, 0.5–1 mm diameter . . . . **70. A. arborea**

15a. Leaf: base truncate or emarginate to cuneate; disc-like glands absent. Inflorescences: glomerules subglobose; flowers rather laxly set 16

b. Leaf: base emarginate to subcordate; disc-like glands occasionally present, small, along the margin (Fig. 3.3b). Inflorescences: glomerules ellipsoid; flowers densely set . . . . **88. A. spec. F**

16a. Stipules strongly oblique, rather long persistent. Leaf: base truncate to emarginate; marginal glands often distinct; apex acuminate to cuspidate. Inflorescences: peduncle 0–1 mm long; glomerules at base not or only slightly interrupted . . . . **85. A. selangorica**

b. Stipules narrowly ovate, some slightly oblique, present in young stages only. Leaf: base emarginate to cuneate; marginal glands often indistinct; apex cuspidate to caudate. Inflorescences: peduncle 2–4 mm long; glomerules at base interrupted for 0.5–1.5 mm . . . . **87. A. subcaudata**

17a. Inflorescences: peduncle distinct, 0.5–4 mm long; glomerules at least at base distinctly interrupted (1–3 mm), (sub)globose, 1–2.5 by 1–1.5 mm; bracts distinct or indistinct 18

b. Inflorescences: peduncle absent or minute, 0–2 mm long; glomerules indistinct, continuously set, or evenly slightly interrupted (up to 0.1 mm), or only at the very base slightly interrupted (up to 1 mm), ellipsoid and 1.5–2.5 by 0.5–1 mm, or subglobose and 0.5–1.2 by 0.5–0.7 mm; bracts mostly indistinct 22

18a. Leaf: texture leathery, often brittle; dots densely set, distinct. Flowers 1–3.5 mm long; anthers 0.3–0.6 mm long 19

b. Leaf: texture leathery to papery, not brittle; dots irregularly set, often fading or indistinct. Flowers 0.3–1.5 mm long; anthers 0.1–0.3 mm long 20

19a. Branchlets, petiole, and leaves subglabrous. Flowers 2–3.5 mm long; anthers 0.5–0.6 mm long. — West Java . . **86b. A. sphaeridiophora** var. **campanulata**

b. Branchlets, petiole, and leaves on midrib (sparsely) puberulous beneath and above. Flowers 1–2 mm long; anthers 0.3–0.4 mm long. — Peninsular Malaysia, Singapore, Sumatra . . . . **82. A. nervosa**

20a. Leaf: nerves 7–12 pairs. Inflorescences 1–2.5 mm diam.; glomerules 1–2.5 by 1–2 mm 21

b. Leaf: nerves 4–6 pairs. Inflorescences 1–1.3 mm diam.; glomerules 0.7–1.2 by c. 0.5 mm . . . . **69. A. antennifera**

21a. Stipules often early caducous. Leaf: only midrib near base tomentose above, glabrescent; dots distinct, but often fading. Inflorescences: bracts inconspicuous, shorter than the flowers; flowers 0.5–1 mm long; stamens (2 or) 3 (or 4) . . . . **83. A. penangensis**

b. Stipules often present in young stages. Leaf: midrib and nerves tomentose above, glabrescent; dots often indistinct. Inflorescences: bracts often conspicuous, as long as to longer than the flowers; flowers 0.3–0.5 mm long; stamens 2 . . . . **87. A. subcaudata**

22a. Leaf: margin at least near the apex glandular-crenate, glandular-serrate, or glandular-dentate; disc-like glands present, scattered within marginal vein arches (Fig. 3.3d) 23

b. Leaf: margin lowly undulate to lowly glandular-crenate; disc-like glands absent or present, few along the margin (Fig. 3.3b) 25

23a. Leaf: margin (lowly) glandular-dentate or (lowly) glandular-crenate (Fig. 3.1b, c), marginal glands surrounded by hairs 24

b. Leaf: margin more or less distinctly glandular-serrate (Fig. 3.1d), marginal glands not surrounded by hairs . . . . **27c. A. octandra** var. **malesiana**

24a. Leaves 7–20 cm long; margin lowly glandular-crenate (Fig. 3.1b); papery; nervation above flat or mostly only nerves near the margin (slightly) sunken. — Altitude 0–360 m . . . . **21. A. globifera**

b. Leaves 15–21 cm long; margin often glandular-serrate (Fig. 3.1c); slightly leathery; nerves and often veins (slightly) sunken. — Altitude 750–900 m . . . . **29. A. pseudoficifolia**

25a. Leaves up to 28 cm long; apex acuminate to cuspidate, sometimes cuspidate to caudate; nerves 8–12 pairs 26

b. Leaves up to 14 cm long; apex cuspidate to caudate; nerves 4–8 pairs 28

26a. Inflorescences 1.8–3.5 mm diam.; glomerules ellipsoid or indistinct; flowers densely set 27

b. Inflorescences 1–2 mm diam.; glomerules (sub)globose; flowers laxly set . . . . **87. A. subcaudata**

27a. Petiole 4–14 mm long, basal glands absent. Leaf: base cuneate to slightly attenuate; drying yellowish green, not darkening with age; disc-like glands often present, small, along the margin (Fig. 3.3b). Inflorescences 2–3.5 mm diam.; glomerules more concentrated apically; drying (light) yellow . . . . **4. A. frutescens**

b. Petiole 9–32 mm long, basal glands present, small. Leaf: base rounded to acute; drying green or brown, blackening with age; disc-like glands absent. Inflorescences 1.8–2.5 mm diam.; glomerules evenly distributed along the rachis; drying brownish . . . . **26. A. nigricans**

28a. Stipules early caducous, narrowly triangular, symmetric. Leaves drying bluish green above, brown beneath, often blackening with age; nerves 4–7 pairs . . 29

b. Stipules present in young stages, narrowly ovate, slightly oblique. Leaves drying orcheous-grey on both sides, not blackening with age; nerves 6–8 pairs . . . . **80. A. maingayi**

29a. Leaf: nerves 4–6 pairs, marginal arches fading; venation densely reticulate. Inflorescences 9–23 mm long; peduncle 0.5–2 mm long; glomerules distinct at base . . . . **69. A. antennifera**

b. Leaf: nerves 5–7 pairs, marginal arches distinct; venation laxly reticulate-scalariform. Inflorescences 6–14 mm long; peduncle 0–0.5 mm long; glomerules indistinct . . . . **81. A. microstachya**

Pistillate specimens

1a. Ovary (mostly) 2-locular 2

b. Ovary (mostly) 3- or more locular 18

2a. Septae and column (sparsely) hairy 3

b. Septae and column glabrous 8

3a. Leaves completely glabrous; basal glands present, often distinct; texture often rather leathery, drying shiny yellow-green to dull dark-green. Ovary glabrous or sparsely puberulous. Fruit glabrous or sparsely puberulous 4

b. Leaves at least sparsely puberulous beneath; basal glands absent or present but indistinct; texture often papery, drying dull dark-green or green-brown. Ovary puberulous. Fruit sparsely puberulous 7

4a. Petiole: basal glands large, black. Leaves drying shiny yellowish green to yellow; marginal glands absent. Up to 3 flowers per inflorescence. Fruits globose . . . . **16. A. aurea**

b. Petiole: basal glands small, greyish. Leaves drying slightly shiny yellowish green to green or brownish, often darkening with age; marginal glands present, small, greyish. Up to 7 flowers per inflorescence. Fruits (broadly) ovoid to globose, seldom ellipsoid . . . . 5 (**24. A. lucida**)

5a. Ovary glabrous. Fruit glabrous, ellipsoid or (broadly) ovoid to globose. — Peninsular Malaysia, Singapore, Sumatra 6

b. Ovary sparsely puberulous. Fruit (broadly) ovoid to globose, sparsely puberulous. — Mostly Java . . . . **24c. A. lucida** var. **pubescens**

6a. Fruit (broadly) ovoid to globose. — Peninsular Malaysia, Singapore, Sumatra . . . . **24a. A. lucida** var. **lucida**

b. Fruit ellipsoid. — North Sumatra . . . . **24b. A. lucida** var. **ellipsoidea**

7a. Leaves 12–28 cm long; margin (lowly) glandular-crenate (Fig. 3.1b); only sparsely hirsute beneath; drying green or brown, blackening with age; disc-like glands absent. Fruits drying dark brown to black with light sutures . . . . **26. A. nigricans**

b. Leaves 5–16 cm long; margin more or less distinctly glandular-serrate (Fig. 3.1d); (sparsely) puberulous above and beneath; drying brownish or yellowish green, not blackening with age; disc-like glands present, many, scattered in centre of marginal vein arches (Fig. 3.3d). Fruits drying orange-brown **27c. A. octandra** var. **malesiana**

8a. Flowers and fruits distinctly pedicelled, laxly set along the rachis (Fig. 3.6n, r–t) 9

b. Flowers and fruits (sub)sessile, densely clustered along the rachis (Fig. 3.6a–j, l, m) 13

9a. Branchlets, petiole, and leaves completely glabrous. Leaves drying light greyish green to yellowish green above and beneath, nervation beneath drying often in a lighter colour 10

b. Branchlets, petiole, and leaves at least beneath on midrib sparsely puberulous. Leaves drying greenish to dark bluish brown above, (dark) brown beneath, nervation beneath drying rather darkish 11

10a. Leaf: nerves 5–8 pairs; texture slightly leathery, drying dull greyish green to dark green; dots densely set, greyish. Up to 5 flowers per inflorescence, ovary mostly 3-locular, seldom 2-locular. Fruits ovoid, 12–15 by 10–13 mm, often drying irregularly ridged and corrugated; apex of endocarp caudate . . . . **7. A. prainiana**

b. Leaf: nerves 7–10 pairs; texture papery, drying shiny yellowish green or dark green; dots indistinct. Up to 11 flowers per inflorescence, ovary 2- or 3-locular. Fruits ellipsoid, 9–13 by 8–11 mm, drying smooth to punctulate; apex of endocarp acute . . . . **12a. A. symplocoides** var. **symplocoides**

11a. Leaf: base obtuse to cuneate; apex acuminate to cuspidate; nerves 6–9 pairs; dots distinct. Ovary 2- and 3-locular (seldom 4-locular); stigmas sessile to slightly raised, 0.5–1.5 mm long. Fruit ellipsoid to ovoid, not stiped, not beaked . . . 12

b. Leaf: base often (slightly) attenuate; apex cuspidate to caudate; nerves 4–6 pairs; dots indistinct. Ovary always 2-locular; stigmas raised, 2–5.5 mm long (Fig. 3.8r). Fruit narrowly ellipsoid, shortly stiped and beaked (Fig. 3.11i) . . . . **69. A. antennifera**

12a. Branchlets, petiole, and leaves on midrib (sparsely) puberulous beneath and above. Fruit ellipsoid to ovoid, sparsely hairy. — Peninsular Malaysia, Singapore, Sumatra . . . . **55. A. nervosa**

b. Branchlets, petiole, and leaves subglabrous. Fruit ellipsoid, glabrous. — West Java . . . . **86b. A. sphaeridiophora** var. **campanulata**

13a. Stipules narrowly triangular, seldom slightly oblique, mostly early caducous, sometimes present in young stages. Ovary and fruit smooth to punctulate, glabrous to sericeous 14

b. Stipules (narrowly) ovate, oblique, often rather persistent. Ovary and fruit ruminate-verrucate, puberulous (Fig. 3.9a, b) . . . . **85. A. selangorica**

14a. Pistillate flowers sessile or subsessile; ovary ellipsoid; stigmas sessile, 0.3–1.5 mm long, flattened on top of the ovary or perpendicular to the sides of the ovary. Fruit (sub)sessile, ellipsoid, not beaked 15

b. Pistillate flowers subsessile; ovary ovoid; stigmas slightly raised, 1.5–2.5 mm long, flattened to the sides of the ovary. Fruit subsessile, (narrowly) ovoid, beaked . . . . **81. A. microstachya**

15a. Stipules present in young stages, some (slightly) oblique. Leaf: either base emarginate to subcordate and apex acuminate to cuspidate or base obtuse to attenuate and apex cuspidate to caudate; dots irregularly or laxly set, greyish, fading or indistinct. Flowers and fruits sessile 16

b. Stipules mostly early caducous. Leaf: base obtuse to slightly attenuate; apex acuminate to cuspidate; dots densely set, blackish, often fading. Flowers and fruits subsessile . . . . **83. A. penangensis**

16a. Leaf: base subcordate or emarginate to cuneate; nerves 8–17 pairs; drying greyish green to blackish above, (light) brown beneath 17

b. Leaf: base attenuate; nerves 6–8 pairs; drying dull orcheous-grey to greenish grey above, brownish grey beneath . . . . **80. A. maingayi**

17a. Leaf: base obtuse to cuneate; apex cuspidate to caudate; disc-like glands absent. Flower: stigmas densely laciniate. Fruit ellipsoid to ovoid, 8–12 mm long . . . . **87. A. subcaudata**

b. Leaf: base subcordate to emarginate; apex acuminate to cuspidate; disc-like glands occasionally present, small, along the margin (Fig. 3.3b). Flower: stigmas ribbed, papillate. Fruit unknown, possibly larger than in *A. subcaudata.* — Swampy ground, Johore . . . . **88. A. spec. F**

18a. Inflorescences and infructescences bearing only one single flower resp. fruit on top of the rachis (Fig. 3.6u). Stigmas broad, ribbed, flattened on top of the ovary (Fig. 3.8p). Fruits globose with often flat or sunken stigma (Fig. 3.11l); pericarp 0.5–5 mm thick, fleshy 19

b. Inflorescences and infructescences bearing more than one flower resp. fruit along the rachis. Stigmas elongated or broad, smooth to laciniate, on top of the ovary to ascending from the sides of the ovary. Fruits subglobose, ovoid or ellipsoid, stigmas not sunken; pericarp 0.2–3 mm thick, not or slightly fleshy 22

19a. Branchlets, petiole, and leaves sparsely puberulous to tomentose. Inflorescences and infructescences (sparsely) tomentose; ovary and fruit (sparsely) puberulous, glabrescent 20

b. Branchlets, petiole, and leaves completely glabrous. Inflorescences and infructescences sparsely tomentose, glabrescent; ovary and fruit glabrous 21

20a. Branchlets and leaves tomentose. Leaves 9–25 cm long; nerves 10–14 pairs. Inflorescences and infructescences tomentose. Fruits 16–21 mm long, (sparsely) puberulous . . . . **3. A. confusa**

b. Branchlets and leaves sparsely puberulous. Leaves 6–20 cm long; nerves 8–10 pairs. Inflorescences and infructescences (sparsely) tomentose. Fruits 9–15 mm long, sparsely hairy, glabrescent . . . . **4. A. frutescens**

21a. Flower: ovary 4- (or 3- or 5-)locular. Fruit globose, 15–21 mm long (25–30 mm when fresh); pericarp 3–4 mm thick . . . . **8. A. quadrilocularis**

b. Flower: ovary 3-locular. Fruit ovoid to subglobose, 14–16 mm long; pericarp 1–2 mm thick . . . . **14. A. spec. E**

22a. Stipules caducous or persistent, narrowly triangular, sometimes slightly oblique, or large and falcate with scattered disc-like glands along the margin beneath. Ovary and fruit smooth to punctulate, glabrous to sericeous 23

b. Stipules (narrowly) ovate, oblique, often rather persistent. Ovary and fruit ruminate-verrucate, puberulous (Fig. 3.9c, d) . . . . **85. A. selangorica**

23a. Leaf: margin lowly glandular-serrate to glandular-crenate, marginal glands distinct, surrounded by hairs. Pistillate flowers sessile, densely set along the rachis (Fig. 3.6a, b, c, i). Fruit globose; septae and column sparsely puberulous, but often glabrescent 24

b. Leaf: margin subentire to lowly glandular-crenate, marginal glands indistinct or if distinct, then not surrounded by hairs. Pistillate flowers subsessile or distinctly pedicelled, laxly set along the rachis or only densely set at apical 7/8–3/4 part of the rachis (Fig. 3.6e–h, j–m, r–t). Fruit ovoid or ellipsoid; septae and column glabrous 25

24a. Leaves 7–20 cm long; margin lowly glandular-crenate (Fig. 3.1b); papery; nervation flat above or mostly only nerves near the margin (slightly) sunken. — Altitude 0–360 m . . . . **21. A. globifera**

b. Leaves 15–21 cm long; margin often glandular-serrate (Fig. 3.1d); slightly leathery; nerves and often veins (slightly) sunken. — Altitude 750–900 m . . . . **29. A. pseudoficifolia**

25a. Branchlets, petiole, and leaves completely glabrous 26

b. Branchlets, petiole, and leaves at least beneath sparsely puberulous 28

26a. Leaves 6–17 cm long, papery to slightly leathery; nerves 5–10 pairs. Flowers and fruits evenly laxly set along the rachis (Fig. 3.6s, t). Ovary ovoid; stigmas elongated, perpendicular to or ascending from the sides of the ovary, not resembling a 6-rayed disc 27

b. Leaves 15–33 cm long, rather leathery; nerves 10–14 pairs. Flowers and fruits rather densely set mostly at apical part of the rachis (Fig. 3.6g). Ovary cylindrical; stigmas broad, flattened on and connate to the top of the ovary, resembling a 6-rayed disc (cf. Fig. 3.8o) .... **10. A. stellifera**

27a. Leaf: nerves 5–8 pairs; texture slightly leathery, drying dull greyish green to dark green; dots densely set, greyish. Flowers up to 5; ovary often rather lobed. Fruits ovoid, 12–15 by 10–13 mm, often drying irregular ridged and corrugate; apex of endocarp caudate .... **7. A. prainiana**

b. Leaf: nerves 7–10 pairs; texture papery, drying shiny yellowish green or dark green; dots indistinct. Flowers up to 11; ovary not lobed. Fruits ellipsoid, 9–13 by 8–11 mm, drying smooth to punctulate; apex of endocarp acute .... **12a. A. symplocoides** var. **symplocoides**

28a. Stipules large, falcate, often rather persistent. Flowers and fruits mostly rather densely set at apical 7/8–3/4 part of the rachis, (sub)sessile (Fig. 3.6h, k). Stigmas smooth, flattened to the sides of the ovary, 1–5 mm long (Fig. 3.8q) 29

b. Stipules narrowly ovate, sometimes oblique, mostly caducous. Flowers and fruits laxly set along the rachis, (shortly) pedicelled (Fig. 3.6m, s, t). Stigmas ribbed to papillate, perpendicular to or ascending from the sides of the ovary, 0.5–1.5 mm long 31

29a Leaves glabrous or only sparsely hairy beneath; nerves slightly prominent to flat above 30

b. Leaves (sparsely) hirsute on both sides; nerves more or less sunken above ....**39. A. lunata**

30a. Stipules 6–20 by 11–37 mm, often long persistent. Petiole: upper pulvinus swollen, 5–11 by 3–6 mm. Leaves 14–47 cm long; base cordate; nerves beneath strongly prominent, not fading towards the margin .... **36. A. benthamiana**

b. Stipules 4–8 by 11–18 mm, present in young stages. Petiole: upper pulvinus distinct, but not extremely so, 2–6 by 1.5–2.5 mm. Leaves 8–25 cm long; base emarginate to rounded; nerves beneath prominent, fading towards the margin .. .. **38. A. falcifera**

31a. Leaves drying greenish, brownish, or bluish above, brownish beneath; dots (rather) densely set, blackish, distinct, sometimes fading. Inflorescences and infructescences (sparsely) puberulous 32

b. Leaves drying greyish green on both sides; dots absent. Inflorescences and infructescences subglabrous .... **13. A. whitmorei**

32a. Petiole 8–21 mm long. Leaf: nerves 6–9 pairs. Inflorescences 5–9 mm long; ovary ellipsoid, 2- and 3-locular (seldom 4-locular). Infructescences 7–40 mm long; fruiting pedicel 0.5–8 mm long 33

b. Petiole 14–51 mm long. Leaf: nerves 11–16 pairs. Inflorescences 12–36 mm long; ovary ovoid to globose, 3-locular (seldom 4-locular). Infructescences 15–82 mm long; fruiting pedicel 5–12 mm long .... **70. A. arborea**

33a. Branchlets, petiole, and leaves on midrib (sparsely) puberulous above and beneath. Fruit ellipsoid to ovoid, sparsely hairy. — Peninsular Malaysia, Singapore, Sumatra . . . . **82. A. nervosa**

b. Branchlets, petiole, and leaves subglabrous. Fruit ellipsoid, glabrous. — West Java . . . . **86b. A. sphaeridiophora** var. **campanulata**

10.3.5 – ***Key to the species of Borneo***

Staminate specimens

1a. Staminate inflorescences strongly interrupted; all individual glomerules distinct, widely set along the rachis (Fig. 3.5k, l) 2

b. Staminate inflorescences continuous to more or less interrupted at base; individual glomerules at least at apex of rachis indistinct, not or only slightly spaced (Fig. 3.5a–j) 11

2a. Branchlets, petioles and leaves completely glabrous 3

b. Branchlet, petioles and leaves on midrib beneath sparsely puberulous 6

3a. Leaves 6.5–18 cm long, smooth or young ones irregularly lowly granular beneath 4

b. Leaves 13–32 cm long, strongly white-granular beneath on nervation only . . . . **2. A. chondroneura**

4a. Leaf: nerves 5–10 pairs, drying approximately the same shade of grey-yellow-green as the lamina. Inflorescences: glomerules more or less evenly set along the rachis 5

b. Leaf: nerves 9–12 pairs, drying often beneath lighter green than the lamina. Inflorescences: glomerules apically less spaced than at base . . . . . **9. A. sarawakensis**

5a. Leaf: nerves 5–8 pairs; texture slightly leathery, drying dull greyish green to dark green; dots densely set, greyish . . . . **7. A. prainiana**

b. Leaf: nerves 7–10 pairs; texture papery, drying shiny yellowish green or dark green; dots indistinct . . . . **12. A. symplocoides**

6a. Stipules (narrowly) ovate, sometimes slightly oblique, or falcate; caducous, but still present in young stages. Leaf: base cuneate to rounded; nerves 6–13 pairs .7

b. Stipules falcate, persistent. Leaf: base emarginate-truncate; nerves 14–23 pairs . . . . **76. A. grandistipula**

7a. Branchlets sparsely tomentose to subglabrous. Leaves only sparsely tomentose to subglabrous beneath; drying yellowish green on both sides 8

b. Branchlets tomentose. Leaf: at least (sparsely) tomentose beneath; drying dark brownish to greenish brownish above, brown beneath 9

8a. Leaves 5.5–13.5 cm long; dots irregularly densely set, greyish, fading. Inflorescences clustered up to 5 together, 7–17 mm long, 1.5–2 mm diam.; glomerules globose. — North Borneo, Mt Kinabalu and environments, above 1000 m . . . . **5. A. fulvovittata**

b. Leaves 10–19 cm long; dots absent. Inflorescences clustered up to 15 together, 9–35 mm long, 0.5–1.5 mm diam.; glomerules ellipsoid. — Sarawak, along or partly in rivers or at tidal influence zones . . . . **11. A. stenostachys**

9a. Stipules (narrowly) ovate, present in young stages. Leaf: marginal glands few, small, indistinct; texture rather papery; (sparsely) hirsute on both sides. Inflorescence rachis 0.3–0.5 mm diam.; glomerules 0.8–1.2 by 0.5–0.8 mm 10

b. Stipules falcate, often early caducous. Leaf: marginal glands many, large, distinct; texture rather leathery; only (sparsely) tomentose beneath. Inflorescence rachis 0.8–1.5 mm diam.; glomerules 1.5–2.5 by 1.5–2.5 mm ...... **78. A. illustris**

10a. Leaves 11–25 by 5–11 cm. Inflorescences 10–20 clustered together, 11–47 mm long .... **75. A. elmeri**

b. Leaves 5.5–13 by 2–4.5 cm. Inflorescences 2–5 clustered together, 7–12 mm long .... **84. A. rhacostyla**

11a. Staminate rachis continuously floriferous from apex to base, though individual glomerules sometimes minutely spaced; peduncle absent, seldom minute (Fig. 3.5a, b) 12

b. Staminate rachis at least at base free of flowers; peduncle more than 1 mm long (Fig. 3.5c–j) 14

12a. Petiole and leaf at least beneath puberulous. Inflorescences continuous, glomerules uninterrupted, indistinct 13

b. Petiole and leaf completely glabrous. Inflorescences continuous, glomerules slightly interrupted, distinct .... **24. A. lucida**

13a. Leaves 12–28 cm long; margin (lowly) glandular-crenate (Fig. 3.1b); only sparsely hirsute beneath; drying green or brown, blackening with age; disc-like glands absent .... **26. A. nigricans**

b. Leaves 5–16 cm long; margin more or less distinctly glandular-serrate (Fig. 3.1d); (sparsely) puberulous on both sides; drying brownish or yellowish green, not blackening with age; disc-like glands many, scattered in centre of marginal vein arches (Fig. 3.3d) .... **27c. A. octandra** var. **malesiana**

14a. Stipules falcate, persistent or caducous. Leaf: marginal glands in margin, small and indistinct; disc-like glands often present, distinct, along the margin (Fig. 3.3c); nerves 9–18 pairs. Inflorescences (when mature) brush-like due to exserted stamens, glomerules indistinct, densely set at apical 3/4–7/8 of the rachis (Fig. 3.5c). Flowers: stamens strongly exserted, c. thrice as long as the sepals (Fig. 3.7n); anthers 0.1–0.2 mm long 15

b. Stipules narrowly ovate, oblique or not, seldom falcate (but then leaf nerves up to 9 pairs or inflorescences interrupted), caducous but sometimes still present in young stages. Leaf: marginal glands often rather distinct; disc-like glands absent or occasionally present, then indistinct, along margin (Fig. 3.3b), seldom scattered at base within marginal vein arches (Fig. 3.3a). Inflorescences (when mature) not brush-like, glomerules at least at base distinct, slightly to strongly interrupted (if glomerules continuous and indistinct, then either flowers laxly set or stamens not exserted or inflorescences clavate-shaped) (Fig. 3.5d–j). Stamens not to slightly exserted (up to twice as long as the sepals), if exserted, then anthers 0.3–0.6 mm long 19

15a. Leaves glabrous or only beneath sparsely hairy; nerves slightly prominent to flat above 16

b. Leaves: above at least on midrib (sparsely) hirsute, beneath (sparsely) hirsute; nerves more or less sunken above 17

16a. Stipules 6–20 by 11–37 mm, often long persistent. Petiole: upper pulvinus swollen, 5–11 by 3–6 mm. Leaves 14–47 cm long; base cordate; nerves raised beneath, not fading towards the margin .... **36. A. benthamiana**

b. Stipules 4–8 by 11–18 mm, present in young stages. Petiole: upper pulvinus distinct, but not extremely so, 2–6 by 1.5–2.5 mm. Leaves 8–25 cm long; base emarginate to rounded; nerves prominent beneath, fading towards the margin . . . . **38. A. falcifera**

17a. Nervation strongly sunken above, giving the leaf a bullate appearance 18

b. Only nerves sunken, sometimes near margin and apex some veins sunken, otherwise leaves flat, smooth above . . . . **39. A. lunata**

18a. Leaves 9–20 cm long . . . . **37. A. bullatissima**

b. Leaves 21–29 cm long . . . . **40. A. sylvestri**

19a. Branchlets and petiole very sparsely puberulous to glabrous; leaves completely glabrous or only very sparsely puberulous on midrib beneath near base. Inflorescences: rachis (sub)glabrous 20

b. Branchlets and petiole (sparsely) puberulous; leaves at least on midrib beneath (sparsely) puberulous to tomentose. Inflorescences: rachis (sparsely) puberulous to tomentose 25

20a. Leaves 6–20 by 1.5–8 cm. Inflorescences cylindric or interrupted (Fig. 3.5d–i), 5–41 mm long, 0.8–3.5 mm diameter 21

b. Leaves 15–33 by 5–13 cm. Inflorescences clavate (Fig. 3.5j), 12–36 mm long, apical head 3–8 mm diameter . . . . **6. A. nitida**

21a. Leaf: apex acuminate to cuspidate; texture papery or leathery; drying greyish to yellowish green on both sides, sometimes greenish or brownish above, brown beneath but then apex acuminate and texture leathery; nerves 7–12 pairs. Glomerules interrupted at base, or if only minutely spaced at base, then inflorescences more then 2 mm diam.; inflorescences drying yellowish or brownish 22

b. Leaf: apex cuspidate; texture papery; drying greenish or bluish brown above, often blackening, (light) brown beneath; nerves 4–6 pairs. Glomerules only at base slightly spaced and inflorescences 1–1.3 mm diam.; inflorescences drying dark brownish . . . . **69. A. antennifera**

22a. Leaf: texture papery, dull; drying greyish green to yellowish green on both sides; dots absent or indistinct. Glomerules 0.8–2 mm long. Flowers drying yellowish; stamens not to slightly exserted, shorter than to slightly longer than sepals . 23

b. Leaf: texture leathery, shiny; drying greenish to brownish above, brownish beneath; dots often irregularly set, distinct, but often fading. Glomerules 2–3 mm long. Flowers drying brownish; stamens exserted, c. twice as long as sepals (Fig. 3.7j) . . . . **72. A. caloneura**

23a. Branchlets, petiole, and leaf on midrib beneath very sparsely puberulous. Inflorescences 5–22 mm long, 1–3.5 mm diam.; glomerules ellipsoid, at base interrupted, distinct, apically continuous, indistinct 24

b. Branchlets, petiole, and leaf completely glabrous. Inflorescences 14–41 mm long, 0.8–1.2 mm diam.; glomerules subglobose, strongly interrupted at base, at apex less, but distinct throughout . . . . **9. A. sarawakensis**

24a. Inflorescences 1–1.5 mm diam.; glomerules rather distinctly interrupted at base of rachis (Fig. 3.5g) . . . . **1. A. banahaensis**

b. Inflorescences 2–3.5 mm diam.; glomerules at base only slightly interrupted (Fig. 3.5i) . . . . **4. A. frutescens**

25a. Inflorescences 1–6 clustered together; glomerules subglobose to ellipsoid, distinct to indistinct, (slightly) interrupted at base, decreasingly spaced towards the apex 26

b. Inflorescences 4–14 clustered together; glomerules ellipsoid, distinct, spaced rather evenly interruptedly along the rachis. — Inflorescences 9–35 mm long, 0.5–1.5 diam.; glomerules 1–1.5 by 0.5–0.8 mm. Sarawak, along or partly in rivers or at tidal zones . . . . **11. A. stenostachys**

26a. Leaves drying greyish green to yellowish green. Inflorescences 2–9 mm diam.; glomerules clustered strongly apically on fleshy rachis (Fig. 3.5i, j); drying yellowish 27

b. Leaves drying greenish or brownish. Inflorescences 0.5–2.2 mm diam.; glomerules not clustered densely apically (Fig. 3.5d–h); drying light to dark brown . . . 28

27a. Branchlets and leaves tomentose. Leaf: nerves 10–14 pairs. Inflorescences 12–32 mm long, tomentose; apical head 5–9 mm diameter . . . . **3. A. confusa**

b. Branchlets and leaves sparsely tomentose. Leaf: nerves 8–10 pairs. Inflorescences 5–22 mm long, (sparsely) tomentose; apical head 2–3.5 mm diameter . . . . **4. A. frutescens**

28a. Leaves: nerves 4–10 pairs 29

b. Leaves: nerves 10–17 pairs 35

29a. Leaf: apex acuminate to cuspidate; texture (rather) leathery; dots blackish, often distinct. Inflorescences 14–57 mm long; glomerules distinct, at least at base distinctly interrupted, 1.5–2.5 by 1.5–2 mm 30

b. Leaf: apex cuspidate to caudate; texture (rather) papery; dots greyish, often indistinct or fading. Inflorescences 5–23 mm long; glomerules distinct or not, distinctly or only slightly interrupted at base, 0.5–1.5 (seldom up to 2.5) by 0.3–1.5 mm, or indistinct and flowers seemingly continuously laxly set along the rachis . 31

30a. Stipules falcate, early caducous or still present in young stages. Leaf: dots irregularly set, fine; midrib sparsely tomentose above. Inflorescences: glomerules distinctly interrupted throughout. Stamens 3 or 4 . . . . **78. A. illustris**

b. Stipules narrowly ovate, (slightly) oblique, early caducous. Leaf: dots densely set, large; glabrous above. Inflorescences: glomerules at base strongly interrupted, less at apex. Stamens 2 or 3 . . . . **82. A. nervosa**

31a. Stipules slightly asymmetric, mostly early caducous, sometimes present in young stages. Branchlets, petiole, and leaf only on midrib beneath sparsely puberulous 32

b. Stipules slightly to strongly oblique, present in young stages or longer. Branchlets, petiole, and leaf at least on midrib above and beneath (sparsely) tomentose . 33

32a. Petiole 7–15 mm long. Leaves drying rather shiny greenish on both sides, not blackening with age; nerves 7–10 pairs . . . . **68. A. alia**

b. Petiole 4–8 mm long. Leaves drying above greenish to brown, beneath brown, blackening with age; nerves 4–6 pairs . . . . **69. A. antennifera**

33a. Stipules slightly to strongly oblique, caducous, present in young stages only. Leaves above only on midrib (sparsely) puberulous to (sparsely) tomentose. Inflorescences: glomerules at least at base distinct, globose, compact (Fig. 3.5d, e); stamens not to slightly exserted 34

b. Stipules strongly oblique, often rather long persistent. Leaves above sparsely hirsute. Inflorescences: glomerules lax, indistinct, flowers seemingly continuously laxly set along the rachis (Fig. 3.5h); stamens exserted . . . **79. A. lagenocarpa**

34a. Leaf: base often slightly attenuate; drying greenish grey to greenish brown above, greyish brown beneath; nerves 6–8 pairs; nervation laxly reticulate, slightly scalariform. Inflorescences 5–9 mm long; glomerules c. 1 by 0.5 mm . . . . **77. A. granularis**

b. Leaf: base cuneate to emarginate; drying (dark) greenish brown above, brown beneath; nerves 8–17 pairs; nervation distinct, often distinctly reticulate-scalariform. Inflorescences 9–23 mm long; glomerules 1–2.5 by 1–1.5 mm . . . . **87. A. subcaudata**

35a. Branchlets (sparsely) tomentose. Petiole 5–38 mm long, (sparsely) tomentose. Leaves at least (sparsely) tomentose beneath 36

b. Branchlets sparsely puberulous. Petiole 14–51 mm long, sparsely puberulous. Leaves only on midrib sparsely puberulous beneath . . . . **70. A. arborea**

36a. Stipules narrowly ovate, sometimes oblique. Petiole 5–17 mm long. Leaves: texture (rather) papery; dots indistinct or fading. Glomerules interrupted at base only, rather continuously set apically (Fig. 3.5e, g), subglobose or ellipsoid, 1–2.5 by 1–1.5 mm 37

b. Stipules falcate. Petiole 8–38 mm long. Leaves: texture rather leathery; dots irregularly set, fine. Glomerules mostly distinctly interrupted throughout, globose, 1.5–2.5 by 1.5–2.5 mm . . . . **78. A. illustris**

37a. Leaf: nerves 10–12 pairs; nervation laxly reticulate. Inflorescences 18–47 mm long; glomerules ellipsoid . . . . **71. A. basilanensis**

b. Leaf: nerves 8–17 pairs; nervation densely reticulate, (slightly) scalariform. Inflorescences 9–23 mm long; glomerules (sub)globose . . . . **87. A. subcaudata**

Pistillate specimens

1a. Ovary (mostly) 2-locular 2

b. Ovary (mostly) 3- or more locular 17

2a. Septae and column (sparsely) hairy 3

b. Septae and column glabrous 5

3a. Petiole and leaves at least sparsely puberulous beneath. Ovary (sparsely) tomentose. Fruit ovoid to ellipsoid, (sparsely) tomentose 4

b. Petiole and leaves completely glabrous. Ovary glabrous. Fruit globose, glabrous . . . . **24a. A. lucida** var. **lucida**

4a. Leaves 12–28 cm long; margin (lowly) glandular-crenate (Fig. 3.1b); only sparsely hirsute beneath; drying green or brown, blackening with age; disc-like glands absent. Fruits drying dark brown to black with light sutures . . . . **26. A. nigricans**

b. Leaves 5–16 cm long; margin more or less distinctly glandular-serrate (Fig. 3.1d); (sparsely) puberulous on both sides; drying brownish or yellowish green, not blackening with age; disc-like glands many, scattered within marginal vein arches (Fig. 3.3d). Fruits drying orange-brown . . . . **27c. A. octandra** var. **malesiana**

5a. Ovary and fruit (sub)sessile, pedicel up to 0.5 mm long 6

b. Ovary and fruit distinctly pedicelled, pedicel more than 1 mm long 11

6a. Stipules early caducous or present in young stages only, (narrowly) ovate, sometimes oblique. Ovary ellipsoid, densely to sparsely sericeous or puberulous; stigmas 0.5–1.5 mm long. Fruits narrowly ovoid or ellipsoid, seldom globose, not beaked, (sparsely) tomentose to subglabrous 7

b. Stipules often rather persistent, narrowly ovate, strongly oblique to falcate. Ovary narrowly ovoid, flask-shaped to subfusiform, densely tomentose; stigmas 4.5–6 mm long (Fig. 3.8o). Fruits flask-shaped to subfusiform, beaked, (sparsely) tomentose (Fig. 3.11k) . . . . **79. A. lagenocarpa**

7a. Stipules (narrowly) ovate, symmetric. Flowers and fruits rather laxly set along the whole rachis (Fig. 3.6p, q) 8

b. Stipules narrowly ovate, more or less oblique. Flowers and fruits rather densely set at least at apical part of the rachis (Fig. 3.6e, j, l, m) 9

8a. Leaves 11–25 by 5–11 cm. Inflorescences 10–42 mm long; stigmas flattened on top and to the sides of the ovary, densely laciniate. Infructescences 16–57 mm long . . . . **75. A. elmeri**

b. Leaves 5.5–13 by 2–4.5 cm. Inflorescences 10–23 mm long; stigmas at first ascending from top to an apical bunch before flattening to the sides of the ovary, ribbed and papillate. Infructescences 12–33 mm long . . . . . . **84. A. rhacostyla**

9a. Leaf: nerves 6–10 pairs. Inflorescences 0.5–0.8 mm diam., (sparsely) sericeous. Ovary sparsely sericeous at base, glabrescent; stigma lowly papillate to laciniate. Fruits sparsely sericeous at base only, glabrescent, granular 10

b. Leaf: nerves 8–17 pairs. Inflorescences 1.5–2 mm diam., tomentose. Ovary densely sericeous; stigmas densely laciniate. Fruits (sparsely) sericeous, punctate . . . . **87. A. subcaudata**

10a. Stipules slightly asymmetric, early caducous, sometimes still present in young stages. Leaves drying rather shiny greyish green on both sides; marginal glands distinct, black to grey; above glabrous, beneath only midrib and nerves puberulous . . . . **68. A. alia**

b. Stipules slightly to strongly oblique, present in young stages. Leaves drying greenish grey to greenish brown above, greyish brown beneath; marginal glands indistinct; above at least midrib sparsely puberulous, beneath sparsely puberulous . . . . **77. A. granularis**

11a. Branchlets, petiole, and leaf completely glabrous. Leaves drying yellowish to greyish green on both sides. Ovary glabrous; stigmas 0.2–1 mm long. Fruits glabrous, drying yellowish; pericarp 0.2–1 mm thick 12

b. Branchlets, petiole, and leaf at least on midrib beneath sparsely puberulous. Leaves drying dark greyish, greenish, bluish, or brownish above, brownish beneath. Ovary sericeous to sparsely puberulous at base only, if glabrous than stigmas longer than 1.5 mm; stigmas 0.8–5.5 mm long. Fruits sericeous to glabrous, drying dark to orange-brown; pericarp 0.5–1.5 mm thick 14

12a. Leaf: nerves 7–11 pairs, regularly set; dots indistinct. Flowers up to 11; ovary not lobed. Fruits ellipsoid or fusiform, 9–13 by 8–11 mm or 14–17 by 7–10 mm, drying smooth to punctulate; apex of endocarp acute 13 (**12. A. symplocoides**)

b. Leaf: nerves 5–9 pairs, with often larger gap between 3rd and 4th pair; dots densely set, fine, greyish. Flowers up to 5; ovary lowly lobed. Fruits ovoid, 12–15 by 10–13 mm, often drying irregularly ridged and corrugated; apex of endocarp caudate . . . . **7. A. prainiana**

13a. Fruits fusiform, 14–17 mm long; pedicel 11–35 mm long . . . .**12b. A. symplocoides** var. **chalarocarpa**

b. Fruits ovoid, 9–13 mm long; pedicel 2–7 mm long . . . .**12a. A. symplocoides** var. **symplocoides**

14a. Leaf: dots indistinct or fading, if distinct then laxly irregularly set. Flower: pedicel 1–3 mm long; ovary (narrowly) ovoid; stigmas more or less raised, 1.5–5.5 mm long, free, perpendicular. Fruit (narrowly) ovoid to slightly flask-shaped or fusiform, slightly stiped and/or beaked 15

b. Leaf: dots densely set, large, black. Flower: pedicel 0.8–1 mm long; ovary ellipsoid; stigmas sessile, 0.8–1.2 mm long. Fruit ellipsoid to subglobose, not stiped nor beaked . . . . **82. A. nervosa**

15a. Leaf: apex acuminate; drying greenish or reddish brown above; nerves 7–12 pairs. Ovary 2- and 3-locular; stigmas 1.5–2.5 mm long. Fruits not or only very slightly stiped, 13–22 mm long; pericarp 0.8–1.5 mm thick 16

b. Leaf: apex cuspidate; drying dark greenish blue above; nerves 4–6 pairs. Ovary 2-locular, never 3-locular; stigmas 2.5–5.5 mm long. Fruits shortly stiped, 7–10 mm long; pericarp 0.5–0.8 mm thick . . . . **69. A. antennifera**

16a. Branchlets, petioles, and leaves only on midrib and nerves beneath very sparsely puberulous, glabrescent. Leaf: texture leathery; dots irregularly set, distinct. Ovary rugose, (sub)glabrous. Fruits (sub)glabrous; apex of endocarp acute . . . . **72. A. caloneura**

b. Branchlets, petioles and leaves beneath (sparely) tomentose. Leaf: texture papery; dots often indistinct. Ovary smooth, (sparsely) sericeous. Fruits sparsely puberulous; apex of endocarp caudate . . . . **71. A. basilanensis**

17a. Leaf: disc-like glands absent or only at base or along the margin (Fig. 3.3a–c). Flowers and fruits densely set only at apical part of rachis, or laxly set along the rachis (Fig. 3.6e–t); subsessile to distinctly pedicelled. Fruit: septae and column glabrous 18

b. Leaf: disc-like glands scattered within the marginal vein arches (Fig. 3.3d). Flowers and fruits densely set along the rachis (Fig. 3.6c, i), sessile. Fruit: septae and column sparsely sericeous . . . . **24d. A. lucida** var. **trilocularis**

18a. Flowers and fruits subsessile, densely set only along apical 7/8–3/4 of the rachis (Fig. 3.6h, k). Stigmas sessile, smooth, flattened to the sides of the ovary (Fig. 3.8q). Fruits ovoid with stigma remnant ascending. Leaf: disc-like glands distinct, along the margin (Fig. 3.3c) 19

b. Flowers and fruits distinctly pedicelled, set rather laxly along the whole rachis (Fig. 3.6s, t) or singly apically (Fig. 3.6u, v). Stigmas sessile to raised, ribbed to laciniate, perpendicular to, or ascending from the sides of the ovary. Fruits ellipsoid to globose, if ovoid, then distinctly pedicelled and stigma remnants usually not ascending. Leaf: disc-like glands absent, or only a few distinct ones along the margin, sometimes few scattered near base within the marginal vein arches (Fig. 3.3a, b) 23

19a. Leaves glabrous or only sparsely hairy beneath; nerves slightly prominent to flat above 20

b. Leaves at least on midrib and beneath (sparsely) hirsute above; nerves more or less sunken above 21

20a. Stipules 6–20 by 11–37 mm, often long persistent. Petiole upper pulvinus swollen, 5–11 by 3–6 mm. Leaves 14–47 cm long; base cordate; nerves beneath raised, not fading towards the margin .... **36. A. benthamiana**

b. Stipules 4–8 by 11–18 mm, present in young stages. Petiole upper pulvinus distinct, but not extremely so, 2–6 by 1.5–2.5 mm. Leaves 8–25 cm long; base emarginate to rounded; nerves beneath prominent, fading towards the margin .. .. **38. A. falcifera**

21a. Nerves and venation strongly impressed above and giving the leaf a bullate appearance 22

b. Only nerves impressed, sometimes near margin and apex some veins impressed, leaves flat, smooth above ....**39. A. lunata**

22a. Leaves 9–20 cm long ....**37. A. bullatissima**

b. Leaves 21–29 cm long .... **40. A. sylvestri**

23a. Inflorescences and infructescences bearing usually only one single flower or fruit respectively on top of the rachis (Fig. 3.6u, v) (seldom few clustered apically). Stigmas broad, raised or sunken (if narrow, then altitude > 1000 m, Mt Kinabalu or other mountains in northern Borneo). — Fruit sometimes globose with sunken stigmas and thick fleshy pericarp 24

b. Inflorescences and infructescences bearing more than one flower or fruit respectively along the rachis (Fig. 3.6s, t). Stigmas narrow 30

24a. Fruits ellipsoid or (broadly) ovoid with prominent stigmas, seldom subglobose; pericarp 0.5–1.5 mm thick. Ovary ovoid, stigmas slightly raised, ribbed and margins laciniate, or cylindric and stigmas broad and prominent (Fig. 3.8o); stigmas 1–2 mm long 25

b. Fruits globose with sunken stigmas (Fig. 3.11l), seldom ovoid, but then sutures ridged; pericarp 0.5–6 mm thick. Ovary globose, stigmas broad, flat, 0.5–1 mm long, slightly ribbed or laxly laciniate (Fig. 3.8p) 27

25a. Branchlets, petiole, and leaves on midrib and nerves beneath sparsely hairy. Inflorescences and flowers (sparsely) puberulous to tomentose. Infructescences and pedicels sparsely puberulous. Fruits (broadly) ovoid to globose, 8–12 mm long; apex of endocarp acute 26

b. Branchlets, petiole, and leaves completely glabrous. Inflorescences and flowers subglabrous. Infructescences and pedicels glabrous. Fruits ovoid to ellipsoid, 13–21 mm long; apex of endocarp caudate ....**9. A. sarawakensis**

26a. Leaf: 5.5–13.5 cm long; dots irregularly densely set, greyish, fading. Stigmas slightly raised, narrow, not prominent. Fruits glabrous, drying brownish with light yellow-brown sutures; stigmas narrow, not extremely thick. — North Borneo, Mt Kinabalu and environments, above 1000 m .... **5. A. fulvovittata**

b. Leaf: 10–19 cm long; dots absent. Stigmas sessile, broad, prominent. Fruits sometimes sparsely puberulous near base, drying light yellowish; stigmas broad, thick. — Sarawak, along or partly in rivers or tidal zones ..**11. A. stenostachys**

27a. Branchlets and leaves (sparsely) hairy to glabrous. Leaf: nerves 8–13 pairs. Inflorescences sparsely tomentose to subglabrous. Ovary sparsely puberulous to glabrous. Fruits sparsely puberulous to glabrous 28

b. Branchlets and leaves tomentose. Leaf: nerves 10–14 pairs. Inflorescences tomentose. Ovary puberulous. Fruits (sparsely) puberulous ...... **3. A. confusa**

28a. Branchlets and leaves (very) sparsely puberulous, glabrescent. Leaves 6.5–21 cm long, papery; nerves 8–11 pairs. Ovary mostly 3-locular, occasionally 4-locular, sparsely puberulous to glabrous. Fruits 9–18 mm long; pericarp 0.5–3(–6) mm thick 29

b. Branchlets and leaves completely glabrous. Leaves 15–33 cm long, leathery; nerves 9–13 pairs. Ovary 4–6-locular, seldom 7-locular, glabrous. Fruits 21–28 mm long; pericarp 3–5 mm thick . . . . **6. A. nitida**

29a. Branchlets and leaves beneath very sparsely puberulous, glabrescent. Inflorescences subglabrous. Ovary glabrous; stigmas papillate to laciniate. Infructescences subglabrous. Fruits young ones ridged, mature ones smooth, glabrous, stigmas not sunken . . . . **1. A. banahaensis**

b. Branchlets and leaves sparsely puberulous, glabrescent. Inflorescences (sparsely) tomentose. Ovary sparsely hairy, glabrescent; stigmas ribbed. Infructescences (sparsely) tomentose. Fruits young and mature ones smooth, sparsely hairy, glabrescent, stigmas flat to sunken . . . . **4. A. frutescens**

Mostly *A. frutescens* is distinct by its stronger indument and smaller fruits from the typical subglabrous and large-fruited *A. banahaensis*. However, in places were *A. banahaensis* and *A. frutescens* co-occur, as in Sabah, the differences between the species fade: *A. frutescens* becomes glabrescent and the fruit of *A. banahaensis* does not get as large as in, e.g., Mindanao.

30a. Branchlets, petioles, and leaves completely glabrous. Leaves drying greyish green to yellowish green on both sides. Ovary glabrous; stigma up to 1 mm long. Fruits glabrous, yellowish when dry 31

b. Branchlets, petioles, and leaves at least on midrib beneath very sparsely puberulous to tomentose. Leaves drying (dark) greyish green, bluish green, or brownish above, brownish beneath. Ovary at least at base sparsely puberulous (if (sub)glabrous, then stigmas 1.5–2.5 mm long, or nerves 14–23 pairs); stigmas 0.7–2.5 mm long. Fruits sparsely puberulous to glabrous, brownish to black when dry 34

31a. Leaves 6.5–18 cm long, smooth or young ones irregularly lowly granular beneath 32

b. Leaves 13–32 cm long, strongly white-granular beneath on nervation only . . . . **2. A. chondroneura**

32a. Leaf: nerves 7–11 pairs, regularly set; dots indistinct. Flowers up to 11; ovary not lobed. Fruits ellipsoid or fusiform, 9–13 by 8–11 mm or 14–17 by 7–10 mm, drying smooth to punctulate; apex of endocarp acute 33 (**12. A. symplocoides**)

b. Leaf: nerves 5–9 pairs, with often larger gap between 3rd and 4th pair; dots densely set, fine, greyish. Flowers up to 5; ovary lowly lobed. Fruits ovoid, 12–15 by 10–13 mm, often drying irregular ridged and corrugate; apex of endocarp caudate . . . . **7. A. prainiana**

33a. Fruits fusiform, 14–17 mm long; pedicel 11–35 mm long . . . . **12b. A. symplocoides** var. **chalarocarpa**

b. Fruits ovoid, 9–13 mm long; pedicel 2–7 mm long . . . . **12a. A. symplocoides** var. **symplocoides**

34a. Stipules (narrowly) ovate, symmetric or slightly oblique, early caducous (if falcate and persistent, then nerves 8–13 pairs). Leaf: base rounded to cuneate, very base never cordate; nerves 6–16 pairs. Inflorescences sparsely puberulous to (sparsely) tomentose. Ovary (sparsely) puberulous to subglabrous. Fruits sparsely puberulous to glabrous; pericarp 0.8–5 mm thick 35

b. Stipules falcate, often persistent. Leaf: base emarginate or cuneate with very base cordate; nerves 14–23 pairs. Inflorescences subglabrous. Ovary glabrous. Fruits glabrous; pericarp 0.5–1 mm thick . . . . **76. A. grandistipula**

35a. Petiole 6–38 mm long. Leaf: texture papery or (slightly) leathery; disc-like absent, or few present along the margin; nerves 6–13 pairs. Inflorescences axillary to just below the leaves 36

b. Petiole 14–51 mm long. Leaf: texture papery; disc-like glands often present, along the margin (Fig. 3.3b); nerves 12–16 pairs. Inflorescences below the leaves or on the branches . . . . **70. A. arborea**

36a. Branchlets, petioles, and leaves at least beneath (sparsely) tomentose to (sparsely) puberulous. Ovary smooth, at base (sparsely) tomentose to puberulous, glabrescent towards apex. Fruits sparsely puberulous 37

b. Branchlets, petioles, and leaves only on midrib and nerves beneath very sparsely puberulous, glabrescent. Ovary rugose, (sub)glabrous. Fruits (sub)glabrous . . . . **72. A. caloneura**

37a. Leaf: dots often distinct, large or small. Ovary ovoid or ellipsoid; stigmas sessile, 0.8–2.2 mm long. Fruits ellipsoid to (sub)globose, not stiped or beaked; apex of endocarp acute 38

b. Leaf: dots indistinct. Ovary narrowly ovoid; stigmas slightly raised, 2–2.5 mm long. Fruits ovoid to slightly flask-shaped, beaked, 13–19 mm long; apex of endocarp caudate . . . . **71. A. basilanensis**

38a. Leaf: dots irregularly set, fine; nerves 8–13 pairs. Stipules falcate, sometimes persistent. Flowers: sepals 3; ovary 3-locular (seldom 4-locular); stigmas 1.5–2.2 mm long. Fruits: pericarp 1–5 mm thick . . . . **78. A. illustris**

b. Leaf: dots laxly set, large; nerves 6–9 pairs. Stipules caducous. Flowers: pedicel 0.8–1 mm long; ovary 2- and 3-locular; stigmas 0.8–1.2 mm long. Fruits: pericarp 0.8–1.5 mm thick . . . . **82. A. nervosa**

10.3.6 – ***Key to the species of the Philippines, Sulawesi, and the Moluccas***

Staminate specimens

1a. Inflorescences (when mature) brush-like due to long exserted stamens, glomerules indistinct, densely set at apical 3/4–7/8 of the rachis (Fig. 3.5c). Stamens strongly exserted, c. thrice as long as the sepals. Leaf: margin subentire, marginal glands indistinct, in margin; disc-like glands distinct, along the margin (Fig. 3.3c) . . . 2

b. Inflorescences not brush-like, glomerules distinct, spaced at least at base of rachis, or more or less continuously set along the rachis, interrupted by distinct bracts (Fig. 3.5a, g). Stamens not exserted or only exserted to twice the sepal length. Leaf: margin glandular-crenate to lowly undulate, marginal glands distinct, along the margin; disc-like glands distinct and scattered within the vein arches, or indistinct, occasionally along the margin (Fig. 3.3b, d) 3

2a. Stipules 6–20 by 11–37 mm, often long persistent. Petiole upper pulvinus swollen, 5–11 by 3–6 mm. Leaves 14–47 cm long; base cordate; nerves raised beneath, not fading towards the margin . . . . **36. A. benthamiana**

b. Stipules 4–8 by 11–18 mm, present in young stages. Petiole upper pulvinus distinct, but not extremely so, 2–6 by 1.5–2.5 mm. Leaves 8–25 cm long; base emarginate to rounded; nerves prominent beneath, fading towards the margin **38. A. falcifera**

3a. Inflorescences floriferous to base; glomerules more or less continuously set along the rachis (Fig. 3.5a), bracts indistinct, shorter than glomerules 4

b. Inflorescences peduncled; glomerules at least at base of rachis interrupted, bracts indistinct or distinct, shorter than or as long as glomerules, or if glomerules more or less continuously set along the rachis, then bracts distinct, longer than glomerules (Fig. 3.5g) 6

4a. Petioles and leaves completely glabrous. Leaf: margin subentire, lowly undulate or lowly glandular-crenate 5

b. Petioles and leaves sparsely hirsute. Leaf: margin often glandular-serrate (Fig. 3.1d) . . . . **27c. A. octandra** var. **malesiana**

5a. Leaf: basal glands fading. Glomerules ellipsoid, slightly interruptedly set along the rachis. — Sulawesi: Sula Isl. . . . . **24. A. lucida**

b. Leaf: basal glands distinct. Glomerules indistinct, continuously set along the rachis. — Philippines . . . . **31. A. symplocifolia**

6a. Branchlets, petiole, and leaf beneath tomentose 7

b. Branchlets, petiole, and leaf beneath glabrous or sparsely puberulous 8

7a. Stipules caducous. Leaves glabrous above. Inflorescences 18–47 mm long, 1.5–2.2 mm diam., tomentose; glomerules 1.5–2 by 1–1.5 mm. Stamens 2 or 3, not to slightly exserted, 0.8–1 mm long . . . . **71. A. basilanensis**

b. Stipules falcate, often rather persistent. Leaves sparsely tomentose above. Inflorescences 14–59 mm long, 2–3 mm diam., densely (reddish) tomentose; glomerules 2–4 by 1.2–2 mm. Stamens 4, exserted, 1.2–1.8 mm long . . . . **54. A. leytensis**

8a. Leaf: dots absent; drying yellowish or greyish green on both sides; young leaves lowly white granular beneath, mature ones smooth 9

b. Leaf: dots distinct, sometimes fading; drying greyish, greenish, or brownish above, brownish beneath; young and mature leaves smooth .10

9a. Inflorescences 1–1.5 mm diam.; peduncle 1.5–2.5 mm long, subglabrous; glomerules subglobose, spaced 0.5–2 mm at base . . . . **1. A. banahaensis**

b. Inflorescences 2–3.5 mm diam.; peduncle 0.5–1.5 mm long, sparsely puberulous; glomerules ellipsoid, spaced 0.5–1 mm at base . . . . **4. A. frutescens**

10a. Leaf: disc-like glands scattered (mostly at base) within marginal vein arches (Fig. 3.3a) 11

b. Leaf: disc-like glands absent or occasionally few present along margin (Fig. 3.3b) 12

11a. Branchlets and leaves completely glabrous. Nerves 7–9 pairs. — Moluccas . . . . **73. A. dendroidea**

b. Branchlets and leaves on nerves (very) sparsely puberulous beneath. Nerves 9–13 pairs. — Central Sulawesi . . . . **54. A. leytensis**

12a. Inflorescences: 28–74 mm long, sparsely puberulous; glomerules distinctly, up to 3 mm, spaced at base. — Philippines 13

b. Inflorescences: 11–26 mm long, subglabrous; glomerules not or slightly, up to 1 mm, spaced at base — Moluccas: Seram . . . . **43. A. brevicaudata**

13a. Leaves 6.5–15 cm long; marginal glands present, but not extremely large; dots densely set . . . . **86a. A. sphaeridiophora** var. **sphaeridiophora**

b. Leaves 11–20 cm long; marginal glands thick, black, protruding; dots irregularly laxly set . . . . **89. A. spec. G**

Pistillate specimens

1a. Flowers and fruits (sub)sessile, densely set along the whole rachis or at apical part only (Fig. 3.6b, c, h, i, k) 2
b. Flowers and fruits distinctly pedicelled, (rather) laxly set along the rachis or singly apically (Fig. 3.6n, o, u) 6
2a. Flowers and fruits 3-locular; stigmas 2–2.5 mm long, curving downwards to the sides of the ovary, slightly rough (Fig. 3.8q); septae and column glabrous. Leaf: disc-like glands along the margin (Fig. 3.3c). Stipules falcate, (shortly) persistent 3
b. Flowers and fruits 2-locular; stigmas 0.5–1.2 mm long, straight, papillate to laciniate; septae and column sparsely hairy. Leaf: disc-like glands scattered within marginal vein arches (Fig. 3.3d). Stipules (narrowly) ovate, early caducous . . 4
3a. Stipules 6–20 by 11–37 mm, often long persistent. Petiole: upper pulvinus swollen, 5–11 by 3–6 mm. Leaves 14–47 cm long; base cordate; nerves beneath raised, not fading towards the margin . . . . **36. A. benthamiana**
b. Stipules 4–8 by 11–18 mm, present in young stages. Petiole: upper pulvinus distinct, 2–6 by 1.5–2.5 mm. Leaves 8–25 cm long; base emarginate to rounded; nerves beneath prominent, fading towards the margin . . . . **38. A. falcifera**
4a. Branchlets sparsely puberulous to glabrous. Petiole and leaf glabrous. Leaf: margin subentire, lowly undulate or lowly glandular-crenate. Ovary and fruit sparsely sericeous to glabrous 5
b. Branchlets, petiole, and leaf sparsely hirsute. Leaf: margin often glandular-serrate (Fig. 3.1d). Ovary and fruit sparsely sericeous **27c. A. octandra** var. **malesiana**
5a. Leaf: basal glands fading. Ovary and fruit sparsely sericeous (?glabrous). — Moluccas . . . . **24(c). A. lucida** (?var. **pubescens**)
b. Leaf: basal glands distinct. Ovary and fruit glabrous. — Philippines . . . . **31. A. symplocifolia**
6a. Flowers and fruits singly set at apical end of rachis (Fig. 3.6u); stigmas 0.5–1 mm long, broad, connate to top of ovary 7
b. Flowers and fruits (rather) laxly arranged throughout the rachis (Fig. 3.6n, o); stigmas 0.8–2.5 mm long, narrow, free 8
7a. Ovary glabrous; stigmas prominent, papillate to laciniate. Young fruits ovoid, 12–16 by 12–16 mm, mature fruits globose, 23–27 by 23–28 mm, punctulate; stigmas prominent, irregularly sculptured and ridged on sutures; pericarp 0.5–1.5 mm thick when immature to 4–6 mm thick when mature . . . . **1. A. banahaensis**
b. Ovary glabrescent; stigmas flat, lowly papillate. Young and mature fruits globose, 9–15 by 10–15 mm, smooth, stigmas sunken; pericarp 0.5–2.5 mm thick . . . . **4. A. frutescens**
8a. Branchlets, petiole, and leaf beneath tomentose 9
b. Branchlets, petiole, and leaf beneath glabrous or sparsely puberulous 10
9a. Stipules caducous. Leaves glabrous above. Flowers 2-locular; stigmas 2–2.5 mm long, perpendicular, curving towards the ovary sides (Fig. 3.8f) . . . . **71. A. basilanensis**
b. Stipules falcate, often rather persistent. Leaves sparsely tomentose above. Flowers 3- (seldom 2-)locular; stigmas 1–1.5 mm long, perpendicular, slightly recurved (Fig. 3.8e) . . . . **54. A. leytensis**

10a. Ovary ovoid. Fruit ovoid to globose 11
b. Ovary narrowly ovoid. Fruit fusiform. — (Sometimes?/usually?) hermaphrodite . . . . **43. A. brevicaudata**
11a. Leaf: disc-like glands scattered (mostly at base) within marginal vein arches (Fig. 3.3a) 12
b. Leaf: disc-like glands absent or occasionally few present along margin (Fig. 3.3b) 13
12a. Branchlets and leaves completely glabrous. Nerves 7–9 pairs. Stigmas 1–2.5 mm long, tetrafid, tree-like (Fig. 3.8b). Fruits ovoid to globose, 9–13 mm long, distinctly beaked. — Moluccas . . . . **73. A. dendroidea**
b. Branchlets and leaves on nerves (very) sparsely puberulous beneath. Nerves 9–13 pairs. Stigmas 1–1.5 mm long, bifid, not tree-like. Fruits ovoid, 12–17 mm long, slightly beaked. — Central Sulawesi . . . . **54. A. leytensis**
13a. Inflorescences 7–16 mm long. Flowers 2- or 3-locular, singly set per bract; petal-like structures absent; stigmas sessile, 0.8–1.2 mm long. — Fruits not beaked, pericarp 0.3–0.5 mm thick . . . **86a. A. sphaeridiophora** var. **sphaeridiophora**
b. Inflorescences 24–58 mm long. Flowers 3-locular, sometimes 2 per bract; petal-like structure sometimes distinct; stigmas raised, 2.5–3 mm long. — Fruits unknown . . . . **89. A. spec. G**

10.3.7 – *Key to the species of Papua Barat, Papua New Guinea, and the Solomons*

Introduction

The New Guinea species are different from the West Malesian ones. The arrangement of the glomerules or pistillate flowers along the rachis and the foliar glands are the most important delimiting and grouping factors for the West Malesian species. In contrast, the New Guinean species have almost all (rather) densely set glomerules or flowers, regularly set marginal glands, and disc-like glands along the margin. They are most easily divided into three size-groups: one with large leaves, thick inflorescences and 3-locular large fruits, one with small leaves, narrow inflorescences and 2-locular small fruits, and a third, intermediate group with intermediate leaves, intermediate inflorescences and 2- and 3-locular, intermediately sized fruits. This third intermediate group overlaps at one end with the large-sized group, and at the other with the small-sized group. Because of this, very few characters are fit to use in a dichotomous key. Almost every character – be it vegetative or staminate or pistillate – separates the large species from the small species, but leaves the intermediate species in between.

The dichotomous key presented beneath is based on the few characters that at least divide part of the intermediate group. Because of the numerous combinations that these characters show in the species, it was not possible to describe all combinations of characters. The characters that are presented should thus be strictly used, and it is recommended to use the synoptic key or refer to the descriptions when in doubt. Many species have exceptions besides the typical features, and these are not always present in the key.

Some of the more peculiar characters and the species possessing them are given in the list of spot characters. Another striking feature of the New Guinean species is the occurrence of hermaphrodites. These are besides their appearance in the dichotomous key also listed separately.

List of spot-characters

- Ovary and fruit lamellate (Fig. 3.9c, d): **50. A. lamellata**
- Leaf beneath scattered with numerous black disc-like glands, often found in swampy area: **52. A. ledermanniana**
- Petiole > 30 mm long, leaves large, 17–34 cm long, shiny: **60. A. praegrandifolia**
- Petiole 3–8 mm long, often entirely pulvinate: **43. A. brevicaudata**, **59. A. parvula**, **62. A. sclerophylla** (3)

Hermaphrodites

1a. Ovary 2-locular (sometimes 2- and 3-locular). Fruit (narrowly) ovoid to fusiform. — Papua New Guinea 2
b. Ovary 3-locular. Fruit (sub)globose. — Bougainville . . . . **49. A. heterodoxa**
2a. Stipules present in young stages, oblique to slightly falcate. Leaf: apex acute to acuminate. Stamens 2 or 3, not exserted; ovary narrowly ovoid. Fruits narrowly ellipsoid to fusiform, 16–19 by 6–9 mm 7
b. Stipules early caducous. Leaf: apex acuminate to cuspidate. Stamens 4 (or 5), exserted; ovary ovoid. Fruits ellipsoid to ovoid, 8–13 by 8–13 mm . . . . **48. A. hermaphrodita**
3a. Petiole 3–8 mm long, often entirely pulvinate. Sepals narrowly ovate; stamens 1.2–2.5 mm long . . . . **43. A. brevicaudata**
b. Petiole 11–26 mm long, pulvinate at base and apex, lower pulvinus often indistinct. Sepals ovate; stamens (?young) 0.5–0.8 mm long . . . . **46. A. egregia**

Key to the species

1a. Nerves 5–10 pairs 2
b. Nerves 10–17 pairs 17
2a. Petioles 3–8 mm long, often entirely pulvinate 3
b. Petioles 5–28 mm long, pulvinate at base and apex 5
3a. Staminate inflorescences (as far as known) 5–10 mm long; anthers 0.4–0.5 mm long. Bracts of staminate and pistillate inflorescences inconspicuous, 0.5–1.5 mm long. Ovary and fruit ovoid to ellipsoid. Fruits 8–10 mm long, not beaked. Petioles 2–5 mm long. Leaves 2.5–5 by 1–2 cm 4
b. Staminate inflorescences 11–26 mm long; anthers 0.6–0.8 mm long. Bracts of staminate and pistillate inflorescences conspicuous, 1.3–2.5 mm long. Ovary and fruit narrowly ovoid to narrowly ellipsoid. Fruits 16–19 mm long, beaked. Petioles 3–8 mm long. Leaves 3–9.5 by 1–4 cm. — Pistillate specimens sometimes with stamens . . . . **43. A. brevicaudata**
4a. Stipules mostly early caducous. Leaves elliptic to obovate, apex acute to acuminate; nerves 5–7 pairs . . . . **59. A. parvula**
b. Stipules mostly shortly persistent. Leaves (narrowly) elliptic, apex acuminate to cuspidate; nerves 7–10 pairs . . . . **62. A. sclerophylla**

5a. Branchlets densely to sparsely tomentose. Leaves above at least on midrib (sparsely) tomentose, beneath (sparsely) tomentose 6

b. Branchlets sparsely puberulous to glabrous. Leaves glabrous or only sparsely puberulous beneath 8

6a. Nerves 7–10 pairs. Ovary often 2- or 3-locular. Staminate inflorescences 7–15 mm long, 1–2 mm diameter. Pistillate pedicel 0.5–1 mm long. Fruiting pedicel 1–4 mm long 7

b. Nerves 9–15 pairs. Ovary mostly 3-locular, seldom 4-locular. Staminate inflorescences 9–92 mm long, 1.5–5 mm diameter. Pistillate pedicel 0.5–4 mm long. Fruiting pedicel 3–9 mm long 26

7a. Leaves above only midrib tomentose. Pistillate pedicel and ovary tomentose. Fruits ellipsoid, very sparsely puberulous; column at base hairy. — Altitude low to 600 m . . . . **41. A. annulata**

b. Leaves above midrib and lamina (sparsely) tomentose. Pistillate pedicel and ovary densely tomentose. Fruits ovoid, patchy tomentose; column glabrous. — Altitude 1300–1700 m . . . . **61. A. reticulata**

8a. Dried leaf: dots distinct; disc-like glands absent or few scattered along the margin; **if** regularly scattered along the margin **then** leaf apex cuspidate to caudate. Staminate inflorescences with distinctly interrupted glomerules throughout the rachis or glomerules continuously set, indistinct. Pistillate flowers and fruits 3-locular, fruits ovoid to globose, sometimes slightly lobed (*A. nigropunctata*), or 2-locular and (broadly) ellipsoid (*A. misimana*), or hermaphroditic flowers and fruits with withered stamens 9

b. Dried leaf: dots indistinct; disc-like glands many scattered along the margin or over the lamina or at base only; **if** indistinct or only few scattered along the margin **then** inflorescences subglabrous. Staminate inflorescences (as far as known) with glomerules at base interrupted at 0.5–1 mm, continuous apically. Pistillate flowers and fruits 2-locular (*A. egregia*), narrowly ovoid or narrowly ellipsoid to fusiform, or 3-locular, ovoid to globose, not lobed 13

9a. Inflorescences with hermaphroditic flowers; fruits with withered stamens. — Altitude > 1000 m 10

b. Staminate and pistillate inflorescences separate; stamens never present in pistillate flowers or fruits. — Altitude up to 600 m 11

10a. Ovary mostly 2-locular (sometimes 2- and 3-locular); stigmas 1.5–2.5 mm long; pedicel 1–3.5 mm long. Fruit ellipsoid to (narrowly) ovoid; pedicel 2–7 mm long; pericarp 0.3–0.5 mm thick. — Papua New Guinea . . . . **48. A. hermaphrodita**

b. Ovary mostly 3-locular (sometimes 2-locular); stigmas 0.8–1.2 mm long; pedicel 0.5–1 mm long. Fruit (sub)globose; pedicel 3–5 mm long; pericarp 0.5–1 mm thick. Fruit. — Bougainville . . . . **49. A. heterodoxa**

11a. Leaf: apex acuminate to cuspidate; dots rather laxly set; disc-like glands occasionally present along the margin. Branchlets, petiole, and midrib beneath glabrous or sparsely puberulous. Staminate inflorescences continuous (Fig. 3.5m). Pistillate flowers and fruits (as far as known) subsessile, very sparsely puberulous to glabrous, mostly 2-locular, seldom 3-locular. Fruits not lobed 12

b. Leaf: apex cuspidate to caudate; dots densely set; disc-like glands regularly present along the margin. Branchlets, petiole, and midrib beneath (sparsely) tomentose.

Staminate inflorescences interrupted. Pistillate flowers and fruits pedicelled, sparsely sericeous to sparsely puberulous, 3-locular. Fruits slightly lobed .... **57. A. nigropunctata**

12a. Branchlets and leaves completely glabrous. Stipules early caducous. Leaf: base cuneate to attenuate; dots grey. Staminate inflorescences 0.5–1 mm diameter. Pistillate flowers and fruits unknown. — North Papua New Guinea .... **53. A. leptochrysandra**

b. Branchlets and midrib of leaves sparsely puberulous. Stipules present in young stages, (slightly) falcate. Leaf: base cordate to cuneate; dots black. Staminate inflorescences 1–1.5 mm diameter. Pistillate flowers and fruits ovoid, subsessile. — Eastern Papuan Islands .... **56. A. misimana**

13a. Leaf: disc-like glands regularly present, along the margin or scattered over the lamina or at base only. Inflorescences sparsely tomentose to puberulous. Staminate inflorescences distinctly (1.5–9 mm) spaced at base (Fig. 3.5q). Pistillate flower (as far as known) mostly 3-locular, seldom 2-locular; ovary ovoid. Fruit (as far as known) ovoid to subglobose, 8–12 mm long 14

b. Leaf: disc-like glands few, occasionally present along the margin. Inflorescences subglabrous. Staminate inflorescences slightly (0.5–1 mm) spaced at base (cf. Fig. 3.5p). Pistillate flower 2-locular; ovary narrowly ovoid. Fruit narrowly ellipsoid to fusiform, 16–19 mm long .... **46. A. egregia**

14a. Leaf: disc-like glands scattered within the marginal vein arches, throughout the lamina or at the base only 15

b. Leaf: disc-like glands scattered along the margin 16

15a. Stipules shortly persistent, narrowly ovate, oblique. Leaf: disc-like glands scattered near base only; base cordate to obtuse. — Staminate inflorescences: glomerules subglobose, spaced at base, continuous apically. Pistillate flower: pedicel either 3–6 or 0–0.5 mm long; ovary sericeous. Fruit beaked, ovoid .... **44. A. carrii**

b. Stipules early caducous. Leaf: disc-like glands scattered over the lamina; base obtuse to cuneate. — Staminate inflorescences unknown. Pistillate flower: pedicel 1–1.5 mm long; ovary sparsely puberulous. Fruit not beaked, possibly globose . ... **64. A. spec. A**

16a. Leaves 6.5–11 by 2.5–3.5 cm; nerves 5–7 pairs. Inflorescences axillary to just below the leaves. — Staminate inflorescences (*ex descr.*) 20–40 mm long, stamens hardly exserted, c. 1 mm long. Pistillate inflorescences 0.3–0.5 mm diameter. Flower: pedicel 0.5–1.5 mm long; ovary 3-locular, glabrous; stigmas slightly recurved, 1–1.5 mm. — Altitude 1000–2200 m .... **47. A. flexuosa**

b. Leaves 12–18.5 by 4–6.5 cm; nerves 7–11 pairs. Inflorescences mostly on the trunk. — Altitude 250–300 m. Staminate inflorescences 19–69 mm long, stamens exserted, 1.2–2 mm long. Pistillate inflorescences and flowers unknown .... **65. A. spec. B**

17a. Leaf: disc-like glands absent or present along the margin or only near base . 18

b. Leaves beneath with scattered black disc-like glands. — Staminate inflorescences: glomerules interrupted, stamens exserted. Pistillate inflorescences: flowers laxly set at base of rachis, clustered at apex. Ovary and fruit 2- or 3-locular, sparsely light hairy. Mostly in swamps or swampy areas .... **52. A. ledermanniana**

18a. Leaves subglabrous or only beneath on midrib sparsely tomentose; disc-like glands mostly many, sometimes only few, along the margin. Branchlets sparsely tomentose to subglabrous 19

b. Leaves above glabrous or on nerves and lamina sparsely to densely tomentose, beneath sparsely to densely tomentose; disc-like glands absent or few near the base. Branchlets (densely) tomentose, seldom sparsely so 22

19a. Petiole 9–42 mm long. Leaves 12–34 by 4–13 cm; apex acuminate; disc-like glands mostly many, along the margin (Fig 3.3c); dots indistinct or absent. Staminate inflorescences 14–69 mm long 20

b. Petiole 3–8 mm long. Leaves 6.5–14 by 1.5–4.5 cm; apex cuspidate to caudate; disc-like glands occasionally few, along the margin (Fig. 3.3b); dots distinct. Staminate inflorescences up to 8 mm long. — Pistillate inflorescences c. 6 mm long; pistillate flower: pedicel minute; stigma 1–1.5 mm long. Fruiting pedicel < 0.5 mm long . . . . **55. A. longicaudata**

20a. Leaves rather leathery, shiny when dry; 17–34 by 4–13 cm. Petiole 11–42 mm long. Inflorescences axillary or on the branches; peduncle 0–3 mm long. — Fruits long pedicelled (but pistillate flowers not!) 21

b. Leaves papery, dull when dry; 12–18 by 4–6.5 cm. Petiole 9–16 mm long. Inflorescences (as far as known) mostly on the trunk, occasionally some axillary; peduncle 4–17 mm long. — Fruits and pistillate flowers unknown . . . . **65. A. spec. B**

21a. Petiole 11–27 mm long. Staminate inflorescences 0.7–1.5 mm diam., sparsely puberulous; glomerules globose, 1–1.5 by 1–1.5 mm, spaced at 1–5 mm along the rachis; bracts inconspicuous, sparsely puberulous. Pistillate inflorescences 13–24 mm long, (sparsely) puberulous, flowers laxly set, pedicel 1–3 mm long. Fruiting pedicel 2–11 mm long; fruit ovoid . . . . **51. A. laxiflora**

b. Petiole 18–42 mm long. Staminate inflorescences 3–3.5 mm diam., (densely) tomentose; glomerules ellipsoid, 3–4 by 2–3 mm, spaced at 0.5–2 mm at base, continuous apically; bracts conspicuous, tomentose. Pistillate inflorescences 2–8 mm long, tomentose, flowers densely set, sessile. Fruiting pedicel 9–17 mm long; fruit globose . . . . **60. A. praegrandifolia**

22a. Indumentum (densely) tomentose. Leaves not or very slightly bullate; margin (lowly) undulate to (lowly) glandular-crenate, not recurved. Stipules persistent or not. Staminate inflorescences (as far as known) 9–92 mm long. Pistillate inflorescences (as far as known) 5–78 mm long, flowers subsessile to pedicelled 23

b. Indumentum (densely) hirsute. Leaves slightly bullate; margin (lowly) glandular-dentate, recurved. Stipules persistent. Staminate inflorescences (young) 5–8 mm long. Pistillate inflorescences 3–5 mm long, flowers sessile . . **45. A. decipiens**

23a. Nerves 11–15 pairs 24

b. Nerves 9–12 pairs 26

24a. Leaves (sparsely) tomentose above, glabrescent; disc-like glands occasionally present at base or along margin, sometimes indistinct. Ovary lowly lobed or not, pedicel 0.5–1.5 mm long. Fruit lobed or not, 10–19 mm broad. — Staminate inflorescences (densely) tomentose, slightly interrupted at base only or almost continuous. Petiole 5–27 mm long. Leaves 7–31 by 3–11 cm 25

b. Leaves glabrous above; disc-like glands absent. Ovary lamellate (Fig. 3.9e), subsessile. Fruit lamellate (Fig. 3.9f), 18–23 mm broad. — Staminate inflorescences unknown. Petiole 11–37 mm long. Leaves 20–32.5 by 6.5–10 cm . . . . **50. A. lamellata**

The three species in leads 24 and 25, *A. lamellata*, *A. brassii*, and *A. papuana*, are almost only separable in fruit.

25a. Leaves sparsely tomentose above, glabrescent; dots irregularly set, grey, fading; disc-like glands occasionally present near base only. Inflorescences axillary to just below the leaves, or on the branches. Staminate inflorescences: glomerules spaced at 1–5 mm at base of rachis, or almost continuous throughout. Pistillate flowers: stigma slightly raised, straight. Fruiting pedicel 3–7 mm long; fruits ovoid, 10–16 by 10–16 mm, not lobed; pericarp 1.5–3 mm thick . . . . **42. A. brassii**

b. Leaves (sparsely) tomentose above; dots indistinct; disc-like glands occasionally present along margin. Inflorescences axillary to just below the leaves, not on the branches. Staminate inflorescences: glomerules approximately continuously spaced. Pistillate flowers: stigma raised, recurved. Fruiting pedicel 2–5 mm long; fruits (broadly) ovoid, 12–18 by 12–19 mm, slightly lobed; pericarp 1–2 mm thick . . . . **58. A. papuana**

26a. Leaf: marginal glands regular, distinct; disc-like glands scattered at base of leaf, sometimes indistinct. Staminate inflorescences with glomerules usually at least at base (slightly) spaced, 9–69 mm long. — Pistillate inflorescences densely to sparsely tomentose, flowers rather densely or rather laxly set along the rachis 27

b. Leaf: marginal glands few, indistinct; disc-like glands absent. Staminate inflorescences with continuously set indistinct glomerules, 27–92 mm long. — Pistillate inflorescences unknown . . . . **66. A. spec. C**

27a. Staminate inflorescences up to 2–5 mm diam.; glomerules mostly only spaced at base to almost continuous 28

b. Staminate inflorescences up to 1.5–2.5 mm diam.; glomerules mostly interrupted throughout 29

28a. Indumentum densely tomentose. Petiole 6–16 mm long. Leaves 11–21 by 4–9.5 cm; base cordate to rounded; dots irregularly set, fading; disc-like glands occasionally present near base, indistinct. Inflorescences often on the branches. Staminate inflorescences 16–69 mm long, 2–4 mm diam., densely tomentose. Stigma slightly raised, straight. Fruits ovoid, beaked; fruiting pedicel 3–7 mm long . . . . **42. A. brassii**

b. Indumentum tomentose. Petiole 5–28 mm long. Leaves 9–26 by 3–12 cm; base rounded to cuneate; dots densely set, fading; disc-like glands scattered mostly at base, often distinct. Inflorescences axillary or in the axils of fallen leaves. Staminate inflorescences 9–29 mm long, 3–5 mm diam., tomentose. Stigma raised, (slightly) recurved. Fruits ovoid to subglobose, not beaked; fruiting pedicel 4–9 mm long . . . . **63. A. vagans**

29a. Indumentum sparsely tomentose. Leaf: nervation not sunken. Staminate inflorescences up to 29 mm long. — Fruits (sub)globose, long pedicelled **63. A. vagans**

b. Indumentum tomentose. Leaf: nervation often sunken. Staminate inflorescences up to 47 mm long. — Fruits unknown . . . . **67. A. spec. D**

10.3.8 – ***Synoptic key to all species***

Used abbreviations

Species names are abbreviated to the first 3 or 4 characters, when needed a 5th character is added.

acum	15. A. *acuminata*
alia	68. A. *alia*
annu	41. A. *annulata*
ante	69. A. *antennifera*
arbo	70. A. *arborea*
aur	16. A. *aurea*
bana	1. A. *banahaensis*
basi	71. A. *basilanensis*
bent	36. A. *benthamiana*
bour	17. A. *bourdillonii*
bras	42. A. *brassii*
brev	43. A. *brevicaudata*
bull	37. A. *bullatissima*
calo	72. A. *caloneura*
card	18. A. *cardiosperma*
carr	44. A. *carrii*
cars	44. *carr.* informal group *subhermaphrodita*
chon	2. A. *chondroneura*
conf	3. A. *confusa*
deci	45. A. *decipiens*
dend	73. A. *dendroidea*
duth	74. A. *duthieana*
egre	46. A. *egregia*
elme	75. A. *elmeri*
falc	38. A. *falcifera*
fici	19. A. *ficifolia*
flex	47. A. *flexuosa*
frut	4. A. *frutescens*
fulv	5. A. *fulvovittata*
fusi	20. A. *fusiformis*
glob	21. A. *globifera*
grand	76. A. *grandistipula*
granu	77. A. *granularis*
herm	48. A. *hermaphrodita*
hete	49. A. *heterodoxa*
illu	78. A. *illustris*
illf	78. *illu.* informal group Sarawak
lage	79. A. *lagenocarpa*
lame	50. A. *lamellata*
lanc	22. A. *lanceolata*
lati	23. A. *latifolia*
laxi	51. A. *laxiflora*
lede	52. A. *ledermanniana*
lept	53. A. *leptochrysandra*
leyt	54. A. *leytensis*
leys	54. *leyt.* informal group *sulawesiensis*
long	55. A. *longicaudata*
luci	24(a). A. *lucida* (var. *lucida*)
luce	24b. *luci.* var. *ellipsoidea*
lucp	24c. *luci.* var. *pubescens*
luct	24d. *luci.* var. *trilocularis*
luna	39. A. *lunata*
macr	25. A. *macrophylla*
main	80. A. *maingayi*
micr	81. A. *microstachya*
misi	56. A. *misimana*
nerv	82. A. *nervosa*
nigc	26. A. *nigricans*
nigp	57. A. *nigropunctata*
nit	6. A. *nitida*
octa	27(a). A. *octandra* (var. *octandra*)
octc	27b. *octa.* var. *chinensis*
octm	27c. *octa.* var. *malesiana*
octy	27d. *octa.* var. *yunnanensis*
papu	58. A. *papuana*
parv	59. A. *parvula*
pena	83. A. *penangensis*
plan	28. A. *planchoniana*
prae	60. A. *praegrandifolia*
prai	7. A. *prainiana*
pseu	29. A. *pseudoficifolia*
quad	8. A. *quadrilocularis*
reti	61. A. *reticulata*
rhac	84. A. *rhacostyla*
sara	9. A. *sarawakensis*
scle	62. A. *sclerophylla*
sela	85. A. *selangorica*

serr	30.	*A. serrata*
spha	86(a).	*A. sphaeridiophora* var. *sphaeridiophora*
spca	86b.	*spha.* var. *campanulata*
stel	10.	*A. stellifera*
sten	11.	*A. stenostachys*
subc	87.	*A. subcaudata*
sylv	40.	*A. sylvestri*
symci	31.	*A. symplocifolia*
symco	12(b).	*A. symplocoides*
symcc	12a.	*symco.* var. *chalarocarpa*
tetr	32.	*A. tetrapleura*
vaga	63.	*A. vagans*
vagl	63.	*vaga.* informal group lowland
vill	33.	*A. villosa*
wall	34.	*A. wallichii*
whit	13.	*A. whitmorei*
yunn	35.	*A. yunnanensis*
spA	64.	*A. spec. A, aff. nigp*
spB	65.	*A. spec. B, aff. flex*
spC	66.	*A. spec. C, aff. papu*
spD	67.	*A. spec. D, aff. vaga*
spE	14.	*A. spec. E, aff. stel*
spF	88.	*A. spec. F, aff. subc*
spG	89.	*A. spec. G, aff. calo*

Index to the key characters

This index gives the type of characters listed below in the synoptical key. The sequence of these is the recommended sequence to attain a quick determination.

Vegetative characters: 27 20 4 5 3 28 8 19 25 26 21 22 23 24 7 18 29 6 10 11 16 17 12 13 14 15 30–36 9
Staminate inflorescence: 43 41 40 39 47 50 51 42 52 44 45 46 48 49 38 37
Staminate flower: 55 59 58 61 53 60 57 54 56 62
Pistillate inflorescence: 69 72 67 66 68 65 71 70 64 37
Pistillate flower: 72 83 80 84 85 86 87 90 91 89 88 92 81 77 76 78 73 82 74 75 79
Hermaphrodites: 63
(Infructescence: cf. pistillate inflorescence: 69 67 68 71 64 37)
Fruit: 103 93 80 99 97 98 100 101 95 94 96 102 104
Geography: 1
Habit: 2
Habitat: 105

Key characters

Bold/Italic type is for species with more than one state. Uncommon states are between brackets; question marks denote unknown states. Varieties and formas are only mentioned if different from the typical form. Then they are in *italics.*

Missing data are only included if they could be guessed from related species.

Thus *A. leptochrysandra* is virtually absent in most of the pistillate or fruiting characters, while the staminate characters of *A. bullatissima* are guessed.

1. Geography
Sri Lanka — ***acum card*** fusi lanc lati
South(west) India — ***acum*** bour ***card***
Himalaya — ***octa wall***
China — ***octa octc octy vill wall yunn***

Burma, Thailand (excl. Peninsular), Laos, Cambodia, Vietnam — ***duth*** fici ***frut*** macr ***micr octa octc octm octy*** plan ***pseu*** serr tetr ***vill wall yunn***
Peninsular Thailand, Peninsular Malaysia, Singapore — ***ante arbo aur bent conf falc frut glob luci luna*** main ***micr nerv nigc octm*** pena ***prai pseu quad*** sela ***stel subc symco whit*** spE spF
Sumatra — ***ante arbo aur bent conf falc frut glob luci*** *luce* ***luna nerv nigc octm prai quad stel subc symco whit***
West Java — ***arbo*** *spca* ***frut lucp luna nerv octm***
Borneo — alia ***ante arbo ?bana basi bent*** bull calo chon ***conf*** elme ***falc frut*** fulv grand granu illu lage ***luci*** *luct* ***luna nerv nigc*** nit ***octm prai*** rhac sara sten ***subc*** sylv ***symco*** *symcc*
Philippines — ***bana basi bent frut leyt octm*** spha symci spG
Sulawesi — ***falc frut leyt*** *leys* ***lucp octm***
Ambon, Buru, Ceram, Sula Isl. — ***brev*** dend ***frut lucp***
Papua Barat, Papua New Guinea — annu bras ***brev*** carr deci egre flex herm lame laxi lede lept long misi nigp ***papu*** parv prae reti scle vaga spA spB spC spD
Bougainville, Solomon Islands — hete ***papu***

2. Habit
Tree, up to 21–30 m high or more — acum ante arbo aur basi bent bras brev bull calo carr falc frut herm illu lage luna nerv papu pena subc symco vaga
Tree, up to 12–20 m high — alia annu card chon conf dend duth egre elme fulv fusi glob grand hete lame lati leyt luci misi nigc octa prai prae quad reti sara stel sten sylv tetr vill wall whit spB spC spE
Shrub or small tree, up to 2–10.5 m high — bana deci fici flex granu lanc laxi lede lept long macr main micr nigp plan rhac sela serr spha symci yunn spD

3. Indumentum of branchlets
glabrous — aur (***bana***) (***calo***) card (***carr***) chon (***dend***) (***duth***) (***egre***) (***fulv***) fusi (***hete***) lati lept (***luci***) macr nit ***prae*** (***plan***) prai quad sara stel symci symco tetr (***wall***) yunn spE
sparsely puberulous or sparsely hirsute — acum alia ante arbo ***bana*** bent brev ***calo carr dend duth egre*** falc flex frut ***fulv*** grand granu herm ***hete*** *illf* lanc laxi lede *leys* long ***luci*** main micr misi nerv nigc nigp octa parv pena (prae) ***plan*** sela spha sten vaga ***wall*** whit spA spB spG
(densely) tomentose or (densely) hirsute — annu basi bour bras bull conf deci elme fici glob illu lage lame leyt luna octy papu pseu reti rhac scle serr subc sylv vill spC spD spF

4. Stipule persistence
long — bent deci grand illf lame leyt luna papu prae
shortly/caducous — annu bras brev bull carr conf egre elme falc frut granu illu lage laxi lede long misi rhac scle sela subc sylv (spD) spF

5. Stipule shape
(unknown: ante basi bour calo dend duth glob herm hete lept luci nigc nit pena pseu reti spha spA spB spC spE spG)

falcate, often with disc-like glands along the margin beneath — arbo bent bras bull deci falc grand illu lame laxi leyt luna papu prae sylv vaga spD
(narrowly) ovate, strongly asymmetric — annu bana brev carr chon ***conf*** egre frut fulv lage lede long misi nerv quad scle sela
(narrowly) ovate, some (slightly) oblique — alia ***conf*** flex granu main prai sara ?stel sten ***subc*** symco whit spF
(narrowly) ovate, symmetric — aur elme fici octa parv rhac serr ***subc*** vill wall
(narrowly) triangular, symmetric — acum card fusi lanc lati macr micr nigp plan symci tetr yunn

6. Petiole length
2–5 mm — ***ante brev fici frut long*** parv ***plan sara*** scle
6–17 mm — acum ***alia*** annu ***ante arbo aur bana*** basi ***bent*** bour bras ***brev*** bull ***calo*** card ***carr chon conf*** deci dend duth ***egre elme*** falc ***fici*** flex ***frut*** fulv ***fusi*** glob ***grand*** granu ***herm*** hete ***illu*** lage ***lame*** lanc ***lati laxi*** lede lept leyt ***long luci luna*** main micr misi ***nerv nigc*** nigp ***nit octa papu*** pena ***plan prai pseu quad reti*** rhac ***sara*** sela serr ***spha*** sten subc symci ***symco tetr vaga vill wall*** whit yunn spA spB spC ***spD spE*** spF spG
17–28 mm — ***alia arbo aur bana bent calo carr chon conf egre elme fici fusi grand herm illu lame lati laxi luci luna nerv nigc nit octa papu prae pseu quad reti spha stel*** sylv ***symco tetr vaga vill wall spD spE***
28–38 mm — ***arbo aur calo chon grand illu lame nigc nit prae stel***
38–51 mm — ***arbo grand macr prae***
51–100 mm — ***macr***

7. Pulvini
both distinct — annu arbo aur bana (bent) bour bull card carr chon conf dend falc flex ***fulv*** fusi ***glob*** grand herm hete illu lame lanc lati laxi lept ***leyt*** long luci luna main micr misi nerv nigc nigp nit octa papu pena prae plan quad sara sela spha stel sten subc sylv ***symci*** symco ***tetr*** vaga wall yunn spD spE
lower one indistinct — (acum) alia ante basi calo duth egre frut (fulv) granu (leyt) macr prai reti serr ***symci tetr*** whit spA spB spC spF spG
both (rather) indistinct — ***acum*** bras deci elme fici (***glob***) lage lede pseu rhac vill
upper one large, distinct — bent
petiole entirely pulvinate — brev parv scle

8. Petiole indumentum
glabrous — ***acum arbo*** aur ***bent calo*** card ***carr*** chon ***dend duth egre flex fulv*** fusi ***hete*** lanc lati ***laxi*** lept luci macr nit ***prae*** plan prai quad sara ***spha*** stel symci symco tetr wall yunn ***spB*** spE
sparsely puberulous — (***acum***) alia ante (***arbo***) bana ***bent*** (***bour***) brev (***bull***) (***calo***) (***carr***) (***conf***) (***dend***) (***duth***) (***egre***) falc (***flex***) ***frut*** (***fulv***) (***glob***) grand (***granu***) herm (***hete***) (***illu***) ***laxi*** lede *leys* long main ***micr*** misi nerv nigc ***nigp*** octa parv ***pena prae*** reti scle sela ***spha*** sten ***subc vaga*** (***whit***) spA (***spB***) spD spG
densely tomentose/hirsute — annu basi ***bour*** bras ***bull conf*** deci elme fici (***frut***) ***glob granu illu*** lage lame leyt luna ***micr*** (***nigp***) *octy* papu ***pena*** pseu rhac serr ***subc*** sylv ***vaga*** vill ***whit*** spC spF

9. Leaf shape

narrowly ovate — ***acum alia annu ante arbo aur bana basi bent bour bras bull card carr chon conf duth flex frut fulv herm hete illu lame laxi lede lept leyt long luci main micr nit octa papu pena prae plan prai quad reti spha stel sten symci symco vaga wall vill yunn spA spB spC spE spF spG***

narrowly elliptic — ***acum alia annu ante arbo aur bana basi bent bour bras bull calo card chon conf*** deci ***dend duth egre elme falc fici flex frut fulv glob grand*** granu ***herm hete illu lage lame lanc laxi lede lept leyt long luci luna main micr misi nerv nigc nigp nit octa papu pena prae plan prai quad reti*** rhac ***sara scle sela*** serr ***spha stel sten subc*** sylv ***symci symco tetr vaga wall*** whit ***yunn spB spC spD spE spF spG***

narrowly obovate — ***bour bras brev calo card egre elme grand lage lanc luci luna papu prae sara sela subc spC spF***

ovate — ***carr herm illu*** macr ***spha symci vill spA***

elliptic — ***arbo brev calo conf dend elme fici fusi glob herm hete lati misi nerv nigc nigp octa parv*** pseu ***quad scle spha symci symco tetr vaga vill spD***

obovate — ***brev elme fusi lati parv***

linear elliptic — (***bent***) ***bull*** (***falc***)

10. Leaf length

2–5 cm — ***brev*** parv scle

5–11 cm — ***acum alia annu ante aur brev bull calo card carr conf dend duth*** egre ***falc fici*** flex ***frut fulv fusi glob granu herm lage lanc lati lede lept*** (leyt) ***long luci luna main*** micr ***misi nerv nigp octa papu pena plan prai quad reti rhac sara*** (sela) ***spha*** (sten) ***subc*** symci tetr ***vaga vill wall whit yunn*** spA ***spF***

11–26 cm — ***acum alia annu ante arbo aur*** bana basi ***bent*** bour bras ***bull calo card carr chon conf*** deci ***dend duth*** elme ***falc fici frut fulv fusi glob grand granu herm*** hete ***illu lage lame lanc lati laxi lede lept*** leyt ***long luci luna macr main*** (micr) ***misi nerv nigc nigp nit octa papu pena prae plan prai*** pseu ***quad reti rhac sara*** sela ***serr spha stel*** sten ***subc sylv symco*** (tetr) ***vaga vill wall whit yunn*** spB spC spD spE ***spF*** spG

26–40 cm — ***arbo bent chon grand illu lame laxi luna macr nigc nit papu prae stel sylv vill***

40–50 cm — ***bent***

11. Leaf width

1–4 cm — acum ***alia annu ante aur*** brev ***bull calo card carr deci dend duth egre falc*** flex ***frut fulv fusi glob granu herm lage*** lanc ***lept long luci main*** micr ***misi nerv*** nigp ***octa papu*** parv ***pena*** plan ***prai*** (quad) ***reti*** rhac ***sara*** scle (sela) ***spha sten subc symci symco tetr*** (vaga) (wall) ***whit yunn spA*** (spE)

4–10 cm — ***alia annu ante arbo aur*** bana basi ***bent*** bour bras ***bull calo card carr chon*** conf ***deci dend duth egre elme falc fici frut fulv fusi glob*** grand ***granu herm*** hete ***illu lage*** lame lati laxi lede ***lept*** leyt (long) ***luci luna main misi nerv nigc*** (nigp) ***nit octa papu pena prai prae*** pseu quad ***reti*** (rhac) ***sara*** sela serr ***spha stel sten subc*** sylv ***symci symco tetr vaga vill*** wall ***whit yunn spA*** spB spC ***spD*** spE spF spG

10–17 cm — ***arbo bent chon elme fici illu luna*** macr ***nigc nit papu prae stel vaga vill spD***

12. Leaf base

(sub)cordate — bent bras ***carr*** deci (***falc***) (***lame***) (***laxi***) (***leyt***) macr ***misi*** (***papu***) (***spha***) ***vill*** (***spF***)

rounded to cuneate — ***acum alia*** annu ***ante*** arbo aur ***bana*** basi bour (***bras***) bull ***calo*** card ***carr*** chon conf (***deci***) ***dend*** duth egre ***elme falc*** fici flex ***frut*** fulv fusi glob ***granu herm hete*** illu lage ***lame*** lanc ***lati laxi*** lede ***lept leyt long luci luna main*** micr ***misi nerv*** nigc ***nigp*** nit octa ***papu parv pena*** prae plan ***prai*** pseu ***quad*** reti rhac ***sara*** scle serr stel sten ***subc*** sylv symci ***symco*** tetr vaga ***vill*** wall whit ***yunn*** spA spB spC spD spE spG

emarginate — ***elme grand*** (***lati***) ***luna sela subc spF***

truncate — ***grand sela***

attenuate — (***acum***) (***alia***) (***ante***) (***bana***) brev (***calo***) (***dend***) (***frut***) ***granu*** (***herm***) (***hete***) ***lept*** (***long***) ***luci main nerv*** (***nigp***) *octc* (***parv***) (***pena***) ***prai*** (***quad***) (***sara***) ***spha*** (***symco***) (***yunn***)

13. Leaf margin

subentire — annu aur (***basi***) bent ***bull*** (***dend***) ***falc*** lage ***lati*** lept ***macr main misi*** nigp ***rhac scle*** tetr spB ***spC*** spD (***spF***)

(lowly) undulate — acum ***alia ante*** arbo ***bana*** basi ***bras brev bull calo*** card ***carr chon conf*** dend ***duth egre elme falc fici flex frut fulv glob granu herm hete illu*** (***lage***) ***lame lanc laxi leyt long luci*** luna ***macr main micr misi nerv nigc nit octa papu parv pena prae plan prai quad reti rhac sara sela spha*** stel ***sten*** subc sylv ***symci symco vaga wall whit yunn spC spE*** spF ***spG***

(lowly) glandular-crenate — ***alia ante bana*** bour ***bras brev calo carr chon conf duth egre elme fici flex frut fulv fusi glob grand granu herm hete illu lame lanc lati laxi*** lede ***leyt long luci*** (***macr***) ***micr nerv nigc*** nigp ***nit octa papu parv pena prae plan prai quad sara sela spha sten symci symco vaga vill wall whit yunn*** spA (***spB***) ***spE spG***

(lowly) glandular-serrate — ***fici grand lati leyt octa*** *octc* pseu ***reti scle serr vill spE***

(lowly) glandular-dentate — deci ***fusi serr***

14. Leaf margin

recurved — annu deci fici fusi lati (pseu) reti serr spG

flat — all others

15. Leaf apex

acute — ***egre fici fusi lati parv vill***

acuminate — ***annu arbo aur*** basi ***bent bras*** brev ***bull*** calo card ***chon conf deci dend*** duth ***egre elme*** falc ***fici flex frut*** fulv ***fusi*** glob ***grand herm hete illu lage lame lati*** laxi ***lede lept leyt luci*** luna macr ***misi nerv nigc nit octa papu parv pena prai*** prae pseu ***quad*** reti ***rhac scle sela*** serr ***spha stel sylv symci symco*** tetr ***vaga vill wall whit spA*** spB ***spC spD spE spF spG***

cuspidate — acum ***alia annu*** ante ***arbo aur*** bana ***bent bour bras bull*** carr ***chon conf deci dend elme flex frut grand granu herm hete illu lage lame lanc lede***

lept leyt long luci micr misi nerv nigc nigp nit octa (***papu***) ***pena*** plan ***prai quad rhac scle sela spha stel sten subc sylv symci symco vaga wall whit*** yunn ***spA*** (***spC***) (***spD***) ***spE spF spG***
caudate — ***alia bour granu lanc long*** main ***micr nigp sten subc***

16. Leaf: texture of dried leaf
papery — acum alia annu ante arbo bana basi bour (***carr***) chon ***conf deci dend*** (***duth***) elme (***falc***) flex frut fulv glob grand granu (***herm***) (***hete***) (***illu***) lage ***lame lanc*** (***laxi***) lede lept ***leyt*** long ***luci*** (***macr***) main micr misi (***nerv***) ***nigc*** nigp ***octa papu*** (***parv***) ***pena*** (***prae***) plan ***prai quad reti rhac*** sara (***scle***) sela (***spha***) (***stel***) sten ***subc*** symco ***vaga wall*** whit yunn spA spB (***spC***) (***spD***) spE ***spF*** (***spG***)
leathery — aur bent bras brev bull calo card ***carr*** (***conf***) (***deci***) (***dend***) ***duth*** egre ***falc*** fici fusi ***herm hete illu*** (***lame***) (***lanc***) lati ***laxi*** (***leyt***) (***luci***) luna ***macr nerv*** (***nigc***) nit ***octa*** (***papu***) ***parv*** (***pena***) ***prae*** (***prai***) pseu (***quad***) (***reti***) (***rhac***) ***scle*** serr ***spha stel*** (***subc***) sylv symci tetr (***vaga***) vill (***wall***) ***spC spD*** (***spF***) ***spG***

17. Leaf: glossiness of dried leaf
dull — ante arbo basi bour bras brev ***card*** chon conf deci dend elme frut fusi glob grand ***granu*** herm hete illu lage lame lati lede lept leyt long main micr nerv ***nigc*** nigp ***octa*** papu parv pena plan prai pseu ***quad*** rhac sara scle serr spha sten subc ***symco*** vaga vill whit yunn spA spB ***spC*** spD ***spE spF*** spG
(slightly) shiny — (acum) alia annu aur bana bent bull calo (***card***) carr duth (egre) falc fici flex fulv (***granu***) lanc laxi luci luna (macr) (misi) (***nigc***) nit (***octa***) prae (***quad***) reti (sela) stel sylv symci (***symco***) tetr (wall) ***spC*** (***spE***) (***spF***)

18. Leaf: smoothness of surface of dried leaf
strongly bullate above — bull sylv
(older leaves) (slightly) bullate above — bras (conf) deci fici luna (macr) pseu (serr) (subc) (vaga) spD
lowly (white) granular above and/or beneath — bana conf frut fulv (glob) nit prai quad sara (?sela) sten symco whit spE
strongly white granular nervation beneath — chon

19. Leaf: colour when dry
yellow on both sides — aur ***lanc luci nit sten*** symci ***tetr***
yellowish green on both sides — (aur) ***frut fulv lanc luci nit*** (octa) plan ***sara stel sten*** symco ***tetr*** (vill) wall
greyish green on both sides — acum alia ***bana*** chon conf ***frut fulv*** glob ***luci nit*** prai quad ***sara stel*** symco whit (yunn) spE
greyish, greenish, or brownish above, greyish or (dark) brownish beneath — annu ***basi*** bent ***bras bull*** calo card carr ***duth falc fici*** flex fusi ***grand*** granu herm hete illu ***lage lame lati*** laxi lede lept ***leyt luna*** macr main misi ***nerv*** nigp octa ***papu parv*** pena ***prae*** pseu reti ***scle sela*** serr spha ***subc*** sylv ***vaga*** vill yunn spA spB spC spF spG
dark green or dark brown to almost blackish above — ante bour ***bras*** brev (carr) ***deci duth*** egre elme ***fici lage*** long ***luci nigc*** rhac ***scle sela subc spD***

bluish green or bluish brown above — ante arbo ***deci*** herm ***grand lame leyt*** micr ***nerv nigc papu parv vaga***
reddish above — ***basi bras bull falc lati luna octa prae spD***

20. Leaf: basal glands
black or grey, distinct — aur fusi lanc lati tetr **yunn**
brownish, often indistinct — luci nigc octa plan prai sara symci symco vill wall ***yunn***
surrounded by hairs — acum card fici serr

21. Leaf: marginal glands in margin, nervules leading to indistinct glands
(aur) bent bull luna sylv spC

22. Leaf: relative frequency of marginal glands
few — acum annu basi brev card dend duth egre elme flex granu herm hete lept long macr main misi nigp parv pena plan quad rhac scle sylv symci symco tetr spA spB spC spD spE spF
regular — alia ante arbo bana bent bour bras bull calo carr chon conf falc fici frut fulv ***lame*** lanc lati ***laxi leyt*** luci luna micr nerv nigc nit octa prai prae ret sara sela serr spha stel sten ***vaga*** vill wall yunn spG
many — deci fusi glob grand illu ***lame laxi*** lede ***leyt*** papu pseu subc ***vaga*** whit

23. Leaf: relative size of marginal glands
thick, large — ***egre illu*** nerv ***spha***
distinct — alia ante ***arbo bour*** bras bull calo ***chon*** deci duth ***egre*** fusi ***grand illu*** lame lanc lati laxi leyt luci nigc nit octa papu prae plan prai pseu ***quad*** reti sela serr ***spha*** sten sylv ***symci symco*** vaga vill wall ***yunn*** spG
small — ***acum*** annu ***arbo*** bana ***basi*** bent ***bour brev card carr*** conf ***elme*** flex frut ***fulv grand granu herm lede long*** luna ***macr main*** micr ***misi*** parv ***pena quad rhac*** sara ***scle stel subc*** sylv ***symci symco tetr*** spA spB ***spE spF***
indistinct — ***acum*** (***arbo***) aur ***basi brev card carr*** (***chon***) dend ***elme*** falc ***fulv granu herm*** hete lage ***lede*** lept ***long macr main misi*** nigp ***pena rhac scle*** (***stel***) ***subc tetr*** whit (***yunn***) spC spD ***spE spF***

24. Leaf: drying colour/consistency of marginal glands
grey(ish) — ***bras*** card carr flex ***frut*** fulv granu herm hete lede lept ***leyt micr*** misi ***octa*** parv ***reti*** stel ***vaga*** whit spC
brown(ish) — ***alia*** (***arbo***) bana conf ***lanc*** luci ***nit plan*** sela ***sten*** subc symci
black(ish) — annu ***ante arbo*** basi bent bour ***bras*** brev bull calo chon conf ***deci*** duth egre falc ***frut*** fusi grand ***illu*** lame ***lanc*** lati laxi ***leyt*** luna main ***micr*** nerv ***nigc*** nigp ***nit octa*** papu pena prae ***plan*** prai quad ***reti*** sara scle spha ***sten*** sylv symco tetr ***vaga*** vill wall yunn spB spG
surrounded by hairs — (***alia***) (***ante***) ***deci*** fici glob (***illu***) (***leyt***) (***nigc***) pseu serr

25. Leaf: distinctness of dots
distinct — acum arbo ***bour*** brev ***calo*** card dend duth ***egre*** (***fici***) fulv fusi (***glob***) grand ***herm hete*** illu ***lanc*** lati lept ***leyt*** long luci misi nerv nigc nigp octa parv plan prai scle spha ***symci*** tetr vaga yunn

fading or indistinct — alia annu ante aur basi bent (***bour***) bras bull (***calo***) carr ***chon*** deci ***egre*** elme falc ***fici*** flex ***glob*** granu (***herm***) (***hete***) lage lame (***lanc***) lede ***leyt*** luna macr main micr (***nerv***) ***nit*** octa papu (***parv***) pena prae pseu reti (***rhac***) ***sara*** sela ***serr*** (***spha***) ***stel*** subc sylv (***symci***) ***symco*** vill wall ***whit*** spC spD spF spG

absent — bana (***chon***) conf frut laxi (***nit***) quad rhac (***sara***) (***serr***) (***stel***) sten (***symco***) (***whit***) spA spB spE

26. Leaf: density of dots

densely set, large, blackish — brev calo card dend duth fusi hete lati lept long misi nerv nigp parv plan scle spha tetr vaga

densely set, fine, greyish — arbo basi bras egre elme fici fulv grand herm illu lage lame lanc ***micr*** nigc pena prai subc symci

laxly set, fine, greyish — acum alia ante ***bull*** chon deci granu lede luci ***main*** nit octa papu prae sara sela ***serr*** symco wall whit yunn spC spD spF (***spG***)

irregularly set — annu aur bent bour ***bull*** carr falc flex glob leyt luna macr ***main micr*** pseu reti ***serr*** stel sylv vill ***spG***

27. Leaf: disc-like glands

along margin, distinct, many — bent bull falc flex ***grand*** laxi luna (***nigp***) ***prae scle*** sylv spB

along margin, small, few, irregularly present — arbo bana ***basi*** brev (***calo***) chon ***conf*** duth egre frut fulv ***fusi grand*** (***hete***) illu ***lati*** lept long ***main micr*** misi ***nigp*** nit papu parv prai ***prae*** quad sara (***scle***) ***spha*** stel sten ***symco spE*** spF

at base, small, few — ***annu*** bras carr ***reti vaga*** spD

scattered within marginal arches, regularly present — acum ***annu*** aur bour card dend ***fici fusi glob*** lanc ***lati*** lede leyt luci macr nit octa plan prai pseu ***reti*** serr sten symci tetr ***vaga*** vill wall yunn spA

absent — alia ante ***basi calo*** (***conf***) deci elme (***fici***) (***glob***) granu herm ***hete*** lage lame ***main micr*** nerv nigc pena rhac sela (***spha***) subc (***symco***) whit spC (***spE***) spG

28. Leaf: indumentum

completely glabrous — aur (***bana***) card chon dend fusi lanc lati ***laxi*** lept luci macr nit ***prae*** plan prai quad sara stel symci symco tetr wall yunn spB spE

hairs present beneath on midrib and nerves — alia ante ***arbo bana*** bent calo carr duth egre falc flex grand hete (***laxi***) lede *leys* long misi nigp parv pena (***prae***) scle spha sten spA spG

hairs present beneath — basi fulv herm illu lame nigc

hairs present above on midrib and nerves, and beneath — annu ***arbo*** bour brev bull deci glob granu main micr nerv pseu sela subc sylv whit spC spF

hairs present on both sides — acum bras conf elme fici frut lage leyt luna octa papu reti rhac serr vaga vill spD

29. Nervation: pairs of nerves

4–7 — ante ***carr*** duth ***egre*** flex fusi ***granu*** (***herm***) ***hete lage lati lept main*** micr ***nerv nigp*** parv ***prai rhac spha symco tetr*** spA

7–10 — acum alia annu ***aur bana*** bour ***bras*** brev ***bull calo*** card ***carr chon*** dend ***egre elme*** fici frut fulv ***glob granu herm hete illu lage lanc lati lept leyt luci macr***

main misi ***nerv nigc nigp nit octa*** pena ***plan prai pseu*** quad reti ***rhac sara*** scle serr ***spha sten subc*** symci ***symco tetr vaga vill*** wall ***whit*** yunn ***spB spC spD spE spG***

10–12 — ***aur bana*** basi ***bras bull*** (***calo***) ***chon conf elme falc glob illu lanc laxi*** lede ***leyt long luci luna macr nigc nit octa papu plan pseu sara stel sten subc*** sylv ***vaga vill whit spB spC spD spE***

12–16 — arbo ***bent bras conf*** deci ***falc grand illu*** lame ***laxi leyt long luna nit papu prae*** sela ***stel subc whit*** spF

16–23 — ***bent grand prae subc***

30. Nervation: marginal arches

distinct — acum alia arbo bana basi bent bour bras brev bull calo carr chon conf deci dend egre elme ***falc*** fici flex frut fulv fusi glob grand granu ***herm*** hete illu lage lame lanc lati lept leyt long luci luna macr main micr misi nerv nigc nigp nit octa parv plan pseu quad rhac sara scle sela serr spha stel sten subc sylv symci symco tetr vaga vill wall whit ***yunn*** spA spB spC spD spE spF

fading — annu ante aur card duth (***falc***) (***herm***) laxi lede papu pena prai prae reti ***yunn*** spG

31. Nervation: marginal arches curving at

0.5–3 mm — ***acum alia*** annu ante ***arbo aur*** bana basi bour bras brev bull ***calo card*** carr chon conf deci ***dend*** duth egre elme falc flex frut fulv ***fusi*** glob ***grand*** granu herm ***hete illu*** lage lame lanc ***lede lept leyt long luci luna*** main micr misi nerv ***nigc*** nigp ***octa*** papu parv pena plan prai pseu quad reti rhac sara scle ***sela serr spha stel*** sten subc ***sylv symci*** symco ***tetr vaga wall*** whit yunn spA ***spB*** spC ***spD*** spE ***spF spG***

3–5 mm — ***acum alia arbo aur bent calo card dend fici fusi grand hete illu lati laxi lede lept leyt long luci luna macr nigc*** nit ***octa prae sela serr spha stel sylv symci tetr vaga vill wall spB spD spF spG***

5–8 mm — ***arbo bent fici fusi lati laxi luci macr vill***

32. Nervation: nerves sunken above

slightly — arbo (aur) (bras) egre glob granu illu lame leyt long main (nit) sara subc spF

distinctly — bull deci fici luna (pseu) serr sylv (vaga) spD

33. Nervation: nerves almost flat beneath

symci tetr

34. Nervation: reticulation

slightly scalariform — ***alia annu ante arbo bras bull calo carr chon conf elme falc fulv grand granu*** (***herm***) ***illu lame lanc lede leyt luna main nerv nigc papu pena prai prae quad reti rhac sara stel sylv vaga whit spC spD spE spF spG***

strongly scalariform — ***subc***

densely reticulate — acum ***alia annu ante arbo*** aur bent ***bras calo carr chon conf elme falc*** frut ***fulv*** glob ***grand herm lame lanc*** laxi ***lede leyt*** long luci ***luna main*** misi ***nigc*** nigp nit ***papu pena prai prae quad reti sara*** scle sela serr spha ***stel*** sten ***subc sylv*** symci symco ***vaga*** wall ***whit*** spA spB ***spC spD spE spF*** laxly reticulate — bana basi bour brev ***bull*** card deci dend duth egre fici flex fusi ***granu*** hete ***illu*** lage lati lept macr micr ***nerv*** octa parv plan ***rhac*** tetr vill yunn ***spG***

35. Nervation: distinctness

distinct — acum alia ante arbo bent bras bull calo chon deci elme fici flex frut fulv glob grand granu illu lage lame ***lanc*** laxi ***luci*** luna macr misi nigc nigp prae pseu ***quad*** scle ***sela*** serr ***stel*** subc sylv symco vaga ***whit*** yunn ***spA*** spB spC spD spE spF spG

fading — annu aur bana basi carr conf dend egre falc fusi herm hete ***lanc*** lept leyt long ***luci*** main micr nerv nit octa papu parv pena plan prai (***quad***) reti rhac sara ***sela*** spha ***stel*** sten symci tetr vill wall (***whit***) (***spA***)

indistinct — bour brev card duth lati lede

36. Nervation: second and third order sunken above

slightly — bras conf deci (elme) macr (nigc)

distinctly — bull fici luna (pseu) serr sylv (vaga) spD

37. Inflorescences

axillary or in the axes of fallen leaves — acum alia annu ante ***arbo*** aur bana basi bour ***bras*** brev bull calo card carr chon conf deci dend duth egre elme falc fici flex frut fulv fusi glob grand granu herm hete illu lage ***lame*** lanc lati laxi lede lept leyt long luci luna ***macr*** main micr ***misi*** nerv nigc nigp ***nit*** octa papu parv pena prae plan prai pseu quad reti rhac sara scle sela serr spha stel sten subc sylv symci symco tetr vaga vill wall whit yunn spA (***spB***) spC spD ***spE*** spF spG

on the branches — ***arbo*** bent ***bras lame macr misi nit spE***

on the trunk — ***spB***

38. Staminate inflorescence: clustering

1–6 — acum alia annu ante arbo aur bana basi bour bras brev bull calo card carr chon conf deci egre falc fici frut fulv fusi glob grand granu herm ***hete*** illu lage lanc lati laxi lede lept leyt long ***luci*** luna macr main micr misi nerv nigc nigp nit octa papu parv pena prae plan prai pseu quad reti rhac ***sara*** scle sela serr spha ***stel*** (***sten***) ***subc*** symci ***symco*** tetr vaga vill wall yunn (spB) spC spD spE spF spG

6–10 — bent ***?hete luci sara stel sten*** (***subc***) ***symco spB***

10–20 — elme ***sten spB***

39. Staminate inflorescence: length

4–16 mm — acum alia annu ***ante aur*** bana ***bent bour brev bull calo card carr*** (***chon***) ***conf*** ?deci ***egre elme*** falc (***fici***) ***frut fulv fusi*** glob ***grand*** granu ***lage*** lanc ***laxi lede lept leyt*** long ***luci*** (***luna***) main micr misi ***nerv nigc nigp nit*** (***papu***) parv pena ***plan prai*** (***pseu***) ***quad*** ?reti rhac ***sara*** scle sela ***serr stel sten subc symci symco tetr vaga vill whit*** spE ***spF***

16–50 mm — ***ante arbo aur*** basi ***bent bour bras brev bull calo card carr chon conf egre elme fici*** flex ***frut*** (***fulv***) ***fusi grand*** illu ***lage laxi lede lept leyt luci luna macr nerv nigc nigp nit*** octa ***papu*** prae ***plan prai pseu quad sara serr spha stel sten subc symci symco tetr vaga vill*** wall ***whit*** yunn ***spB spC*** spD ***spF spG***

50–100 mm — ***arbo bras grand leyt macr nerv prai spha symco vill spB spC spG***

40. Staminate inflorescence: diameter
0.2–0.5 mm — chon elme grand rhac whit
0.5–1.5 mm — alia ante arbo bana card granu illu lage laxi lept long ***luci*** main micr misi nigp ***plan prai*** reti sara scle ***sela*** sten ***subc*** symco spB ***spE***
1.5–3.5 mm — acum annu aur basi ***bent*** bour ***bras*** brev ***bull*** calo carr deci egre falc frut fulv fusi glob lanc lede leyt ***luci*** luna macr nerv nigc ***nit*** octa ***papu*** parv pena prae ***plan prai*** pseu ***quad sela*** serr spha stel ***subc*** symci tetr ***vaga*** vill wall yunn spC spD ***spE*** spF spG
3.5–5 mm — ***bent bras bull*** fici ***nit papu quad vaga***
5–9 mm — conf ***nit quad***

41. Staminate inflorescence: indumentum
(sub)glabrous — bana brev chon egre flex fulv grand lept nit prai quad sara stel symco whit spE
(sparsely) puberulous — alia ante ***aur*** bent bull calo ***card*** dend elme falc frut granu herm hete lanc ***lati*** laxi luci luna main micr misi nerv nigp octa ***parv plan*** rhac scle spha sten sylv symci ***tetr*** wall spB ***spG***
sparsely to densely tomentose or sericeous — acum annu arbo ***aur*** basi bour bras ***card*** carr conf deci duth fici fusi glob illu lage lame ***lati*** lede leyt long macr nigc papu ***parv*** pena prae ***plan*** pseu reti sela serr subc ***tetr*** vaga vill yunn spC spD spF ***spG***

42. Staminate inflorescence: peduncle length
absent — aur card ?deci fici fusi glob lanc lati lept luci macr misi octa plan serr symci tetr vill wall yunn
0–0.5 mm — acum ***annu main*** micr ***nigc papu prae pseu sela*** (***spC***)
0.5–3 mm — alia ***annu*** ante arbo bana (***basi***) ***bent brev calo*** chon ***conf*** egre elme ***falc*** frut fulv grand granu (***illu***) laxi ***lede leyt*** long ***luna main nerv nigc nigp nit papu*** parv pena prai ***prae pseu quad*** rhac ***sela spha*** stel ***sten subc*** symco whit ***spC*** spE ***spF*** spG
3–10 mm — ***basi bent*** bour ***bras brev*** bull ***calo*** carr ***conf falc illu*** lage ***lede leyt luna nerv nigp nit quad*** sara ***spha sten subc*** vaga ***spB spC*** spD ***spF***
10–24 mm — ***bras nit spB***

43. Staminate inflorescence: distribution of glomerules
continuously floriferous to base — acum aur card ?deci fici fusi glob lanc lati lept luci macr ***main micr*** misi nigc octa ***papu plan*** pseu ***sela*** serr symci tetr vill wall yunn spC
continuously flowered at apical 3/4 to 2/3 — (***alia***) bent bour ***brev*** bull falc ***granu*** lage long luna ***main micr parv scle sela*** sylv
interrupted at base, continuous at apex — ***alia*** annu ante arbo bana basi bras ***brev*** calo ***carr*** ?dend ?duth egre ?flex ***frut granu*** (***illu***) ?lame lede leyt nerv ***papu parv*** pena ***prae*** (***plan***) reti sara ***scle*** spha stel (***sten***) subc vaga ?spA spB spE spF spG

massed in a apical head — conf ***frut*** nit quad
strongly interrupted throughout — (***carr***) chon elme fulv grand ***illu*** laxi nigp prai ***prae*** rhac ***sten*** symco whit spD

44. Staminate inflorescence: conspicuousness of bracts
conspicuous — aur bour bras brev fici fusi lati macr octa papu prae pseu serr spha ***subc*** symci tetr vill wall yunn
indistinct — acum alia annu ante arbo bana basi bent bull calo card chon conf egre elme falc frut fulv glob granu illu lage lanc laxi lede lept leyt long luci luna main micr misi nerv nigc nigp nit parv pena plan prai quad reti rhac sara scle sela stel sten ***subc*** symco vaga whit spB spC spD spE spF spG

45. Staminate inflorescence: bracts length
0.2–0.5 mm — alia ante arbo conf elme ***frut*** granu ***lage lept*** luci nit ***plan*** ?quad ***sara sten*** spE
0.5–1.2 mm — acum annu aur bana basi bent ***brev*** calo card ***carr*** chon egre falc ***frut*** fulv glob grand illu ***lage*** lanc lati laxi lede ***lept*** leyt long ?luna main ?micr misi nerv nigc nigp octa ***papu*** parv pena ***plan*** prai pseu rhac ***sara*** scle sela serr spha stel ***sten subc*** ?sylv symci symco tetr ***wall*** whit yunn spB spC ***spD*** spF
1.2–2 mm — bras ***brev*** *spca* ***carr*** fusi macr ***papu*** prae reti ***subc*** vaga ***vill wall spD*** spG
2–3 mm — bour fici ***vill***

46. Staminate inflorescence: bracts indumentum outside
glabrous to very sparsely puberulous — aur bana brev chon egre frut fulv fusi grand granu lanc lati lept long luci macr nit parv pena plan prai ?quad sara scle spha stel tetr whit yunn spE
sparsely puberulous/villose/sericeous/tomentose — acum alia ante arbo bour bras calo card carr conf glob illu laxi lede leyt main ?micr misi nerv nigc nigp octa reti rhac sela serr symci symco vaga ***vill*** spB spD spF spG
tomentose/puberulous/sericeous/villose/hirsute — annu basi bent ?bull elme falc lage prae pseu sten ?sylv ***vill*** wall spC
densely sericeous/tomentose/puberulous — fici papu subc

47. Staminate inflorescence: glomerule shape
ellipsoid — arbo (***aur***) basi (***bent***) bras (***bull***) card conf (***falc***) frut ?lame leyt luci (***luna***) nigc nit papu prae plan quad stel sten ***spB*** spE spF
(sub)globose — alia annu ante bana bour brev calo carr chon egre elme fici ?flex fulv fusi (***glob***) grand granu illu lanc laxi lede long (***macr***) (***main***) (***micr***) nerv nigp (***octa***) parv pena prai (***pseu***) reti rhac sara scle sela serr spha subc symco (***symci***) (***tetr***) vaga (***vill***) (***wall***) whit (***yunn***) ***spB*** spD spG
indistinct — acum ***aur bent bull falc glob*** lage lati lept ***luna macr main micr*** misi ***octa pseu symci tetr vill wall yunn*** spC

48. Staminate inflorescence: glomerule length
0.5–1.5 mm — acum alia ante bana chon elme fulv glob grand granu lanc laxi ?macr main micr prai rhac sara sten ***subc*** symco whit

1.5–3 mm — annu arbo aur basi bour ***bras*** brev calo carr egre frut fusi illu lede ***leyt*** luci nerv nigc nigp nit octa papu pena plan quad serr spha ***stel subc*** symci tetr vaga ***spB*** spD spE spF **spG**
3–6 mm — bent ***bras*** fici ***leyt*** prae ***stel spB spG***

49. Staminate inflorescence: glomerule width
0.3–0.8 mm — alia ante elme frut granu main micr plan rhac ***sara stel*** sten spE
0.8–1.5 mm — acum annu arbo aur bana basi brev ***carr*** chon fulv glob grand lanc laxi ***lede leyt*** luci macr ***nerv*** nigc ***nigp nit*** octa pena prai quad ***sara*** spha ***stel*** subc symco symci ***tetr*** whit spF
1.5–3.5 mm — bent bour bras calo ***carr*** egre fici fusi illu ***lede leyt nerv nigp nit*** papu prae serr ***tetr*** vaga spB spD spG

50. Staminate inflorescence: number of flowers per glomerule
2–5 — brev ***egre*** glob granu lage lanc lept ***main misi*** parv ***plan pseu*** scle spC
5–10 — acum alia annu ante aur ***bana*** (***basi***) calo card ***carr*** chon ***egre*** elme (***falc***) fici frut fulv fusi ***grand*** lati ***laxi leyt*** long macr ***main*** micr ***misi*** nerv nigp ***nit*** octa pena ***plan*** prai ***pseu quad*** reti rhac sara sela ***serr*** spha ***stel*** sten subc symci symco tetr (***vaga***) vill wall whit yunn spD spE spF
10–15 — (***bana***) ***basi*** bent bour bull ***carr*** conf ***falc grand*** illu ***laxi*** lede ***leyt*** luci luna ***nigc nit quad serr stel vaga*** spB spG
15– >> 20 — arbo bras **nigc** papu prae

51. Staminate inflorescence: setting of flowers in glomerules
laxly — acum alia ante bour brev calo card carr ?duth egre fusi lage ?lati lept macr misi nerv octa parv pena pseu reti sara scle sela spha subc symci tetr vill wall yunn spC spD spG
densely — annu arbo aur bana basi bent bras bull chon conf ?deci elme falc fici flex frut fulv ?glob grand granu illu ?lame lanc laxi lede leyt long luci luna main micr nigc nigp nit papu prae plan prai quad rhac serr stel sten ?sylv symco vaga whit spB spE spF

52. Staminate inflorescence: spacing of glomerules (at base)
not — acum aur bent bour bull card ***conf*** falc fici fusi glob lage lanc lati lept long luna macr micr misi ***nit*** octa papu parv pseu sela symci tetr vill wall yunn ***spC***
0–1 mm — alia annu ante ***arbo bana bras*** brev ***chon*** (***conf***) egre frut granu ***luci*** main nigc (***nit***) (***prae***) plan ***quad*** rhac serr ***spha*** stel ***subc symco whit*** spE ***spG***
1–4 mm — ***arbo bana*** basi ***bras calo*** carr ***chon*** elme fulv ***grand*** illu ***laxi lede*** leyt ***luci*** nerv nigp pena prai ***prae quad sara spha*** sten ***subc symco*** vaga ***whit spB*** (***spC***) ***spD*** spF ***spG***
4–9 mm — ***bras calo grand laxi lede sara*** (***symco***) ***spB spD***

53. Staminate flower: length
0.3–0.5 mm — alia ***arbo elme frut*** granu ***long luci*** main ***micr nigc nit quad*** rhac ***stel*** sten subc
0.5–1 mm — ***arbo bour chon*** conf egre ***elme frut*** fulv glob grand illu ***lanc laxi long luci micr nigc nit*** octa pena plan ***prai quad*** reti? sara sela ***serr*** (***stel***) ***symci*** symco ***tetr*** whit spE spF

1–2.5 mm — acum annu ante bent ***bour*** bras brev bull calo card carr ***chon*** falc fici fusi lage ***lanc*** ?lati ***laxi*** lede lept leyt luna macr misi nerv nigp ***papu*** parv ***prai prae*** pseu scle ***serr spha symci tetr vaga*** vill wall yunn spB spC spD spG

2.5–3.5 mm — ***papu prae spha vaga***

54. Staminate flower: number of sepals

3 — ***bour*** (***brev***) (***elme***) (***frut***) ***luci*** (***nigc***) ***parv*** (***plan***) (***sten***) ***wall spE spG***

4 — ***acum*** annu ante ***arbo*** aur ***bana basi bent bour bras brev*** bull calo ***card carr chon conf*** egre ***elme falc fici frut*** glob ***grand*** granu ***herm*** hete illu lage lanc lati (***laxi***) ***lede*** lept ***leyt*** long ***luci luna macr main*** micr misi ***nerv nigc*** nigp nit octa papu ***parv*** pena ***prae plan prai pseu quad*** reti rhac ***sara*** scle sela ***serr*** spha stel ***sten*** subc symci symco tetr vaga vill ***wall whit yunn spB*** spC spD ***spE*** spF ***spG***

5 — (***acum***) alia ***arbo bana basi*** (***bent***) ***bour*** (***bras***) (***card***) (***carr***) ***chon conf falc fici fulv*** fusi (***grand***) (***herm***) ***laxi*** (***lede***) (***leyt***) ***luna macr*** (***main***) ***nerv*** (***nigc***) ***prae*** (***prai***) ***pseu*** (***quad***) (***sara***) ***serr*** (***sten***) ***whit*** (***yunn***) (***spB***)

6 — ***fulv*** (***plan***)

7 — ***fulv***

55. Staminate flower: sepal connectivity

free — acum aur card fici fusi lanc ?lati luci octa plan pseu serr symci tetr vill wall yunn

connate at base only — alia ante arbo bana basi bour calo chon conf ?dend ?duth elme ?flex frut fulv glob grand granu illu laxi leyt long macr main micr nigc nit pena prai quad rhac sara sela stel sten subc symco whit spE spF spG

connate to c. halfway — annu bent bras brev bull carr ?deci egre falc lage ?lame lede lept luna misi nerv nigp papu parv prae reti scle spha ?sylv vaga spB spC spD

56. Staminate flower: sepal length

0.3–0.8 mm — alia annu ante arbo bana bent ***bour*** (***bras***) bull card ***carr*** conf egre elme falc frut (***fulv***) ***glob*** grand granu ***lage*** (***lati***) laxi ***lede*** lept long luci ***luna*** main micr misi nigc nigp nit (***octa***) ***papu prae*** plan quad ***reti*** rhac ***sara*** sela serr stel sten ***subc symco*** (***wall***) ***spB*** spE ***spF***

0.8–1.8 mm — acum aur basi ***bour bras*** brev calo ***carr*** chon fici ***fulv*** fusi ***glob*** illu ***lage*** lanc (***lede***) leyt ***luna*** macr nerv ***octa papu*** parv pena (***prae***) prai pseu ***reti*** (***sara***) scle spha ***subc*** symci (***symco***) tetr vaga vill ***wall*** whit yunn ***spB*** spC spD (***spF***) spG

57. Staminate flower: sepal indumentum outside

glabrous to very sparsely puberulous — aur bana brev chon egre frut fulv grand lanc lede lept luci macr ***octa*** parv plan prai sara scle sela stel symci symco tetr whit yunn spE

sparsely puberulous/sericeous/tomentose/villose/hirsute — acum alia annu ante arbo basi bent bour bras calo card carr conf elme falc fici fusi granu illu lage lati laxi leyt long luna misi nerv nigc nigp nit ***octa papu*** pena prae pseu quad reti rhac serr spha sten vaga vill wall spB spC spD spF spG

tomentose/sericeous/puberulous — bull glob main micr ***papu*** subc

58. Staminate flower: number of stamens

2 — acum ***alia*** ante arbo aur ***bana*** basi (***bent***) ***bour bras brev*** bull ***calo card chon*** conf ***egre elme falc fici*** flex ***frut*** fusi glob granu hete lage lanc lati ***lede*** lept long luci ***luna*** macr main micr misi ***nerv*** nigc ***nigp*** nit octa ***papu*** parv ***prae*** plan ***prai*** pseu quad rhac sara scle sela ***serr spha*** stel sten subc ***symci*** symco tetr (***vaga***) ***vill*** wall ***whit*** yunn ***spB spC spD*** spE spF

3 — (***alia***) ***annu bana bent bour bras*** (***brev***) ***calo*** (***card***) carr ***chon*** (***egre***) (***elme***) ***falc fici*** (***frut***) ***fulv grand illu laxi lede luna nerv nigp papu*** pena ***prae*** (***prai***) ***reti spha*** (***symci***) ***vaga vill whit*** (***spB***) (***spC***) ***spD spG***

4 — ***annu bras*** (***brev***) *cars* ***falc fulv*** (***grand***) ***herm illu laxi*** leyt ***nerv prae*** (***prai***) ***reti*** (***serr***) (***vaga***) ***spD spG***

5 — *cars* ***fulv*** (***herm***) ***prae spD***

6 — ***fulv prae spD***

7 or 8 — ***prae***

59. Staminate flower: stamen exsertion

not or slightly exserted, c. 0.75–1.25 times the sepal length — acum alia arbo aur bana basi bour brev chon conf egre elme fici frut fulv fusi glob grand granu illu lanc ?lati long luci macr main micr nigc nigp nit octa pena plan prai pseu quad ?reti rhac sara scle sela serr stel sten subc symci symco tetr vill wall whit spE spF

exserted, c. twice the sepal length — annu ante bras calo card carr ?deci lage ?lame laxi lede lept leyt misi nerv parv ***prae*** spha vaga yunn spB spC spD spG

strongly exserted, c. thrice the sepal length — bent bull falc luna papu ***prae*** ?sylv

60. Staminate flower: stamen length

0.2–1 mm — ***acum*** alia arbo aur bana basi ***bour*** chon conf egre elme ?flex frut ***fulv*** glob grand granu hete illu lanc long luci (***macr***) main micr nigc ***nigp*** nit **octa** pena plan prai pseu quad ?reti rhac sara sela serr stel sten subc ***symci*** symco tetr whit spE spF

1–2 mm — ***acum annu*** ante ***bent bour bras brev*** bull calo card ***carr*** falc fici ***fulv fusi herm*** lage ?lati laxi lede lept leyt luna ***macr*** misi ***nigp octa papu*** parv ***prae*** scle ***symci vaga*** vill ***wall yunn*** spB ***spC*** spD ***spG***

2–4 mm — ***annu bent bras brev carr fusi herm*** nerv ***papu prae*** spha ***vaga wall yunn spC spG***

61. Staminate flower: anther length

0.1–0.2 mm — alia bana bent bull conf elme falc frut glob granu luna main micr nigc nit prai quad rhac sara sela stel sten subc symco spE

0.2–0.4 mm — acum annu ante arbo aur basi bour bras calo card chon fici fulv grand illu lage lanc lati laxi lede lept leyt long luci macr misi nerv nigp octa papu pena prae plan pseu reti serr ***spha*** symci tetr vaga ***vill wall*** whit yunn spB spC ***spD*** spF

0.4–0.6 mm — *spca* carr egre fusi herm hete parv scle ***spha vill wall spD*** spG

0.6–0.8 mm — brev

62. Staminate flower: pistillode
absent — acum alia ante aur card conf egre frut fulv fusi glob lage lanc lati lede lept long macr main micr misi nit papu parv prai pseu quad rhac scle spha stel sten symci tetr vill whit spC
minute — bana chon falc granu octa plan sara symco yunn
hairy tuft — bour brev illu serr spD
lumpy — arbo basi elme fici grand laxi leyt luci nerv nigc pena reti sela subc spE spF
cylindric — annu bent bras calo carr luna nigp prae vaga wall spB spG

63. Hermaphrodites
(brev) (egre) herm hete

64. Pistillate inflorescence: clustering
1–6 — acum alia annu ante arbo aur bana basi bent bour bras brev ?bull calo card carr chon conf deci dend duth egre (***elme***) falc fici flex frut fulv fusi glob grand granu herm ***hete*** illu lage lame lanc lati laxi lede leyt long luci luna macr main micr misi nerv nigc nigp nit octa papu parv pena prae plan prai pseu quad reti rhac ***sara*** scle sela serr spha stel sten subc sylv symci symco tetr vaga vill wall whit yunn spA spD spE spF spG
6–10 — ***elme hete*** (***sara***)

65. Pistillate inflorescence: length
2–6 mm — acum ***annu*** (***ante***) aur bana ***brev bull*** card conf deci ***fici flex frut fulv*** fusi glob granu (***herm***) ***lage*** lanc lati ***long*** luci ***macr main*** micr misi (***nerv***) ***nigc*** nit ***octa*** (**pena**) ***prae*** plan pseu quad ***sara*** serr ***stel subc*** (***sylv***) ***sylv symci*** (***vaga***) vill ***wall*** yunn ***spF***
6–15 mm — alia ***annu ante arbo*** bent bour ***bras brev*** (***bull***) (***calo***) ***chon*** dend duth ***elme*** falc (***fici***) (***flex***) (***frut***) ***fulv grand herm hete illu lage lame laxi*** lede ***long luna*** (***macr***) (***main***) ***nerv nigc*** nigp ***octa papu pena prai prae rhac sara*** scle sela ***spha stel*** sten ***subc sylv symci symco vaga wall whit spA spF***
15–37 mm — ***arbo basi bras calo*** carr ***chon*** egre ***elme fulv grand herm hete illu lame laxi*** leyt ***luna papu prai rhac*** (***spha***) ***symco vaga whit spA*** spD ***spG***
37–80 mm — ***basi calo elme lame luna spG***

66. Pistillate inflorescence: diameter
0.2–1 mm — alia annu ante (***arbo***) bana basi brev bull carr chon dend duth ***egre*** elme falc flex ***fulv*** grand granu herm hete illu ***lame*** laxi lede long misi ***nerv*** nigp nit ***papu pena plan*** prai quad rhac sara scle ***sela*** stel sten symco ***vaga*** whit spA
1–2 mm — acum ***arbo*** aur ***bent*** bour bras bull calo card ***conf*** deci ***egre*** frut ***fulv*** fusi glob lage ***lame*** lanc lati leyt luci luna main micr ***nerv*** nigc octa ***papu pena*** prae ***plan*** pseu ***sela*** serr spha subc sylv symci ***vaga vill*** wall yunn spD spF spG
2–4 mm — ***bent conf*** fici macr ***vill***

67. Pistillate inflorescence: indumentum
(sub)glabrous — bana chon egre flex fulv grand nit prai quad sara stel symco whit spE

(sparsely) puberulous — ***acum*** alia ante ***aur*** bent brev bull calo ***card carr*** dend elme falc frut granu herm hete lanc ***lati*** laxi (*leys*) luci luna main micr misi nerv nigp octa ***parv plan*** rhac scle spha sten sylv symci ***tetr*** wall spA ***spG***

sparsely to densely (red) tomentose or sericeous — ***acum*** annu arbo ***aur*** basi bour bras ***card carr*** conf deci duth fici fusi glob illu lage lame ***lati*** lede leyt long macr nigc papu ***parv*** pena prae ***plan*** pseu reti sela serr subc ***tetr*** vaga vill yunn spD spF ***spG***

68. Pistillate inflorescence: number of flowers per inflorescence

1 — bana bour? conf frut fulv nit quad sara sten spE

up to 5 — aur bour? brev fici flex fusi glob lanc lati micr parv prai pseu tetr yunn

up to 11 — acum alia annu ante arbo basi bull calo card carr chon deci dend duth egre falc grand granu herm illu lage laxi lede leyt long luci macr main misi nerv nigc nigp octa pena prae plan reti scle sela serr stel symci symco vaga vill wall whit spA spD spF

up to 15 — bent bras hete papu rhac spha subc

up to 19 — lame

up to 21 — elme spG

69. Pistillate inflorescence: distribution of flowers

flowers densely clustered throughout — acum aur deci fici fusi glob lanc lati luci macr ***main*** nigc octa prae plan pseu serr ***subc*** symci tetr vill wall yunn ***spF***

flowers rather densely clustered throughout — annu bras card lame leyt ***long nerv*** papu pena reti vaga ***spD***

flowers densely clustered apically, laxly so or absent below — alia bent bour ***brev*** bull dend duth ***egre*** falc granu hete lage lede ***long*** luna ***main*** micr misi ***nerv parv*** scle sela spha stel ***subc*** sylv ***spF***

flowers laxly clustered throughout — ante arbo basi ***brev*** calo carr chon ***egre*** elme flex grand herm illu laxi nigp ***parv*** prai rhac symco whit spA ***spD*** spG

one flower apically — bana conf frut fulv nit quad sara sten spE

70. Pistillate inflorescence: bract length

0.3–0.5 mm — ante arbo ***dend*** elme falc ***flex*** glob grand granu lage ***laxi luci*** luna ***micr misi*** nit quad rhac ***scle stel subc*** sylv

0.5–1.2 mm — acum alia annu aur bana bent ***calo*** card carr chon conf deci ***dend*** duth egre ***flex*** frut fulv fusi ***herm*** hete illu lanc lati ***laxi*** lede leyt long ***luci*** main ***micr misi*** nerv ***nigc*** nigp octa papu ***parv*** pena plan prai reti sara ***scle*** sela serr spha ***stel*** sten ***subc*** symci symco tetr vaga ***vill*** wall whit yunn spA spE spF

1.2–2 mm — basi bras brev ***calo*** fici ***herm lame nigc parv prae vill*** spD spG

2–3 mm — bour ***lame*** macr ***prae***

71. Pistillate inflorescence: bract indumentum outside

(sub)glabrous — ***ante*** bana brev calo chon flex fulv fusi grand lanc ***lati*** luci nit ***octa*** parv plan prai sara ***stel*** symci symco tetr whit yunn spE ***spG***

(very) sparsely puberulous/tomentose — acum alia ***ante*** arbo aur bour card carr dend duth egre falc frut granu herm hete illu ***lati*** laxi lede leyt long nerv nigc nigp ***octa papu*** pena quad rhac scle sela serr spha ***stel*** sten sylv vaga wall spA spD ***spG***

tomentose/puberulous/sericeous/villose — annu basi bent bras ?bull conf elme glob luna macr main micr misi ***papu*** prae ?pseu reti subc vill spF
densely tomentose/villose — deci fici lage lame

72. Pistillate flower: pedicel length
absent — acum aur alia deci fici glob granu lage lanc lati macr main octa prae plan pseu sela serr subc symci tetr vill wall yunn spF
minute, 0–0.5 mm long — aur bent ?bour ***brev*** *cars* ?duth elme lame long luci micr misi ***nigc*** pena rhac sylv
0.5–3 mm long — annu ante arbo bana basi bras ***brev*** bull calo card ***chon conf*** dend egre falc flex frut ***fulv*** fusi ***herm*** hete illu laxi lede leyt luna nerv ***nigc*** nigp ***nit*** (octa) papu parv prai quad reti sara scle spha stel ***sten symco vaga*** whit spA spD ?spE spG
3–6 mm long — carr ***chon*** ?***conf fulv*** grand (***herm***) ***nit sten symco vaga*** (spG)

73. Pistillate flower: length
1–2 mm — alia ***aur bull chon*** elme ***frut*** granu main ***micr*** rhac scle ***subc symco***
2–4 mm — acum annu ante ***arbo aur*** bana basi bent brev ***bull*** calo card ***carr chon*** ?conf deci dend ***egre*** falc fici flex ***frut fusi*** grand ***herm*** hete ***illu lage*** lame lanc lati lede ***leyt*** long luci luna ***micr misi*** nerv ***nigc*** nigp nit ***octa papu*** parv pena prae ***plan*** prai ***pseu*** quad reti ***sara sela*** ser spha ***stel subc*** sylv ***symci symco vaga vill wall*** whit spA spD spF
4–6.5 mm — ***arbo*** bras ***carr egre fusi herm illu lage*** laxi ***leyt*** macr ***misi nigc octa papu plan pseu sara sela stel*** sten (***symci***) ***vaga vill wall*** yunn spG

74. Pistillate flower: sepal number
3 — ***acum ante bour calo card*** duth (***fusi***) illu (***lanc***) macr (***nigc***) (papu) ***parv plan symci symco*** wall ***yunn***
4 — ***acum alia*** annu ***ante aur*** basi (***bent***) ***bour*** bras brev (***calo***) ***card*** carr chon deci dend egre ***elme falc fici fusi*** granu ***herm*** hete lage ***lanc*** laxi lede leyt long ***luci main*** micr ***misi*** nerv ***nigc*** nigp octa papu ***parv*** pena ***plan*** prai pseu ***reti*** rhac ***sara scle*** sela ***serr*** spha subc ***symci symco*** tetr ***vaga*** vill ***yunn spA spD spE*** spF ***spG***
5 — ***alia*** arbo ***aur*** bana ***bent bull*** *cars* (***elme***) ***falc fici flex frut*** fulv glob grand (***herm***) lame lati ***luci luna*** (***main***) (***misi***) ***nit*** prae ***quad reti sara scle*** (***serr***) ***stel sten*** sylv ***vaga whit spA spD spE spG***
6 — ***bull conf flex*** (***frut***) ***luna nit quad stel sten whit***
7 — ***conf***

75. Pistillate flower: sepal length
0.3–1 mm — alia annu ante arbo ***aur*** bent ***bras*** bull ***calo*** card carr dend ***duth*** egre elme falc flex glob ***grand*** granu ***hete lage lame lanc laxi*** lede ***leyt*** long luci luna ***main*** micr misi ***nerv nigp*** nit octa papu ***parv prae*** plan ***prai*** quad ***reti*** rhac ***sara*** scle serr ***stel subc*** sylv symci symco tetr ***vaga*** whit ***yunn*** spA spE spG
1–2.2 mm — acum ***aur*** bana basi bour ***bras*** brev ***calo*** chon conf deci ***duth*** fici frut fulv fusi ***grand*** herm ***hete*** illu (***lage***) ***lame lanc*** lati ***laxi leyt*** (***main***) ***nerv*** nigc ***nigp parv*** pena ***prai prae*** pseu ***reti sara*** sela spha ***stel*** sten ***subc vaga*** vill wall (***yunn***) spD spF
2.5–3.5 mm — macr

76. Pistillate flower: sepal direction
ascending — annu aur bras brev *cars* egre flex hete lanc misi octa parv prae plan symci tetr wall yunn
perpendicular — acum alia ante arbo basi bent bour bull calo card carr deci dend duth elme falc fici fusi glob grand granu herm illu lage lame lati laxi lede leyt long luci luna macr main micr nerv nigc nigp papu pena prai pseu reti rhac scle sela serr spha sten subc sylv symco vaga vill whit spA spD spE spF spG
reflexed — bana chon conf frut fulv nit quad sara stel

77. Pistillate flower: sepal indumentum outside
(sub)glabrous — aur bana chon ***egre*** flex fulv grand lanc nit ***octa*** parv plan ***prai*** sara stel symci symco tetr ***whit*** yunn spE ***spG***
(very) sparsely puberulous/tomentose — acum alia annu ante arbo bour brev calo card carr dend duth ***egre*** elme falc frut fusi granu herm hete illu laxi lede leyt long luci luna main misi nerv nigp ***octa prai*** quad rhac scle sela spha sten vaga vill wall ***whit*** spA spD ***spG***
tomentose/sericeous/puberulous/hirsute — basi bent bull conf fici glob lame lati micr nigc papu pena prae pseu reti serr subc sylv spF
densely tomentose/hirsute/villose — bras deci lage macr

78. Pistillate flower: sepal fleshy
at base only — *cars* fulv luci nigc octa plan symci tetr vill
completely — bana chon frut lati prai quad sara spha stel sten symco (whit) spE

79. Pistillate flower: petal-like structures occasionally present
alia bull carr fulv luci luna nigc octa plan pseu sara stel sten sylv yunn spG

80. Pistillate flower: locule number
2 — acum alia ***annu*** ante aur ***basi*** brev ***calo carr*** duth egre elme fici fusi granu ***herm hete*** lage lanc ***lede*** (***leyt***) luci macr main micr ***misi nerv*** nigc octa pena plan (***prai***) ***reti*** rhac scle ***sela*** serr ***spha*** subc symci ***symco*** tetr vill wall yunn spF
3 — ***annu arbo bana*** (***basi***) ***bent*** bour ***bras*** bull ***calo*** card (***carr***) chon ***conf*** deci dend falc flex frut fulv glob grand (***herm***) ***hete illu lame*** lati ***laxi lede leyt*** long *luct* ***luna*** (***misi***) ***nerv*** nigp ***papu prai prae*** pseu (***quad***) (***reti***) sara ***sela spha stel*** sten sylv ***symco*** vaga whit spA spD spE spG
4 — (***arbo***) (***bana***) (***bent***) ***bras conf*** (***illu***) ***lame*** (***laxi***) (***luna***) (***nerv***) ***nit*** (***papu***) (***prae***) ***quad*** (***stel***)
5 — ***lame nit*** (***quad***)
6 (or 7) — ***nit***

81. Pistillate flower: ovary shape
globose — arbo ***bana conf lame quad*** sela ***serr***
cylindric — ***quad*** sara stel ?spE
ovoid — annu basi bour bras calo card carr ***chon*** dend duth flex fulv fusi grand herm hete illu lanc lati laxi lede leyt long luci macr ***micr*** misi nigp papu parv prae plan prai reti scle spha sten symci symco tetr vaga ***wall*** whit spA spD spG

ellipsoid — acum alia aur ***bana*** bent bull ***chon conf*** deci elme falc fici frut glob granu ***lame*** luna main nerv nigc nit octa pena pseu rhac ***serr*** subc sylv vill spF
narrowly ovoid/flask-shaped — ante brev egre lage (***micr***) ***wall*** yunn

82. Pistillate flower: ovary length
1–2 mm — alia ***annu*** aur bana ***brev*** bull ***card*** chon ***deci dend*** egre elme ***flex frut*** granu ***herm hete lame lanc lede luci luna*** main micr ***nerv*** nigp ***pena prai prae quad reti*** rhac scle ***serr*** subc ***symci symco whit*** spA ***spD***
2–4 mm — acum ***annu*** ante arbo basi bent bour bras ***brev*** calo ***card*** carr ?conf ***deci dend*** ?duth falc fici ***flex frut*** ?fulv fusi ?glob grand ***herm hete*** illu lage ***lame lanc*** lati laxi ***lede*** leyt long ***luci luna*** macr misi ***nerv*** nigc nit octa papu parv ***pena prae*** plan ***prai*** pseu ***quad reti*** sara sela ***serr*** spha stel sten sylv ***symci symco*** ?tetr vaga vill wall ***whit*** yunn ***spD*** spF spG

83. Pistillate flower: ovary indumentum
glabrous — aur bana calo chon (***falc***) flex fulv fusi grand lanc lati luci nit plan prai quad sara spha stel symci symco tetr ***wall*** whit yunn spE
(sparsely) puberulous to sericeous at base only, glabrescent towards apex — acum ante bent brev bull card dend egre granu herm hete illu long misi nerv ***octa*** *octc* (***wall***) spG
evenly (sparsely) puberulous to sericeous — alia arbo basi conf duth ***falc*** frut laxi lede *leys lucp* micr nigp ***octa*** *octm* parv pena scle sela sten *vagl* spA
(densely) sericeous or tomentose — annu bour bras carr deci elme fici glob lage lame leyt luna macr main nigc *octy* papu prae pseu reti rhac serr subc sylv vaga vill spD spF

84. Pistillate flower: ovary-stigma transition
distinctly contracted/stigma raised — annu ante bour calo carr dend herm laxi leyt nigp papu vaga wall yunn spA spG
slightly contracted/stigma slightly raised — acum arbo basi bras brev card chon deci duth egre flex fulv fusi glob grand hete illu lame lati lede long luci micr misi ***nigc*** octa parv plan prai reti scle sela symci symco tetr vill whit
direct/stigma sessile — alia aur bana bent bull conf elme falc fici frut granu lage lanc luna macr main nerv ***nigc*** nit pena prae pseu quad rhac sara serr spha stel sten subc sylv spD spE spF

85. Pistillate flower: stigma shape
narrow — acum alia annu ante arbo aur basi bent bour bras brev bull calo card carr chon deci dend duth egre elme falc fici flex fulv fusi glob grand granu herm hete illu lage lame lanc lati laxi lede ?lept leyt long luci luna macr micr misi nerv nigc nigp octa papu parv prae plan prai pseu reti rhac scle sela serr spha subc sylv symci symco tetr vaga vill wall whit yunn spA ?spB ?spC spD spG
broad — bana conf frut main nit pena quad sara stel sten spE spF

86. Pistillate flower: stigma direction
perpendicular to the sides of the ovary — alia annu ante arbo aur bana basi bent bour bras brev bull calo card carr chon conf deci dend duth ***egre*** elme falc flex frut fulv fusi grand granu herm hete illu lage lame ***lanc*** lati laxi lede ?lept leyt

long luna ***macr*** main micr misi nerv nigp nit octa papu parv pena prai prae pseu quad reti sara scle sela serr ***spha*** stel sten subc sylv ***symco*** vaga vill wall whit yunn spA spD spE spF spG
ascending from the sides of the ovary — acum (***egre***) fici glob ***lanc*** luci (***macr***) nigc plan rhac (***spha***) symci (***symco***) tetr

87. Pistillate flower: stigma curvation
straight — acum alia ***aur*** bana bour bras brev conf deci egre ***elme*** fici frut fulv ***fusi*** glob ***lage*** lame lanc luci macr nigc nit prae plan pseu quad serr stel sten ***symci*** symco tetr vill ***spD*** spE spF ***spG***
slightly recurved — annu ***arbo aur*** basi card carr chon duth flex ***fusi*** herm hete ***lage*** laxi lede leyt nerv nigp parv prai scle spha ***symci wall*** whit ***spD spG***
recurved — ante ***arbo*** calo dend grand lati long misi octa papu reti vaga ***wall*** yunn spA
flattened to the sides of the ovary — bent bull ***elme*** falc granu illu luna main micr pena (***rhac***) sara sela subc sylv
raised in a apical bunch before flattening to the ovary sides — ***rhac***

88. Pistillate flower: stigma incision apically
lobed — flex frut herm lati sara symco
to c. halfway — annu ante arbo bana bour card carr chon dend duth fici glob hete laxi lede leyt long luna macr misi plan pseu scle sten wall whit spA spD
to near base — alia aur basi bent bras brev bull calo deci egre falc fulv fusi grand granu illu lage lame lanc main micr nerv nigp octa papu parv pena prai prae quad reti rhac sela sylv symci tetr vaga vill yunn spE spF spG
(almost) divided — acum conf elme luci nigc nit serr spha stel subc

89. Pistillate flower: stigma length
0.3–0.5 mm — aur ***luci*** (***macr***) main (***prai***) ***symco***
0.5–1.5 mm — acum alia arbo bana ***bent brev*** card chon conf ***dend*** elme fici flex frut ***fusi*** glob grand ***granu*** hete ***illu*** lanc ***laxi lede*** leyt long ***luci macr*** nerv nigc ***nigp*** nit ***octa*** parv pena prae plan ***prai*** pseu quad rhac ***sara*** scle serr spha stel ***sten*** subc symci ***symco*** tetr ***vaga*** vill whit ***spD*** spE spF
1.5–3 mm — annu ***ante*** basi ***bent*** bras ***brev*** bull calo carr deci ***dend*** duth egre falc fulv ***fusi granu*** herm ***illu*** lame lati ***laxi lede*** luna micr misi ***nigp octa*** papu ***reti sara*** sela ***sten*** sylv ***vaga*** wall yunn spA ***spD*** spG
3–6 mm — ***ante bent*** bour lage ***reti***

90. Pistillate flower: stigma sculpture above
(sub)smooth — bent bull ***calo nerv nit***
ribbed — ***annu arbo basi*** brev ***carr*** falc ***fulv fusi herm illu lage lanc laxi luci*** luna ***macr nigp nit parv pena*** quad ***rhac sara scle sela spha sten*** sylv symco ***tetr whit yunn spA spD spE spF spG***
margins papillate or laciniate — ***basi calo dend herm lanc luci macr nerv nigp parv rhac scle spha***
(laxly or lowly) papillate — acum ***annu*** ante ***arbo*** aur ***bana bour card*** chon ***conf dend duth*** egre ***flex*** frut ***fulv fusi glob*** grand ***granu*** hete ***illu*** lati ***laxi*** leyt ***long***

- ***misi nigc octa plan*** prai ***pseu reti sela*** serr stel ***sten symci tetr*** vill ***wall yunn spD spE spF spG***
- (laxly) laciniate — alia ***bana bour card carr conf duth*** fici ***flex glob granu illu lage*** lede ***long misi nigc octa pena*** prae ***plan pseu reti sara symci tetr*** vaga ***wall whit yunn spA***
- densely laciniate/feathered — bras deci elme lame main micr papu subc

91. Pistillate flower: style remnant beneath
    - not observable: lower side of stigma directly attached to ovary — bana conf frut nit quad sara stel sten spE
    - present on central part of lower side of stigma — aur bour bras brev card *cars* chon deci dend egre fici flex fulv fusi glob hete lame lanc lati laxi lede ?lept leyt luci misi nerv nigc octa papu parv pena plan prai scle serr spha symci symco tetr vaga vill wall whit yunn spA
    - completely absent — acum alia annu ante arbo basi bent bull calo carr duth elme falc grand granu herm illu lage long luna macr main micr nigp prae pseu reti rhac sela subc sylv spD spF spG

92. Pistillate flower: stigmatic sculpturing beneath
    - (unknown since style remnant present) — aur bour bras brev card carr deci dend egre fici flex fulv fusi glob hete lame lanc lati laxi lede ?lept leyt luci misi nerv nigc octa papu parv pena plan prai scle serr spha symci symco tetr vaga vill wall whit yunn spA
    - (unknown since stigma completely attached to ovary) — bana conf frut nit quad sara stel sten spE
    - smooth — acum alia annu arbo bent bull carr elme falc ***grand*** granu herm lage luna macr main micr nigp prae pseu rhac sela subc sylv spD spF
    - ribbed — ***duth grand*** illu long ***reti*** spG
    - lowly papillate — ante basi calo ***duth reti***

93. Fruit: pedicel length
    - absent — acum alia fici glob granu lanc lati main plan pseu symci tetr wall yunn
    - 0–0.5 — deci lage long luci micr misi ***octa pena*** rhac vill
    - 0.5–2 — aur ***bent*** elme fusi (***lame***) (***luna***) nigc parv reti ***sara*** sela subc spA
    - 2–6 mm — annu ante (***arbo***) bana basi ***bent*** bour ***bras*** brev calo card carr ***chon conf*** dend duth egre falc frut ***fulv grand herm*** hete illu ***lame laxi*** lede leyt ***luna nerv*** nigp ***nit*** papu ***prai quad sara*** scle spha stel sten ***symco vaga*** whit ***spE***
    - 6–10 mm — ***arbo bras chon conf fulv grand herm laxi nerv nit prai prae quad symco vaga spE***
    - 10–20 mm — ***arbo chon fulv*** (***laxi***) ***prai prae*** *symcc*
    - 20–35 mm — *symcc*

94. Fruit: shape
    - (sub)globose — acum ***arbo*** aur ***bana card*** conf ***dend*** fici frut ***glob*** hete ***illu*** lanc ***laxi luci*** ?macr ***nerv nigp*** nit (***octa***) prae pseu quad ***sela*** spha ***vaga*** spA? ***spE***
    - ovoid — ***alia bana*** bent bour bras bull ***calo*** carr ***chon*** deci ***dend*** falc grand ***herm illu lati laxi leyt*** long ***luna micr misi*** nigc ***nigp octa papu plan*** prai reti ***sara scle sela*** sten ***subc*** sylv ***symci symco tetr vaga vill wall whit yunn spE***

narrowly ovoid — ***alia basi calo lage micr wall***
broadly ovoid — ***card*** fulv ***glob lati*** (***leyt***) ***luci misi papu***
ellipsoid — annu ***ante arbo calo*** duth elme granu ***herm*** lede *luce* main ***nerv octa*** parv pena ***plan*** rhac ***sara scle*** stel ***subc symci symco tetr vill whit yunn***
narrowly ellipsoid — (***ante***) brev ***egre fusi*** *symcc*
broadly ellipsoid — ***chon*** lame
flask-shaped — ***basi lage*** (***luna***)
fusiform — ***egre fusi*** *symcc*

95. Fruit: length
6–11 mm — acum ***annu ante*** aur ***card carr chon deci dend duth elme falc frut fulv*** granu ***herm*** lanc lede long luci ***luna*** main ***micr*** misi (***nerv***) ***nigc*** nigp ***octa*** parv ***pena*** plan ***pseu*** reti ***rhac*** scle ***spha*** sten ***subc*** symci ***symco*** vill wall ***yunn*** spA
11–22 mm — alia ***annu*** (***ante***) arbo ***bana*** basi bent bour bras brev calo ***card carr chon*** conf ***deci dend duth*** egre ***elme falc*** fici ***frut fulv*** fusi glob grand ***herm*** hete illu lage lame ***lati*** laxi leyt ***luna micr nerv nigc nit octa*** papu ***pena*** prai prae ***pseu*** quad ***rhac*** sara sela ***spha*** stel ***subc symco*** *symcc* tetr vaga whit ***yunn*** spE
22–28 mm — ***bana lati nit***

96. Fruit: width
5–12 mm — acum alia annu ante ***arbo*** aur ***basi*** (***bent***) ***bras*** brev ***calo card carr*** chon deci ***dend*** duth egre elme falc fici ***frut fulv*** fusi ***grand*** granu ***herm hete illu*** lage lanc lede (***leyt***) long luci ***luna*** main micr misi ***nerv*** nigc nigp octa (***papu***) parv pena plan ***prai*** pseu reti rhac sara scle ***sela spha*** sten subc symci symco tetr ***vaga*** vill wall whit yunn spA ***spE***
12–22 mm — ***arbo bana basi bent*** bour ***bras calo card carr*** conf ***dend frut fulv*** glob ***grand herm hete illu lame*** lati laxi ***leyt luna nerv papu prai*** prae quad ***sela spha*** stel ***vaga spE***
22–27 mm — ***bana lame*** nit

97. Fruit: stiped
slightly when young — acum calo octa pena wall
slightly — alia ante card plan *symcc*
distinctly — fusi

98. Fruit: beaked
slightly when young — arbo calo carr octa
slightly — annu deci duth herm hete lage leyt luci micr reti *symcc* tetr
distinctly — ante basi bour bras brev card dend fusi misi nigp papu wall yunn

99. Fruit: sculpture
smooth — ***ante*** arbo aur ***bana bent*** bras ***calo card*** carr conf ***falc fici*** frut ***illu lage*** lati ***leyt long luna*** nerv ***nigc*** nit ***papu pena*** quad ***sara symco whit*** spA
punctulate — annu ***ante*** basi ***bent*** brev ***calo card*** deci ***dend*** egre ***falc fici*** fulv fusi glob ***herm*** hete ***illu lage*** lanc lede ***leyt long luci luna*** micr ***nigc nigp pena*** prae ***plan*** pseu sten ***symco*** vaga ***whit***
punctate — acum ***chon dend*** duth elme ***grand herm*** laxi ***luci*** main misi octa parv ***plan prai*** reti rhac spha ***stel*** subc symci ***tetr*** vill wall ***yunn spE***
(lowly) granular — alia granu *luct* ***yunn***

irregularly corrugate-papillate — ***prai stel***
ruminate-verrucate — sela
tuberculate — bour
striate & lamellate — lame
ridged — ***bana chon*** (***grand***) ***prai sara tetr spE***
lobed — ***nigp papu***

100. Fruit: indumentum
glabrous — aur bana calo chon dend ***falc*** ?flex fulv fusi grand lanc lati ***lede*** ?lept luci ***misi*** nit plan prai quad sara spha stel symci symco tetr wall whit yunn spE
(very) sparsely puberulous (at base only) — annu ante arbo (***bent***) card carr duth egre ***falc*** granu herm hete ***lede*** *leys* ***misi octa*** sten ?spG
sparsely tomentose/puberulous/sericeous/hirsute — acum alia basi ***bent*** bour bras brev conf ***deci*** elme ***falc*** frut glob illu lage ***lame*** laxi leyt long *lucp* luna main micr nerv nigc nigp ***octa*** papu parv pena prae pseu rhac scle sela subc ?sylv vaga vill spA ?spD ?spF
(densely) sericeous/hirsute — ***deci*** fici ***lame*** ?macr reti ?serr

101. Fruit: pericarp thickness
0.2–0.8 mm — acum alia annu ante aur ***bent*** bour brev ***card*** carr ***deci dend*** duth ***elme*** falc ***frut fulv*** fusi ***grand*** granu herm ***hete lage*** lanc laxi lede ***leyt long*** luci ***luna*** main micr ***misi nigc nigp*** octa parv ***pena prae*** plan ***prai pseu*** scle ***sela spha*** sten ***subc*** symci symco ***tetr vaga*** vill wall yunn
0.8–1.5 mm — arbo ***bana*** basi ***bent*** calo ***card*** chon ***deci dend egre elme*** fici ***frut fulv glob grand hete illu lage lame leyt long luna misi*** nerv ***nigc nigp papu pena prai prae pseu*** reti rhac sara ***sela subc tetr vaga*** whit spA ***spE***
1.5–3 mm — ***bana bent*** bras ***conf deci egre frut glob illu lame leyt papu*** (***spha***) stel ***vaga spE***
3–7 mm — ***bana conf illu*** lati nit quad

102. Fruit: apex of endocarp caudate
basi prai sara stel

103. Fruit: indument of septae and column
only column at base hairy — annu
both (sparsely) hairy — acum aur bour card fici fusi glob lanc lati luci macr nigc octa plan pseu serr symci tetr vill wall yunn

104. Fruit: number of seeds
often only one — acum ***alia*** annu ***ante brev*** duth egre ***elme fusi*** granu ***herm*** lage lanc ***lede luci main micr misi octa parv*** pena ***plan reti*** rhac scle ***subc symci*** vill ***wall yunn*** ?spA
usually one per locule — ***alia*** (***ante***) arbo aur bana basi bent bour bras ***brev*** ?bull calo card carr chon conf deci dend (***elme***) falc fici frut fulv ***fusi*** glob grand ***herm*** hete illu lame lati laxi ***lede*** leyt long ***luci*** luna ?macr (***main***) (***micr***) ***misi*** nerv nigc nigp nit (***octa***) papu ***parv*** prae (***plan***) prai pseu quad ***reti*** sara sela ?serr ***spha*** stel sten (***subc***) ?sylv ***symci*** symco ***tetr*** vaga ***wall*** whit ***yunn*** ?spD spE ?spG
occasionally two per locule — ?fici (***spha***) (***tetr***)

105. Habitat

altitude above 1000 m — acum (ante) ***basi*** (bent) ***bras*** brev ***bull calo*** carr ***chon*** egre ***falc frut*** fulv fusi herm ***hete illu lame*** lanc ***luci luna octa papu*** parv ***prai*** reti scle ***spha subc vaga vill wall yunn*** spD
swamps — lede ?spF
riverine — sten

10.4 – **Species descriptions**

10.4.1 – *Section Aporosa*

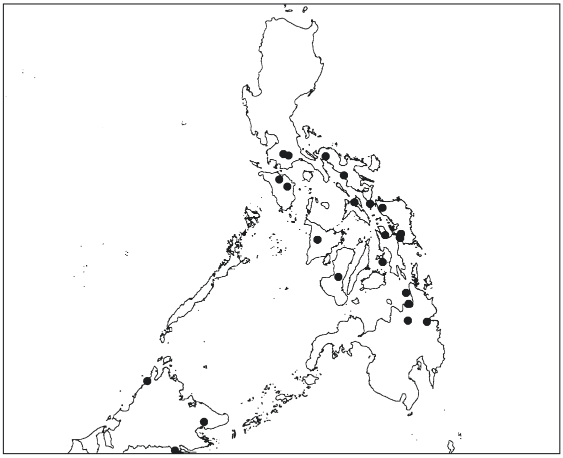
1. Aporosa banahaensis (Elmer) Merr. — Fig. 3.5g; Map 10.1

Aporosa banahaensis (Elmer) Merr., Enum. Philipp. Flow. Pl. 2 (1923) 410. — *Baccaurea banahaensis* Elmer, Leafl. Philipp. Bot. 4 (1912) 1475; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 70. — Type: *Elmer 9106* (iso BM, BO, L), Philippines, Luzon, Lucban.

Aporosa similis Merr., Philipp. J. Sci., Bot. 9 (1914) 472; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 92. — Type: *FB (Everett) 7279* (iso P), Philippines, Negros.

Aporosa agusanensis Elmer, Leafl. Philipp. Bot. 7 (1915) 2636. — Type: *Elmer 13415* (iso A, BM, BO, L, P), Philippines, Mindanao, Cabadbaran.

Shrub or small tree, up to 15 m high, up to 30 cm diameter. *Bark* smooth. Young branches very sparsely puberulous. *Stipules* not seen, caducous, probably slightly oblique. *Petiole* terete, adaxially lowly grooved, 9–24 by 0.8–1.2 mm, sparsely hirsute, glabrescent, lower pulvinus 1.5–3.5 by 1.2–2 mm, upper pulvinus 5–10 by 1.2–2 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 11–21.5 by 4.3–8.5 cm; base rounded to acute, sometimes slightly attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, small, brownish; apex cuspidate; blade thinnish, young leaves lowly irregular granular above and beneath, sometimes slightly shiny, not brittle, drying greenish grey, greenish yellow, or brown above and beneath, nervation lighter below, glabrous above, midrib very sparsely hairy at base, only midrib and nerves sparsely hirsute beneath, glabrescent; dots absent; disc-like glands few, small, along margin. *Nervation*: midrib prominent above, raised beneath; nerves 9–11 pairs, slightly prominent above, prominent beneath, marginal arches distinct, 1.5–3 mm from the margin; veins and venation fading, laxly reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–4 clustered together, 7–11 by 1–1.5 mm, very sparsely hairy, glabrescent; peduncle 1.5–2.5 mm long, 0.3–0.5 mm diam.; bracts broadly triangular, inconspicuous, 1–1.2 mm long, glabrous, margin ciliate; glomerules subglobose, 0.8–1.5 by 0.8–1 mm, consisting of 7–11 densely set flowers, spaced at 0.5–2 mm at base, decreasing to 0 mm at apical end of rachis; pedicel minute. *Staminate flowers* 0.3–0.5 mm long; sepals 4 or 5, obovate, connate at base, 0.5–0.7 mm long, glabrous; stamens 2 or 3, slightly exserted, 0.3–0.4 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode minute. *Pistillate inflorescences* 1 or 2 clustered together, 4–5 by 0.5–0.8 mm, very sparsely hairy, glabrescent; flowers single at apical end of rachis; bracts broadly triangular, 0.7–1 mm long, glabrous, margin ciliate; bracteoles triangular, 0.4–0.6 mm long, glabrous, margin ciliate; pedicel 1–2 mm, sparsely hairy. *Pistillate flowers* 2–2.5 mm long; sepals 5, ovate, reflexed, 1.2–1.5 mm long, fleshy, glabrous, margin ciliate; ovary ellipsoid



Map 10.1. Distribution of *Aporosa banahaensis* (Elmer) Merr.

to globose, 1.5–2 mm, 3- (or 4-)locular, punctulate, glabrous; stigmas sessile, broad, apically bifid to c. halfway, flattened on top of the ovary, straight, 0.5–1 mm long, papillate to laciniate above, glabrous, connate to ovary beneath. *Infructescences* 3–11 by c. 0.8 mm, sparsely tomentose, glabrescent; fruiting pedicel 2–5 mm long, sparsely tomentose, glabrescent. *Fruits* subovoid to globose, not stiped, not beaked, 12–25 by 12–25 mm, smooth, young ones ridged along the sutures, drying light yellow-brown, glabrous; pericarp 0.5–6 mm thick, fleshy when mature; septae and column glabrous. *Seeds* 2 or 3, half-terete, ovoid, 9–10 by 8–9 by c. 4 mm.

Distribution — Malesia: ?North Borneo, Philippines.

Habitat & Ecology — Virgin or secondary forest or old logging areas; in lower storey. Soil (brown) clay. Altitude: 35–380 m. Flowering: February to April; fruiting: April to September and November. The fruit is recorded odourless and edible.

Vernacular names — Mayagbon (Siti Bis.).

Notes — 1. Airy Shaw (1972) united *A. banahaensis*, including its synonyms *A. similis* and *A. agusanensis*, with *A. frutescens*, but in my view they represent distinct species. *Aporosa banahaensis*, though similar in foliage, has interrupted staminate inflorescences and pistillate flowers with papillate to laciniate stigmas. The fruits are characteristic in their two phases: the ovoid, thin, young ones (‘*A. similis*’) and the mature globose, thick fleshy ones (‘*Baccaurea banahaensis*’). Many species in the section *Aporosa* are inseparable in foliage, but differ in shape and size of stigmas and fruits, and in interruptions of the staminate glomerules. *Aporosa banahaensis* differs in all these characters from *A. frutescens*, and is consequently kept separate. The state of the type of *A. banahaensis*, one immature, malformed fruit, may have added to the confusion of these two species.

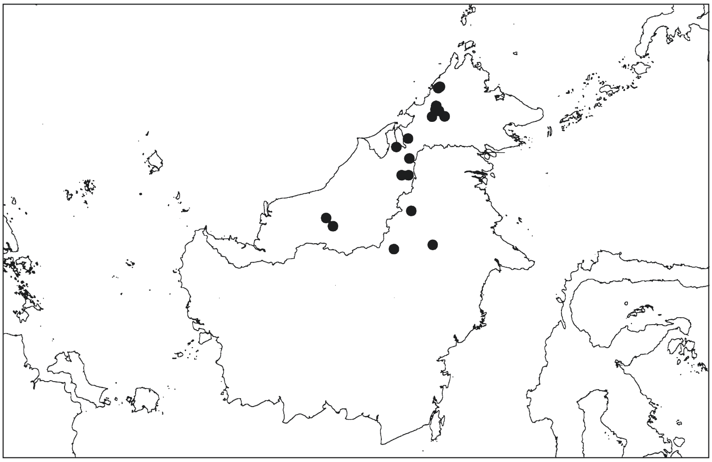
2. In the areas were *A. frutescens* and *A. banahaensis* co-occur the foliar distinction is even less: *A. frutescens* has a lesser indumentum on Luzon than on Borneo, and *A. banahaensis* on Luzon has smaller and thinner leaves than elsewhere in the Philippines. The similar subglabrous leaves of *A. frutescens* occur also in Sabah. Two specimens from Sabah, Tawau, *SAN 30541* and *Maidin 4138*, bear immature staminate inflorescences whose interruptions appear to exclude *A. frutescens*. A further two collections from

Sandakan, *SAN 36602* and *SAN 36921*, have young fruits with prominent laciniate stigmas. These four collections may be *A. banahaensis*, but additional evidence is needed to reliably show that *A. banahaensis* occurs in Sabah.

2. Aporosa chondroneura (Airy Shaw) Schot — Fig. 4.2b, 4.5c; Map 10.2

Aporosa chondroneura (Airy Shaw) Schot, Blumea 40 (1995) 451. — *Aporusa prainiana* King ex Gage var. *chondroneura* Airy Shaw, Kew Bull. 25 (1971) 476. — *Aporusa symplocoides* (Hook.f.) Gage var. *chondroneura* (Airy Shaw) Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 42. — Type: *S (Paie) 25808* (holo K; iso L), Sarawak, 3rd division.

Tree, up to 15 m high, up to 13 cm diameter. *Bark* (pale) brown, yellowish, or grey, smooth to rough; inner bark pale brownish or green. *Wood* yellowish to whitish. Young branches glabrous. *Stipules* not seen, caducous, recorded as reniform (= narrowly ovate, oblique). *Petiole* terete, lowly grooved, 16–35 by 1.2–2 mm, glabrous, lower pulvinus 2–5 by 1.2–3 mm, upper pulvinus 3–6 by 1.5–3.5 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 13–32 by 5–14 cm; base rounded to acute, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, blackish, sometimes indistinct; apex acuminate to cuspidate; blade thin, lowly white granular above, venation regularly white granular beneath, dull, not brittle, drying dark green-grey above and beneath, nervation lighter, completely glabrous; dots irregularly set, fine, grey, mostly indistinct; disc-like glands few, small, along margin. *Nervation*: midrib (slightly) prominent above, prominent beneath; nerves 8–11 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.5–2.5 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly scalariform, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 15–43 by 0.2–0.4 mm, very sparsely tomentose, glabrescent; peduncle 1.5–2.5 by 0.5–0.8 mm; bracts broadly triangular, 0.8–1 mm long, inconspicuous, glabrous, margin ciliate; glomerules subglobose, 1–1.5 by 0.8–1.2 mm, consisting of 6–10 densely set flowers, spaced at 0.5–2 mm along the rachis; pedicel minute. *Staminate flowers* 0.8–1.2 mm long; sepals 4 or 5, obovate, 0.8–1.2 mm long, connate at base, glabrous, margin ciliate; stamens 2 or 3, slightly exserted, 0.6–0.9 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode minute, lumpy. *Pistillate inflorescences* 1–3 clustered together, 7–32 by 0.3–0.8 mm, very sparsely tomentose at base, glabrescent; flowers up to 9, laxly set along the rachis; bracts broadly triangular, 0.6–0.8 mm long, glabrous outside, hairy at base only inside, margin ciliate; bracteoles ovate, 0.3–0.5 mm long, glabrous outside, hairy at base only inside, margin ciliate; pedicel 1.5–6 mm long, sparsely tomentose. *Pistillate flowers* 1.5–3 mm long; sepals 4, ovate, reflexed, 1.2–1.5 mm long, rather fleshy, glabrous outside, hairy at base only inside, margin ciliate; ovary ovoid to ellipsoid, 1.5–2 mm long, 3-locular, smooth, glabrous; stigmas slightly raised, elongated, perpendicular to sides of ovary, slightly recurved, apically bifid to c. halfway, 0.8–1 mm long, lowly papillate above, glabrous, smooth beneath, style remnant present. *Infructescences* 14–54 by 0.8–1.2 mm, glabrous; fruiting pedicel 2–14 mm long, sparsely tomentose. *Fruits* ovoid to ellipsoid, not stiped, not beaked, 10–13 by 8–11 mm, punctate, slightly ridged at sutures, drying (light) brownish yellow, glabrous; pericarp 0.8–1.2 mm thick, not fleshy; septae and column glabrous. *Seeds* 1–3, half-terete, ellipsoid, 7.5–9 by 6.5–7 by 3–3.5 mm.



Map 10.2. Distribution of *Aporosa chondroneura* (Airy Shaw) Schot.

Distribution — Malesia: Borneo.

Habitat & Ecology — Primary, evergreen, (un)disturbed dipterocarp forest; on (steep) hills, small mountain tops, submontane forest, and along riverbanks; in (heavy) sloping country. Soil: sandy, sandstone, or basalt; brown or yellow. Altitude: 450–1250 m. Flowering: March, August to October; fruiting: April to October, December. Fruit said to have acid smell and bitter taste.

Vernacular names — Bua kelabo, janggau (Iban); Kayu Lieng (Pujungan).

3. Aporosa confusa Gage — Fig 4,6b, 10.1; Map 10.3

Aporosa confusa Gage, Rec. Bot. Surv. India 9 (1922) 229; Ridl., Fl. Malay Penins. 3 (1924) 238; Meijer, Bot. News. Bull. Sandakan 7 (1967) 35; Whitmore, Tree Fl. Malaya 2 (1973) 59; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 34; Kew Bull. 36 (1981) 254. — Lectotype (proposed here): *Ridley 6486* (holo SING; iso K), Singapore, Bukit Timah.

Aporosa mollis Merr., Pl. Elmer. Born. (1929) 144; Meijer, Bot. News. Bull. Sandakan 7 (1967) 35. — Type: *Elmer 21765* (holo A; iso L), Sabah, Tawau.

Tree, up to 20 m high, up to 28 cm diameter. *Bark* blackish, (dark) brown, pale reddish, green to grey, or whitish, thin, smooth; inner bark light brown, greenish brown, or yellowish white. *Wood* orange, (pale) yellow, or whitish. Young branches tomentose. *Stipules* narrowly ovate, oblique, 3–5 by 8–9 mm, black glands along margin beneath, sparsely hairy, present in young stages. *Petiole* terete, grooved, 8–19 by 1–2 mm, tomentose, glabrescent, lower pulvinus 2–3 by c. 2 mm, upper pulvinus 3 –7 by 1.8–3.5 mm, both distinct. *Leaves* narrowly ovate to (narrowly) elliptic, 9–25.5 by 4–10 cm; base rounded to acute, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands many, distinct, black or brown; apex acuminate to cuspidate; blade thinnish, young leaves lowly granular above and beneath, dull, not brittle, drying (dark) grey-green above and beneath, sometimes brownish or yellowish, nervation lighter below, sparsely hirsute, midrib and nerves hirsute beneath,

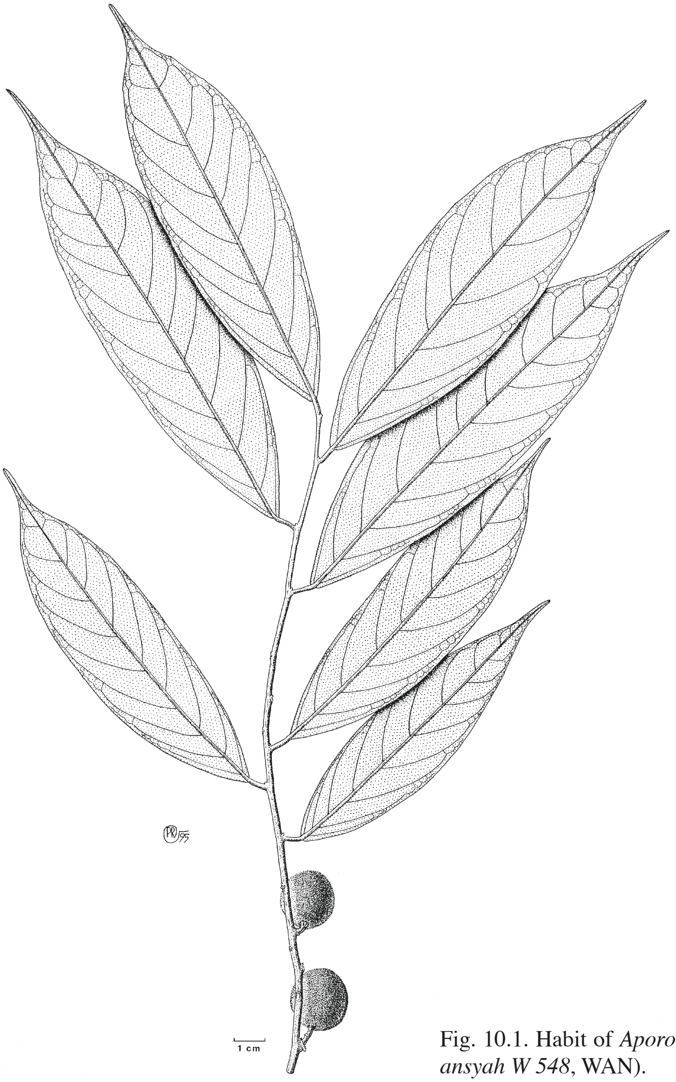


Fig. 10.1. Habit of *Aporosa confusa* Gage (*Ambriansyah W 548*, WAN).

glabrescent; dots irregularly set, fine, grey, mostly indistinct; disc-like glands seldom few, small, greyish, along the margin. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 10–14 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.2–2 mm from the margin; tertiary veins and venation distinct, fading above, rather densely reticulate, slightly scalariform, flat to slightly sunken above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 12–32 by 5–9 mm, tomentose; peduncle 0.5–8 by 1–1.5 mm; bracts inconspicuous, broadly triangular, 0.3–0.5 mm long, sparsely puberulous; glomerules sometimes slightly interrupted at base of rachis, densely massed at apical end of rachis, ellipsoid, indistinct, consisting of more than

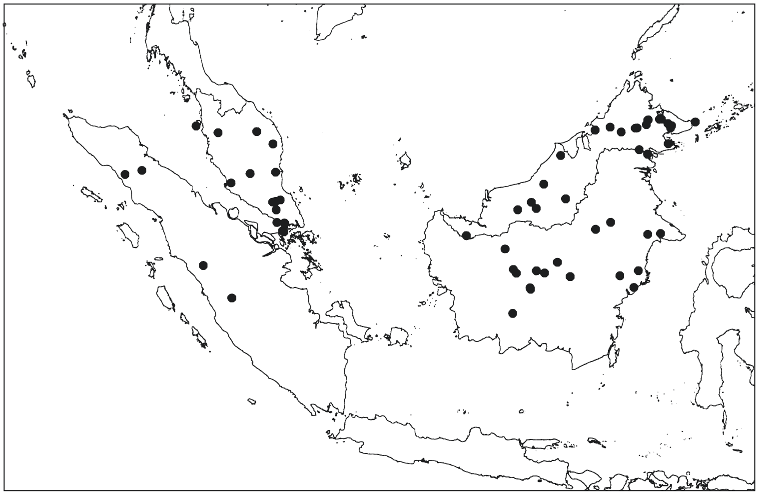
10 densely set flowers; pedicel absent. *Staminate flowers* 0.5–0.8 mm long; sepals 4 or 5, ovate, 0.3–0.6 mm long, connate at base, sparsely hairy outside, glabrescent, glabrous inside, margin ciliate; stamens 2, slightly exserted, 0.5–1 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* not seen, induced from infructescences to be 1 or 2 clustered together, tomentose, flowers single at apical end of rachis; bracts broadly triangular, 0.5–0.8 mm long, puberulous; bracteoles ovate, 0.3–0.5 mm long, puberulous; pedicel present, tomentose. *Pistillate flowers* not seen; sepals in young fruit 6 or 7, ovate, reflexed, 1.2–1.5 mm long, fleshy, puberulous; ovary probably globose to ellipsoid, 3- (or 4-)locular, smooth, puberulous; stigmas sessile, broad, apically almost completely divided, flattened on top of the ovary, straight, 0.8–1 mm long, apically laciniate to papillate above, glabrous, connate to the ovary beneath. *Infructescences* 3–6 by 1.5–2.5 mm, tomentose; fruiting pedicel 3–9 mm long, tomentose. *Fruits* globose to broadly elliptic, not stiped, not beaked, 16–21 by 16–22 mm, smooth, drying brownish orange, sparsely tomentose; pericarp 2–5.5 mm thick, fleshy; septae and column glabrous. *Seeds* 1–4, half-terete, ellipsoid, 9–12 by 8–10 by 4–5 mm.

Distribution — Malesia: Peninsular Malaysia, Singapore, Sumatra, Borneo.

Habitat & Ecology — Primary, secondary, open bamboo, and disturbed (dense) forest; on hillsides, low ridges, ridge tops, along rivers, roadsides, and in orchards; undulating or flatland. Soil: clay, loamy, lime, sandstone, or basalt, brownish to black. Altitude: low to 575 m. Flowering: March to May, August, October, December; fruiting: April to January. Fruit said to be edible.

Vernacular names — Peninsular Malaysia: Sebasah, panatan (Malay). Sumatra: Punding undang, limpaung, medang bubu. Borneo: Janggau, jangit, kayu masam (Iban); kayu untut ayam (Jelai); lumbit (Muru); kayu bloo tui, kayu puchat, kayu untut ayam (Temuan).

Uses — Wood for house building.



Map 10.3. Distribution of *Aporosa confusa* Gage.

Notes — 1. *Aporosa confusa* is most quickly recognized by the grey-green tomentose leaves with often lighter coloured venation on the lower side. The sunken venation can superficially resemble that of *A. lunata*.

2. Sometimes the mucilage cells in the leaf are so large that the younger leaves show a clear punctation analogue to the oil dots of Rutaceae.

4. **Aporosa frutescens** Blume — Fig. 3.5i, 3.6v, 3.7c, 3.8p, 3.11l, 4.6c, 4.7a; Map 10.4

Aporosa frutescens Blume, Bijdr. (1825) 514; Miq., Fl. Ind. Bat. 1, 2 (1859) 431; Müll.Arg. in DC., Prod. 15, 2 (1866) 476 (species dubia); Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 229; Koord., Exkurs.-Fl. Java 2 (1912) 480; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 91; Ridl., Fl. Malay Penins. 3 (1924) 241; S. Moore, J. Bot. Brit. & For. 63, Suppl. (1925) 97; Merr., Pl. Elmer. Born. (1929) 143; Corner, Wayside Trees Malaya 1 (1940) 237; Backer & Bakh.f., Fl. Java 1 (1964) 457; Meijer, Bot. News Bull. Sandakan 7 (1967) 33; Airy Shaw, Kew Bull. 26 (1972) 216 (excl. *A. banahaensis*); Whitmore, Tree Fl. Malaya 2 (1973) 59, 60; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 216; Kew Bull. 36 (1981) 255, 37 (1982) 7. — Lectotype (proposed here): *Blume 1704* (holo L, barcode L 0041512), Java.

Leiocarpus fruticosa Blume, Bijdr. (1825) 582; Hassk., Hort. Bog. Descr. (1858) 57; Bull. Soc. Bot. France 6 (1859) 714; Miq., Fl. Ind. Bat. 1, 2 (1859) 362; Fl. Ind. Bat., Suppl. (1860) 178, 443. — *Aporosa fruticosa* (Blume) Müll.Arg. in DC., Prod. 15, 2 (1866) 475; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278. — Lectotype (proposed here): *Blume 2136* (holo L, barcode L0041510; iso K), Java.

Shrub or tree, up to 27 m high, up to 30 cm diameter. *Bark* black, (dark) brown chocolate, greyish brown, grey-green, or (dark) grey, smooth, slightly scaly; inner bark outside (pale) reddish to pale (yellow) brown, inside turning pale green, pale yellow, or whitish, thin, fibrous. *Wood* brownish yellow or pale grey to white. Young branches sparsely hirsute. *Stipules* narrowly ovate, oblique, 1.5–2 by 5–7 mm, sparsely hairy outside, present in young stages. *Petiole* terete, smooth to adaxially lowly grooved, 4–14 by 0.8–1.5 mm, hirsute, glabrescent, lower pulvinus 1–1.5 by c. 1.5 mm, mostly indistinct, upper pulvinus 2–5 by 1.5–2 mm, distinct. *Leaves* narrowly ovate to narrowly elliptic, 6.5–20 by 1.5–7.5 cm; base cuneate to slightly attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, small, greyish or blackish; apex acuminate to cuspidate; blade thin, lowly granular above and beneath, dull, not brittle, drying greyish green to yellowish green above and beneath, nervation lighter beneath, very sparsely puberulous, midrib and nerves (sparsely) hirsute, glabrescent; dots irregularly set, fine, greyish, mostly indistinct; disc-like glands occasionally few, small, along margin. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 8–10 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.5–2.5 mm from the margin; tertiary veins and venation often distinct, rather densely reticulate, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–4 clustered together, 5–22 by 2–3.5 mm, (sparsely) puberulous; peduncle 0.5–1.5 by 0.7–1 mm; bracts broadly triangular, 0.4–0.7 mm long, inconspicuous, very sparsely hairy outside, glabrescent, glabrous inside, margin ciliate; glomerules ellipsoid, consisting of 7–10 densely set flowers, c. 2 by 0.5 mm, spaced at 0.5–1 mm at base, apically slightly massed in a cylindric head; pedicel absent.

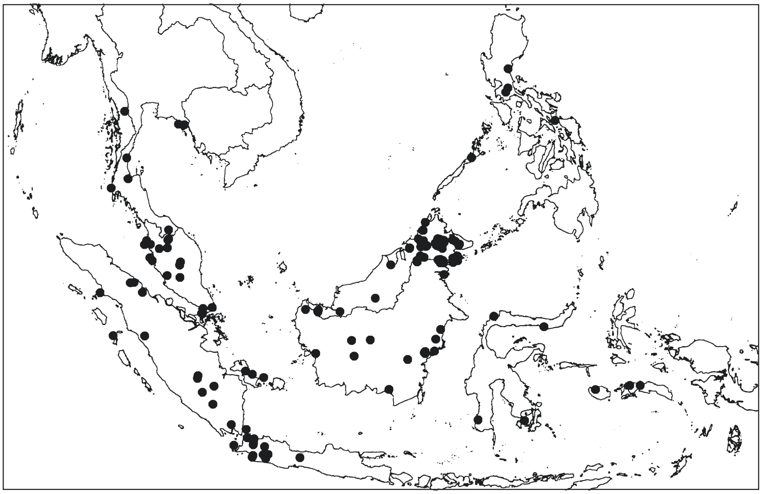
Staminate flowers 0.3–0.7 mm long; sepals (3 or) 4, obovate, 0.2–0.4 mm long, connate at base, glabrous, margin ciliate at apex; stamens 2 (or 3), 0.3–0.6 mm long, slightly exserted; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 2–7 by 0.7–1 mm, (sparsely) puberulous; flowers single at apical end of rachis; bracts broadly triangular, 0.5–0.8 mm long, sparsely puberulous outside, glabrous inside; bracteoles ovate, c. 0.5 mm long, sparsely hirsute outside, glabrous inside; pedicel 1.5–2 mm long, puberulous. *Pistillate flowers* 1.5–3 mm long; sepals 5 (or 6), ovate, subequal, reflexed, 1.2–1.5 mm long, fleshy, sparsely puberulous; ovary ellipsoid, 1.5–2.5 mm, 3-locular, slightly punctulate, sparsely puberulous to subglabrous; stigmas sessile, broad, apically lowly lobed, flattened on top of ovary, straight, 0.5–1 mm long, lowly papillate above, glabrous, connate to the ovary beneath. *Infructescences* 3–11 by 0.8–1.2 mm, sparsely puberulous, glabrescent; fruiting pedicel 2–6 mm long. *Fruits* juicy, globose, often with sunken stigmas, not stiped, not beaked, 9–15 by 10–15 mm, smooth, drying light or brownish yellow, sparsely puberulous to glabrous; pericarp 0.5–3 mm thick, fleshy; septae and column glabrous. *Seeds* 2–4, half-terete, ellipsoid, 8–11 by 6–9 by 3–5 mm.

Distribution — Burma (Tenasserim), Peninsular Thailand, Malesia: Peninsular Malaysia, Singapore, Sumatra, Java, Borneo, Philippines, Sulawesi, and the Moluccas.

Habitat & Ecology — Primary, secondary, disturbed, logged over forest and kerangas; on hilltops, hillsides, hill ridges, along river banks, roads, lakes, and forest margins; in dry, swampy, or shaded areas. Soil: a granitic or yellow-red loamy sand, red clay, blackish stony or a silty clay brown laterite. Altitude: 0–1500 m. Flowering and fruiting throughout the year. Fruits apparently eaten by squirrels.

Vernacular names — Sumatra: Kayu si marlilin, kayu si topu aek (east coast); kayu malam (Bangka). Java: Sassa lumbut, sassa benar. Borneo: Girak (Banggi); liposu gobuk, rambai rambai (Dusun); kalumanjat (Dusun Kinabatangan); lamog lamog (Murut). Philippines: Ragsik (Bic.). Moluccas: Ai mbalute (Ceram).

Notes — 1. The specimens of Blume's herbarium as conserved in Leiden are mostly



Map 10.4. Distribution of *Aporosa frutescens* Blume.

mixed up. Only one (staminate) is accompanied by the name *Aporosa frutescens* in Blume's own handwriting, *Blume 1704*, and this one I selected as lectotype. All other specimens are labelled, in Blume's handwriting, *Leiocarpus fruticosa*. Only one of these bears fruits, *Blume 2136*, which I have selected as lectotype of *A. fruticosa*. The other specimens of the latter species are mixtures of staminate and pistillate flowering material. Apparently, Blume identified some staminate specimens as *L. fruticosa* after his publication (1825). These he united with the earlier identified pistillate specimens, and (re?)numbered them *2223a* and *2233a*.

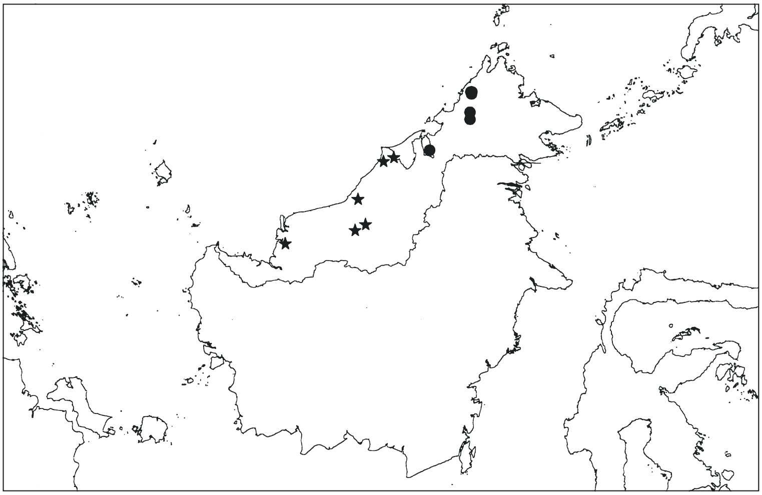
2. The Malayan, Bornean, and Philippine specimens have a much lesser indumentum on all parts of the plant than the more southern specimens. This makes the distinction with the Philippine *A. banahaensis* extremely difficult: see note 2 under that species.

3. Specimen *A 3437* from Sabah has inflorescences with up to 4 pistillate flowers clustered at the apex. The flowers themselves are, however, characteristically those of *A. frutescens*. It is not uncommon for the uniflorous inflorescences to develop some of the lower buds when some mechanical disturbance destroys the top flower.

5. **Aporosa fulvovittata** Schot — Map 10.5

Aporosa fulvovittata Schot, Blumea 40 (1995) 455. — Type: *Chew & Corner RSNB 4532* (holo L; iso K), Sabah, Mt Kinabalu.

Tree, up to 18 m high, up to 20 cm diameter. *Bark* pink brownish, smooth; inner bark brownish, yellowish pink, or white. *Wood* white. Young branches very sparsely hairy. *Stipules* ovate, slightly oblique, 4–6 by 3–4 mm, sparsely puberulous beneath, early caducous. *Petiole* terete, adaxially lowly grooved, 8–14 by 1–1.5 mm, very sparsely puberulous, glabrescent, lower pulvinus 1.5–2.5 by 1.2–2 mm, sometimes indistinct, upper pulvinus 2–3.5 by 1.2–2 mm, distinct. *Leaves* narrowly ovate to narrowly elliptic, 5.5–13.5 by 2–5.5 cm; base rounded to acute, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, small, greyish, often indistinct; apex acuminate; blade thin, lowly granular above and beneath, mostly dull, not brittle, drying (light) grey-green, greenish yellow, or brownish green above and beneath, glabrous above, very sparsely puberulous beneath, midrib and nerves sparsely puberulous, glabrescent; dots irregularly densely set, fine, grey, mostly indistinct; disc-like glands often few, small, distinct, along margin. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 7–10 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1–2 mm from the margin; tertiary nerves and venation often distinct, rather densely reticulate, slightly scalariform, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 7–17 by 1.5–2 mm, very sparsely puberulous, glabrescent; peduncle 1–3 mm by 0.3–0.5 mm; bracts broadly triangular, 0.5–0.8 mm long, inconspicuous, glabrous, margin ciliate; glomerules globose, 1–1.2 by 1–1.2 mm, consisting of 6–8 densely set flowers, spaced at 1–2 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 0.7–1 mm long; sepals 5–7, obovate, 0.7–1.2 mm long, connate at base, glabrous, margin ciliate; stamens 3–6, slightly exserted, 0.8–1.2 mm long, filaments sometimes connate to more than halfway; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* not seen, induced from infructescences to be 1–3 clustered together, sparsely puberulous; flowers single



Map 10.5. Distribution of *Aporosa fulvovittata* Schot (●) and *A. stenostachys* Airy Shaw (★).

at apical end of the rachis; bracts broadly triangular, 0.8–1 mm long, glabrous outside, hairy at base only inside, margin ciliate; bracteoles ovate, 0.7–0.8 mm long, glabrous; pedicel present, sparsely puberulous. *Pistillate flowers* not seen; sepals in young fruit 5, ovate, reflexed, 1.2–1.5 mm long, fleshy at base, glabrous, margin ciliate; staminodes occasionally 3, 0.2–0.3 mm long; ovary probably ovoid-globose, 3-locular, punctulate, glabrous; stigmas in young fruit 3, slightly raised, elongated, perpendicular to the sides of the ovary, apically bifid to near base, straight to slightly recurved, 1.5–2 mm long, longitudinally ribbed and papillate above, glabrous, smooth beneath, style remnant present. *Infructescences* 4–31 by 0.8–1.2 mm, sparsely puberulous, glabrescent; fruiting pedicel 4–14 mm long, sparsely puberulous, glabrescent. *Fruits* broadly ovoid, not stiped, not beaked, 9–12 by 11–14 mm, finely punctulate, drying yellow-brownish, lighter at sutures, glabrous; pericarp 0.5–1.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ellipsoid, 6–8 by 5–6 by 2.5–4 mm.

Distribution — Malesia: Borneo.

Habitat & Ecology — Primary or montane forest; on ridges, mountain slopes; in rocky, open, moist areas. Altitude: 1200–1700 m. Flowering: April, May, September; fruiting: February to June, September to November.

6. Aporosa nitida Merr. — Fig 3.5j, 10.2; Map 10.6

Aporosa nitida Merr., Pl. Elmer. Born. (1929) 143; Meijer, Bot. News. Bull. Sandakan 7 (1967) 33; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 39. — Type: *Elmer 21773* (iso BM, BO, L, P), Sabah, Sandakan.

Shrub or tree, up to 25 m high, up to 30 cm diameter. *Bark* black, (dark) brown to (patchy) greyish, greenish, yellowish, or whitish, smooth or lenticellate; inner bark (pale) brownish, pale greenish, or (pale) yellowish to greyish white. *Wood* yellow to white. *Twigs* brown, young ones green, glabrous. *Stipules* not seen, early caducous. *Petiole*

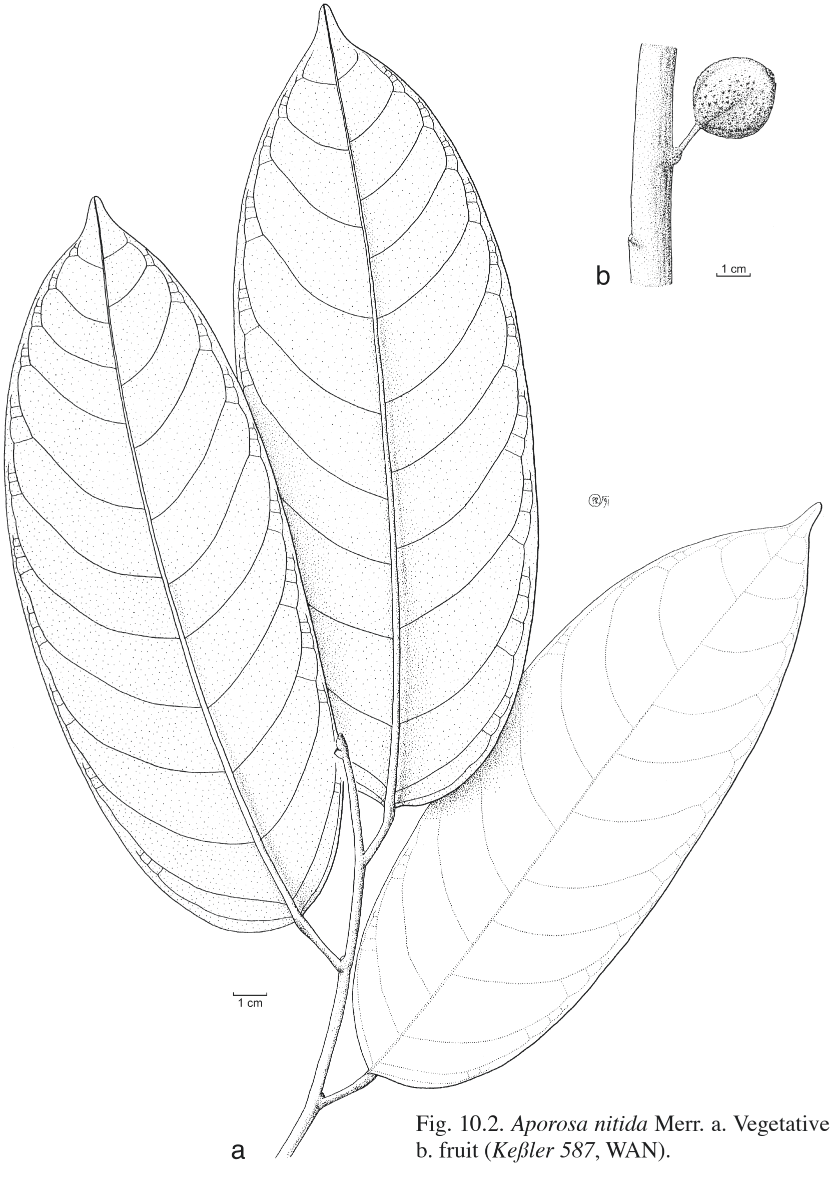
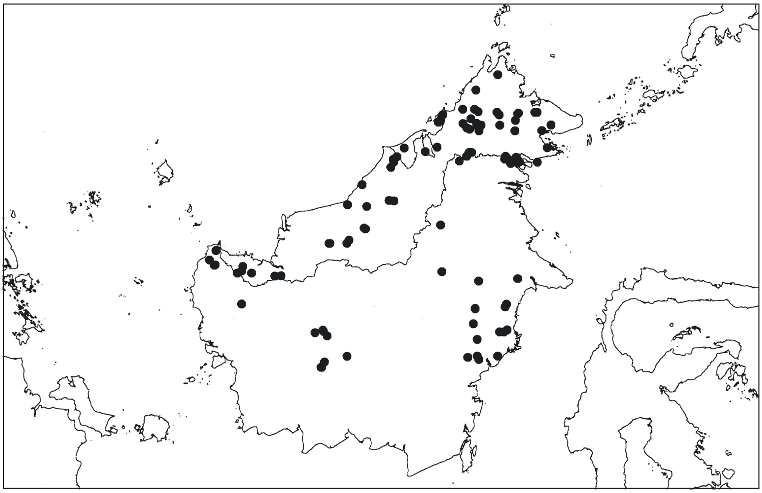


Fig. 10.2. *Aporosa nitida* Merr. a. Vegetative branch; b. fruit (*Keßler 587*, WAN).

terete, adaxially lowly grooved, 13–36 by 1.5–2.5 mm, glabrous, lower pulvinus 3–6 by 2–3 mm, upper pulvinus 8–12 by 2.5–3.5 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 15–32.5 by 5–13 cm; base obtuse to acute, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, distinct, brownish to black; apex acuminate to cuspidate; blade thick, young leaves lowly white granular on nerves, shiny, not brittle, drying greyish green or yellowish green above and beneath, glabrous; dots laxly set, fine, greyish, fading; disc-like glands minute, brownish, occasionally scattered along the margin and at base within marginal arches, often indistinct. *Nervation*: midrib prominent to flat above, prominent beneath; nerves 9–13 pairs, prominent to flat above, sometimes slightly sunken, prominent beneath, marginal arches distinct, 3–5 mm from the margin; tertiary veins and venation fading, rather densely reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 12–36 by 3–8 mm, subglabrous; peduncle 2–24 by 0.7–1 mm; bracts broadly triangular, inconspicuous, 0.3–0.5 mm long, ?glandular, glabrous, margin ciliate; glomerules ellipsoid, 2–3 by c. 1.5 mm, consisting of 9–13 densely set flowers, sometimes spaced at 0.5–1.5 mm at base of rachis, densely massed apically; pedicel c. 0.2 mm. *Staminate flowers* 0.3–0.7 mm long; sepals 4, narrowly obovate, 0.2–0.5 mm long, connate at base, sparsely hairy outside, glabrous inside; stamens 2, slightly exserted, 0.3–0.7 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 2 or 3 clustered together, 2–4 by 0.8–1 mm, subglabrous; flowers single at apical end of rachis; bracts broadly triangular, 0.3–0.5 mm long, fleshy, glabrous outside, hairy at base only inside; bracteoles ?as bracts; pedicel 1.5–5 mm long, sparsely puberulous. *Pistillate flowers* 3–3.5 mm long; sepals 5 or 6, subequal, ovate, reflexed, 0.5–0.8 mm long, fleshy, glabrous, margin ciliate; ovary ellipsoid, 2–3 mm long, 4–6(–7)-locular, smooth, glabrous; stigmas sessile, broad, flattened on top of the ovary, straight, almost completely divided, 0.5–1 mm long, smooth to slightly ribbed above, glabrous, connate to the ovary beneath. *Infructescences* 9–12 by 1.2–2 mm, sparsely tomentose, glabrescent; fruiting pedicel 3–9 mm long, sparsely puberulous. *Fruits* globose, not stiped, not beaked, 21–28 by 22–27 mm, but recorded up to 27–30 mm diam. when fresh, smooth, drying light yellow to orange brown, glabrous; pericarp 3–5 mm thick, fleshy; septae and column glabrous. *Seeds* 3–6, half-terete, ellipsoid, 9–11 by 5–8 by 4–5 mm.

Distribution — Malesia: Borneo.

Habitat & Ecology — Primary, secondary, riverine, or recently logged over forest; on hill sides, hill tops, ridges, road sides, and along river banks or swamps; in low or undulating country, rolling land, marshy or moist areas, or alluvial. Soil: clay, sandstone,



Map 10.6. Distribution of *Aporosa nitida* Merr.

sandy clay loam, loam with lime, silty clay, laterite, or stony, granodiorite derived, yellowish to reddish. Altitude: low to 1000 m. Flowering: March to December; fruiting throughout the year. The fruit is edible but sour.

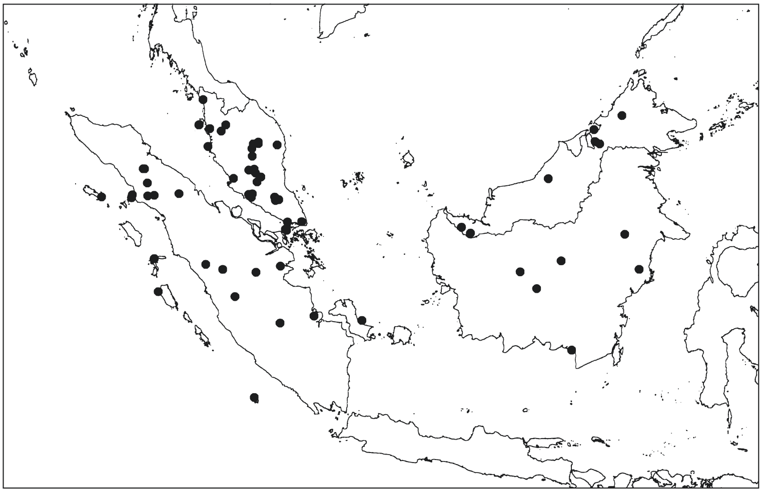
Vernacular names — Kayu besi (Bukit Baka); bilung, susu-diangas (Dusun rongos); janggau, janggau daun besar man (Iban); mata rusu (Malay); ? punu-punu.

7. **Aporosa prainiana** King ex Gage — Fig. 3.5k, 3.6s, 4.4; Map 10.7

Aporosa prainiana King ex Gage, Rec. Bot. Surv. India 9 (1922, before March) 228; Ridl., Fl. Malay Penins. 3 (1924) 240; S. Moore, J. Bot. Brit. & For. 63 Suppl. (1925) 97; Meijer, Bot. News Bull. Sandakan 7 (1967) 34; Airy Shaw, Kew Bull. 25 (1971) 476; Whitmore, Tree Fl. Malaya 2 (1973) 60; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 40; Kew Bull. 36 (1981) 257. — Type: *Curtis 1476* (holo SING), Peninsular Malaysia, Penang.

Aporosa prainiana Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922, second half) 92. — Type: *Ridley s.n.* (holo BM; iso BO), Singapore, Botanic Gardens Jungle.

Shrub or tree, up to 18 m high, up to 20 cm diameter. *Bark* brownish, greyish, grey-green, grey-white, or whitish mottled, smooth to finely fissured or rugose, (slightly) flaky, c. 0.5 mm thick; inner bark dull cream, whitish, (pale) yellow, greenish, or brownish, granular, c. 1 mm thick. *Wood* white, whitish, yellow, (dark) ochre, pale orange, or pale brown. (Young) twigs dark green or brownish, glabrous. *Stipules* not seen, early caducous. *Petiole* terete, adaxially lowly grooved, 5–15 by 0.8–1.5 mm, glabrous, lower pulvinus 1–3 by 1–2 mm, often indistinct, upper pulvinus 2.5–7 by 1–3 mm, distinct. *Leaves* narrowly ovate to narrowly elliptic, 7.5–17 by 2.5–6.5 cm; base obtuse to attenuate, basal glands variably present, small, flat, black; margin lowly undulate to lowly crenate, marginal glands regular, black; apex acuminate to cuspidate; blade thickish, smooth, dull, not brittle, drying light or dark greenish grey above and beneath, sometimes brownish yellow, completely glabrous; dots densely set, fine, greyish black, fading in older leaves; disc-like glands few, small, along the margin, sometimes present. *Nervation*: midrib (slightly) prominent above, prominent beneath; nerves 6–9 pairs, slightly prominent to flat above, prominent beneath, marginal arches fading, 0.5–3 mm from the margin; tertiary veins and venation fading, densely reticulate, slightly prominent to flat. *Inflorescences* axillary to just beneath the leaves. *Staminate inflorescences* clustered 1–6 together, 9–56 by 1–1.8 mm, glabrous; peduncle 0.5–2 by 0.2–0.4 mm; bracts inconspicuous, broadly triangular, 0.5–0.8 mm long, glabrous, margin ciliate; glomerules subglobose, dense, 0.8–1.2 by 1–1.5 mm, consisting of less than 10 flowers, spaced at 1–2.5 mm along the rachis; pedicel absent. *Staminate flowers* 0.8–1.5 mm long; sepals 4 (or 5), narrowly obovate, 1–1.5 mm long, connate at base only, glabrous, margin sparsely ciliate; stamens 2 (or 3), slightly or not exserted, 0.4–0.9 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* clustered 1–3 together, 6–22 by 0.5–0.8 mm, sparsely tomentose at base, glabrescent; flowers up to 5, laxly arranged along the rachis; bracts broadly triangular, 0.5–0.8 mm long, glabrous, margin sparsely ciliate; bracteoles ovate, 0.3–0.5 mm long, glabrous, margin ciliate; pedicel 1.5–3 mm long, sparsely tomentose. *Pistillate flowers* 2–3.5 mm long; sepals 4, patent, ovate, 0.8–1.2 mm long, sparsely hairy outside, glabrous inside; ovary ovoid, 1.5–2.5 mm long, (2- or) 3-locular, slightly (2- or) 3-lobed, glabrous; stigmas slightly raised, elongated, apically bifid to near base, perpendicular to the sides of the ovary, slightly recurved, 0.4–0.8



Map 10.7. Distribution of *Aporosa prainiana* King ex Gage.

mm long, papillate above, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 9–37 by 0.8–1.8 mm, glabrous; fruiting pedicel 4–17 mm long, very sparsely tomentose, glabrescent. *Fruits* fleshy, ovoid, not stiped, not beaked, 12–15 by 10–13 mm, corrugate to punctate (see note), slightly ridged at sutures, glabrous; pericarp 0.5–1 mm thick, slightly fleshy; apex of endocarp caudate; septae and column glabrous. *Seeds* 2 or 3, half-terete, ellipsoid, 9–10 by 6–7 by 3–4 mm.

Distribution — Malesia: Peninsular Malaysia, Singapore, Sumatra, Borneo.

Habitat & Ecology — Primary, (old) secondary, disturbed, logged over dipterocarp forest or kerangas; on hill sides, ridges, and along river banks; flat land, low undulating land, dry land, or riverine land. Soil: tuff, sandstone, loamy, shale granite, or granitic sand, brown or yellow-red. Altitude: sea level to 1350 m. Flowering: February to April, July to October; fruiting: May to January. Fruit sour.

Vernacular names — Sumatra: Bangka: Kayu malam. Borneo: Janggau (Iban); onyak loki (Kalimantan Barat, Bukit Raya).

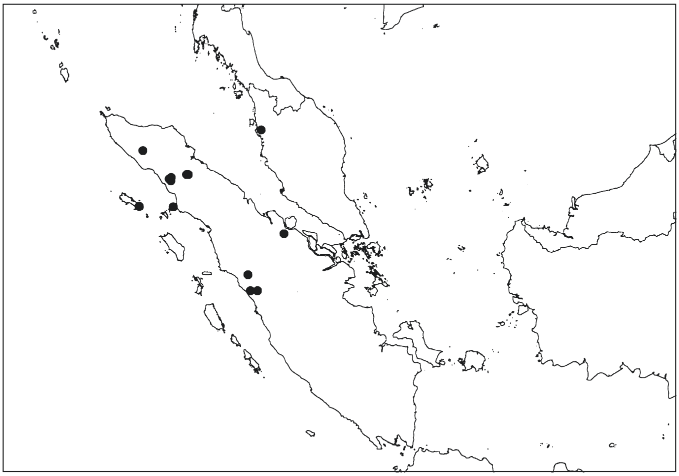
Note — *Aporosa prainiana* and *A. symplocoides* are difficult to distinguish. In literature two characters are mostly used. However, the first, fruits single or fruits many, is based on a misinterpretation of Gage's 'flowers single' (he meant, single in the axis of the bracts!) and on Pax & Hoffmann's 'fruits single', but the type specimen in BM shows distinct scars were other fruits and/or unfertilised pistillate flowers have fallen off. The other character frequently used for separating the species is 2- or 3-locular ovaries (following the example set by Pax & K. Hoffm., 1922). But *A. symplocoides* is both 2- and 3-locular (even according to Pax & K. Hoffmann's description!), which makes distinction with this character impossible. The real difference is the lobed pistillate flower and the larger fruit of *A. prainiana*. This fruit is irregularly corrugate-punctate in the dried state, but probably larger, smooth, and juicy when fresh, whereas the fruit of *A. symplocoides* is thin walled and not fleshy. In addition, *A. prainiana* has often thicker leaves with densely set, distinct dots; *A. symplocoides* has thin leaves with irregularly set dots, which are mostly indistinct.

8. Aporosa quadrilocularis (Miq.) Müll.Arg. — Map 10.8

Aporosa quadrilocularis (Miq.) Müll.Arg. in DC., Prod. 15, 2 (1866) 476; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 92; Airy Shaw, Kew Bull. 32 (1978) 363; 36 (1981) 257. — *Leiocarpus quadrilocularis* Miq., Fl. Ind. Bat., Suppl. (1860) 178, 443. — Type: *Diepenhorst HB 1368* (holo U), W Sumatra, Priaman.

Aporusa claviflora Airy Shaw, Kew Bull. 32 (1978) 364. — Type: *Sidek bin Kiah 263* (holo K; iso L), Peninsular Malaysia, Kedah.

Shrub or tree, up to 20 m high, up to 10 cm diameter. *Bark* greyish brown; inner bark greenish white. *Wood* pale yellowish. *Twigs* grey-brown or green, glabrous. *Stipules* not seen, early caducous. *Petiole* terete, adaxially grooved, 9–24 by 1–1.5 mm, glabrous, lower pulvinus 1.5–3.5 by 1.5–2 mm, upper pulvinus 3–8 by 1.5–2 mm, both distinct. *Leaves* narrowly ovate to (narrowly) elliptic, 9–20 by 3.5–7 cm; base cuneate to slightly attenuate, basal glands absent; margin very lowly undulate to lowly glandular-crenate, marginal glands few, small, black, distinct; apex acuminate to cuspidate; blade thinnish, young leaves lowly white granular, dull or slightly shiny, not brittle, drying dark to light greyish green above and beneath, sometimes yellowish brown, completely glabrous; dots laxly set, fine, greyish, indistinct; disc-like glands seldom few, small, greyish, along the margin. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 7–10 pairs, slightly prominent to flat above, prominent beneath, marginal arches often distinct, 1.5–3 mm from the margin; tertiary veins and venation distinct, sometimes fading, rather densely reticulate, slightly scalariform, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–4 clustered together, 7–28 by 3–6 mm, sparsely tomentose, glabrescent; peduncle 2–7 by 0.8–1.5 mm; bracts not seen; glomerules ellipsoid, 2–3 by 1–1.2 mm, consisting of 9–13 densely set flowers, spaced at 0.5–1.5 mm at base of rachis, densely massed apically; pedicel minute. *Staminate flowers* 0.4–0.6 mm long; sepals 4 (or 5), narrowly obovate, 0.2–0.4 mm long, connate at base only, sparsely hairy outside, glabrous inside,



Map 10.8. Distribution of *Aporosa quadrilocularis* (Miq.) Müll.Arg.

margin ciliate; stamens 2, slightly exserted, 0.3–0.6 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 2–4 by 0.8–1 mm, sparsely tomentose, glabrescent; flowers single at apical end of rachis; bracts broadly triangular, 0.3–0.5 mm, sparsely hirsute outside, glabrous inside, margin ciliate; bracteoles ovate, 0.3–0.5 mm long, sparsely hirsute outside, glabrous inside; pedicel 1.5–2 mm long, sparsely puberulous. *Pistillate flowers* 2–2.5 mm long; sepals 5 or 6, ovate, reflexed, 0.3–0.5 mm long, fleshy, sparsely hirsute outside, glabrous inside, margin ciliate; ovary cylindric to subglobose, 1.5–2.5 mm long, (3- or) 4- (or 5-)locular, smooth, glabrous; stigmas sessile, broad, flattened on top of the ovary, straight, apically bifid to near base, 0.5–1.5 mm long, ribbed towards the base above, glabrous, connate to the ovary beneath. *Infructescences* 8–13 by 1–1.5 mm, sparsely tomentose, glabrescent; fruiting pedicel 3–7 mm long, sparsely tomentose. *Fruits* globose, not stiped, not beaked, 15–21 by 16–22 mm, but recorded to be 25–30 mm diam. when fresh, smooth, drying yellowish or orangish, glabrous; pericarp 3–4 mm thick, fleshy; septae and column glabrous. *Seeds* 4 (or 5), half-terete, ellipsoid, 8–11 by 5–9 by 3–4 mm.

Distribution — Malesia: Sumatra; twice found in Peninsular Malaysia, Kedah.

Habitat & Ecology — Logged over, degraded, or montane forest; on hills, along forest edges, river sides, or roads; in flat, rolling, or dry to alluvial land. Soil: yellow-red loamy or sandy clay with stones. Altitude: 40–1000 m. Flowering: March to April, July to September; fruiting: February, May to September.

9. **Aporosa sarawakensis** Schot — Fig. 3.6u, 3.8o, 4.5a, 10.3; Map 10.9

Aporosa sarawakensis Schot, Blumea 40 (1995) 458. — Type: *S (Paie) 22905* (holo L; iso BO, K), Sarawak, 3rd Division, Marudi.

Shrub or tree, up to 12 m high, up to 20 cm diameter. *Bark* whitish, grey, (light) brownish, green(ish), yellowish, or pink mottled, smooth, slightly dippled, thin; inner bark cream or yellowish, thin, brittle. *Wood* white, yellow, or orange-cream. Twigs (dark) green, glabrous. *Stipules* not seen, early caducous. *Petiole* terete, sometimes adaxially lowly grooved, 4–17 by 0.8–1.8 mm, glabrous, lower pulvinus 1.5–3 by 1–2 mm, upper pulvinus 3–6 by 1.5–3 mm, both distinct. *Leaves* narrowly elliptic to narrowly obovate, 9.5–20 by 2.5–8 cm; base obtuse to slightly attenuate, basal glands indistinct, black; margin lowly undulate to lowly glandular-crenate, marginal glands regular, small, blackish; apex cuspidate to caudate; blade thin, young leaves lowly granular, dull, not brittle, drying greyish green above and beneath, sometimes yellowish green, nervation lighter beneath, completely glabrous; dots laxly set, fine, grey, indistinct; disc-like glands occasionally few, small, along the margin. *Nervation*: midrib (slightly) prominent above, prominent beneath; nerves 9–12 pairs, slightly prominent to slightly sunken above, prominent beneath, marginal arches distinct, 1–3 mm from the margin; tertiary veins and venation distinct, fading, densely reticulate, slightly scalariform, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* clustered 3–8 together, 14–41 by 0.8–1.2 mm, very sparsely puberulous, glabrescent; peduncle 3–6 by 0.2–0.4 mm; bracts broadly triangular, inconspicuous, 0.3–0.7 mm long, subglabrous outside, glabrous inside, margin ciliate; glomerules subglobose, 0.8–1.2 by 0.5–1 mm, consisting of 5–10 rather laxly

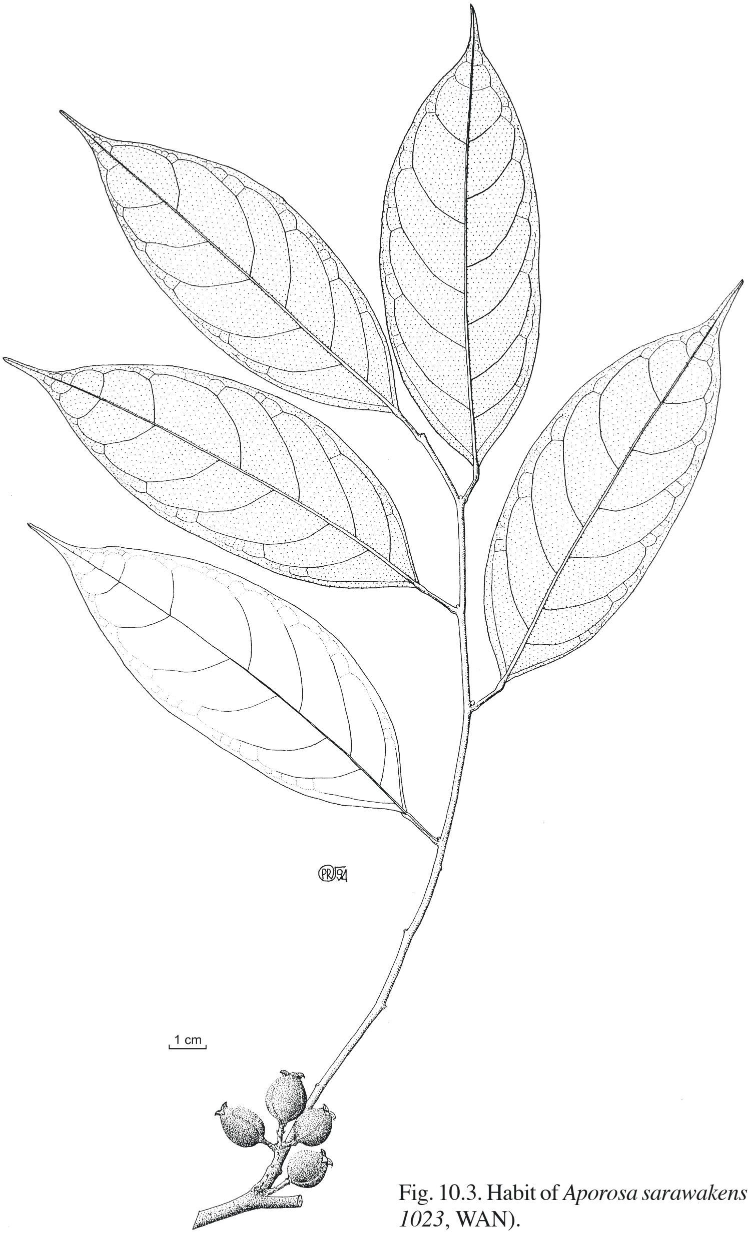


Fig. 10.3. Habit of *Aporosa sarawakensis* Schot (*Sidiyasa 1023*, WAN).

set flowers, spaced at 2–6 mm at base of rachis, decreasing to 0 mm apically; pedicel absent. *Staminate flowers* 0.5–1 mm long; sepals 4 (or 5), narrowly obovate, 0.6–0.9 mm long, connate at base only, glabrous, apex ciliate; stamens 2, slightly exserted, 0.6–1 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode minute, lumpy, resembling an undeveloped stamen. *Pistillate inflorescences* 1–5 (11) clustered together, 4–13 by 0.3–0.5 mm, very sparsely puberulous, glabrescent, flowers 1 (seldom 2), at apical end of the rachis; bracts broadly triangular, 0.5–0.8 mm long, subglabrous outside, glabrous inside, margin ciliate; bracteoles not seen; pedicel 1–2.5 mm long, subglabrous. *Pistillate flowers* 3–5 mm long; sepals 4 or 5, ovate, slightly reflexed, 0.6–1.5 mm long, fleshy, glabrous, margin sparsely ciliate; staminodes occasionally 1–3 present; ovary subcylindric, 2–4 mm long, 3-locular, smooth, glabrous; stigmas sessile, broad, apically lowly bifid, flattened on top and to the sides of the ovary, straight, 1–2 mm long, ribbed above, laciniate, glabrous, connate to ovary beneath, smooth, glabrous. *Infructescences* 4–12 by 0.8–1.2 mm, glabrous; fruiting pedicel 1–5 mm long, glabrous. *Fruits* hard, sometimes slightly fleshy, ovoid to ellipsoid, not stiped, not beaked, 13–21 by 8–12 mm, smooth, ridged at sutures when young, drying light orangish to yellow, glabrous; pericarp 0.8–1.5 mm thick, ?fleshy; apex of endocarp caudate; septae and column glabrous. *Seeds* 1–3, (half-)terete, ellipsoid to subglobose, 8–9.5 by 6–7.5 by 3.5–5 mm.

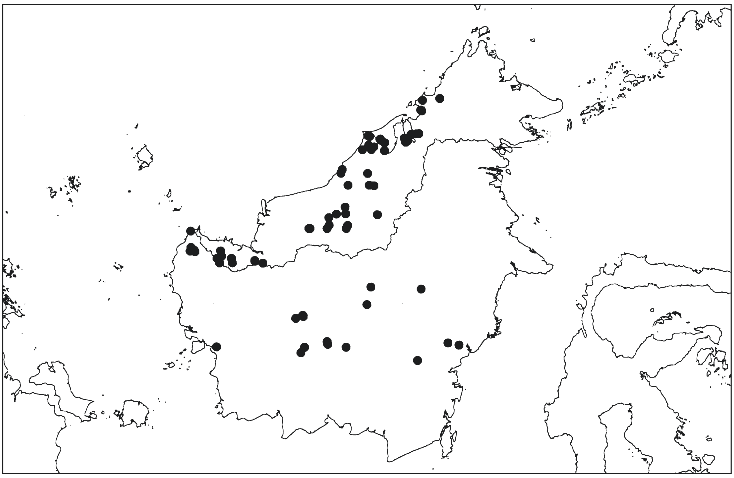
Distribution — Malesia: Borneo (mainly Sarawak).

Habitat & Ecology — Primary, secondary, logged over, and disturbed rain forest or belukar; flat land, undulating land, open places, alluvial; on hillsides, ridges, near streams and at forest edges. Soil: igneous, limestone, or granodiorite derived; clayey, sandy, loamy or basalt; stony, with rocks; yellow to dark brown or red. Altitude: low to 900 m. Flowering: March, July to November; fruiting throughout the year.

Vernacular names — Simpit minyak, hansi burung (Bukit Baka); morok, tamahas (Dayak); buah sabong, enkunik, janggit, janggau, kayu malam (Iban); dawi, salibut (Kayan); tekam garam (Malay).

Notes — 1. This species includes the specimens from Borneo that were often identified as *A. prainiana* because they only have one fruit (see also note under *A. prainiana*).

2. One deviating specimen was seen, *Nooteboom 1112*, which is staminate, but in which part of the inflorescences bear a single pistillate flower at the apex. In other features, the specimen is 'normal'.



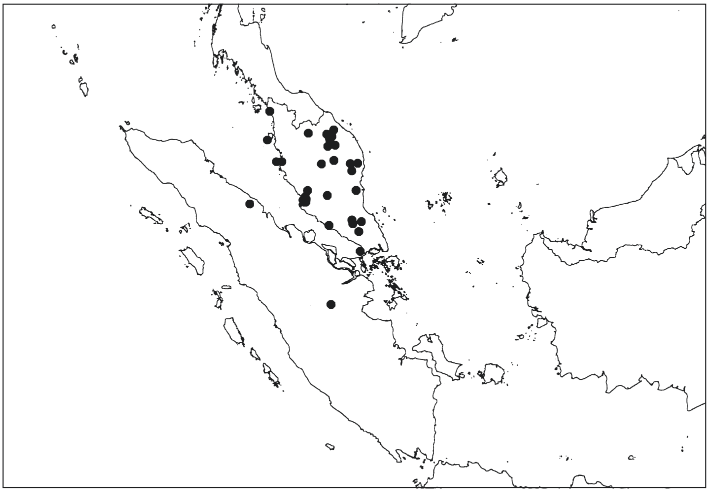
Map 10.9. Distribution of *Aporosa sarawakensis* Schot.

10. Aporosa stellifera Hook.f. — Fig. 3.5f, 3.6g; Map 10.10

Aporosa stellifera Hook.f., Fl. Brit. India 5 (1887) 352; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 60; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 85; Ridl., Fl. Malay Penins. 3 (1924) 239; Whitmore, Tree Fl. Malaya 2 (1973) 60. — Lectoype (proposed here): *King's Collector 1642* (holo K), Peninsular Malaysia, Penang, 1500–1800 ft.

Aporosa nitida auct. non Merr.: Whitmore, Tree Fl. Malaya 2 (1973) 60.

Shrub or tree, up to 18 m high, up to 25 cm diameter. *Bark* black, brown, fawn, or pale greyish green, smooth, with minute rugose scales; inner bark white to yellowish white to yellow-brown. *Wood* (pale) yellow, cream, or brown. Young branches glabrous. *Stipules* not seen, early caducous. *Petiole* terete, adaxially (lowly) grooved, 18–33 by 1.5–2.5 mm, glabrous, lower pulvinus 1.5–3.5 by 2–3.5 mm, upper pulvinus 6–9 by 2–3.5 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 15.5–33 by 6.5–13 cm; base rounded to acute, basal glands absent; margin lowly undulate, marginal glands few, small, greyish; apex acuminate to cuspidate; blade thickish, smooth, rather shiny, not brittle, drying yellowish green to greyish green above and beneath, completely glabrous; dots absent; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 10–14 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 2–4 mm from the margin; tertiary nerves and venation fading, densely reticulate, flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 3–10 clustered together, 9–44 by 1.5–2.5 mm, sparsely tomentose, glabrescent; peduncle 1.5–3 by 0.8–1 mm; bracts broadly triangular, inconspicuous, 0.7–1.2 mm long, glabrous, margin ciliate; glomerules ellipsoid, 1.5–3.5 by 0.5–1.5 mm, consisting of less than 10 flowers, spaced at 0.5–1 mm at base of the rachis, decreasing to 0 mm apically; pedicel 0.1–0.2 mm long. *Staminate flowers* 0.3–0.6 mm long; sepals 4, narrowly obovate, 0.4–0.8 mm long, connate at base only, glabrous, margin sparsely ciliate; stamens 2, not to slightly exserted, 0.3–0.6 mm long; anthers 0.1–0.2 mm long, connective



Map 10.10. Distribution of *Aporosa stellifera* Hook.f.

glabrous; pistillode absent. *Pistillate inflorescences* 2–6 clustered together, 4–7 by 0.7–1 mm, very sparsely puberulous, glabrescent; flowers up to 7, at apical end of the rachis; bracts triangular, 0.4–0.6 mm long, glabrous, margin ciliate; bracteoles ovate, 0.4–0.6 mm long, subglabrous outside, glabrous inside, margin ciliate; pedicel 1–3 mm, sparsely hairy. *Pistillate flowers* 3–4.5 mm long; sepals 5 or 6, ovate, reflexed, thick fleshy, 0.8–1.2 mm long, glabrous, margin ciliate; staminodes occasionally 2 or 3 present, 0.2–0.7 mm long; ovary cylindrical, 2.5–3 mm long, 3- (seldom 4-)locular, smooth, glabrous; stigmas sessile, broad, almost completely divided, flattened on top of the ovary, straight, 0.8–1.5 mm long, smooth, lowly papillate above, glabrous, connate to the ovary beneath, smooth, glabrous. *Infructescences* 8–16 by 1–1.5 mm, sparsely tomentose, glabrescent; fruiting pedicel 2–4 mm long, sparsely tomentose. *Fruits* ellipsoid, not stiped, not beaked, 15–21 by 13–18 mm, punctate to lowly papillate, glabrous; pericarp 1.5–3 mm thick, fleshy; apex of endocarp caudate; septae and column glabrous. *Seeds* 3, half-terete, ellipsoid, 10–10.5 by 8.5–10 by 3.5–5 mm.

Distribution — Malesia: Peninsular Malaysia and Sumatra.

Habitat & Ecology — Primary, disturbed, bamboo or riverine forest, belukar; on hills, ridges, ridges, along river banks, and road sides; in lowland, or seasonal swampy areas. Soil: granite or granitic rock. Altitude: 30–300 m. Flowering: February to April, July to September; fruiting: March to November.

Vernacular names — Peninsular Malaysia: Sebasah, semasak (Malay).

11. **Aporosa stenostachys** Airy Shaw — Map 10.5

Aporusa stenostachys Airy Shaw, Kew Bull. 29 (1974) 285; Kew Bull., Addit. Ser. 4 (1975) 41. — Type: *S (Senada) 10113* (holo K; iso BO, L, SING), Sarawak, Bintulu.

Tree, up to 18 m high, up to 15 cm diameter. *Bark* chocolate to greyish brown, smooth. Twigs brownish green, sparsely hirsute. *Stipules* narrowly ovate, slightly oblique, c. 1.5 by 3–4 mm wide, sparsely hairy, caducous. *Petiole* terete, adaxially lowly grooved, 8–15 by 0.8–1 mm, sparsely hirsute, lower pulvinus 1–2 by c. 1 mm, upper pulvinus 1.5–4 by 1–1.2 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 10–19 by 3–5.5 cm; base obtuse to acute, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, distinct, brownish to black; apex cuspidate to caudate; thin, young leaves lowly granular, dull, not brittle, drying greenish yellow above and beneath, nervation lighter beneath, glabrous above, only midrib and nerves sparsely hirsute beneath, glabrescent; dots absent; disc-like glands absent. *Nervation*: midrib prominent above, prominent beneath; nerves 9–12 pairs, flat above, prominent beneath, marginal arches fading, 1–2 mm from the margin; tertiary nerves and venation fading, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 4–14 clustered together, 9–35 by 0.5–1.5 mm, sparsely puberulous; peduncle 2–6 by 0.5–0.8 mm; bracts broadly triangular, inconspicuous, 0.4–0.6 mm long, puberulous outside, glabrous inside; glomerules ellipsoid, 1–1.5 by 0.5–0.8 mm, consisting of less than 10 flowers, spaced at 2–4 mm at base of rachis, decreasing to 0 mm apically; pedicel minute. *Staminate flowers* 0.3–0.5 mm long; sepals 4 (or 5), narrowly obovate, connate at base only, sparsely puberulous outside, glabrous inside; stamens 2 (or 3), slightly exserted, 0.2–0.4 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 2–5 clustered together, 6–13 by 0.8–1 mm, sparsely puberulous; flowers single at apical end of rachis; bracts broadly triangular, 0.8–1 mm long, sparsely hairy outside, glabrous inside; bracteoles not seen; pedicel 2–5 mm long, sparsely puberulous. *Pistillate flowers* 4–6 mm long; sepals 5 (or 6), subequal, ovate, ascending, 1.8–2.2 mm long, sparsely hairy; staminodes erratically 1 present; ovary ovoid, 3.5–4 mm long, 3-locular, punctulate, sparsely hairy at base; stigmas sessile, broad, apically bifid to c. halfway, flattened on top of the ovary, straight, 1.2–2 mm long, ribbed and papillate above, glabrous, connate to the ovary beneath, smooth, glabrous. *Infructescences* 8–14 by 1–1.2 mm, sparsely puberulous; fruiting pedicel 2–4 mm long, sparsely puberulous. *Fruits* ovoid to globose, not stiped, not beaked, 8–11 by 8–11 mm, slightly punctulate, very sparsely puberulous; pericarp 0.5–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ellipsoid, 7–9 by 5.5–7 by 3–4 mm.

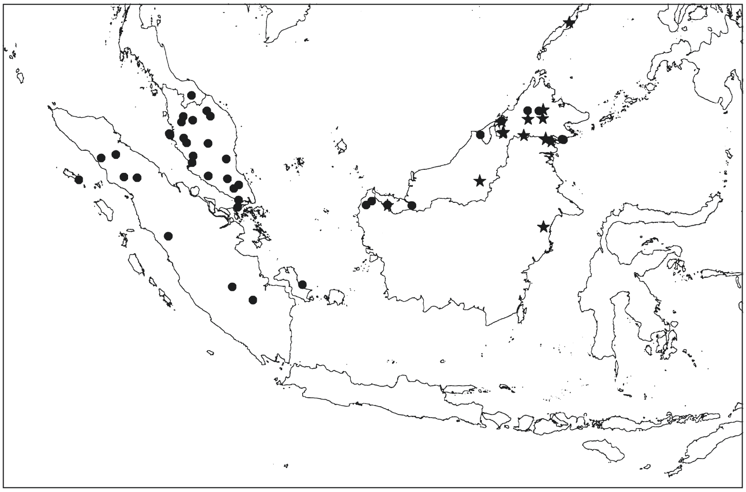
Distribution — Malesia: Borneo.

Habitat & Ecology — Riverine forest; along river banks, or in tidal zone; leaning over the water, sometimes partly under water. Soil rich. Altitude: low to 250 m. Flowering: April, May, October; fruiting: March, October. Fruits apparently eaten by squirrels.

12. **Aporosa symplocoides** (Hook.f.) Gage — Fig. 3.6t; Map 10.11

Aporosa symplocoides (Hook.f.) Gage, Rec. Bot. Surv. India 9 (1922) 229; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 90; Ridl., Fl. Malay Penins. 3 (1924) 240; S. Moore, J. Bot. Brit. & For. 63 Suppl. (1925) 97; Meijer, Bot. News Bull. Sandakan 7 (1967) 34; Airy Shaw, Kew Bull. 26 (1972) 218; Whitmore, Tree Fl. Malaya 2 (1973) 60; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 41, excl. var. *chondroneura* (Airy Shaw) Airy Shaw; Kew Bull. 36 (1981) 257. — ?*Baccaurea symplocoides* Hook.f., Fl. Brit. India 5 (1887) 376. — Type: *King's Collector* (holo K), Peninsular Malaysia, Perak.

Shrub or tree, up to 24 m high, up to 30 cm diameter. *Bark* brownish, reddish, grey, white, or green-white, smooth to slightly flaky or scaly fissured; inner bark pale grey, pale brown, cream, yellow, orange, or reddish brown, speckled. *Wood* white, cream, brownish, or yellow, hard. Young branches glabrous. *Stipules* not seen, early caducous. *Petiole* terete, adaxially grooved, 12–26 by 0.5–1.2 mm, glabrous, lower pulvinus 1.5–3 by 1–1.5 mm, upper pulvinus 2–5 by 1.2–2 mm, both distinct. *Leaves* narrowly ovate to (narrowly) elliptic, 6–17 by 2.5–7 cm; base rounded to slightly attenuate, basal glands sometimes present, small, black, flat; margin lowly undulate to lowly crenate, marginal glands few, small, greyish to black; apex acuminate to cuspidate; blade thin, young leaves lowly granular above and beneath, dull, not brittle, sometimes slightly shiny, drying (dark) grey-green above and beneath, sometimes yellowish green, completely glabrous; dots irregularly set, fine, brownish or blackish, indistinct; disc-like glands small, along the margin, irregularly present. *Nervation*: midrib (slightly) prominent above, prominent beneath; nerves 6–9 pairs, slightly prominent above, prominent beneath, marginal arches distinct, 2–3 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly prominent to flat. *Inflorescences* axillary or just beneath the leaves. *Staminate inflorescences* clustered 1–10 together, 12–62(–98) by 0.8–1.2 mm, subglabrous; peduncle 1.5–3 by 0.5–0.8 mm; bracts broadly triangular, 0.5–0.8 mm long, inconspicuous, sparsely puberulous outside, glabrous inside, margin



Map 10.11. Distribution of *Aporosa symplocoides* (Hook.f.) Gage: var. *symplocoides* (●), var. *chalarocarpa* (Airy Shaw) Schot (★).

ciliate; glomerules globose, 1–1.2 by 0.8–1.2 mm, consisting of 4–8 flowers, spaced at 0.5–3(–7) mm along the rachis; pedicel minute. *Staminate flowers* 0.5–0.9 mm long; sepals 4, narrowly obovate, 0.5–0.9 mm long, connate at base, glabrous, margin sparsely ciliate; stamens 2, not or slightly exserted, 0.3–0.7 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode indistinct. *Pistillate inflorescences* clustered 1–3 together, 7–33 by 0.5–0.8 mm, sparsely puberulous at base, glabrescent; flowers up to 11, laxly arranged along the rachis; bracts broadly triangular, 0.5–0.8 mm long, glabrous outside, hairy at base inside, margin ciliate; bracteoles ovate, 0.4–0.6 mm long, glabrous outside, hairy at base inside; pedicel 1–4 mm long, very sparsely puberulous. *Pistillate flowers* 1.5–3 mm long; sepals 3 or 4, ovate, subequal, 0.5–1 mm long, glabrous, margin ciliate, fleshy; ovary ovoid, 1.2–2.2 mm long, 2- or 3-locular, smooth, glabrous; stigmas slightly raised, elongated, perpendicular to or slightly ascending from the sides of the ovary, apically bifid to near base, straight, 0.2–1 mm long, ribbed above, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 9–114 by 0.5–1 mm, glabrous; fruiting pedicel 2–35 mm long, very sparsely puberulous. *Fruits* (narrowly) ellipsoid to ovoid, not (lowly) stiped, sometimes beaked, 9–19 by 6.5–11 mm, punctulate to almost smooth, glabrous; pericarp 0.2–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 1–3, half-terete, ovoid, 6–9 by 4–7 by 2–4 mm.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia, Singapore, Sumatra, Borneo.

Habitat & Ecology — Primary, somewhat disturbed or logged over, evergreen forest; on hill sides, hill tops, along road sides, or by streams; in undulating land, in open, dense, or (partly) shaded areas, sometimes in seasonal swamps. Soil: granitic or sandy, rich, black. Altitude: low to 500 m. Flowering: March to October; fruiting: March to January.

Vernacular names — Peninsular Malaysia: Sebasah (Malay). Borneo: Bantas (Iban); atang (kayan).

Notes — 1. See note under *A. prainiana*.

2. The variety *A. symplocoides* var. *chalarocarpa* differs from typical *A. symplocoides* only in the elongated infructescences, pedicels, and fruits. There are no differences in vegetative characters or in staminate flowers (one staminate specimen, *SAN 40618*, has inflorescences up to 98 mm long, but differs in no other character from the typical form). Some specimens (from Sarawak and Simalur) are even intermediate in having the fusiform fruits of *A. chalarocarpa* combined with the short inflorescences and pedicels of *A. symplocoides*.

Key to the varieties

1a. Infructescences 34–114 mm long. Fruiting pedicel 13–35 mm long. Fruit narrowly ellipsoid to fusiform, 16–19 by 6.5–10 mm, shortly stiped and beaked . . . . **b.** var. **chalarocarpa**

b. Infructescences 9–46 mm long. Fruiting pedicel 2–7 mm long. Fruit ellipsoid to ovoid, 9–13 by 8–11 mm, not stiped, not beaked . . . . **a.** var. **symplocoides**

a. var. **symplocoides**

For nomenclature see under species.

Infructescences 9–46 mm long; fruiting pedicel 2–7 mm long. *Fruits* ellipsoid to ovoid, 9–13 by 8–11 mm, not stiped, not beaked.

b. var. **chalarocarpa** (Airy Shaw) Schot

Aporosa symplocoides (Hook.f.) Gage var. *chalarocarpa* (Airy Shaw) Schot, Blumea 40 (1995) 453. — *Aporusa chalarocarpa* Airy Shaw, Kew Bull. 20 (1966) 380; Meijer, Bot. News Bull. Sandakan 7 (1967) 34; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 34. — Type: *SAN (Meijer) 19411* (holo K; iso BO, L), Sabah, Tawau.

Infructescences 34–114 mm long; fruiting pedicel 13–35 mm long. *Fruits* narrowly ellipsoid to fusiform, 16–19 by 6.5–10 mm, lowly stiped and beaked.

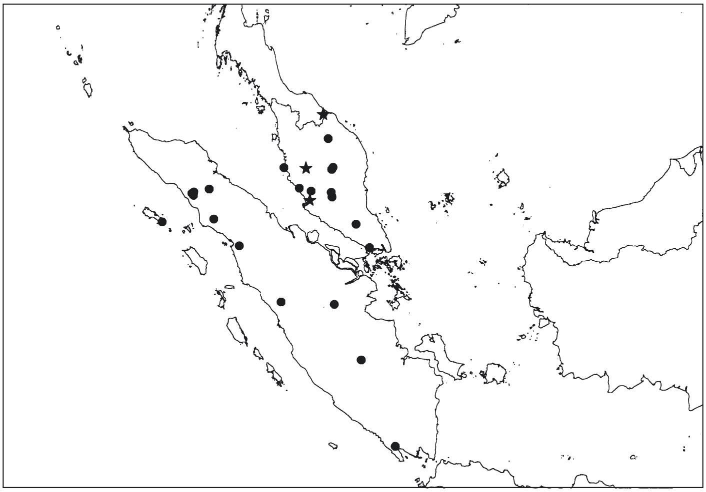
13. Aporosa whitmorei Airy Shaw — Fig. 3.8c; Map 10.12

Aporusa whitmorei Airy Shaw, Kew Bull. 32 (1978) 361. — Type: *KEP-FRI 4935* (holo K; iso L, SING), Peninsular Malaysia, Pahang.

?*Aporosa spec. nov.* S. Moore, J. Bot. Brit. & For. 63 Suppl. (1925) 97. — Specimen: *Forbes 1783* (K), Sumatra, Lampong, Penanggoengan.

Tree, up to 18 m high, up to 30 cm diameter. *Bark* grey or greyish green, smooth, scaly, c. 0.1 mm thick; inner bark pale yellow, whitish green, or pink, c. 1.5 mm thick. *Wood* (pale) yellow. Young branches (sparsely) tomentose. *Stipules* narrowly ovate, slightly oblique, 3–5 by 2–3 mm, at base and centre densely tomentose, glabrescent, caducous. *Petiole* terete, ridged, 6–11 by 0.8–1.2 mm, tomentose, glabrescent, lower pulvinus 1–1.5 by 1–1.2 mm, upper pulvinus 2–3 by 1–1.2 mm, both indistinct under indumentum. *Leaves* narrowly elliptic, 8–20 by 3–7 cm; base rounded to cuneate, basal glands absent; margin subentire, marginal glands many, greyish, hardly visible; apex acuminate to cuspidate; blade thin, young leaves lowly granular above, dull, not brittle, drying (dark) greyish green above and beneath, only midrib and nerves sparsely tomentose above, glabrescent, sparsely tomentose beneath, glabrescent; dots absent; disc-like glands absent. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 9–14 pairs, flat above, prominent beneath, marginal arches distinct, 1.5–3 mm from the margin; tertiary veins and venation distinct, laxly reticulate, flat above, (slightly) prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–4 clustered together, 7–28 by 0.3–0.5 mm, very sparsely tomentose, glabrescent; peduncle 1–3 by 0.3–0.5 mm; bracts triangular, c. 1 mm long, inconspicuous, glabrous, margin ciliate; glomerules globose, 0.8–1.2 by 0.8–1.2 mm, consisting of less than 10 flowers, spaced at 0.5–2.5 mm along the rachis; pedicel minute. *Staminate flowers* 0.8–1 mm long; sepals 4 or 5, obovate, 1–1.2 mm long, almost free, glabrous; stamens 2 or 3, not exserted, 0.8–1 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 7–21 by 0.3–0.7 mm, sparsely tomentose; flowers up to 7, laxly arranged along the rachis; bracts broadly triangular, 0.5–0.8 mm long, glabrous, margin ciliate; bracteoles ovate, 0.3–0.4 mm long, glabrous, margin ciliate; pedicel 1–2 mm long, sparsely tomentose. *Pistillate flowers* 2–3 mm long; sepals 4 or 5, ovate to elliptic, 0.8–1 mm long, very sparsely hairy outside, glabrous inside, margin ciliate; ovary ovoid, 1.5–2.5 mm long, 3-locular, smooth, very sparsely puberulous, glabrescent; stigmas sessile, elongated, apically bifid to slightly less than halfway, perpendicular to the sides of the ovary, slightly recurved, 0.5–1 mm long, ribbed above, laxly laciniate, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 7–23 by 0.8–1.2 mm, sparsely tomentose, glabrescent; fruiting pedicel 2–5 mm long, sparsely tomentose, glabrescent. *Fruits* hard fleshy, ovoid to ellipsoid, not stiped, not beaked, 11–13 by 9–12 mm, punctate to almost smooth, glabrous; pericarp 0.8–1.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 1–3, ovoid, half-terete, 8–9 by 6–7 by 3–5 mm.

Distribution — Malesia: Peninsular Malaysia, Sumatra.



Map 10.12. Distribution of *Aporosa whitmorei* Airy Shaw (●) and *A. spec. E* (★).

Habitat & Ecology — Primary, (un)disturbed, or depleted rain forest or riverine forest; on flat land, sloping country or alluvial; on ridge tops, in valleys, along forest edges, road sides, and along rivers. Soil: deep stony sandy or clayey. Altitude: 25–400 m. Flowering: March, July to September; fruiting: May to November. Fruits eaten by Orang Utang.

14. Aporosa spec. E (aff. *A. stellifera* Hook.f. or *A. frutescens* Blume) — Map 10.12

Specimens: *Larsen & Larsen 33022* (AAU, K, L), Peninsular Thailand, Narathiwat, Sungai Kolok, Nikom Waeng; *KEP-FRI (Kochummen) 18380* (K, L, SING), Peninsular Malaysia, 54th mile Gap Road; *KEP-FRI (Loh) 19189* (K, L), Peninsular Malaysia, NW Pahang, Cameron Highlands, path Boh Tea-Kampuong Mensums; *KL (Teo & P.) 3401* (K, L), Peninsular Malaysia, Selangor, Ulu Gombak, 35 km Juanda Baiks.

Tree, up to 20 m high, up to 30 cm diameter. *Bark* dark grey to pale brown, smooth; inner bark cream. *Wood* cream. Young branches glabrous. *Stipules* not seen, early caducous. *Petiole* terete, often adaxially lowly grooved, 9–23 by 0.8–1.5 mm, glabrous, lower pulvinus 1.5–3 by 1.2–1.9 mm, upper pulvinus 3–6 by 1.2–2 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 11–20 by 3.5–7.5 cm; base rounded to cuneate, basal glands absent; margin lowly undulate to subentire, marginal glands few, small, indistinct; apex acuminate to cuspidate; blade thin, lowly granular above and beneath, dull, not brittle, sometimes slightly shiny, drying greyish green above and beneath, nervation lighter, completely glabrous; dots absent; disc-like glands seldom few along the margin. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 8–12 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.5–2.5 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* born just below the leaves or on the branches. *Staminate inflorescences* clustered 1–4 together, 7–16 by 1.2–1.8 mm, subglabrous; peduncle 1–3 by 0.5–0.8 mm; bracts broadly triangular, inconspicuous, 0.3–0.5 mm long, glabrous, margin ciliate; glomerules ellipsoid, 1.5–2 by c. 0.5 mm, consisting of 7–10 densely set flowers, spaced at 0.5–1 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 0.5–0.9 mm long; sepals 3 or 4, obovate, 0.5–0.7 mm long, connate at base, fleshy, glabrous, apex ciliate; stamens 2, slightly exserted, 0.6–0.9 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode minute, lumpy, resembling undeveloped stamen. *Pistillate inflorescences* not seen, induced from infructescence to be single, subglabrous; flowers single at apical end of rachis; bracts in fruit broadly triangular, 0.5–0.8 mm long, glabrous; bracteoles not seen; pedicel present, subglabrous. *Pistillate flowers* not seen; sepals in fruit 4 or 5, ovate, 0.7–1 mm long, fleshy, glabrous; ovary probably ellipsoid, 3-locular, smooth, glabrous; stigmas in fruit sessile, broad, flattened on top of the ovary, apically bifid to near base, straight, 1–1.5 mm long, ribbed and laxly papillate above, glabrous, connate to the ovary beneath. *Infructescences* 9–13 by 1–1.5 mm, glabrous; fruiting pedicel 3–7 mm long, glabrous. *Fruits* ovoid to subglobose, not stiped, not beaked, 14–16 by 11–16 mm, irregularly punctate, young slightly ridged on the sutures, glabrous; pericarp 1–2 mm thick, fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ovoid, 6.5–9.5 by 5.5–6.5 by c. 3 mm.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia.

Habitat & Ecology — Evergreen forest, on hillsides. Altitude: 300–400 m. Flowering: March; fruiting: July, September and October.

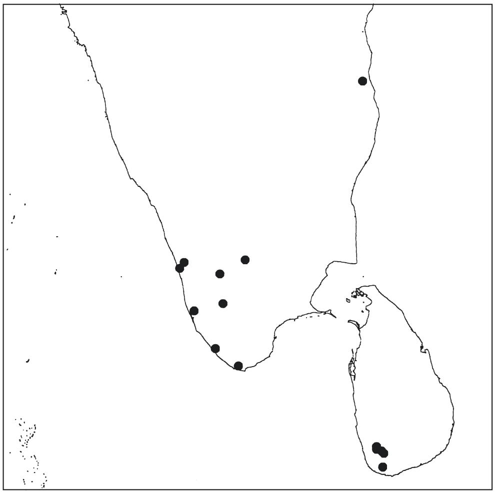
Note — Four collections seen, three in fruit (*KEP-FRI 18380* & *19189*; *KLU 3401*) and one with staminate inflorescences (*Larsen & Larsen 33022*). The leaves are reminiscent of a glabrous *A. frutescens,* but the fruits are like those of *A. sarawakensis*, and the staminate inflorescences fit somewhere between *A. frutescens* and *A. stellifera*. Perhaps young specimens of this latter species?

10.4.2 – ***Section Appendiculatae Pax & K. Hoffm.***

15. Aporosa acuminata Thwaites — Map 10.13

Aporosa acuminata Thwaites, Enum. Pl. Zeyl. (1861) 288; Müll.Arg. in DC., Prod. 15, 2 (1866) 473; Bedd., Fl. Sylv. S. India (3 = For. Man.) (1873) 199; Hook.f., Fl. Brit. India 5 (1887) 348; Trimen, Handb. Fl. Ceylon 4 (1898) 41; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 102; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 42; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 158. — Type: *Thwaites CP 2530* (holo BM; iso P), Sri Lanka, Abagamowa.

Tree or shrub, up to 25 m high, up to 10 cm diameter. *Bark* dark brown to light grey, (shallowly) fissured; inner bark green. Young branches sparsely hairy, glabrescent. *Stipules* narrowly triangular, 8–11 by 4–6 mm, glabrous, caducous. *Petiole* terete, smooth, 6–12 by 0.8–1 mm, very sparsely hairy, glabrescent, lower pulvinus 1–2 by 1–1.2 mm, upper pulvinus 2–3 by 1–1.2 mm, both almost indistinct. *Leaves* narrowly ovate to narrowly elliptic, 6–15 by 2–4 cm; base cuneate to slightly attenuate, basal glands present, hairy; margin lowly undulate, marginal glands few, small, often indistinct; apex cuspidate; blade thin, approximately smooth, slightly shiny, not brittle, drying greenish grey above and beneath, subglabrous, midrib sparsely hairy, glabrescent; dots laxly set, fine, grey, often indistinct; disc-like glands regular, scattered within marginal arches. *Nervation*: midrib prominent; nerves 8–10 pairs, (slightly) prominent above, prominent beneath, marginal arches rather indistinct, 2–4 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–5 clustered together, 4–9 by 1.5–2 mm, probably tomentose; peduncle minute or absent; bracts broadly triangular, inconspicuous, 0.8–1.1 mm long, sparsely hairy outside, glabrous inside, margin ciliate; glomerules (sub)globose, indistinct, consisting of 5–9 laxly set flowers, continuously set along the rachis; pedicel absent. *Staminate flowers* 1–2.5 mm long; sepals 4 (or 5), narrowly obovate, 0.8–1.2 mm long, free, connate to rachis, very sparsely hairy outside, glabrous inside, margin ciliate; stamens 2, not to slightly exserted, 0.5–2.5 mm long; anthers c. 0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* single (or 2 clustered together), 2–4 by 1–1.5 mm, sericeous, flowers up to 7, densely set along the rachis; bracts ovate, 0.75–1 mm long, sparsely puberulous outside, glabrous inside; bracteoles ovate, 0.5–1 mm long, sparsely puberulous outside, glabrous inside; pedicel absent. *Pistillate flowers* 2–3.5 mm long; sepals 3 or 4, ovate, patent, 1.5–2 mm long, thin, sparsely puberulous outside, glabrous inside; ovary ellipsoid, c. 3 mm long, 2-locular, smooth, sparsely sericeous at base, glabrescent towards apex; stigmas slightly raised, elongated, ascending from the sides of the ovary, apically divided, straight, 0.5–1.5 mm long, papillate above,



Map 10.13. Distribution of *Aporosa acuminata* Thwaites.

glabrous, smooth beneath, sparsely sericeous, style remnant absent. *Infructescences* 3–5 by 1.5–2 mm, sericeous; fruiting pedicel absent. *Fruits* subglobose, slightly stiped when young, not beaked, 8–11 by 7.5–10 mm, punctate, drying light brownish, sparsely puberulous; pericarp 0.2–0.5 mm thick, not fleshy; septae and column sparsely hairy. *Seeds* 1, half-terete to terete, ellipsoid, 7.5–9 by 6–7 by c. 4.5 mm.

Distribution — South India (Kerala) and Sri Lanka.

Habitat & Ecology — Primary evergreen forest and sholas, rather dry; on steep slopes or along roads. Altitude: c. 1100 m. Flowering: March; fruiting: February, March, June.

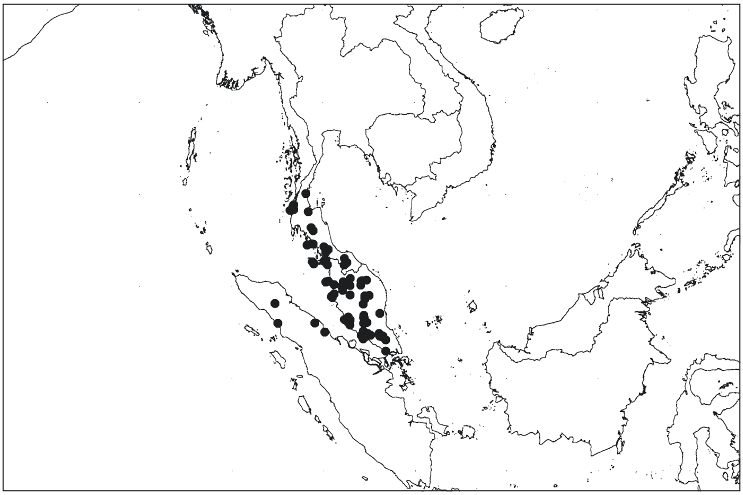
16. **Aporosa aurea** Hook.f. — Fig. 3.6c, 4.6d; Map 10.14

Aporosa aurea Hook.f., Fl. Brit. India 5 (1887) 351 (p.p., excl. *A. microstachya* sensu Kurz = *A. wallichii* Hook.f.); Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 279; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 87; Ridl., Fl. Malay Penins. 3 (1924) 240; Airy Shaw, Kew Bull. 26 (1972) 214; Whitmore, Tree Fl. Malaya 2 (1973) 59; ?Airy Shaw, Kew Bull. 36 (1981) 254. — Type: *Griffith KD 4959* (K; A, P), Malacca.

Excoecaria? integrifolia Roxb., Fl. Ind. 3 (1832) 757, nom. rej. (Int. Code Bot. Nomencl., 2000: 399). — Type: *Roxburgh s.n.* (BR).

Shrub or (small) tree, up to 24 m high, up to 25 cm diameter. *Bark* whitish, yellowish, (greenish) grey, (light) brown, or reddish, smooth to slightly fissured and (finely) flaking, thin, soft; inner bark yellow, or pink, or red, or (dark or pale) brown. *Wood* creamy white, or yellow, or pale orange to (light) brown Young branches whitish to greyish, glabrous. *Stipules* (narrowly) triangular, 4–5 by 2–3 mm, glabrous, caducous. *Petiole* terete, smooth, 7–38 by 1–1.5 mm, glabrous, lower pulvinus 1–3 by 1–2 mm, upper pulvinus 1.5–7 by 1.2–2.5 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 6–25 by 2–9.5 cm; base rounded to acute, basal glands distinct, large, black; margin subentire, marginal glands seldom few in margin; apex acuminate to cuspidate; blade thick, smooth, shiny, rather brittle, drying yellow to light greenish above and beneath, completely glabrous; dots indistinct; disc-like glands few, scattered within marginal arches. *Nervation*: midrib (slightly) prominent above, prominent beneath; nerves 8–12 pairs, slightly prominent to flat above, sunken in older leaves, prominent beneath, marginal arches often fading, 2–5 mm from the margin; tertiary veins and venation fading, densely reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–6 clustered together, 10–19 by 1.5–2 mm, probably tomentose; peduncle absent; bracts broadly triangular, 0.6–1 mm long, inconspicuous, subglabrous outside, glabrous inside, margin ciliate; glomerules indistinct, consisting of 8–10 densely set flowers, continuously spaced along the rachis; pedicel absent. *Staminate flowers* 0.7–1 mm long; sepals 4, narrowly obovate to spathulate, 1–1.5 mm long, free, connate to rachis, base fleshy, glabrous; stamens 2, not exserted, 0.5–0.8 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 2–4 by 1.2–1.5 mm, tomentose, flowers up to 5, densely set along the rachis; bracts broadly triangular, 0.6–1 mm long, subglabrous outside, glabrous inside, margin ciliate; bracteoles triangular, 0.3–0.5 mm long, sparsely hairy outside, glabrous inside; pedicel minute, densely sericeous. *Pistillate flowers* 1.8–2.5 mm long; sepals 4 or 5, ovate to elliptic, patent, 0.7–1.2 mm long, fleshy at base, sparsely hairy outside, glabrous inside; ovary ovoid, 1.5–2 mm long, 2-locular, smooth, glabrous; stigmas sessile, elongated, perpendicular to slightly ascending from the sides of the ovary, apically bifid to near base, straight to slightly recurved, 0.4–0.5 mm long, ribbed and laxly papillate above, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 4–6 by 1.2–1.8 mm, puberulous; fruiting pedicel 0.5–2 mm long, puberulous. *Fruits* globose, not stiped, not beaked, 8–11 by 8–11 mm, almost smooth, young fruits ridged at sutures, drying brownish to black, glabrous; pericarp 0.5–0.8 mm thick, not fleshy; septae, mostly at (inner) margins, and column sericeous. *Seeds* 1 or 2, half-terete, subglobose, 6–8 by 7–8 by 3–4.5 mm.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia, North Sumatra.



Map 10.14. Distribution of *Aporosa aurea* Hook.f.

Habitat & Ecology — Primary, secondary, disturbed, or logged evergreen or (mixed) deciduous forest; in shaded and partly open areas; on steep or shallow hill sides, or hill tops, low undulating or flat country; along cascades, rivers, trails, or along seashore. Soil: granite, sandy, basalt derived sand-clay, or sandstone with limestone boulders; periodically flooded. Altitude: sea level to 500 m. Flowering: December to July; fruiting: January to October.

Uses — Wood used for furniture.

Vernacular names — Peninsular Malaysia: Sebasah (Malay).

Notes — 1. Airy Shaw (1975) includes Borneo in the distribution of *A. aurea*. I have found no evidence for this: Merrill's *A. frutescens* (1929) is distinctly *A. frutescens*, not *A. aurea*; other collections also turned out to be either *A. frutescens* or *A. nitida*. It is easy to distinguish between *A. nitida* and *A. aurea* in vegetative characters: the former has a much thicker petiole that lacks the distinct large black basal glands of the latter.

2. I have seen only three collections from Sumatra, all from Atjeh, so I am not sure if Airy Shaw's citation (1981) is truly *A. aurea*.

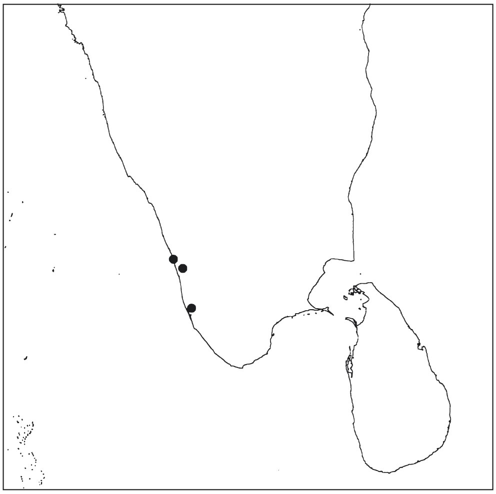
3. Kurz's *A. microstachya* (1877), referred to *A. aurea* by Hooker (1887), is *A. wallichii* (as suggested by Airy Shaw, 1969).

4. See note under *A. lucida*.

17. Aporosa bourdillonii Stapf — Fig. 3.9a, b; Map 10.15

Aporosa bourdillonii Stapf, Hook. Icon. Pl. 23 (1894) t. 2204; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 104; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 42; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 158; Airy Shaw, Kew Bull. 25 (1971) 481, in obs. — Type: *Bourdillon 9* (holo K), S. India, Malabar, Travancore.

Small tree. Young branches tomentose. *Stipules* not seen, caducous. *Petiole* terete, smooth, 10–16 by 0.8–1.2 mm, tomentose, glabrescent, lower pulvinus 1.5–3 by 1–1.5 mm, upper pulvinus 3–6 by 1.2–1.8 mm, both rather distinct. *Leaves* narrowly elliptic to narrowly obovate, 11–16 by 3.5–5.5 cm; base rounded, basal glands absent; margin lowly glandular-crenate, marginal glands regular, small, blackish; apex cuspidate to caudate; blade thin, smooth, dull, not brittle, drying greyish brown to dark-brown above and beneath, ?only midrib sparsely tomentose above, midrib and nerves tomentose beneath, glabrescent; dots irregularly laxly set, blackish, fading; disc-like glands few, scattered within marginal arches, small. *Nervation*: midrib flat above, prominent beneath; nerves 8–10 pairs, flat above, prominent beneath, marginal arches rather distinct, 1.5–3 mm from the margin; tertiary veins and venation indistinct, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–5 clustered together, 12–27 by 2.5–3.5 mm, (sparsely) tomentose; peduncle 3–5 by c. 1 mm; bracts elliptic, conspicuous, 2–3 mm long, sparsely puberulous outside, glabrous inside; glomerules (sub)globose, 2–3 by 2–3 mm, consisting of more than 10 laxly set flowers, spaced continuously at apical 3/4th of rachis; pedicel absent. *Staminate flowers* 0.8–1.5 mm long; sepals 3–5, elliptic, 0.5–1 mm long, connate at base, sparsely tomentose; stamens 2, slightly exserted, 0.8–1.2 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode a minute hair tuft. *Pistillate inflorescences* not seen, induced from infructescences to be single, tomentose; flowers seemingly 1 apically, probably 3–5 laxly set mostly apically; bracts



Map 10.15. Distribution of *Aporosa bourdillonii* Stapf.

elliptic, 2–3 mm long, sparsely tomentose outside, glabrous inside; bracteoles narrowly elliptic, 2–2.5 mm long, sparsely tomentose outside, glabrous inside; pedicel short, tomentose. *Pistillate flowers* not seen; sepals in fruit 3 or 4, elliptic, patent, 1.5–2 mm long, thin, sparsely tomentose; ovary probably ovoid, 3-locular, tuberculate, tomentose; stigmas in fruit raised, elongated, perpendicular to the sides of the ovary, apically to c. halfway bifid, straight, 5–6 mm long, laxly papillate to laciniate above, glabrous, smooth beneath, (sparsely) tomentose, style remnant present. *Infructescences* 12–15 by c. 1 mm, tomentose; fruiting pedicel 1–2 mm long, tomentose. *Fruits* ovoid, not stiped, beaked, c. 19 by 18 mm, tuberculate, drying light brown, sparsely tomentose; pericarp 0.3–0.8 mm thick, not fleshy; septae at inner margins and column sparsely hirsute. S*eeds* 3, only immature ones seen.

Distribution — South India (Kerala).

Habitat & Ecology — Moist evergreen forest. Altitude: low. Flowering: December.

18. Aporosa cardiosperma (Gaertn.) Merr. — Fig. 3.11c; Map 10.16

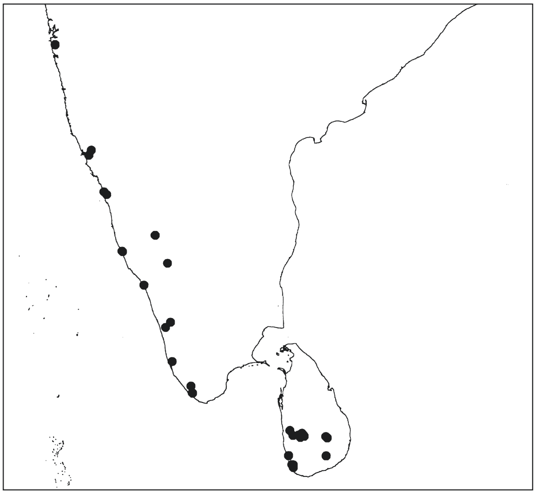
Aporosa cardiosperma (Gaertn.) Merr., J. Arnold Arbor. 35 (1954) 139; Schot, Blumea 40 (1995) 451. — *Croton cardiospermum* Gaertn., Fruct. 2 (1791) 120, pl. 107, f. 11; Hallier, Rec. Trav. Bot. Neerl. 15 (1918) 35, in obs. — Type: *Koenig ?629* (holo L, fruits only), Sri Lanka.

Scepa lindleyana Wight, Ic. Pl. Ind. (1840) t. 361. — *Aporosa lindleyana* (Wight) Baill., Étude Gén. Euphorb. (1858) 645; Thwaites, Enum. Pl. Zeyl. (1861) 288; Müll.Arg. in DC., Prod. 15, 2 (1866) 473; Bedd., Fl. Sylv. S. India (3 = For. Man.) (1873) 199, t. 286; Hook.f., Fl. Brit. India 5 (1887) 349; Trimen, Handb. Fl. Ceylon 4 (1898) 40; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 96; Worth., Ceylon Trees (1959) 377; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 42; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 164. — Type: *Wight KD 2653* (holo K; iso L, P), S. India, Kerala.

Aporosa affinis Baill., Étude Gén. Euphorb. (1858) 645, nomen. — Specimen: *Thwaites CP 2153* (BM, BO, BR, K, P), Sri Lanka.

Aporosa sphaerocarpa Müll.Arg., Flora 47 (1864) 519; in DC., Prod. 15, 2 (1866) 473; Bedd., Fl. Sylv. S. India (3 = For. Man.) (1873) 199, in obs. — Type: *Hohenacker 860* (holo P; iso L), S. India, near Mangalor.

Tree or shrub, up to 20 m high, up to 35 cm diameter. *Bark* 0.5–1 mm thick, (pale) brown, smooth, fine fibrous, furrowed, or vertically deeply to shallowly fissured; inner bark 4–5 mm thick, (light) brown, reddish to pink brown, or dark red. *Sapwood* light brown to cream. Young branches (sub)glabrous. *Stipules* narrowly triangular, 8–12 by 2–3 mm, glabrous, caducous. *Petiole* half-terete, smooth, 7–15 by 1–1.5 mm, glabrous, lower pulvinus 1–1.5 by c. 1.5 mm, upper pulvinus 3–4 by c. 1.5 mm, both distinct. *Leaves* narrowly ovate to narrowly obovate, 6–15 by 2.5–6.5 cm; base obtuse to cuneate, basal glands present, hairy, fading in older leaves; margin lowly undulate to irregularly lowly (glandular-)crenate, marginal glands few, small, greyish, often indistinct; apex acuminate; blade thick, smooth, sometimes slightly bullate, hardly shiny, brittle, drying brownish to greyish above and beneath, glabrous above, midrib subglabrous beneath; dots densely set, fine, blackish, fading; disc-like glands few, scattered within marginal arches. *Nervation*: midrib prominent on both sides; nerves 7–9 pairs, slightly prominent to flat above, prominent beneath, marginal arches fading, 2–4 mm from the margin; tertiary veins and venation indistinct, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 13–35 by 1–1.5 mm, puberulous; peduncle absent; bracts broadly triangular, inconspicuous, 0.7–0.9 mm long, sparsely hairy outside, glabrous inside; glomerules indistinct, consisting of 5–7 rather laxly set flowers, spaced continuously along rachis; pedicel absent. *Staminate flowers* 1.2–1.5 mm long; sepals 4 (or 5), elliptic, 0.5–0.7 mm long, almost free, sparsely hairy outside, glabrous inside; stamens 2 (or 3), exserted, 1–1.5 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 2–6 by1–1.2 mm, red puberulous, the flowers up to 7, densely arranged at the apical end of the rachis; bracts broadly triangular, 0.6–0.8 mm long, sparsely hairy outside, glabrous inside except for the base; bracteoles ovate, 0.6–0.8 mm long, sparsely hairy outside, glabrous inside except for the base; pedicel 1–2.5 mm long, puberulous. *Pistillate flowers* 2–3 mm long; sepals 3 or 4, subequal, ovate, patent, 0.5–0.7 mm long, thin, sparsely sericeous outside, glabrous inside except for the base; ovary ovoid,



Map 10.16. Distribution of *Aporosa cardiosperma* (Gaertn.) Merr.

1.5–2.5 mm long, 3-locular, smooth, sparsely sericeous at base, glabrescent towards apex; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, slightly recurved, apically bifid to c. halfway, 0.5–0.8 mm long, papillate to laciniate above, glabrous, smooth beneath, sparsely sericeous, style remnant present. *Infructescences* 5–13 by 0.8–1.2 mm, puberulous; fruiting pedicel 2–5 mm long, puberulous. *Fruits* globose to broadly ovoid, slightly stiped, beaked, 10–12 by 10–13 mm, punctulate to smooth, drying reddish to dark brown, very sparsely short hairy at base; pericarp 0.5–1 mm thick, not fleshy; septae and column (sparsely) villose. *Seeds* 2 or 3, half-terete, ellipsoid, 6–8 by 5–6 by 2–4 mm.

Distribution — South India (Kerala) and Sri Lanka.

Habitat & Ecology — In (slightly) disturbed wet evergreen, intermediate semi-evergreen, or dry deciduous forest; on steep slopes and near rivers; in dark shade. Altitude: low to 800 m. Flowering: January, March, June; fruiting: March to June.

Vernacular names — Kebelle, kebella (Sinhalese).

Notes — 1. Merrill (1954) based his new combination for *Croton cardiospermum* on a remark by Hallier (1918), who argued that *C. cardiospermum* was identical to *Aporosa latifolia*. Though Hallier was right in moving Gaertner's species to *Aporosa*, the globose pedicelled fruit is clearly that of *A. cardiosperma*, and not of *A. latifolia*.

2. There is some uncertainty about the type specimen of *A. lindleyana*: *Wight KD 2653*, which is not in a very good condition, and the label does not show any locality. The K and P duplicates are staminate, and without locality the identification is presumptive; if the staminate collections came from North India they may just as well be *A. octandra*. The L duplicate is a mixture of a staminate and a pistillate specimen. The pedicelled pistillate flowers undoubtedly indicate *A. cardiosperma*. Thus, the identification of the holotype from Kew is made on base of the pistillate L duplicate, and, on base of this identification, assumed to have been collected in South India.

19. **Aporosa ficifolia** Baill. — Fig. 3.7i; Map 10.17

Aporosa ficifolia Baill., Adansonia 11 (1873–1876) 177; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 94; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 558; Airy Shaw, Kew Bull. 26 (1972) 215. — Lectotype (proposed here): *Lefèvre 286* (holo P), Vietnam, Saigon.

(Small) tree, up to 10 m high, up to 8 cm diameter. Young branches densely tomentose, glabrescent. *Stipules* ovate, 7–11 by 4–8 mm, sparsely puberulous above, tomentose beneath, caducous. *Petiole* terete, smooth, 4–24 by 1.5–3 mm, densely tomentose, lower pulvinus c. 2 by 2 mm, upper pulvinus 5–6 by 2.5–3.5 mm, both indistinct under indumentum. *Leaves* (narrowly) elliptic, 8–25 by 4.5–12 cm; base rounded to acute, basal glands present, hairy; margin lowly undulate to lowly glandular-crenate or glandular-serrate, recurved, marginal glands regular, hairy; apex acute to acuminate; blade thick, smooth, older leaves bullate, shiny when glabrous, brittle, drying greenish or brownish above and beneath, sparsely tomentose above, nervation tomentose, glabrescent, tomentose beneath, nervation densely tomentose; dots laxly set, very fine, grey, often indistinct; disc-like glands occasionally few, small, scattered within marginal arches, often indistinct under indumentum. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 8–10 pairs, slightly prominent to flat above, sunken in older leaves, prominent beneath, marginal arches distinct, 3–8 mm from the margin;

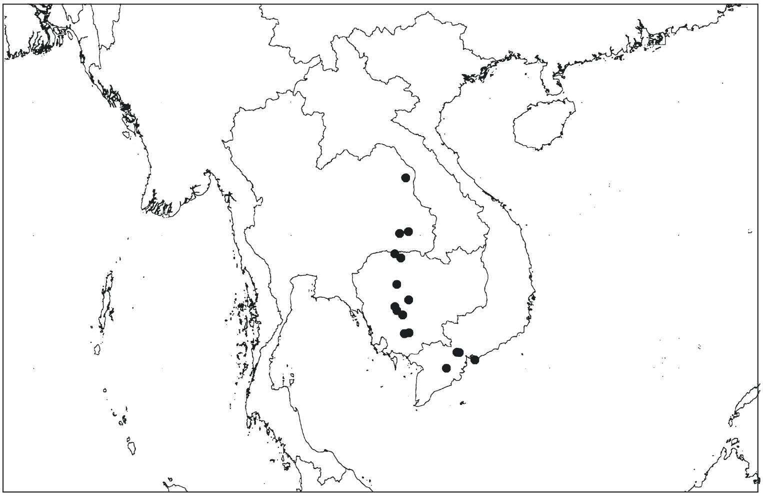
tertiary veins and venation distinct, laxly reticulate, flat above, sunken in older leaves, prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1 or 2 clustered together, 15–26 by 3.5–5 mm, densely sericeous; peduncle absent; bracts conspicuous, broadly triangular, 2–2.5 mm long, densely sericeous outside, glabrous inside; glomerules subglobose, 3–4 by 2.5–3.5 mm, consisting of 6 or 7 densely set flowers, continuously set along the rachis; pedicel 0.3–1 mm long. *Staminate flowers* 1.5–2 mm long; sepals 4 or 5, narrowly obovate, 1.2–1.8 mm long, almost free, sparsely hairy outside, ?glandular inside; stamens 2 or 3, slightly exserted, 1–1.5 mm long; anthers 0.3–0.4 mm long, connective glabrous; pistillode minute, lumpy. *Pistillate inflorescences* 1 or 2 clustered together, 4–7 by 2–3.5 mm, sericeous, flowers up to 5, densely set along the rachis; bracts broadly triangular, 1.5–1.8 mm long, densely tomentose outside, glabrous inside; bracteoles ovate, 0.8–1.2 mm long, tomentose outside, glabrous inside; pedicel absent. *Pistillate flowers* 3.5–4 mm long; sepals 4 or 5, ovate, patent, 1.5–2.2 mm long, thin, puberulous outside, sparsely puberulous inside; ovary ellipsoid, 2-locular, densely tomentose; stigmas sessile, elongated, ascending from the sides of the ovary, straight, apically bifid to c. halfway, 1–1.5 mm long, laxly laciniate above, glabrous, smooth beneath, tomentose, style remnant present. *Infructescences* 8–12 by 2.5–4 mm, densely sericeous; fruiting pedicel absent. *Fruits* globose, not stiped, not beaked, 11–13 by 10–12 mm, subsmooth, drying dark brown, densely sericeous; pericarp 0.8–1.2 mm thick, not fleshy; septae and column hairy. *Seeds* ?4, half-terete, ellipsoid, c. 7.5 by 4 by 3 mm.

Distribution — Cambodia, Thailand.

Habitat & Ecology — Evergreen, mixed, or dry deciduous forest; on planes. Altitude: c. 200 m. Flowering: January to March; fruiting: February to June.

Vernacular names — Cambodia: Krong.

Note — The descriptions of *A. ficifolia* and *A. pseudoficifolia* are often mixed, causing a lot of confusion: the *A. ficifolia* of Hooker (1887), Boerlage (1900), and Chakrabarty & Gangopadhyay (1993) are all *A. pseudoficifolia*. The species can be



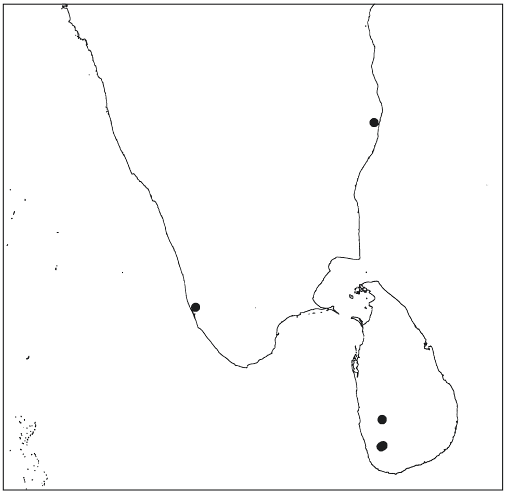
Map 10.17. Distribution of *Aporosa ficifolia* Baill.

distinguished as follows: *A. ficifolia* has thick, often somewhat bullate leaves, inflorescences with densely tomentose conspicuous bracts, and 2-locular ovaries. *Aporosa pseudoficifolia* has more papery, non-bullate leaves, inflorescences with less conspicuous bracts, and 3-locular ovaries. The species are also geographically separated.

20. **Aporosa fusiformis** Thwaites — Map 10.18

Aporosa fusiformis Thwaites, Enum. Pl. Zeyl. (1861) 288; Müll. Arg. in DC., Prod. 15, 2 (1866) 471; Bedd., Fl. Sylv. S. India (3 = For. Man.) (1873) 199; Hook.f., Fl. Brit. India 5 (1887) 351; Trimen, Handb. Fl. Ceylon 4 (1898) 41; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 90; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 42; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 160. — Type: *Thwaites CP 30* (holo BM; iso A, BO, K, P), Sri Lanka, Adam's Peak.
Aporosa thwaitesii Baill., Étude Gén. Euphorb. (1858) 645, nomen.

Tree, c. 15 m high. Young branches glabrous. *Stipules* narrowly triangular, 6–12 by 2–4.5 mm, glabrous, caducous. *Petiole* subterete, ribbed, 5–27(–37) by 0.8–2.2 mm, glabrous, lower pulvinus 1.5–2.5 by 1.5–2 mm, upper pulvinus 2–4 by 1.5–2.2 mm, both distinct. *Leaves* elliptic to obovate, 5–13(–20) by 2.5–8(–9.5) cm; base obtuse to cuneate, basal glands small, greyish; margin lowly glandular-crenate to glandular-dentate, reflexed, marginal glands many, distinct, black; apex acute to acuminate; blade thick, smooth, dull, not brittle, drying greyish green to greyish brown above, lighter beneath, completely glabrous; dots densely set, rather large, greyish to black, fading; disc-like glands many, distinct, black, scattered within marginal arches and along margin. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 5 or 6 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 2.5–6 mm from the margin; tertiary veins and venation fading, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 12–27 by 2–3 mm, tomentose; peduncle absent; bracts broadly triangular, conspicuous, 1.5–2 mm long, glabrous, margin ciliate; glomerules globose, 1.5–2 by c. 1.5 mm, consisting of less than 10 laxly set flowers, spaced continuously along the rachis; pedicel absent. *Stami-*



Map 10.18. Distribution of *Aporosa fusiformis* Thwaites.

nate flowers 1.5–2.2 mm long; sepals 5, narrowly obovate, 1.2–1.8 mm long, almost free, connate to rachis, sparsely tomentose outside, very sparsely puberulous inside; stamens 2, slightly exserted, 1.5–2.2 mm long; anthers 0.4–0.6 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 2–3 by 1.2–1.5 mm, densely tomentose; flowers up to 5, densely arranged along the rachis; bracts broadly triangular, 1–1.2 mm long, glabrous, margin ciliate; bracteoles not seen; pedicel c. 1 mm long, tomentose. *Pistillate flowers* 3–5 mm long; sepals (3 or) 4, ovate, perpendicular, 1–1.5 mm long, thin, sparsely tomentose outside, glabrous inside; ovary ovoid, 2–3.5 mm long, 2-locular, smooth, very sparsely puberulous at base, glabrescent; stigmas slightly raised, elongated, apically bifid to near base, perpendicular to the sides of the ovary, very slightly recurved to straight, 1.2–2 mm long, ribbed and papillate above, glabrous, smooth beneath, sparsely hairy, style remnant present. *Infructescences* 4–6 by c. 2 mm, tomentose; fruiting pedicel c. 1 mm long, tomentose. *Fruits* narrowly ellipsoid to fusiform, stiped, beaked, 14–17 by 7–9 mm, punctulate, drying black, glabrous; pericarp 0.5–0.8 mm thick, not fleshy; septae and column sparsely sericeous. *Seeds* 1 or 2, (half-)terete, ovoid, immature c. 8 by 4.5 by 2.5 mm.

Distribution — South India and Sri Lanka.

Habitat & Ecology — Evergreen forest. Altitude: 1200–1800 m. Flowering: March, April, September; fruiting: March.

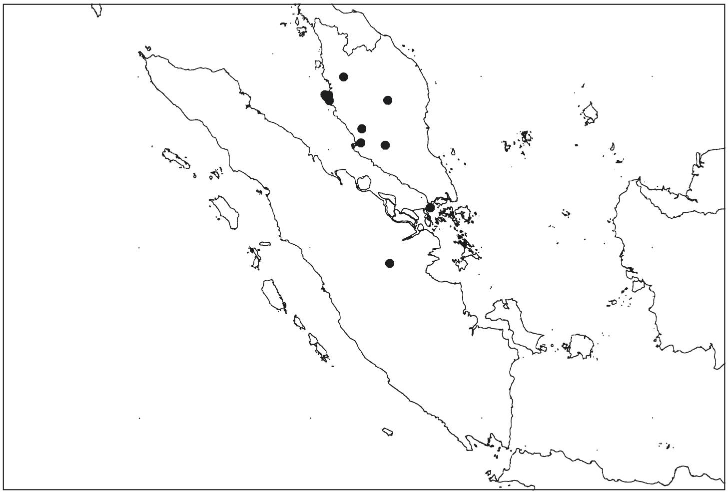
Note — Very close to *A. latifolia*, differing only in its fusiform, 2-locular fruit. The leaves are often smaller, though I found one specimen with the uppermost leaves up to 13 cm long, and the lower placed leaves up to 20 cm long; thus this is a very unreliable character.

21. **Aporosa globifera** Hook.f. — Fig. 4.3b; Map 10.19

Aporosa globifera Hook.f., Fl. Brit. India 5 (1887) 347; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 94; Ridl., Fl. Malay Penins. 3 (1924) 237; Whitmore, Tree Fl. Malaya 2 (1973) 59. — Lectotype (proposed here): *King's Collector 7607* (holo K; iso BO, P), Peninsular Malaysia, Perak.

Aporusa lophodonta Airy Shaw, Kew Bull. 33 (1978) 25. — Type: *M. Shah MS 1530* (holo K; iso L), Peninsular Malaysia, Pahang.

Small tree, up to 12 m high, up to 10 cm diameter. *Bark* brown(-greyish) to black, c. 2 mm thick, approximately smooth; inner bark orange-brown or red-brown. *Sapwood* pale brown to yellow. Young branches tomentose. *Stipules* narrowly ovate, slightly oblique, 3.5–5 by 1.5–2 mm, sparsely hirsute, caducous. *Petiole* terete, smooth, 6–16 by 1–1.5 mm, hirsute, glabrescent, lower pulvinus 1.5–2 by 1–1.5 mm, upper pulvinus 3–4 by 1–1.5 mm, both indistinct under indumentum. *Leaves* (narrowly) elliptic, 7–19.5 by 2–7.5 cm; base obtuse to acute, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands many, hairy; apex acuminate; blade thinnish, smooth (young leaves very lowly white granular above and beneath) , dull, not brittle, drying light greenish above and beneath, only midrib hirsute above, glabrescent, sparsely hirsute beneath, midrib and nerves hirsute, glabrescent; dots irregularly patchy densely set, very fine, greyish, often indistinct; disc-like glands few to regular, brownish, hairy, within marginal arches, often indistinct. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 8–11 pairs, flat to sunken above, prominent beneath, marginal arches distinct, 1–2 mm from the margin; tertiary veins



Map 10.19. Distribution of *Aporosa globifera* Hook.f.

and venation distinct, densely reticulate, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–6 clustered together, 7–16 by 1.5–2 mm, tomentose; peduncle absent; bracts broadly triangular, 0.5–0.8 mm long, inconspicuous, only sparsely sericeous at base; glomerules globose, indistinct, consisting of 3–5 laxly set flowers, set rather continuously along the rachis; pedicel absent. *Staminate flowers* 0.5–0.8 mm long; sepals 4, narrowly obovate, 0.5–0.9 mm long, connate at base, puberulous outside, glabrous inside; stamens 2, slightly exserted, 0.4–0.7 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 3–4 by c. 1.2 mm, densely tomentose, flowers up to 3, densely set along the rachis; bracts broadly triangular, 0.3–0.5 mm long, tomentose outside, sparsely tomentose inside; bracteoles ovate, 0.2–0.3 mm long, tomentose outside, sparsely tomentose inside; pedicel absent. *Pistillate flowers* not seen; sepals in fruit 5, ovate, patent, 0.5–0.8 mm long, thin, tomentose outside, sparsely tomentose inside; ovary probably ellipsoid, 3-locular, smooth, sericeous; stigmas slightly raised, elongated, ascending from the sides of the ovary, straight, apically bifid to c. halfway, 0.8–1 mm long, papillate to laciniate above, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* c. 4 by 1.5 mm, densely sericeous; fruiting pedicel absent. *Fruits* globose to broadly ovoid, not stiped, not beaked, 11–14 by 13–16 mm, punctulate, drying (dark) reddish brown, sparsely hairy; pericarp 1–2 mm thick, not fleshy; septae and column very sparsely hairy at base and (central) margin, glabrescent. *Seeds* (2 or) 3, half-terete, ellipsoid, 8–9 by 6–7 by 3–5 mm.

Distribution — Malesia: Peninsular Malaysia, Singapore, Sumatra.

Habitat & Ecology — Primary or disturbed forest, swampy areas, shady areas. Altitude: 5–360 m. Flowering: March; fruiting: January, April, May, November.

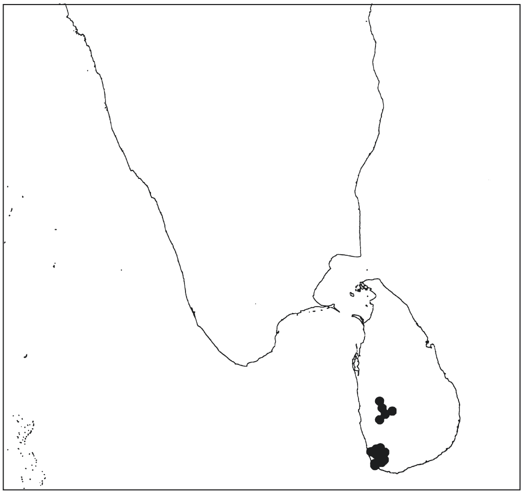
Vernacular names — Peninsular Malaysia: Kayu senawai bukit (Temuan).

Note — The recorded resemblance between *A. lophodonta* and *A. whitmorei* (Airy Shaw, 1978) is caused by a superficial likeness in leaf texture, which is true for many other species of *Aporosa*.

22. Aporosa lanceolata (Tul.) Thwaites — Fig. 3.7g, 3.11d; Map 10.20

Aporosa lanceolata (Tul.) Thwaites, Enum. Pl. Zeyl. (1861) 288; Müll.Arg. in DC., Prod. 15 (1866) 475, p.p.; Bedd., Sylv. Madr.; Hook.f., Fl. Brit. India 5 (1887) 351; Trimen, Handb. Fl. Ceylon. 4 (1898) 40; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 87; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 43; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 163. — *Lepidostachys lanceolata* Tul., Ann. Sci. Nat. 3me ser. 15 (1851) 253. — Type: *Macrae 614* (P), Sri Lanka.

Shrub or small tree, up to 5 m high, up to 10 cm diameter. *Bark* below smooth. Young branches sparsely puberulous. *Stipules* narrowly triangular, 3–6 by 1.5–2 mm, very sparsely hairy at base beneath, caducous. *Petiole* half-terete, ridged, 6–10 by 0.5–0.8 mm, glabrous, lower pulvinus 1–1.5 by 0.8–1 mm, upper pulvinus 1.5–2 by 0.8–1 mm, both variably distinct. *Leaves* narrowly elliptic to narrowly obovate, 5.5–13.5 by 2–4.5 cm; base obtuse to cuneate, basal glands small, black, distinct; margin lowly undulate to lowly glandular-crenate, marginal glands regular, brownish to black, distinct; apex cuspidate to caudate; blade thinnish, smooth, often shiny, not brittle, drying yellowish green above and beneath, completely glabrous; dots rather densely set, fine, greyish black, fading; disc-like glands minute, brownish, occasionally present within marginal arches. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 9–12 pairs, slightly prominent above, (slightly) prominent beneath, marginal arches distinct, 1–3 mm from the margin; tertiary veins and venation distinct, fading, densely reticulate, slightly scalariform, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 8–11 by 1.5–2 mm, probably puberulous; peduncle absent; bracts broadly triangular, 0.8–1 mm long, base lobed, inconspicuous, glabrous, margin sparsely ciliate; glomerules indistinct, consisting of less than 10 (?3–5) laxly set flowers, continuously set along the rachis; pedicel absent. *Staminate flowers* 0.8–1.2 mm long, connate to



Map 10.20. Distribution of *Aporosa lanceolata* (Tul.) Thwaites.

rachis; sepals 4, narrowly obovate, 0.9–1.1 mm long, almost free, glabrous; stamens 2, not exserted, 0.7–0.9 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 1.5–4 by 1–1.2 mm, puberulous, flowers up to 5, densely arranged along the rachis; bracts broadly triangular, 0.5–0.7 mm long, glabrous, margin ciliate; bracteoles ovate, 0.3–0.5 mm long, glabrous, margin ciliate; pedicel absent. *Pistillate flowers* 2–3 mm long; sepals (3 or) 4, ovate, ascending, 0.8–1.3 mm long, base fleshy, glabrous, margin ciliate; ovary ovoid, 1.5–2.5 mm long, 2-locular, smooth, glabrous; stigmas sessile, elongated, perpendicular to ascending from the sides of the ovary, straight, apically bifid to near base, 0.5–1 mm long, ribbed above, margins papillate, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 2–5 by 1–1.5 mm, puberulous; fruiting pedicel absent. *Fruits* (sub)globose, not stiped, not beaked, 6–8 by 7–8 mm, punctulate, drying blackish, glabrous; pericarp 0.3–0.5 mm thick, not fleshy; septae and column sericeous. *Seeds* 1, (half-)terete, globose, 4–6 by 5–6 by 2–2.5 mm.

Distribution — Sri Lanka.

Habitat & Ecology — Primary, secondary, and disturbed wet, evergreen, tropical forest; on gentle to steep slopes. Altitude: low to 1600 m. Flowering: August, October to December; fruiting: February to April, September, December.

Vernacular names — Kalamadua (Sinhalese).

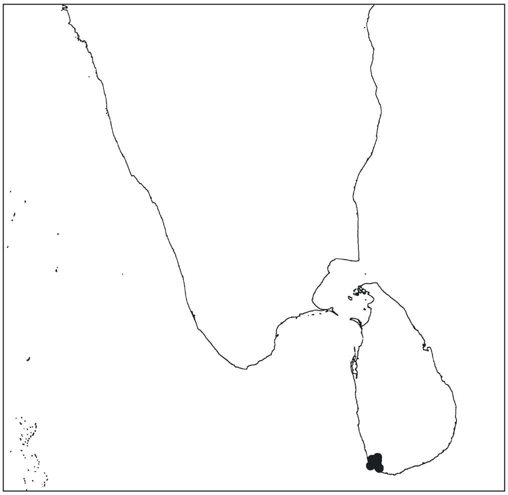
Note — Kurz's (1877) *A. lanceolata* is *A. planchoniana*; Hance's (1879) *A. lanceolata* is *A. yunnanensis*.

23. **Aporosa latifolia** Moon ex Thwaites — Map 10.21

Aporosa latifolia Moon ex Thwaites, Enum. Pl. Zeyl. (1861) 288; Müll.Arg. in DC., Prod. 15, 2 (1866) 470; Bedd., Fl. Sylv. S. India (3 = For. Man.) (1873) 199; Hook.f., Fl. Brit. India 5 (1887) 347; Trimen, Handb. Fl. Ceylon 4 (1898) 39; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 96; Worth., Ceylon Trees (1959) 376; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 43; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 163; Schot, Blumea 40 (1995) 451. — *Agyneia latifolia* Moon, Cat. Pl. Ceyl. (1824) 65, nomen. — Type: *Thwaites CP 3433* (holo BM; iso P), Sri Lanka.

Aporosa cardiosperma auct. non (Gaertn.) Merr.: Merr., J. Arnold Arbor. 35 (1954) 139.

Tree, up to 20 m high, up to 40 cm diameter. *Bark* dark to light brown or grey, 1–5 mm thick, hard, smooth, cracked, or fissured, peeling off in large narrow strips of 1–2 cm wide; inner bark 3–5 mm thick, red brown to pinkish straw. Young branches glabrous. *Stipules* narrowly triangular, c. 8 by 3 mm, glabrous, caducous. *Petiole* terete, ribbed, 9–27 by 2.2–3 mm, glabrous, lower pulvinus 2–3 by 3–4.5 mm, upper pulvinus 5–7 by 3–4 mm, both more or less distinct. *Leaves* elliptic to obovate, 6.5–17 by 4.5–10 cm; base slightly emarginate to obtuse, basal glands small, black, fading; margin subentire to irregularly glandular-crenate to glandular-serrate, recurved, marginal glands regular, black; apex truncate to acuminate; blade thick, smooth, dull, brittle, drying greenish or reddish brown above, (golden) brownish beneath, completely glabrous; dots rather densely set, fine, distinct, grey to blackish; disc-like glands regular, often distinct, scattered at base within marginal arches and along the margin. *Nervation*: midrib prominent on both sides; nerves 6–8 pairs, slightly prominent to flat above, prominent beneath, marginal arches often distinct, 3–6 mm from the margin; tertiary veins and venation indistinct, laxly reticulate, flat above, slightly prominent beneath.



Map 10.21. Distribution of *Aporosa latifolia* Moon ex Thwaites.

Inflorescences axillary or just below the leaves. *Staminate inflorescences* and *staminate flowers* not seen. *Pistillate inflorescences* single, c. 2 by 1.2 mm, red puberulous; flowers up to 3, densely set along the rachis; bracts broadly triangular, 0.5–0.7 mm long, very sparsely hairy outside, glabrous inside; bracteoles not seen; pedicel absent. *Pistillate flowers* 2.5–3.5 mm long; sepals 5, ovate, patent, 1–1.5 mm long, fleshy, densely red puberulous; ovary ovoid, 2–3 mm long, 3-locular, smooth, glabrous; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, (slightly) recurved, apically lowly bifid, 2–2.5 mm long, lowly papillate above, glabrous, ribbed beneath, glabrous, style remnant present. *Infructescences* 2–8 by 1.5–3 mm, red puberulous to sericeous; fruiting pedicel absent. *Fruits* ovoid, not stiped, not beaked, 20–24 by 17–21 mm, almost smooth, drying reddish brown, glabrous; pericarp 5–7 mm thick, fleshy; septae and column (sparsely) sericeous. *Seeds* 3, half-terete, ellipsoid, 9–10 by 6–8 by 3–4 mm.

Distribution — Sri Lanka.

Habitat & Ecology — Secondary, wet, evergreen forest, forest edges. Altitude: low to 400 m. Fruiting: February, May, July.

Notes — 1. See note 1. under *A. cardiosperma*.

2. *Aporosa latifolia* differs from *A. fusiformis* in the large, ovoid, fleshy, 3-locular fruit (see note under latter).

24. **Aporosa lucida** (Miq.) Airy Shaw — Fig. 3.6i, 10.4; Map 10.22

Aporusa lucida (Miq.) Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 38; Kew Bull. 32 (1978) 362; 36 (1981) 255; 37 (1982) 8. — *Tetractinostigma lucidum* Miq., Fl. Ind. Bat., Suppl. (1860) 471. — Type: *Teysmann HB 4558* (holo U; ?iso BO), Sumatra.

Aporosa miqueliana Müll.Arg. in DC., Prod. 15, 2 (1866) 474; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 103; Ridl., Fl. Malay Penins. 3 (1924) 241; Meijer, Bot. News Bull. Sandakan 7 (1967) 34; Whitmore, Tree Fl. Malaya 2 (1973) 61. — Type: *Teysmann s.n.* (BO, n.v.), Sumatra.

Aporosa microsphaera Hook.f., Fl. Brit. India 5 (1887) 350; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 279; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 243; Koord., Exkurs.-Fl. Java 2 (1912)

481; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 86; Backer & Bakh.f., Fl. Java 1 (1964) 456. — Lectotype (proposed here): *King's Collector 7933* (holo P; iso ?BO), Peninsular Malaysia, Perak.

Aporosa borneensis Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 87. — Type: *Korthals s.n.* (iso L), Borneo.

Leiocarpus arboreus auct. non Blume: Miq., Fl. Ind. Bat., Suppl. (1860) 443.

(Small) tree or shrub, up to 18 m high, up to 25 cm diameter. *Bark* (pale or dark) brown, (pale) fawn, (pale) grey, fawn-grey, reddish yellow, yellowish, whitish, or greenish, grey mottled, dippled, smooth, scaly, or lenticellate to rugose, thin, papery flaky; inner bark (pale) brown, (pale) yellow, yellowish brown, red-brown, or greenish brown, thin, fibrous. *Sapwood* (pale) brown, (pale) yellow, yellowish, light orange, or white, hard. Young branches white, very sparsely puberulous. *Stipules* not seen, caducous. *Petiole* half-terete, ridged, 6–25 by 0.8–1.5 mm, glabrous, lower pulvinus 1.5–3 by 1–2 mm, upper pulvinus 2–5 by 1–2.2 mm, both distinct. *Leaves* narrowly ovate to narrowly obovate, 5.5–24 by 2–9 cm; base obtuse to attenuate, basal glands present, fading; margin lowly undulate to lowly glandular-crenate, marginal glands regular, distinct, brownish; apex acuminate to cuspidate; thin, smooth, sometimes brittle, rather shiny, drying yellow-brown to dark green above and beneath; completely glabrous; dots rather laxly set, fine, greyish to black, fading; disc-like glands small, few, scattered within marginal arches, fading. *Nervation*: midrib prominent on both sides; nerves 8–11 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.5–6 mm from the margin; tertiary veins and venation distinct, fading in older leaves, densely reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–8 clustered together, 9–30 by 1–2 mm, puberulous; peduncle absent; bracts broadly triangular, 0.3–0.5 mm long, inconspicuous, glabrous, margin ciliate; glomerules ellipsoid, 1.5–2.2 by c. 1 mm, consisting of more than 10 densely set flowers, approximately continuously set along the rachis or spaced at 0.5–2 mm at base of rachis, continuous apically; pedicel minute. *Staminate flowers* 0.4–0.8 mm long; sepals 3 or 4, obovate, 0.5–0.7 mm long, almost free, very sparsely puberulous outside, glabrous inside, margin sparsely ciliate; stamens 2, not exserted, 0.3–0.5 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode lumpy, minute, ciliate. *Pistillate inflorescences* 1–3 clustered together, 3–5 by 1–1.2 mm, puberulous, flowers up to 9, densely arranged along the rachis; bracts broadly triangular, 0.3–0.6 mm long, glabrous, margin sparsely ciliate; bracteoles ovate, 0.2–0.4 mm long, sparsely puberulous outside, glabrous inside; pedicel minute, tomentose. *Pistillate flowers* 2–3.5 mm long; sepals 4 or 5, ovate, patent, 0.6–1 mm long, base fleshy, sparsely hairy at base outside, glabrous inside; ovary ovoid, 1.5–2.5 mm long, 2- (or 3-)locular, punctulate, glabrous or sparsely hairy; stigmas slightly raised, elongated, slightly ascending from the sides of the ovary, straight, apically almost completely divided, 0.3–0.9 mm long, ribbed above, margins papillate to laciniate, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 3–9 by 0.8–1.5 mm, puberulous; fruiting pedicel 0–0.5 mm long, puberulous. *Fruits* globose to broadly ovoid or ellipsoid, not stiped, sometimes slightly beaked, 7–11 by 6–12 mm, punctulate to finely granular, drying (dark) brown to black, glabrous; pericarp 0.3–0.8 mm thick, not fleshy, taste recorded sweet; septae and column sparsely hirsute at (central) margins (sometimes glabrescent!). *Seeds* 1, 2 (or 3), half-terete, ellipsoid, 5–8 by 6–7 by 3–4 mm; aril juicy, sweetish.

Distribution — Malesia: Peninsular Malaysia, Singapore, Sumatra, Java, Borneo, Sulawesi, and the Moluccas (Sula Islands).

Habitat & Ecology — Primary, secondary, (somewhat) disturbed, and logged over forest, evergreen, mixed dipterocarp, heath or transition between heath and kerangas, submontane forest, fresh water swamp, or periodically inundated; on steep to gentle ridges, hill sides, and hill tops; on flat or (low) undulating land, open, partly shaded, or dry country. Soil: shale, sandy, granitic sand, clayey sand, or clay, yellow or red. Altitude: 0–1200 m. Flowering: March to October; fruiting throughout the year.

Vernacular names — Sumatra: Bangka: Tulang kera. Borneo: Kunau kunau (Brunei); ombah sampori, ubah bunkan (Bukit Baka); kapit kapit, Penatan (Dusun); kayu masam (Iban); pupoo (Tengara).

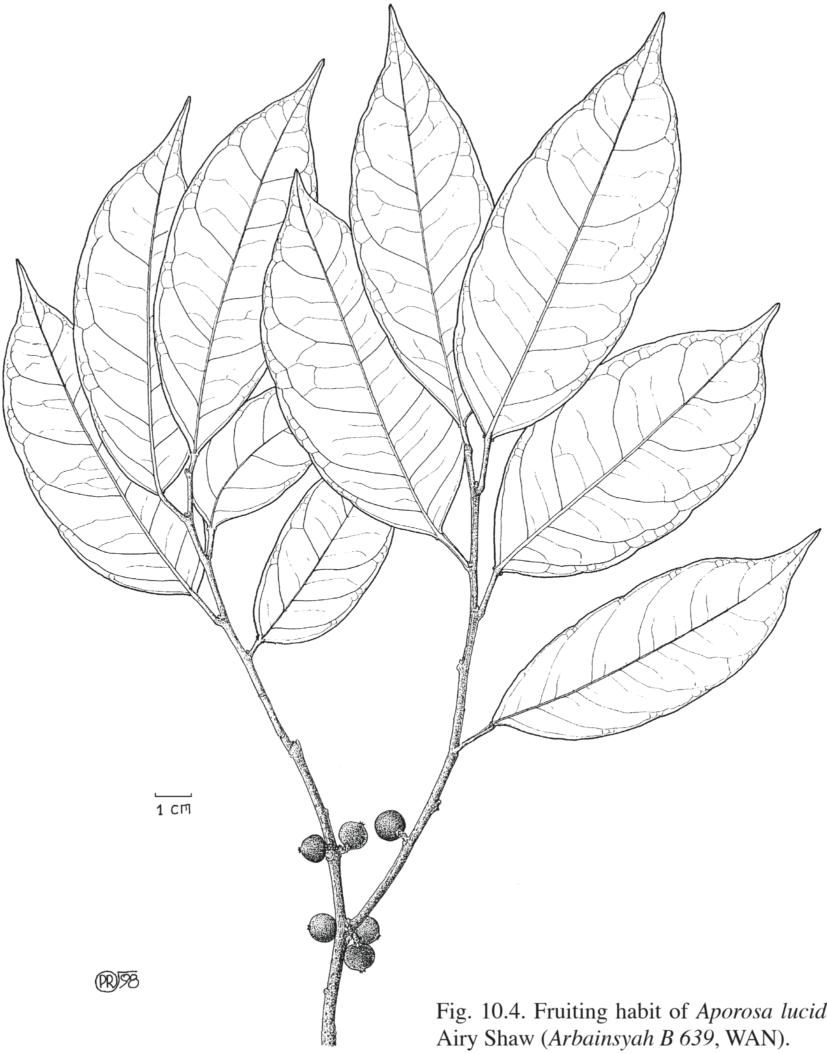
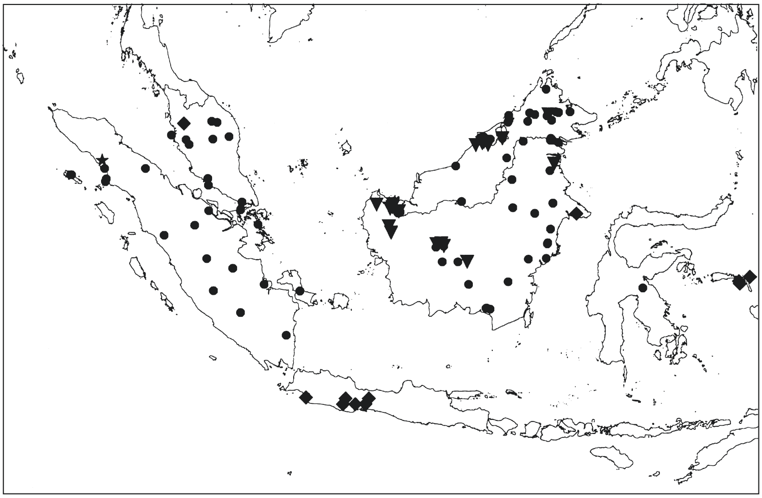


Fig. 10.4. Fruiting habit of *Aporosa lucida* (Miq.) Airy Shaw (*Arbainsyah B 639*, WAN).



Map 10.22. Distribution of *Aporosa lucida* (Miq.) Airy Shaw: var. *lucida* (●), var. *ellipsoidea* Airy Shaw (★), var. *pubescens* Schot (◆), and var. *trilocularis* Schot (▼).

Notes — 1. Separating *A. lucida* and *A. aurea* is rather difficult. *Aporosa aurea* has mostly larger leaves with longer petioles that dry often with a quite lurid shade of yellow, continuously spaced glomerules, and pistillate flower clusters of up to 5. *Aporosa lucida* has smaller, more darker drying leaves, glomerules slightly interrupted, and pistillate flower clusters of up to 9. These differences show, however, variation and overlap. The only trustworthy differentiating character I found is the absence/presence of the marginal glands.

2. *Aporosa lucida* is quite variable in shape and indumentum of the fruit. Airy Shaw (1978) described one fruit type as a variety, the ellipsoid fruits from North Sumatra. To be consistent, I described two new varieties: one with puberulous ovaries from Java and the Sula Islands, and a 3-locular form from Borneo. They are identical in vegetative and staminate characters, and because the difference in globose and ellipsoid fruits is often caused by the number of seeds developing, and as locularity and indumentum of the ovary is variable in other species (e.g., *A. nervosa* and *A. octandra*) I see no reason to distinguish them on a higher level.

Key to the varieties

1a. Ovary and fruit glabrous. — Northern West-Malesia 2
b. Ovary and fruit (sparsely) puberulous. — Southern West-Malesia . . . . **c.** var. **pubescens**
2a. Ovary and fruit (mostly) 2-locular 3
b. Ovary and fruit (often) 3-locular. — Borneo . . . . **d.** var. **trilocularis**
3a. Fruit ellipsoid. — North Sumatra . . . . **b.** var. **ellipsoidea**
b. Fruit globose. — Peninsular Malaysia, Singapore, Sumatra, or Borneo . . . . **a.** var. **lucida**

a. var. **lucida**

For nomenclature see under species.

Pistillate flowers: ovary 2-locular, glabrous. *Fruit* globose, 7–11 by 6–12 mm, punctulate, drying light brown to black, glabrous. *Seeds* mostly 2.

Distribution — Malesia: Peninsular Malaysia, Singapore, Sumatra, Borneo.

b. var. **ellipsoidea** Airy Shaw

Aporusa lucida (Miq.) Airy Shaw var. *ellipsoidea* Airy Shaw, Kew Bull. 32 (1978) 362; 36 (1981) 256. — Lectotype (proposed here): *De Wilde & De Wilde-Duyfjes 12817* (holo K; iso BO, L), Sumatra, Atjeh.

Pistillate flowers: ovary 2-locular, glabrous. *Fruits* ellipsoid, not stiped, not beaked, 10–11 by 7–8 mm, punctulate, drying light to dark brown, glabrous. *Seeds* mostly 1.

Distribution — Malesia: North Sumatra.

c. var. **pubescens** Schot

Aporosa lucida (Miq.) Airy Shaw var. *pubescens* Schot, Blumea 40 (1995) 457. — Type: *Wiriadinata 873* (holo L; iso BO), W Java.

Pistillate flowers: ovary 2-locular, sparsely sericeous. *Fruits* globose to broadly ovoid, 7–11 by 6–12 mm, punctulate, drying (dark) brownish, sparsely hairy. *Seeds* mostly 2.

Distribution — Malesia: Java, the Moluccas (Sula Islands). Once found in Sumatra (Bangka) and Kalimantan, Mentawir region.

Note — The only known Sulawesi collection is unfortunately staminate, so I cannot identify it positively as var. *pubescens*!.

d. var. **trilocularis** Schot

Aporosa lucida (Miq.) Airy Shaw var. *trilocularis* Schot, Blumea 40 (1995) 457. — Type: *Nooteboom 4047* (holo L), Ind. Borneo, Bukit Raya.

Pistillate flowers: ovary 3-locular, glabrous. *Fruits* globose, 10–11 by 10–11 mm, (lowly) granular, drying dark brown to black, glabrous. *Seeds* 3.

Distribution — Malesia: (mostly North) Borneo

Note — Often mistaken for *Drypetes*.

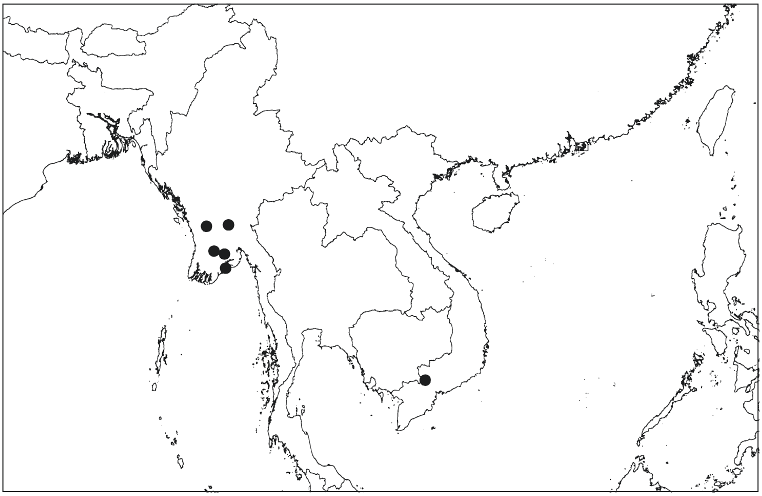
25. Aporosa macrophylla (Tul.) Müll.Arg. — Fig. 3.7h; Map 10.23

Aporosa macrophylla (Tul.) Müll.Arg. in DC., Prod. 15, 2 (1866) 470; Kurz, For. Fl. Brit. Burma 2 (1877) 361; Hook.f., Fl. Brit. India 5 (1887) 346; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 97; Merr., Enum. Philipp. Flow. Pl. 2 (1973) 411, in obs. — *Lepidostachys macrophylla* Tul., Ann. Sci. Nat. 3^{me} sér. 15 (1851) 253. — Type: *Wallich s.n.* (holo K-WALL; iso K), Burma, Prome.

Small tree, c. 3 m high. Young branches glabrous. *Stipules* triangular, c. 5 by 4 mm, glabrous, caducous. *Petiole* terete, finely lineate, 43–91 by 2–3.5 mm, glabrous, lower pulvinus 2.5–4 by 2.5–4 mm, indistinct, upper pulvinus 4–9 by 2.5–4.5 mm, distinct.

Leaves ovate, 12–31 by 11–17 cm; base cordate, basal glands absent; margin lowly undulate to subentire, sometimes glandular-crenate, marginal glands few, small, indistinct; apex acuminate; blade thickish, smooth, lowly bullate, slightly shiny, not brittle, drying green to (dark) greyish brown above, (light) brown beneath, completely glabrous; dots indistinct; disc-like glands occasionally few, small, black, scattered mostly at base within marginal arches. *Nervation*: midrib flat above, prominent beneath; nerves 7–11 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 3–7 mm from the margin; tertiary veins and venation rather distinct, laxly reticulate, slightly prominent to slightly sunken above, slightly prominent beneath. *Inflorescences* axillary or borne on the upper branches . *Staminate inflorescences* 2–6 clustered together, 22–55 by 2–3.5 mm, ?tomentose; peduncle absent; bracts broadly triangular, conspicuous, 1.2–1.5 mm long, claw 0.5–0.8 mm long, glabrous, margin ciliate; glomerules indistinct, globose, c. 1 by 1 mm, consisting of up to 10 laxly set flowers, set continuously along the rachis; pedicel 0.3–0.8 mm long. *Staminate flowers* 1.2–2 mm long; sepals 4 or 5, linearly obovate, 1.2–1.8 mm long, connate at base, glabrous, margin long ciliate; stamens 2, not exserted, 0.9–1.2 mm long; anthers 0.3–0.4 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 4–7 by 3–4 mm, densely tomentose; flowers up to 9, densely set along the rachis; bracts broadly triangular, 2–2.5 mm long, fused with bracteoles, these ovate, 1.5–2 mm long, sericeous at base outside, sparsely sericeous at base inside, margin ciliate; pedicel absent. *Pistillate flowers* 4–6 mm long; sepals 3, ovate, subequal, patent, 2.5–3.5 mm long, thin, densely tomentose outside except for apex, sparsely tomentose at base inside; ovary ovoid, 3.5–5 mm long, 2-locular, smooth, densely tomentose; stigmas sessile, elongated, perpendicular to slightly ascending from the sides of the ovary, straight, apically bifid to c. halfway, 0.4–1 mm long, ribbed above, margins lowly laciniate, glabrous, smooth beneath, (sparsely) tomentose, style remnant absent. *Infructescences*, *fruits*, and *seeds* not seen; septae and column in flower sericeous.

Distribution — Burma (Rangoon).



Map 10.23. Distribution of *Aporosa macrophylla* (Tul.) Müll.Arg.

Habitat & Ecology — In forest with teak (*Tectona grandis* L.f., Verbenaceae). Soil: granitic. Altitude: c. 150 m. Flowering: January, May, September.

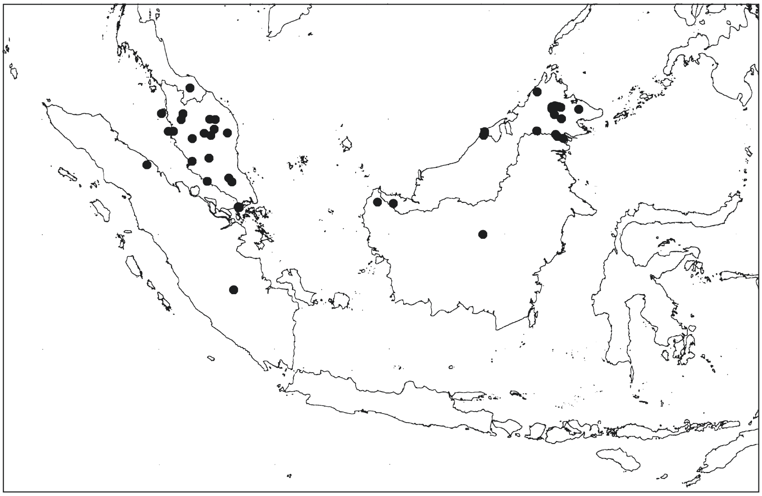
Vernacular names — Burma: Moantlong, Mchin (Shan).

Note — According to Hooker (1887) a deciduous tree.

26. Aporosa nigricans Hook.f. — Map 10.24

Aporosa nigricans Hook.f., Fl. Brit. India 5 (1887) 347; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; Merr., Philipp. J. Sci., Bot. 11 (1916) 65; Enum. Born. Pl. (1921) 330; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 97; Ridl., Fl. Malay Penins. 3 (1924) 239; Merr., Pl. Elmer. Born. (1929) 142; S. Moore, J. Bot. Brit. & For. 63 Suppl. (1925) 97; Meijer, Bot. News Bull. Sandakan 7 (1967) 33; Airy Shaw, Kew Bull. 26 (1972) 217; Whitmore, Tree Fl. Malaya 2 (1973) 61; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 39; Kew Bull. 36 (1981) 256; Chakrabarty & Basu, J. Econ. Tax. Bot. 6 (1985) 432. — Type: *King's Collector 3839* (holo K), Peninsular Malaysia, Perak.

Tree, up to 18 m high, up to 20 cm diameter. *Bark* brownish, greyish, whitish, greenish, light grey, or dull fawn, spotted, smooth, thin papery; inner bark pale yellow, pale brown, (yellow-)pinkish, orange, or white. *Wood* white, yellow, or brown yellow. Young branches sparsely puberulous. *Stipules* caducous. *Petiole* terete, smooth or adaxially lowly grooved, 9–32 by 1.2–1.8 mm, sparsely puberulous, glabrescent, lower pulvinus 1.5–2.5 by 1.5–2 mm, upper pulvinus 2–5 by 1.5–2.5 mm, both distinct. *Leaves* (narrowly) elliptic, 12.5–27.5 by 4.5–14.5 cm; base rounded to acute, basal glands small, brownish (hairy in young leaves), often indistinct; margin lowly undulate to glandular-crenate or glandular-serrate, marginal glands regular, distinct, blackish (hairy in young leaves); apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, sometimes thicker and shiny, drying brownish or greenish above, darker beneath, blackening, glabrous above, sparsely hirsute beneath, glabrescent; dots rather densely set, very fine, black to brown, fading; disc-like glands absent. *Nervation*: midrib (slightly) prominent above, prominent beneath; nerves 8–11 pairs, slightly prominent to flat above, (slightly) prominent beneath, marginal arches distinct, 1.5–5 mm from the margin; tertiary nerves and venation distinct, rather densely reticulate, slightly scalariform, slightly prominent to slightly sunken near the margin above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* clustered 1–6 together, 8–28 by 1.8–2.5 mm, probably tomentose; peduncle 0–2 by c. 1.5 mm; bracts broadly triangular, 0.6–1 mm long, inconspicuous, sparsely hirsute outside, glabrous inside; glomerules ellipsoid, consisting of 13–20 densely set flowers, 1.5–2.5 by c. 1 mm, spaced at c. 0.1 mm along the rachis; pedicel minute, 0.2–0.3 mm long. *Staminate flowers* 0.4–0.6 mm long; sepals (3 or) 4 (or 5), obovate, 0.5–0.8 mm long, connate at base, sparsely hirsute outside, glabrous inside; stamens 2, not to slightly exserted, 0.3–0.6 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode a minute hair tuft. *Pistillate inflorescences* 1–3 clustered together, 2–9 by 1.5–2 mm, tomentose; flowers up to 9, densely arranged along the rachis; bracts broadly triangular, 0.8–1.6 mm long, sparsely hirsute outside, (sub)glabrous inside; bracteoles ovate, 0.5–1.4 mm long, sparsely hirsute outside, subglabrous inside; pedicel small, 0.3–1 mm long, tomentose. *Pistillate flowers* 3–4.5 mm long; sepals (3 or) 4, ovate, patent, 1.2–2 mm long, base fleshy, tomentose outside, glabrous inside; occasionally 1 staminode present, obconical, c. 0.6 mm long; ovary ellipsoid, 2–3.5 mm, 2-locular,



Map 10.24. Distribution of *Aporosa nigricans* Hook.f.

punctulate, densely tomentose; stigmas sessile to slightly raised, elongated, ascending from the sides of the ovary, straight, apically (almost) completely divided, 0.5–1.5 mm long, papillate to laciniate above, glabrous, smooth beneath, tomentose, style remnant present. *Infructescences* 2–11 by 1.8–2.3 mm, sericeous; fruiting pedicel 1–1.5 mm long. *Fruits* ovoid, not stiped, not beaked, 10–12 by 9–12 mm, punctulate to smooth, drying blackish to brownish with yellowish whitish sutures, sparsely hairy; pericarp 0.5–1.5 mm thick, not fleshy; septae and column (sparsely) sericeous, mostly along margins. *Seeds* 2, half-terete, ovoid, 6–8.5 by 6–8 by 3–4 mm.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia, Singapore, Sumatra, Borneo. Also recorded from the Nicobars by Chakrabarty & Basu (1985), but I did not see these collections.

Habitat & Ecology — Primary, secondary, logged over, cleared, or open forest, wet kerangas, or margins of swamp forest; in flat to low undulating land; along road sides, hill sides, hill ridges, steep or gentle slopes. Soil: sandy or sandstone with clay, brown to black. Altitude: 5–600 m. Flowering: April to July, September; fruiting: May to October, December, February.

Vernacular names — Peninsular Malaysia: Tebasah (Malay). Borneo: Sabah: Tampui munyit (Lamag District).

Note — One specimen seen with an ant nest on its leaf.

27. **Aporosa octandra** (Buch.-Ham. ex D. Don) Vickery — Map 10.25

Aporosa octandra (Buch.-Ham. ex D. Don) Vickery, Enum. Fl. Pl. Nepal 3 (1982) 193; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 166. — *Myrica? octandra* Buch.-Ham. ex D. Don, Prod. Fl. Nepal (1825) 56. — Type: *Buchanan-Hamilton s.n.* (holo BM), Central Nepal, Ettaura.

Alnus dioica Roxb., Fl. Ind. 3 (1832) 580. — *Aporosa dioica* (Roxb.) Müll.Arg. in DC., Prod. 15 (1866) 472; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 103; Airy Shaw, Kew Bull. 23 (1969) 3, in obs.; Kew Bull. 26 (1972) 215; Whitmore, Tree Fl. Malaya 2 (1973) 60; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 35; Kew Bull. 36 (1981) 255; 37 (1982) 7; Enum. Philip.

Euph. (1983) 8; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 43; H.S. Qiu, Guihaia 11 (1991) 16. — Type: *Roxburgh s.n.* (K).

Lepidostachys roxburghii Wall. ex Lindl., Nat. Syst. Bot., ed. 2 (1836) 441 — *Aporosa roxburghii* (Wall. ex Lindl.) Baill., Étude Gén. Euphorb. (1858) 645; Kurz, For. Fl. Brit. Burma 2 (1877) 362; Hook.f., Fl. Brit. India 5 (1887) 347; Craib, Kew Bull. (1911) 461; Contr. Fl. Siam. (1912) 188. — Type: *Wallich 6816 (a)* (holo K-WALL; iso K, L), Silhet.

Scepa stipulacea Lindl., Nat. Syst. Bot., ed. 2 (1836) 441. — Type: *Griffith s.n.* (CAM), Burma.

Alnus integrifolia Roxb. [Fl. Ind. 3 (1832) 580, nomen] ex Steud., Nomencl. Bot., ed. 2, 2 (1841) 698. — Type: *Roxburgh s.n.* (K, drawing)

Aporosa lindleyana (Wight) Baill. var. *macrostachya* Müll.Arg., Flora 47 (1847) 519; in DC., Prod. 15, 2 (1866) 473. — Type: *Hooker f. s.n.* (P), Sikkim.

Aporosa oblonga Wall. ex Müll.Arg., Linnaea 32 (1863) 78; in DC., Prod. 15, 2 (1866) 472; Hook.f., Fl. Brit. India 5 (1887) 348; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 103; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 554. — *Lepidostachys? oblonga* Wall., Cat. (1832) 7299, nomen. — Type: *Wallich 7299* (K-WALL; iso K), Burma, Amherst.

Aporosa villosula Kurz, J. Asiat. Soc. Bengal 42, 2, 4 (1873) 239; For. Fl. Brit. Burma 2 (1877) 362; Hook.f., Fl. Brit. India 5 (1887) 347; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 100; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 560. — Lectotype (proposed here): *Helfer KD 4951* (holo K; iso A, P), s.l., Tenasserim & Andamans.

Aporosa clellandii Hook.f., Fl. Brit. India 5 (1887) 348; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 104. — Type: *McClelland s.n.* (K), Burma, Rangoon.

Aporosa spec. nov.: Craib, Cont. Fl. Siam (1912) 188. — *Aporosa wallichii* Hook.f. var. *ambigua* Airy Shaw, Kew Bull. 35 (1980) 384. — Type: *Kerr 958* (holo K; iso L), Thailand, Payap.

?*Aporosa obovata* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 100. — Type: *Meebold 14696* (B†), Burma, Mergui.

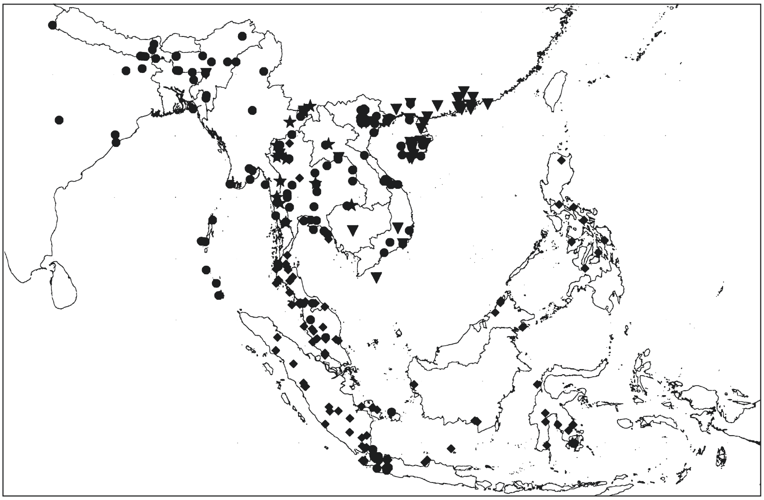
Aporosa microcalyx (Hassk.) Hassk. var. *intermedia* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 102. — Syntypes: *Balansa 3282, 4684* (P), Vietnam, Tonkin.

Shrub or tree, up to 15 m high, up to 30 cm diameter. *Bark* (light) brown to grey or tan, smooth or roughened, thickened, flaky, or vertically (narrowly) ridged and cracked, c. 0.5 cm thick; inner bark pink. *Wood* cream. Young branches sparsely tomentose. *Stipules* (narrowly) ovate, seldom slightly oblique, 6–9 by 3–5 mm, sparsely sericeous at base outside, ciliate, caducous. *Petiole* terete, lowly ribbed, 7–23 by 1–1.5 mm, sparsely puberulous, glabrescent, lower pulvinus 1–3 by 1–1.5 mm, upper pulvinus 3–7 by 1.2–2.5 mm, both distinct. *Leaves* narrowly ovate to (narrowly) elliptic, 5–23.5 by 2–8 cm; base rounded to cuneate, basal glands small, greyish, fading; margin lowly undulate to lowly glandular-crenate or glandular-serrate, sometimes slightly recurved, marginal glands regular, distinct, grey to black; apex acuminate to cuspidate; thinnish, smooth, not brittle, dull or slightly shiny, drying grey-brown or green-brown above, greenish or brownish beneath; dots irregularly densely set, fine, grey, fading; disc-like glands regular, small, grey to black, scattered within marginal arches, variably distinct; very sparsely puberulous, glabrescent, beneath midrib and nerves sparsely puberulous, glabrescent. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 8–11 pairs, slightly prominent above, prominent beneath, marginal arches mostly rather distinct, 1.5–5 mm from the margin; tertiary veins and venation often fading, laxly reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–5 clustered together, 16–46 by 1.5–2.5 mm, puberulous; peduncle absent; bracts broadly triangular, rather conspicuous, c. 0.5 mm long, sparsely puberulous at base outside, glabrous inside, margin ciliate; glomerules indistinct, consisting of 6–8 laxly set flowers, continuously spaced along the rachis; pedicel absent.

Staminate flowers 0.7–1 mm long; sepals 4, narrowly obovate, 0.7–1 mm long, almost free, connate to rachis, sparsely puberulous to glabrous outside, glabrous inside, margin (sparsely) ciliate; stamens 2, slightly exserted, 0.5–1.2 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode indistinct. *Pistillate inflorescences* 1–3 clustered together, 3–11 by 1.2–2 mm, (red) puberulous, flowers up to 11, densely arranged along the rachis; bracts broadly triangular, 0.6–0.9 mm long, sparsely puberulous to glabrous outside, glabrous inside, margin (sparsely) ciliate; bracteoles ovate, 0.4–0.6 mm long, sparsely puberulous to glabrous outside, glabrous inside; pedicel absent. *Pistillate flowers* 3–5 mm long; sepals 4, ovate, patent, 0.7–1 mm long, base fleshy, very sparsely puberulous outside, glabrous inside; staminodes occasionally 2, obconical, 0.2–0.3 mm long; ovary ellipsoid, stiped, 2–2.5 mm long, 2- (or 3-)locular, smooth, (sparsely) sericeous; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, recurved, apically bifid to near base, 0.8–2 mm long, laxly papillate to laciniate above, glabrous, smooth beneath, sparsely sericeous to glabrous, style remnant present. *Infructescences* 6–14 by c. 1.5 mm, (red) puberulous; fruiting pedicel 0–1 mm long. *Fruits* ovoid to ellipsoid (seldom globose, with pedicel 1–3 mm long), young ones slightly stiped, slightly beaked, 9–13 by 6–10 mm, punctate, drying (dark) brown to black, sparsely hairy; pericarp 0.2–0.5 mm thick, not fleshy; septae and column sparsely sericeous. *Seeds* 1 (or 2), terete, ellipsoid, 7–8 by 5–6 by 3–4 mm.

Distribution — From North India and Pakistan southwards to Burma, Thailand, Laos, Vietnam, South China, Cambodia, Nicobar Isl., Malesia.

Habitat & Ecology — Primary, secondary, subtropical, evergreen, or (mixed) deciduous forest, savannah, or belukar, moist to rather dry; in shaded understorey or (partly) open places; on hills, (steep) slopes, forest edges, road sides, plains, thickets, and along streams. Soil: sandy, sandstone, granitic sand, limestone, clay, rocky, or rocky loam;



Map 10.25. Distribution of *Aporosa octandra* (Buch.-Ham. ex D. Don) Vickery: var. *octandra* (●), var. *chinensis* (Champ. ex Benth.) Schot (▼), var. *malesiana* Schot (◆), and var. *yunnanensis* (Pax & K. Hoffm.) Schot (★).

granite or sandstone bedrock. Altitude: 40–1500 m. Flowering and fruiting throughout the year.

Uses — Wood used for house posts and fuel. Leaves used to dye cloth black. Bark chewed as a kind of betel by Karen Hill tribe (Thailand).

Vernacular names — Pakistan: Keechua. China: Tai ip kam (Hainan Isl.); kam shu. Thailand: Grom (Trang Prov.). Peninsular Malaysia: Lalimau (Malay). Sumatra: Kayu pe(a)langas; p(e)(a)langas (Bangka Isl.). Borneo: Sarei, (kayu) rasak (Martapura region). Philippines: Somarog (Bis.).

Note — An extremely variable species in leaf size and indumentum, especially in Thailand, were the different forms co-occur, together with almost every thinkable intermediate form. Though so many intermediates occur between the extremes, I will describe the extremes as three varieties (which is, I think, more manageable than lumping all into a confusing mess). Thus, I have, beside the typical form from North India, Burma, Laos, Cambodia, and Vietnam, described three different geographical varieties: one from South China, one from North China, and the one occurring in the Malesian region. The fact that sharp boundaries cannot be made between any of the varieties, means that the dividing characters have to be used strictly. All intermediates (and there are many!) are thus automatically left simply as *A. octandra*.

Key to the varieties

1a. Branchlets tomentose. Leaves (sparsely) puberulous above, (sparsely) tomentose beneath, nervation tomentose. Ovary tomentose. — Malesia or SE Asia to Yunnan 2

b. Branchlets (sparsely) puberulous. Leaves (sparsely) puberulous. Ovary sparsely puberulous, glabrescent towards the apex. — India, Burma, Thailand, Laos, Cambodia, Vietnam, South China 3

2a. Leaves thinnish, margin rather distinctly glandular-serrate. — Malesia . . . . **c.** var. **malesiana**

b. Leaves thickish, margin slightly glandular-serrate. — Yunnan and North Indo-China, Thailand . . . . **d.** var. **yunnanensis**

3a. Leaves with slightly glandular-serrate margin, drying greyish to brownish above and beneath. — North India, Burma, Thailand, Laos, Cambodia, Vietnam . . . . **a.** var. **octandra**

b. Leaves with distinct glandular-serrate margin, drying bright greenish to greenish brown above, brownish beneath. — South China . . . . **b.** var. **chinensis**

a. var. **octandra**

For nomenclature see under species.

Branchlets puberulous. *Leaves* (narrowly) elliptic to (narrowly) ovate; margin glandular-serrate; thin, mostly dull, drying dull greyish brown on both sides, sparsely puberulous, glabrescent. *Pistillate flowers*: ovary puberulous.

Distribution — North India, China (Yunnan), Burma, Thailand, Cambodia, Laos, Vietnam.

b. var. **chinensis** (Champ. ex Benth.) Schot

Aporosa octandra (Buch.-Ham. ex D. Don) Vickery var. *chinensis* (Champ. ex Benth.) Schot, Blumea 40 (1995) 452. — *Scepa chinensis* Champ. ex Benth., J. Bot. 6 (1854) 72. — *Aporosa sinensis* Baill., Étude Gén. Euphorb. (1858) 645, nom. illig. — *Aporosa microcalyx* (Hassk.) Hassk. var. *chinensis* (Champ. ex Benth.) Müll.Arg. in DC., Prod. 15 (1866) 472; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 102. — *Aporosa chinensis* (Champ. ex Benth.) Merr., Lingnan Sci. J. 13 (1934) 34. — Type: *Champion s.n.* (P?, n.v.), Hong-Kong.

Aporosa leptostachya Benth., Fl. Hongk. (1861) 317. — Type: *Champion s.n.* (K), Hong-Kong.

Aporosa frutescens auct. non Blume: Benth., Fl. Hongk. (1861) 317.

Branchlets sparsely puberulous. *Leaves* narrowly elliptic to narrowly obovate; margin glandular-serrate; thinnish, shiny, drying above bright greenish or greenish brown, beneath brownish, sparsely puberulous. *Pistillate flowers*: ovary sparsely sericeous, glabrescent towards apex.

Distribution — South China, North Vietnam.

Notes — 1. Distinct by its smallish green leaves with serrate margin.

2. One interesting specimen changes sexes, as probably also did Bentham's *Aporosa leptostachya*.

c. var. **malesiana** Schot — Fig. 3.5a, 3.6b

Aporosa octandra (Buch.-Ham. ex D. Don) Vickery var. *malesiana* Schot, Blumea 40 (1995) 452. — *Scepa aurita* Tul., Ann. Sci. Nat. 3^{me} sér. 15 (1851) 254. — *Aporosa aurita* (Tul.) Baill., Étude Gén. Euphorb. (1858) 645; Miq., Fl. Ind. Bat. 1, 2 (1859) 431; Müll.Arg. in DC., Prod. 15, 2 (1866) 474; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 100; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 409; Corner, Wayside Trees Malaya 1 (1940) 235; Backer & Bakh.f., Fl. Java 1 (1964) 456; Meijer, Bot. News Bull. Sandakan 7 (1967) 34. — Type: *Cuming 860* (holo P; iso A, BM, K, L), Philippines, Luzon.

Aporosa cumingiana Baill., Étude Gén. Euphorb. (1858) 645, nomen. — Specimen: *Cuming 1724* (holo P; iso K, L) Philippines, Leyte or Samar.

Tetractinostigma microcalyx Hassk., Hort. Bogor. Descr. (1858) 55; Miq., Fl. Ind. Bat. 1, 2 (1859) 362; Fl. Ind. Bat., Suppl. (1860) 185, 471. — *Aporosa microcalyx* (Hassk.) Hassk., Bull. Soc. Bot. France 6 (1859) 714; Müll.Arg. in DC., Prod. 15, 2 (1866) 471; Hook.f., Fl. Brit. India 5 (1887) 346; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 240; Koord., Exkurs.-Fl. Java 2 (1912) 481; Merr., Enum. Born. Pl. (1921) 330; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 101; Ridl., Fl. Malay Penins. 3 (1924) 238; S. Moore, J. Bot. Brit. For. 63 Suppl. (1925) 97; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 555. — Type: *Hasskarl s.n.*, cult. in Hortus Bogoriensis (Bogor Botanical Garden) sub nom. *Leiocarpus serratus* (L?), Java, Bantam.

Branchlets tomentose. *Leaves* narrowly ovate to narrowly elliptic; margin (lowly) glandular-serrate; thin, slightly shiny; drying above and beneath greyish to brownish, sparsely puberulous, midrib and nerves puberulous beneath. *Pistillate flowers*: ovary tomentose.

Distribution — Thailand, Malesia: Peninsular Malaysia, Sumatra, W Java, Borneo, the Philippines, Sulawesi.

Notes — 1. Distinct by its smallish, (lowly) serrate leaves, like var. *chinensis*, but thinner and puberulous.

2. The large variability of *A. octandra* stops about the Isthmus of Kra, the narrowest part of Peninsular Thailand; southwards the species is quite uniform in the form of *A. octandra* var. *malesiana*.

d. var. **yunnanensis** (Pax & K. Hoffm.) Schot

Aporosa octandra (Buch.-Ham. ex D. Don) Vickery var. *yunnanensis* (Pax & K. Hoffm.) Schot, Blumea 40 (1995) 452. — *Aporosa microcalyx* (Hassk.) Hassk. var. *yunnanensis* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 102. — *Aporosa dioica* (Roxb.) Müll. Arg. var. *yunnanensis* (Pax & K. Hoffm.) H.S. Qiu, Guihaia 11 (1991) 17. — Type: *Henry 1163* (holo K; iso L), China, Yunnan, Szemao.

Branchlets tomentose. *Leaves* narrowly ovate to narrowly elliptic; margin slightly glandular-serrate; thickish, rather shiny, drying above brownish to greyish, sometimes greyish green, beneath brownish to greyish; (sparsely) tomentose, nervation tomentose. *Pistillate flowers*: ovary tomentose.

Distribution — China (Yunnan), Burma, North Thailand, Laos.

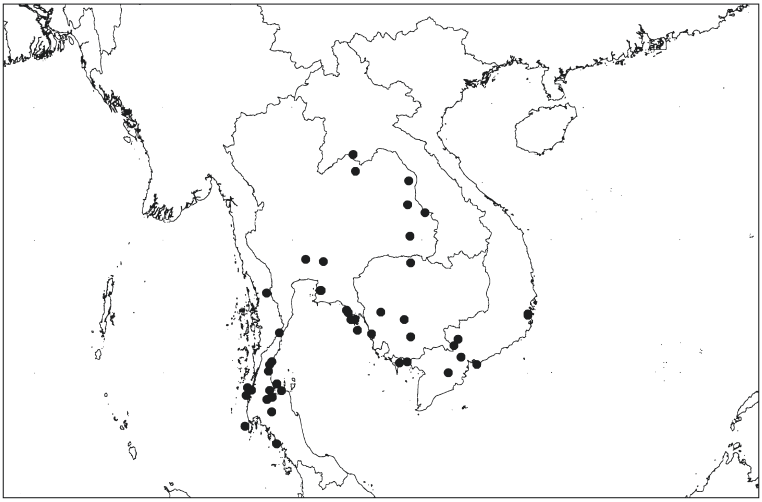
Notes — 1. Distinct by its thick tomentose leaves.

2. Because of the tomentose indumentum the distinction between this variety and *A. villosa* is very difficult to make. The only reliable distinctive character is the ovate leaf with its (lowly) cordate base of *A. villosa*. In addition, as far as I have seen, *A. octandra* var. *yunnanensis* has a more distinct glandular-serrate margin, which is less well developed in *A. villosa*. In case of doubt, a specimen is best identified as *A. octandra*.

28. Aporosa planchoniana Baill. ex Müll. Arg. — Fig. 3.8k, 3.11f; Map 10.26

Aporosa planchoniana Baill. [Étude Gén. Euphorb. (1858) 645, nomen] ex Müll. Arg. in DC., Prod. 15, 2 (1866) 475; Hook. f., Fl. Brit. India 5 (1887) 350; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 279; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 88; Gagnep., Fl. Indo-Chine 5 (1927) 560; Airy Shaw, Kew Bull. 26 (1972) 217. — Type: *Griffith 1095a* (holo P; iso K), Burma, Mergui.
Aporosa lanceolata auct. non Thwaites: Kurz, For. Fl. Brit. Burma 2 (1877) 363, p.p.

Shrub or (small) tree, up to 10 m high, c. 12 cm diameter. Young branches very sparsely puberulous. *Stipules* narrowly triangular, 2–3 by 1.2–1.5 mm, sparsely hairy at base outside, caducous. *Petiole* half-terete, ridged, 3–8 by 0.8–1 mm, glabrous, lower pulvinus 1–1.5 by 0.8–1 mm, upper pulvinus 2–3 by 1–1.2 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 5.5–13 by 1.5–3.5 cm; base acute to cuneate, basal glands small, blackish; margin very lowly undulate to lowly glandular-crenate, marginal glands few, brownish black, often distinct; apex cuspidate; blade thin, smooth, dullish, rather brittle, drying with a green-brown to green-yellow colour above and beneath, completely glabrous; dots densely set, fine, black, distinct; disc-like glands few, scattered within marginal arches, brownish, often indistinct. *Nervation*: midrib prominent above, prominent beneath; nerves 9–11 pairs, prominent above, (slightly) prominent beneath, marginal arches fading, 1.5–3 mm from the margin; tertiary veins and venation fading, rather laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 12–37 by 1.2–1.8 mm, densely puberulous; peduncle absent; bracts inconspicuous, broadly triangular, 0.3–0.7 mm long, (sub)glabrous outside, glabrous inside; glomerules ellipsoid, 1.5–2 by c. 0.5 mm, consisting of 4–6 densely set flowers, spaced at 0–0.7 mm along the rachis; pedicel absent. *Staminate flowers* 0.5–1 mm long; sepals (3–)4(–6), (broadly) obovate, 0.4–0.8 mm long, free, connate to the rachis, glabrous, margin sparsely ciliate; stamens 2, not to slightly exserted, 0.4–0.9 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode a minute lump, often



Map 10.26. Distribution of *Aporosa planchoniana* Baill. ex Müll. Arg.

indistinct. *Pistillate inflorescences* 1 or 2 clustered together, 3–6 by c. 1 mm, densely red puberulous, flowers up to 9, densely set along the rachis; bracts broadly triangular, 0.5–0.8 mm long, (sub)glabrous outside, glabrous inside, margin ciliate; bracteoles triangular, 0.3–0.5 mm long, sparsely hairy at base outside, glabrous inside, margin ciliate; pedicel absent. *Pistillate flowers* 3–5 mm long; sepals 3 or 4, ovate, ascending, 0.4–0.7 mm long, base fleshy, glabrous outside, long hairy at base inside; staminodes 2, occasionally present, minute; ovary ovoid, lowly stiped, 2–3.5 mm long, 2-locular, punctulate, glabrous; stigmas slightly raised, elongated, ascending from the top of the ovary, straight, apically bifid to c. halfway, 0.5–1 mm long, papillate to laciniate above, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 3–8 by 1–1.2 mm, densely puberulous; fruiting pedicel absent. *Fruits* ovoid to ellipsoid, lowly stiped, beaked, 7–11 by 5–7 mm, punct(ul)ate, drying (light) brown, glabrous; pericarp 0.3–0.5 mm thick, not fleshy; septae and column sparsely sericeous. *Seeds* 1 (or 2), terete, ovoid, 5–7.5 by 4–5 by 2–4 mm.

Distribution — Burma, Indo China, Thailand.

Habitat & Ecology — Secondary and disturbed evergreen or mixed deciduous forest; in dry, light, open, or shrubby areas; along rivers, roads, by swamps and in clearings. Soil: sandy. Altitude: 0–400 m. Flowering: January to June; fruiting: November to July.

Vernacular names — Thailand: (Ka) Krim, naam puong.

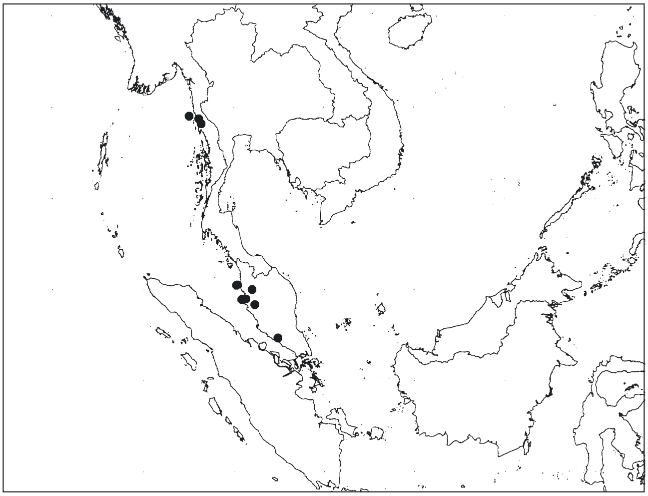
Note — Müller Argoviensis (1866) cites as type specimen *Hooker et T. Thomson 1095A*, however, this should be *Griffith 1095A*, as found in Hooker's herbarium.

29. Aporosa pseudoficifolia Pax & K. Hoffm. — Map 10.27

Aporosa pseudoficifolia Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 94; Ridl., Fl. Malay Penins. 3 (1924) 237; Airy Shaw, Kew Bull. 26 (1972) 217; Whitmore, Tree Fl. Malaya 2 (1973) 59. — Type: *King's Collector 3210* (BM; K) Peninsular Malaysia, Perak, Larut.

Aporosa ficifolia auct. non Baill.: Hook.f., Fl. Brit. India 5 (1887) 346 (pro *Wallich 8017*); ?Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 1 (*Meebold s.n.*).

Shrub, up to 3.5 m high. Young branches tomentose. *Stipules* not seen, caducous. *Petiole* terete, smooth, 14–21 by 1.8–2.3, hirsute, glabrescent, lower pulvinus 1.5–2 by 2–2.5 mm, upper pulvinus 3–5 by 3–3.5 mm, both indistinct under indumentum. *Leaves* elliptic, 15–21 by 5.5–9 cm; base rounded, basal glands absent; margin glandular-serrate, slightly recurved, marginal glands many, distinct, hairy; apex acuminate; blade thick, smooth, slightly bullate, dull, not brittle, drying brownish green above and beneath, only midrib tomentose above, glabrescent, sparsely tomentose beneath, nervation tomentose, glabrescent; dots irregularly set, fine, grey, fading; disc-like glands brownish, hairy, scattered within marginal arches. *Nervation*: midrib prominent to flat above, prominent beneath; nerves 9–12 pairs, prominent to flat above, sunken near the margin, prominent beneath, marginal arches distinct, 1–2.5 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly prominent to flat above, sometimes slightly sunken, prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* and *staminate flowers* not seen. *Pistillate inflorescences* single, 1–3 by 1.5–2 mm, sericeous, flowers up to 5, densely set along the rachis; bracts and bracteoles not seen; pedicel absent. *Pistillate flowers* 3.5–4.5 mm long; sepals 4 (or 5), ovate, patent, 1.5–2 mm long, thin, (sparsely) sericeous outside, glabrous inside; occasionally 1 or 2 staminodes present, obconical, 0.3–0.8 mm long; ovary ellipsoid, 3-locular, smooth, sericeous; stigmas sessile, elongated, perpendicular to slightly ascending from the sides of the ovary, straight, apically bifid to c. halfway, sometimes lowly tetrafid, 1–1.2 mm long, papillate to laciniate above, glabrous, smooth beneath, sparsely sericeous, style remnant absent. Young *infructescences* c. 3 by 2 mm, sericeous; fruiting pedicel absent. Young *fruits* globose, not stiped, not beaked, 8–10 by 8–10 mm, punctulate, drying dark brown, sparsely hairy; pericarp 0.5–1 mm thick,



Map 10.27. Distribution of *Aporosa pseudoficifolia* Pax & K. Hoffm.

not fleshy; septae and column very sparsely hairy at base and apex, glabrescent. *Seeds* 2, half-terete, ellipsoid, no mature ones seen.

Distribution — Burma (Tenasserim); Malesia: Peninsular Malaysia.

Habitat & Ecology — Hill forest. Altitude: 660–1000 m. Flowering: February; fruiting: August, October.

Notes — 1. *Aporosa pseudoficifolia* differs from *A. globifera* only in size and texture of the leaves and may represent specimens from greater altitude of *A. globifera*.

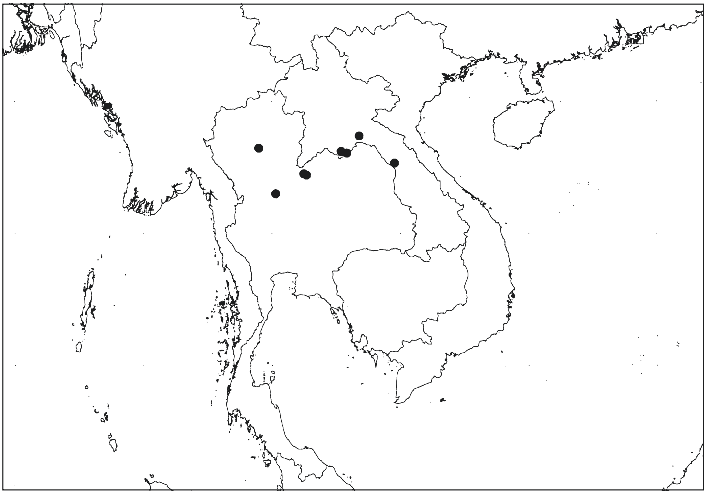
2. The specimens cited by Hooker (1887) as *A. ficifolia* (*Wallich 8017, Maingay KD 1498, King's Collector 3210*) are all 3-locular and belong to *A. pseudoficifolia*. Probably only his description of the globose, 2-locular fruit may pertain to *A. ficifolia* (see also note under latter).

3. Specimen *Wray 3686*, mentioned by Pax & K. Hoffmann (1922) is *A. globifera*.

30. Aporosa serrata Gagnep. — Fig. 3.6a, 3.7f, 3.8l; Map 10.28

Aporosa serrata Gagnep., Bull. Soc. Bot. France 70 (1923) 234; Fl. Gén. Indo-Chine 5 (1927) 557. — Lectotype (proposed here): *Harmand 383* (= *Herb. Pierre 2966*) (P), Cambodia, Kompong Xoai.

(Small) tree or shrub, evergreen, up to 8 m high, 5–6 cm diameter. Young branches tomentose. *Stipules* ovate, 5–7 by 3–4 mm, tomentose outside, caducous. *Petiole* terete, smooth, 9–17 by 1.5–2.5 mm, tomentose, lower pulvinus indistinct, upper pulvinus 2–5 by 2–3 mm. *Leaves* narrowly elliptic, 9–19 by 4–8.5 cm; base obtuse to cuneate, basal glands present, hairy; margin glandular-serrate to glandular-dentate, slightly recurved, marginal glands regular, distinct, hairy; apex acuminate; blade thick, smooth, dull, brittle, drying greenish or brownish above, brownish beneath, (sparsely) tomentose, nervation with denser indumentum, glabrescent; dots irregularly set, fine, grey, indistinct; disc-like glands few, hairy, scattered within marginal arches, indistinct. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 8 or 9 pairs, flat to sunken above, prominent beneath, marginal arches distinct, 1.5–4 mm from the margin; tertiary veins and venation distinct, densely reticulate, flat to sunken above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 9–18 by 2–3 mm, probably sericeous; peduncle absent; bracts conspicuous, broadly triangular, 0.8–1.2 mm long, sparsely hairy outside, glabrous inside, ?glandular; glomerules variably distinct, globose, 1.5–2 by 1.5–2 mm, consisting of 6–12 rather densely set flowers, spaced at 0–0.1 mm along the rachis; pedicel minute. *Staminate flowers* 0.8–1.2 mm long; sepals 4 or 5, narrowly obovate, 0.5–0.8 mm long, almost free, sparsely hairy outside, glabrous inside; stamens 2 (or 4), slightly exserted, 0.5–1 mm long; anthers 0.3–0.4 mm long, connective glabrous; pistillode minute, hairy. *Pistillate inflorescences* 1–3 clustered together, 2–4 by 1.5–2 mm, sericeous; flowers up to 7, densely arranged along the rachis; bracts triangular, 0.8–1 mm long, sparsely sericeous outside, glabrous inside; bracteoles ovate, 0.6–0.8 mm long, sparsely sericeous outside, glabrous inside; pedicel absent. *Pistillate flowers* 2–3.5 mm long; sepals 4 (or 5), ovate, connate at base, 0.8–1 mm long, sericeous outside, sericeous at base only inside; ovary ellipsoid to subglobose, 1.5–2.5 mm long, 2-locular, smooth, sericeous; stigmas apically almost completely divided, ses-



Map 10.28. Distribution of *Aporosa serrata* Gagnep.

sile, flattened to the top of the ovary, 0.5–1 mm long, lowly papillate above, glabrous, smooth beneath, sparsely sericeous, style remnant absent. *Infructescences* c. 5 by 1.5 mm, hirsute; fruiting pedicel absent. *Fruits* ellipsoid, not stiped, not beaked, 8–9 by 5.5–6 mm, subsmooth, drying dark brown, subhirsute; pericarp very thin, not fleshy; septae and column hairy. *Seeds* not seen.

Distribution — Thailand; Malesia: Peninsular Malaysia.

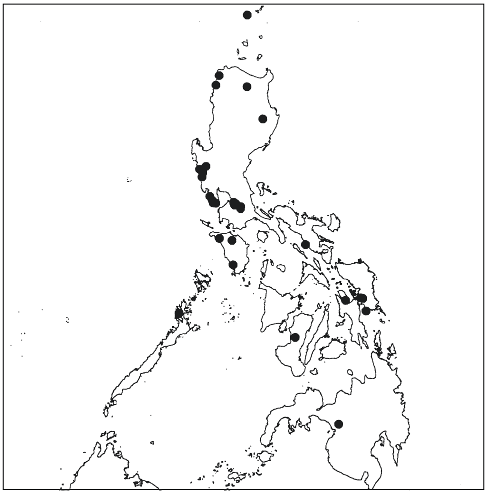
Habitat & Ecology — Evergreen or mixed deciduous forest; in scrubby and moist areas. Altitude: 200–300 m. Flowering: March; fruiting: April, May.

31. **Aporosa symplocifolia** Merr. — Map 10.29

Aporosa symplocifolia Merr., Philipp. J. Sci. 1, Suppl. (1906) 77 (*symplocosifolia*); Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 88; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 410; Airy Shaw, Alphab. Enum. Euphorb. Philip. Isl. (1983) 9. — Lectotype (proposed here): *Whitford 53* (holo K; iso P), Philippines, Luzon, Mt Mariveles.

Aporosa elliptifolia Merr., Philipp. J. Sci., Bot. 9 (1914) 472; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 88, in obs.; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 410; Airy Shaw, Alphab. Enum. Euphorb. Philip. Isl. (1983) 9. — Type: *Merrill 9609* (iso L), Philippines, Palawan.

Small tree, up to 8 m high, c. 8 cm diameter. *Bark* smooth; inner bark fawn. Young branches glabrous. *Stipules* narrowly triangular, 3–4 by 1–1.5 mm, glabrous, caducous. *Petiole* half-terete, ridged, 8–16 by 0.8–1 mm, glabrous, lower pulvinus 1–2 by 0.8–1.2 mm, variably distinct, upper pulvinus 2–4 by 0.8–1.2 mm, distinct. *Leaves* (narrowly) ovate to (narrowly) elliptic, 6–11 by 2.5–5.5 cm; base obtuse to cuneate, basal glands small, brown to grey, distinct; margin lowly undulate to lowly glandular-crenate, marginal glands few, small, brownish, often distinct; apex acuminate to cuspidate; blade thick, smooth, shiny, rather brittle, drying green-yellow above and beneath, subglabrous (sometimes in very young leaves midrib very sparsely hairy beneath); dots rather irregularly densely set, fine, greyish, fading; disc-like glands often present, few, distinct,



Map 10.29. Distribution of *Aporosa symplocifolia* Merr.

within marginal arches. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 7–10 pairs, slightly prominent to flat above, (slightly) prominent to flat beneath, marginal arches often distinct, 1.5–4 mm from the margin; tertiary veins and venation fading, densely reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 9–19 by 1.8–2 mm, probably puberulous; peduncle absent; bracts broadly triangular, 0.5–1 mm long, rather conspicuous, hairy at base only outside, glabrous inside, margin ciliate; glomerules indistinct, consisting of 5–8 laxly set flowers, spaced continuously along the rachis; pedicel absent. *Staminate flowers* 0.8–1.2 mm long; sepals 4, (narrowly) obovate, 0.9–1.3 mm long, free, connate to rachis, glabrous, margin ciliate; stamens 2 (or 3), not exserted, 0.8–1.2 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 3–10 by 1.2–1.5 mm, puberulous, flowers up to 7, densely set along the rachis; bracts broadly triangular, 0.5–0.9 mm long, glabrous outside, hairy at base only inside, margin sparsely ciliate; bracteoles triangular to ovate, 0.3–0.5 mm long, glabrous, margin ciliate; pedicel absent. *Pistillate flowers* 2–4.2 mm long; sepals 4, ovate, subequal, ascending, 0.5–1 mm long, base fleshy, glabrous outside, sericeous at base inside; ovary ovoid, 1.5–3 mm long, 2-locular, smooth, glabrous; stigmas slightly raised, elongated, ascending from the top of the ovary, straight or slightly recurved, apically bifid to near base, 0.5–1 mm long, papillate to laciniate above, glabrous, smooth beneath, style remnant present. *Infructescences* 4–11 by 0.8–1.5 mm, puberulous; fruiting pedicel absent. *Fruits* ovoid to ellipsoid, not stiped, not beaked, 8–11 by 5–9 mm, punctate, drying light brown to black, glabrous; pericarp 0.3–0.5 mm thick, not fleshy; septae and column sericeous, mostly at margins. *Seeds* 1 or 2, (half-)terete, ellipsoid, 7–8 by 5–7 by 2–4 mm.

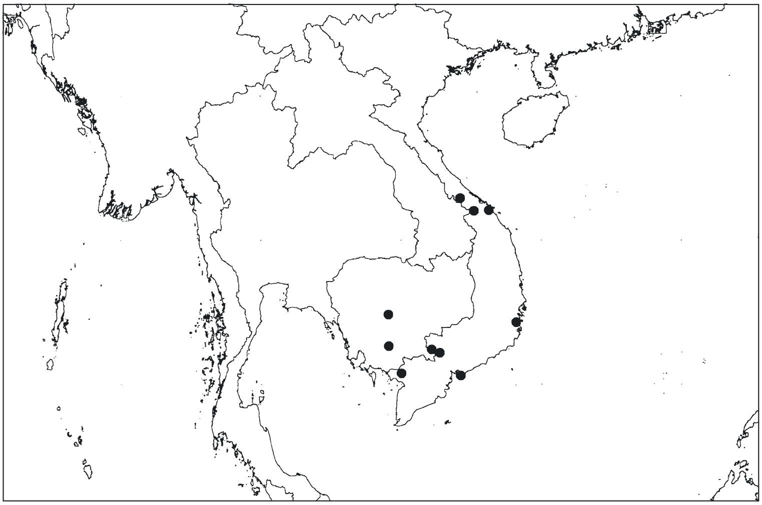
Distribution — Malesia: Philippines.

Habitat & Ecology — In forest; in high, often mossy places; on ridges. Soil: volcanic with sulphur, or riverine rocks and gravel beds, or ?ultrabasic. Altitude: low to 950 m. Flowering: December to March; fruiting: May, June.

32. **Aporosa tetrapleura** Hance — Fig. 4.1a, b; Map 10.30

Aporosa tetrapleura Hance, J. Bot. 14 (1876) 260; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 90; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 561. — Type: *Pierre s.n. (?64) (Herb. Hance 19207)* (holo BM; ?iso K, L, P), ?Cambodia (?Cochinchine).

(Small) tree, up to 12 m high, c. 10 cm diameter. Young branches glabrous. *Stipules* ovate to triangular, 2–3 by 1.5–2 mm, sparsely sericeous at base outside, caducous. *Petiole* half-terete, ridged, 9–21 by 1–1.5 mm, glabrous, lower pulvinus 1–2.5 by 1–1.5 mm, variably distinct, upper pulvinus 2–4 by 1.2–2 mm, distinct. *Leaves* (narrowly) elliptic, 6–12 by 2.5–6 cm; base acute to cuneate, basal glands distinct, black; margin (sub)entire, marginal glands few, small, black, often indistinct; apex acuminate; blade thick, smooth, shiny, rather brittle, drying yellow-green above and beneath, completely glabrous; dots irregularly densely set, fine, grey, fading; disc-like glands small, few, distinct, within marginal arches. *Nervation*: midrib prominent above and beneath; nerves 6–8 pairs, slightly prominent to flat, marginal arches often distinct, 2–4 mm from the margin; tertiary veins and venation fading, rather laxly reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 3–5 clustered together, 13–34 by 2–2.5 mm, densely puberulous; peduncle absent; bracts broadly triangular, 0.7–1 mm long, rather conspicuous, glabrous outside, only puberulous at base inside; glomerules subglobose, 1.5–2.5 by 1–2 mm, often indistinct, consisting of 6–8 laxly set flowers, set approximately continuously along the rachis; pedicel absent. *Staminate flowers* 0.8–1.2 mm long; sepals 4, (narrowly) obovate, 0.8–1.3 mm long, free, connate to the rachis, glabrous, margin ciliate; stamens 2, not exserted, 0.3–0.5 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* not seen, induced from infructescence to be single or 2 clustered together, densely puberulous, the flowers up to 5, densely set along the rachis; bracts in fruit broadly triangular, 0.6–0.8 mm long, glabrous, margin ciliate; bracteoles in fruit not seen; pedicel absent. *Pistillate flowers* not seen; sepals in fruit 4,



Map 10.30. Distribution of *Aporosa tetrapleura* Hance.

ovate, ascending, 0.6–0.9 mm long, base fleshy, glabrous outside, puberulous at base inside, margin ciliate; ovary probably ovoid, 2-locular, glabrous; stigmas in fruit slightly raised, elongated, ascending from the top of the ovary, straight, apically bifid to near base, 0.8–1.1 mm long, ribbed and papillate to laciniate above, glabrous, smooth beneath, style remnant present. *Infructescences* 4–7 by 1.5–2 mm, densely red puberulous; fruiting pedicel absent. *Fruits* ovoid to ellipsoid, not stiped, slightly beaked when immature, 11–14 by 8–12 mm, punctate, ridged at the sutures, drying dark brown to black, glabrous; pericarp 0.5–1.5 mm thick, slightly fleshy; septae and column sericeous. *Seeds* 2 (or 3), half-terete, ellipsoid, 7–8.5 by 6–7 by 2.5–4 mm.

Distribution — Cambodia, Vietnam.

Habitat & Ecology — In forests. Soil: granitic. Altitude: c. 300 m. Flowering: April, December; fruiting: March, June.

Note — The type sheet from Hance's herbarium (no. 19207) as preserved in BM, is also labelled *Pierre s.n.*, Cambodia. Pax & Hoffmann (1922) cited as type *Pierre s.n.*, Cochinchina, but they did not see the specimen. The isotype of *A. tetrapleura* in K, which looks identical to the BM one, labels *Pierre 64*, Cochinchina. However, duplicates of *Pierre 64* from L and P (Cochinchina), have a different leaf colour than the BM and K types. Furthermore, the Cambodian collection of Pierre as cited by Gagnepain (1927) (*Pierre 2587*) is staminate, and cannot be the type. Ostensibly, somehow the labels have become mixed up, and there is, for now, no knowing who and what is correct. The BM collection is holotype, but the duplicates and the collecting locality are questionable.

33. Aporosa villosa (Wall. ex Lindl.) Baill. — Map 10.31

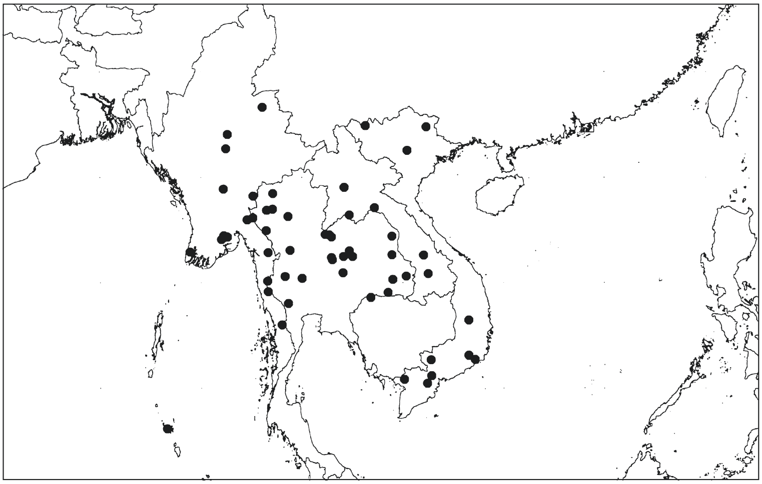
Aporosa villosa (Wall. ex Lindl.) Baill., Étude Gén. Euphorb. (1858) 645; Müll.Arg. in DC., Prod. 15, 2 (1866) 471; Kurz, For. Fl. Brit. Burma 2 (1877) 361; Hook.f., Fl. Brit. India 5 (1887) 345; Craib, Kew Bull. (1911) 461; Contr. Fl. Siam. (1912) 188; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 99; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 559; Airy Shaw, Kew Bull. 26 (1972) 218; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 45; H.S. Qiu, Guihaia 11 (1991) 18. — *Lepidostachys? villosa* Wall., Cat. (1832) 7298(a), nomen. — *Scepa villosa* Wall. ex Lindl., Nat. Syst. Bot., ed. 2 (1836) 441. — Type: *Wallich 7298 (a)* (K-WALL), Moalinga.

Aporosa sphaerosperma Gagnep., Bull. Soc. Bot. France 70 (1923) 234; Fl. Indo-Chine 5 (1927) 557. — Lectotype (proposed here): *Harmand 332* (P), Laos.

Aporosa sphaerosperma Gagnep. var. *cordata* Gagnep., Bull. Soc. Bot. France 70 (1923) 234; Fl. Indo-Chine 5 (1927) 558. — Lectotype (proposed here): *Harmand 438* (P), Laos.

Aporosa glabrifolia Kurz, J. Bot. 13 (1875) 330; Hook.f., Fl. Brit. India 5 (1887) 349; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 102. — Type: *Kurz s.n.* (n.v.), Nicobar Islands, Kamorta.

Shrub or (small) tree, up to 15 m high, up to 15 cm diameter. *Bark* black to light brown, vertically cracked or grooved. Young branches densely tomentose. *Stipules* ovate, 4–6 by 2–3 mm, densely tomentose outside, sparsely tomentose inside, caducous. *Petiole* terete, smooth, 9–25 by 1.2–2.5 mm, densely tomentose, glabrescent, lower pulvinus 2–3 by 2–2.5 mm, upper pulvinus 3–6 by 2–3 mm, both indistinct under indumentum. *Leaves* ovate to elliptic, 8.5–30 by 6–12.5 cm; base slightly cordate to rounded, basal glands small, hairy; margin (lowly) glandular-crenate to lowly glandular-serrate, marginal glands regular, distinct, blackish; apex acute to acuminate; blade thickish, corrugate-reticulate above when dry, smooth beneath, dull, sometimes brittle, drying greyish brown to greenish brown above, sometimes bluish green, reddish brown beneath, sparsely tomentose above, glabrescent, midrib (sparsely) tomentose, tomentose beneath, glabrescent, midrib and nerves tomentose; dots densely set, irregular, black, rather indistinct; disc-like glands few, blackish, scattered within marginal arches, often indistinct under indumentum. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 8–11 pairs, slightly prominent to flat above, prominent beneath, marginal arches mostly distinct, 3–7 mm from the margin; veins and venation fading, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–6 clustered together, 10–57 by 2–3 mm, tomentose; peduncle absent; bracts broadly triangular, rather conspicuous, 1.2–2.2 mm long, (sparsely) puberulous outside, glabrous inside, margin ciliate; glomerules indistinct, consisting of 5–7 laxly set flowers, set continuously along the rachis; pedicel absent (or minute). *Staminate flowers* 1.2–1.8 mm long; sepals 4, narrowly obovate, 1–1.5 mm long, almost free, connate to the rachis, sparsely tomentose outside, glabrous inside, margin ciliate; stamens 2 or 3, slightly exserted, 1.2–1.8 mm long; anthers 0.3–0.5 mm long, connective glabrous; pistillode absent or a minute hair tuft. *Pistillate inflorescences* 1–4 clustered together, 2–4 by 1.5–2.5 mm, tomentose, flowers up to 7, densely set along the rachis; bracts broadly triangular, 1–1.5 mm long, puberulous outside, hairy at base only inside, margin ciliate; bracteoles ovate, 0.5–0.8 mm long, puberulous outside, glabrous inside; pedicel absent. *Pistillate flowers* 2.5–4.5 mm long; sepals 4, ovate, subequal, patent, 1–1.5 mm long, base fleshy, sparsely puberulous outside, glabrous inside; ovary ellipsoid, 2–3.5 mm long, 2-locular, smooth, densely tomentose; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, about straight, apically bifid to near base, 0.8–1.5 mm long, papillate above, glabrous, smooth beneath, sparsely tomentose, style remnant present. *Infructescences* 3–9 by 1.5–2.5 mm, (sparsely) tomentose; fruiting pedicel 0–0.5 mm long, tomentose. *Fruits* ovoid to ellipsoid, not stiped, not beaked, 10–11 by 7–9 mm, punctate, drying reddish to light brown, sparsely tomentose; pericarp 0.2–0.5 mm thick, not fleshy; septae and column sparsely sericeous. *Seeds* 1, terete, ellipsoid, 7–9 by 5–6.5 by 4–5 mm.



Map 10.31. Distribution of *Aporosa villosa* (Wall. ex Lindl.) Baill.

Distribution — Burma, Thailand, Laos, Cambodia, Vietnam.

Habitat & Ecology — Locally common in evergreen, (mixed) deciduous, secondary, disturbed, or seasonal forest; dry or partly swampy; in open country, on planes, forest edges, or along roads. Soil: (poor) sandy, limestone, or silt; bedrock granite. Altitude: 300–1500 m. Flowering: December to March; fruiting: March to June, October.

Uses — Wood used for houses. The fruit is edible (but not so good).

Vernacular names — Burma: Yemein (Hmawbi). Thailand: Muat son (Chiang Mai Prov.); krom (Satun Prov.); meud lode (Ban Ubol).

Note — Distinct from *A. octandra* var. *yunnanensis* only by the shape of the leaves. Intermediates are possible. See note under latter.

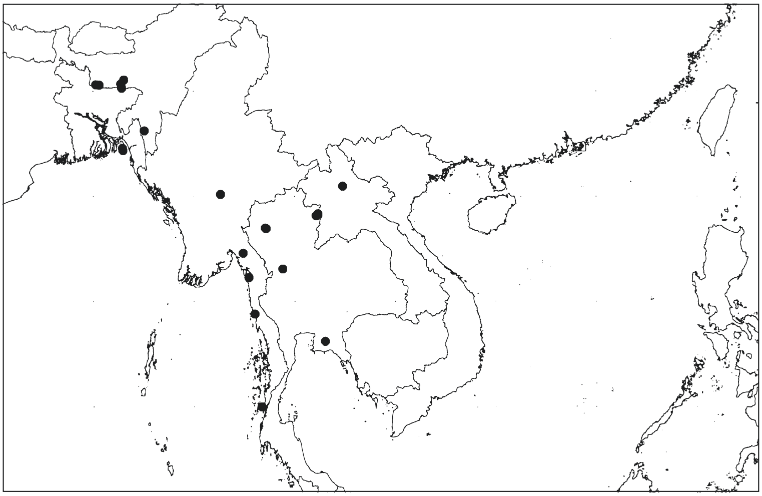
34. **Aporosa wallichii** Hook.f. — Map 10.32

Aporosa wallichii Hook.f., Fl. Brit. India 5 (1887) 350; Craib, Kew Bull. 11 (1911) 461; Contr. Fl. Siam. (1912) 188; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 88; Gagnep., Fl. Gén. Indo-Chine 5 (1927) 562; Airy Shaw, Kew Bull. 26 (1972) 218; Kew Bull. 35 (1980) 384; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 44; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 169. — Type: *Wallich 8019* (K-WALL), Silhet.

Aporosa microstachya auct. non (Tul.) Müll.Arg.: Kurz, For. Fl. Brit. Burma 2 (1877) 36.

Aporosa aurea auct. non Hook.f.: Hook.f., Fl. Brit. India 5 (1887) 36., p.p. (excl. Malaysian specimens).

(Small) tree, up to 15 m high, up to 15 cm diameter. *Bark* (light) brownish, thick, coarse, longitudinally cracked or grooved. Young branches very sparsely puberulous. *Stipules* narrowly ovate, seldom slightly oblique, 5–7 by 1.5–2.8 mm, very sparsely puberulous at margin outside, caducous. *Petiole* terete, smooth, 6–19 by 0.8–1.2 mm, glabrous, lower pulvinus 1.5–2 by 1.2–1.5 mm, upper pulvinus 3–5 by 1.2–2 mm, both rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 9–17.5 by 3.5–6.5 cm; base obtuse to acute, basal glands small, blackish; margin lowly undulate to lowly glandular-crenate, marginal glands regular, black; apex acuminate to cuspidate; blade thin, smooth, slightly shiny, not brittle, drying bright to yellowish green above, seldom reddish green, greenish (or brownish) beneath, glabrous; dots irregularly densely set, fine, greyish, fading; disc-like glands regular to many, brownish, distinct, scattered within marginal arches. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 8–10 pairs, slightly prominent to flat above, prominent beneath, marginal arches rather distinct, 2–4 mm from the margin; tertiary veins and venation fading, rather densely reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 18–43 by 2–2.5 mm, puberulous; peduncle absent; bracts broadly triangular, 0.7–1.5 mm long, rather conspicuous, puberulous outside, sparsely puberulous to subglabrous inside, margin ciliate; glomerules indistinct, consisting of less than 10 laxly set flowers, continuously set along the rachis; pedicel absent. *Staminate flowers* 1.2–2 mm long; sepals 3 or 4, narrowly obovate, 0.7–1.3 mm long, almost free, connate to rachis, thin, apically sparsely tomentose outside, glabrous inside, margin ciliate; stamens 2 (or 3), slightly exserted, 1–2.5 mm long; anthers 0.3–0.5 mm long, connective sometimes sparsely hairy; pistillode cylindric, 0.5–0.8 mm long, at apex hairy. *Pistillate inflorescences* 1 or 2 clustered together, 3–9 by 1.5–2 mm, puberulous, flowers up to 11, densely arranged along the rachis; bracts broadly triangular, 0.8–1.2 mm long, sparsely puberulous outside, glabrous inside,



Map 10.32. Distribution of *Aporosa wallichii* Hook.f.

margin ciliate; bracteoles ovate, 0.4–0.8 mm long, sparsely puberulous outside, glabrous inside, margin ciliate; pedicel absent. *Pistillate flowers* 3–4.5 mm long; sepals 3, ovate, ascending, 1–1.4 mm long, thin, sparsely puberulous outside, sericeous at base inside, margin ciliate; ovary ovoid to fusiform, 2–3 mm long, 2-locular, punctulate, subglabrous (often at base and apex with a few scattered hairs); stigmas raised, elongated, perpendicular to the sides of the ovary, (slightly) recurved, apically bifid to less than halfway, 2–3 mm long, papillate to laciniate above, glabrous or sparsely hairy, smooth beneath, often sparsely hairy, style remnant present. *Infructescences* 3–4 by 1.5–2 mm, (red) puberulous; fruiting pedicel absent. *Fruits* (narrowly) ovoid, young ones stiped, often beaked, 9–11 by 6–9 mm, punctate, drying (dark) brown to black, glabrous; pericarp c. 0.5 mm thick, not fleshy; septae and column sparsely hairy, glabrescent. *Seeds* 1 or 2, half-terete, ovoid, 7–7.5 by 5–6 by 2–3 mm.

Distribution — North India, Burma, Thailand.

Habitat & Ecology — (Dry) evergreen or (mixed) deciduous forest, dry or open, on slopes, or along edge of forest. Soil: granite bedrock. Altitude: 100–1300 m. Flowering: December to February; fruiting: March to May.

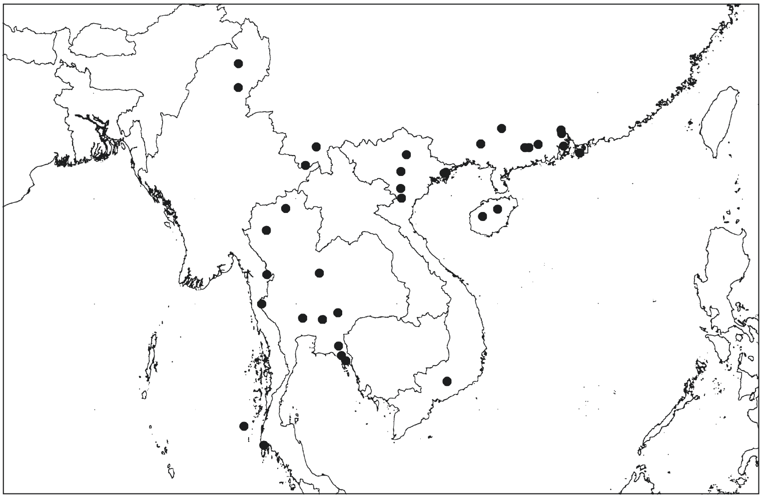
Note — Intermediates with *A. octandra* are specimens with green, but hairy leaves (as the former *A. wallichii* var. *ambigua* Airy Shaw) or specimens with brown, glabrous leaves. Since the specimens with hairy, green leaves also have tomentose ovaries, they are placed in *A. octandra*, while those with glabrous, brown leaves and glabrous ovaries are transferred to *A. wallichii*.

35. **Aporosa yunnanensis** (Pax & K. Hoffm.) F.P. Metcalf — Fig. 3.5b, 3.6d, 3.7e; Map 10.33

Aporosa yunnanensis (Pax & K. Hoffm.) F.P. Metcalf, Lingnan Sci. J. 10 (1931) 486; Merr., Lingnan Sci. J. 13, 1 (1934) 34, p.p., excl. *A. microcalyx* (Hassk.) Hassk. var. *yunnanensis* Pax & K. Hoffm., J. Arnold Arbor. 19 (1938) 40; Airy Shaw, Kew Bull. 26 (1972) 218; Mandal & Panigr., Bull. Bot. Surv. India 26 (1984) 45. — *Aporosa wallichii* Hook.f. var. *yunnanensis* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 90. — Lectotype (proposed here): *Henry 11638E* (holo K), China, Yunnan, Szemao.

Aporosa lanceolata auct. non Thwaites: Hance, J. Bot. 17 (1879) 14; Forbes & Hemsl., J. Linn. Soc. 26 (1894) 428.; Dunn & Tutcher, Fl. Kwangtung (1912) 236; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 88, in obs.

Shrub or (small) tree, up to 8 m high, up to 10 cm diameter. *Bark* tan, finely roughened, thin. Young branches glabrous. *Stipules* narrowly triangular, 2–4 by c. 1 mm, glabrous, caducous. *Petiole* terete, smooth, 5–16 by 0.8–1.2 mm, glabrous, lower pulvinus 1–2.5 by 1–1.5 mm, upper pulvinus 1.5–5 by 1.5–2 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 7.5–17 by 2–5.5 cm; base acute to slightly attenuate, basal glands present, brownish, variably distinct; margin lowly undulate to lowly glandular-crenate, marginal glands present, regular, black, sometimes indistinct; apex cuspidate; blade thin, smooth, dull, not brittle, drying a light greenish brownish above and beneath, nervation lighter beneath, completely glabrous; dots laxly set, fine, grey to black, sometimes fading; disc-like glands occasionally few, within marginal arches, brownish black. *Nervation*: midrib prominent above, prominent beneath; nerves 7–10 pairs, slightly prominent above, prominent beneath, marginal arches variably distinct, 1.5–3 mm from the margin; tertiary veins and venation distinct, laxly reticulate, slightly prominent. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 18–41 by 1.8–2.5 mm, probably sericeous; peduncle absent; bracts broadly triangular, often rather conspicuous, 1–1.2 mm long, glabrous, margin ciliate; glomerules subglobose, indistinct, consisting of c. 5 laxly set flowers, continuously set along the rachis; pedicel absent. *Staminate flowers* 1.2–2 mm long; sepals 4 (or 5), narrowly obovate, 0.8–1.2 mm long, free, connate to rachis, glabrous, margin ciliate; stamens 2, exserted, 1–2.2 mm long; anthers 0.3–0.4 mm long, connective glabrous; pistillode indistinct. *Pistillate inflorescences* single (or 2 clustered together), 2–5 by 1.2–1.5 mm, sericeous, flowers up to 5, densely set along the rachis; bracts broadly triangular, 0.8–1.2 mm



Map 10.33. Distribution of *Aporosa yunnanensis* (Pax & K. Hoffm.) F.P. Metcalf.

long, glabrous, margin ciliate; bracteoles ovate, 0.8–1 mm long, subglabrous outside, glabrous inside; pedicel absent. *Pistillate flowers* 4–6.5 mm long; sepals 3 or 4, ovate, subequal, ascending, 0.6–1.1 mm long, thin, glabrous, margin ciliate; staminodes occasionally 1 seen, 0.2–0.3 mm long; ovary flask-shaped, 2.5–4.5 mm long, 2-locular, smooth, glabrous; stigmas raised, elongated, perpendicular to the sides of the ovary, recurved, apically bifid to near base, 1.5–2.5 mm long, ribbed and papillate to laciniate above, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 2–5 by 1.5–2 mm, sericeous; fruiting pedicel absent. *Fruits* ovoid to ellipsoid, not stiped, beaked, 10–13 by 7–9 mm, punctate to lowly granulate, drying light to reddish brown, glabrous; pericarp 0.5–0.8 mm thick, not fleshy; septae and column sparsely hairy. *Seeds* 1 or 2, (half-)terete, ellipsoid, 7.5–9 by 5–6 by 4–4.5 mm.

Distribution — South China, Burma, Thailand, Laos, Vietnam.

Habitat & Ecology — In evergreen forest; in wet or dry, shaded or open, or high areas; on gentle slopes, along edge of forest, streams, or roads. Soil: sandy or dry clayey; granite bedrock. Altitude: 600–1300 m. Flowering: November to March; fruiting: March to July.

Note — The papery leaves of *A. yunnanensis* with cuspidate apex and greenish grey colour with lighter nervation are reminiscent of those of the section Aporosae. This feature aids the distinction between *A. yunnanensis* and the *A. octandra*-complex. This is for me sufficient reason to keep *A. yunnanensis* as a distinct species, despite Chakrabarty & Gangopadhyay's opinion (1993).

10.4.3 – ***Section Benthamianae Schot***

36. Aporosa benthamiana Hook.f. — Fig. 3.7n, 3.8q, 3.11g, 4.7b; Map 10.34

Aporosa benthamiana Hook.f., Ic. Pl. 16 (1887) t. 1583; Fl. Brit. India 5 (1887) 352; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 279; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 84; Ridl., Fl. Malay Penins. 3 (1924) 236; Corner, Wayside Trees Malaya 1 (1940) 237; Meijer, Bot. News Bull. Sandakan 7 (1967) 33; Whitmore, Tree Fl. Malaya 2 (1973) 59; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 33. — Lectotype (proposed here): *Maingay 2381 KD 1416* (holo K; iso L), Malacca.

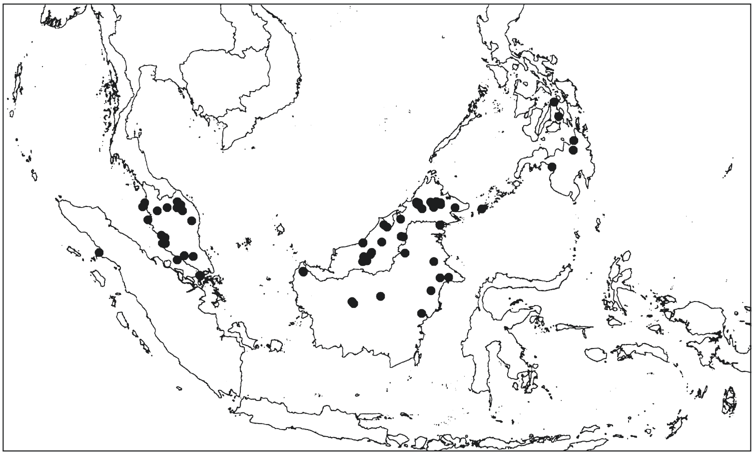
?*Aporosa euphlebia* Merr., Philipp. J. Sci., Bot. 11 (1916) 62; Enum. Born. Pl. (1921) 330; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 84. — Type: *Native Collector 2823* (n.v.), Sarawak.

Aporosa stipulosa Merr., Philipp. J. Sci., Bot. 6 (1920) 547. — *Aporosa lunata* (Miq.) Kurz var. *philippinensis* Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 82. — *Aporosa lunata* (Miq.) Kurz var. *stipulosa* (Merr.) Merr., Enum. Philip. Fl. Pl. 2 (1923) 410, nom. illegit. — Type: *M.S. Clemens 968* (n.v.), Philippines, Mindanao.

Aporosa grandifolia Merr., Pl. Elmer. Born. (1929) 143. — Type: *Elmer 20944* (iso BM, BO, K, L, P), Sabah, Tawau.

Aporosa spec. Merr., Pl. Elmer. Born. (1929) 144. — Specimen: *Elmer 21233* (BO, BM, BR, K, L, M, P), Sabah, Elphinstone Prov., Tawau.

Tree, up to 30 m high, up to 35 cm diameter. *Bark* grey, (chocolate) brown, brown-white, or brown-green mottled, smooth or rough, slightly flaky; inner bark brownish, red, pink, yellow, or white. *Wood* brownish red, ochre, or yellow. *Twigs* white mottled greenish brown, (sparsely) puberulous. *Stipules* falcate, 6–20 by 11–37 mm, black disc-like glands along margin beneath, sparsely hairy at base beneath, glabrescent, often persistent. *Petiole* terete, smooth, 12–28 by 2–4 mm, sparsely pubescent, glabrescent, lower pulvinus 2–4 by 3–4 mm, upper pulvinus 5–11 by 3–6 mm, both distinct. *Leaves* narrowly elliptic to narrowly obovate (to linear elliptic), 14–50 by 4–12 cm; base cordate, basal glands absent; margin subentire to lowly undulate, marginal glands few, small, black, in margin, often indistinct; apex acuminate to cuspidate; blade thick, smooth, shiny, not brittle, drying greenish brown, brownish, or sometimes bluish above, (golden) brown beneath, glabrous above, midrib and nerves sparsely puberulous beneath, glabrescent; dots irregularly laxly set, fine, blackish, fading; disc-like glands regular, distinct, black, along the margin. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 12–18 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 3–6 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* born on the branches. *Staminate inflorescences* 6–10 clustered together, 12–35 by 2–4 mm, puberulous; peduncle 2–4 by 1–1.5 mm; bracts broadly triangular, inconspicuous, 0.5–0.7 mm long, hairy outside, glabrous inside; glomerules indistinct, ellipsoid, consisting of more than 10 densely set flowers, 3–6 by 2–3 mm, continuously spaced along apical part of the rachis; pedicel minute. *Staminate flowers* 1.5–2 mm long; sepals 4 (or 5), elliptic, 0.6–0.8 mm long, connate to c. halfway, sparsely hairy outside, glabrous inside; stamens 2 (or 3), strongly exserted, 1.5–2.5 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode cylindrical, c. 0.3 mm long, hairy at apex. *Pistillate inflorescences* 3–5 clustered together, 6–11 by c. 2 mm, puberulous, flowers up to 15, densely set at upper 3/4 of the rachis; bracts broadly triangular, 0.5–1 mm long, hairy outside, glabrous inside; bracteoles ovate, 0.5–0.7 mm long, sparsely hairy outside, glabrous inside; pedicel 0–0.5 mm long, puberulous. *Pistillate flowers* 2–4 mm long; sepals (4 or) 5, ovate, patent, 0.7–0.9 mm long, thin, hairy outside, glabrous inside; ovary ellipsoid, 2–4 mm long, 3- (or 4-)locular, smooth, sericeous at base, glabrescent towards apex; stigmas sessile, elongated, flattened to the sides of the ovary, apically bifid to near base, straight, 2–5 mm long, smooth above and beneath, glabrous, style remnant absent. *Infructescences* 8–23 by 1.5–3 mm, sparsely puberulous; fruiting pedicel 0.5–4 mm long, sparsely puberulous. *Fruits* ovoid, not



Map 10.34. Distribution of *Aporosa benthamiana* Hook.f.

stiped, not beaked, 13–18 by 11–18 mm, slightly punctulate to smooth, drying (dark) brown, sparsely hairy, glabrescent; pericarp 0.5–3 mm thick, mostly not fleshy; septae and column glabrous. *Seeds* 3, half-terete, ellipsoid, 8–11 by 5–8 by 3–4 mm.

Distribution — Malesia: Peninsular Malaysia, Singapore, Sumatra, Borneo, Philippines.

Habitat & Ecology — In primary, disturbed, and secondary forest; on flat land, hills, or ridges; in lower montane, alluvial, or heath forest. Soil: rich sandy, sandy clay, clay loam, or clay. Altitude: 15–1185 m. Flowering: May to November; fruiting: March to December. Fruit eaten by monkeys.

Vernacular names — Peninsular Malaysia: Kaun semasak, sebasah (Malay). Borneo: Kayu masam (Iban); natu tundu, kayu kadang daun (Kelabit); kumpang (Lundu Distr.); binang (Murut).

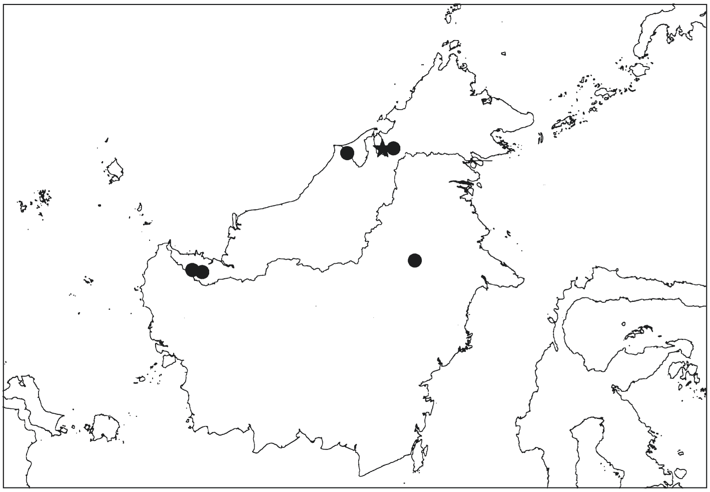
Notes — 1. Two specimens from high altitude have a thick fleshy pericarp.

2. In my opinion the description of the stipules of *A. euphlebia* (Merrill, 1916) hardly points to any *Aporosa* species, though the inflorescence does. It might be a mixtum, but I retain the synonymy, because I was unable to locate the type specimen.

37. **Aporosa bullatissima** Airy Shaw — Map 10.35

Aporusa bullatissima Airy Shaw, Kew Bull. 20 (1966) 379; Kew Bull., Addit. Ser. 4 (1975) 34. — Type: *S (Rosli) 3353* (holo K; iso BO, L, SING), Sarawak, Baram.

Tree, up to 25 m high, up to 30 cm diam.; buttresses up to 2.5 m high. *Bark* grey to red-brown, smooth. *Wood* yellow. Young branches tomentose. *Stipules* falcate, 4–7 by 8–15 mm, present in young stages, black disc-like glands along margin beneath, sericeous at base beneath, glabrescent. *Petiole* terete, smooth, 8–17 by 1.5–2 mm, tomentose, glabrescent, lower pulvinus c. 2 by 2 mm, upper pulvinus 2–3 by 2–2.5 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, some linear elliptic, 9–20 by 2–5 cm; base rounded, basal glands absent; margin subentire to lowly undulate, marginal glands few, black, in margin; apex acuminate to cuspidate; blade thick, smooth, strongly bullate, shiny, sometimes brittle, drying greenish to reddish brown above, brownish beneath, only midrib sparsely hirsute above, sparsely hirsute beneath; dots irregularly set, fine, blackish, fading; disc-like glands present regular, distinct, black, along margin. *Nervation*: midrib sunken above, prominent beneath; nerves 9–11 pairs, sunken above, prominent beneath, marginal arches distinct, 2–3 mm from the margin; tertiary veins and venation distinct, rather laxly reticulate, slightly scalariform, flat to sunken above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 3–5 clustered together, 9–19 by 2.5–4 mm, puberulous; peduncle 3–4 by 1–1.5 mm; bracts not seen; glomerules probably ellipsoid, indistinct, consisting of up to 12 densely set flowers, spaced continuously at apical part of the rachis; pedicel minute. *Staminate flowers* 1.5–1.8 mm long; sepals 4, ovate, 0.3–0.5 mm long, connate to c. halfway, sericeous outside, glabrous inside; stamens 2, strongly exserted, 1.5–2 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode a minute hair tuft. *Pistillate inflorescences* clustering not seen, 4–7 by 0.8–1.2 mm, puberulous, flowers up to 11, densely set at apical 3/4th of rachis; bracts and bracteoles not seen; pedicel 0.5–1 mm long, puberulous. *Pistillate flowers* 1.5–2.2 mm long; sepals 5 or 6, subequal, ovate, patent, 0.5–1 mm long, thin, hairy outside, glabrous inside; staminodes



Map 10.35. Distribution of *Aporosa bullatissima* Airy Shaw (●) and *A. sylvestri* Airy Shaw (★).

erratically 2 or 3 present; ovary ellipsoid, 1.2–2 mm long, 3-locular, smooth, sericeous at base, glabrescent towards apex; stigmas sessile, elongated, flattened to the sides of the ovary, apically bifid to near base, straight, 1.5–2.5 mm long, smooth above and beneath, glabrous, style remnant absent. *Infructescences*, *fruits*, and *seeds* not seen, septae and column in flower glabrous.

Distribution — Malesia: Borneo.

Habitat & Ecology — Primary forest; on hills or ridges. Soil: sandy clay on igneous rock. Altitude: 45–1200 m. Flowering: March, July to September.

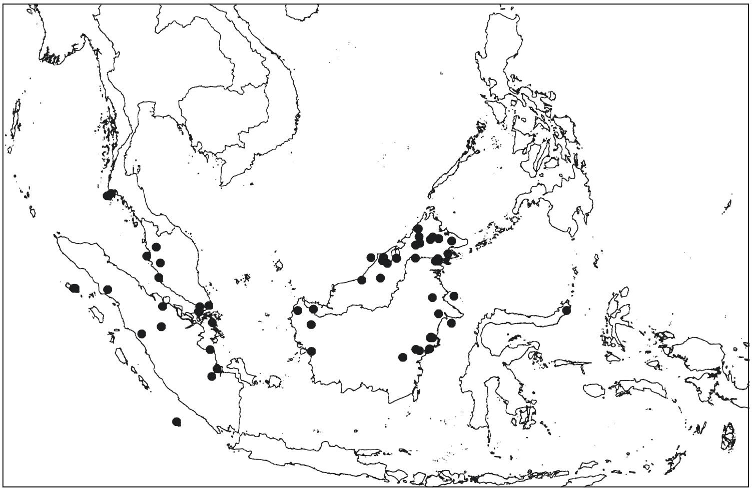
38. **Aporosa falcifera** Hook.f. — Fig. 3.5c, 3.6h; Map 10.36

Aporosa falcifera Hook.f., Fl. Brit. India 5 (1887) 352; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 279; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 83; Ridl., Fl. Malay Penins. 3 (1924) 236; S. Moore, J. Bot. Brit. & For. 63 Suppl. (1925) 97; Meijer, Bot. News Bull. Sandakan 7 (1967) 33; Airy Shaw, Kew Bull. 26 (1972) 215; Whitmore, Tree Fl. Malaya 2 (1973) 60; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 30; Kew Bull. 36 (1981) 255. — Type: *King's Collector 6574* (holo BM; iso BO, K, P), Peninsular Malaysia, Perak.

Aporosa hosei Merr., Philipp. J. Sci., Bot. 11 (1916) 63; Enum. Born. Pl. (1921) 330; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 84. — Type: *Hose 92* (iso K, L, P), Sarawak.

Aporosa acuminatissima Merr., Pl. Elmer. Born. (1929) 142 p.p. (type only), nomen illeg., non Merr., Philipp. J. Sci. 16 (1920) 546 (= *A. sphaeridiophora* Merr.). — *Aporusa merrilliana* Govaerts & Radcl.-Sm., Kew Bull. 51 (1996) 175. — Type: *Elmer 21048* (iso BM, BO, K, L, P), Sabah, Tawau.

Tree, up to 30 m high, up to 40 cm diameter. *Bark* black to grey brown, smooth, flaky, fissured, sometimes lenticelled, not peeling, 1 mm thick; inner bark red to whitish, soft, 2.5 mm thick. *Wood* pale brown, reddish to yellowish, or white. Twigs grey, (sparsely) puberulous. *Stipules* falcate, 4–9 by 11–18 mm, present in young stages, black disc-like glands along margin beneath, puberulous at base beneath, glabrescent. *Petiole* terete, smooth, 9–17 by 1–1.5 mm, sparsely puberulous, lower pulvinus 2–2.5 by c. 2 mm, upper pulvinus 2–6 by 1.5–2.5 mm, both distinct. *Leaves* narrowly elliptic, sometimes linear elliptic, 8–25 by 2.5–7 cm; base subcordate to rounded, basal glands absent; margin subentire to lowly undulate, marginal glands regular, small, blackish, indistinct, in margin; apex acuminate; blade thickish, smooth, shiny, not brittle, drying bluish green above, golden brownish beneath, glabrous above, midrib and nerves sparsely puberulous beneath; dots irregularly set, fine, greyish, fading; disc-like glands regular to many, along margin, black, mostly distinct. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 10–14 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct to slightly fading, 1–3 mm from the margin; tertiary veins and venation fading, densely reticulate, slightly scalariform, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 8–16 by 2–3 mm, puberulous; peduncle 1–4 by 0.5–1 mm; bracts ovate, inconspicuous, 0.7–0.9 mm long, hairy outside, glabrous inside; glomerules indistinct, ellipsoid, consisting of 9–13 densely set flowers, spaced continuously along apical part of the rachis; pedicel minute. *Staminate flowers* 1–2 mm long; sepals 4 or 5, obovate, 0.3–0.6 mm long, connate to halfway, sparsely hairy outside, glabrous inside; stamens 2 (or 3), strongly exserted, 1–1.8 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode often indistinct. *Pistillate inflorescences* 2 or 3 clustered together, 7–15 by 0.8–1 mm, puberulous, flowers up to 11, densely set at apical 3/4th of rachis; bracts broadly triangular, 0.2–0.3 mm long, sparsely hairy outside, glabrous inside; bracteoles ovate, 0.1–0.2 mm long, sparsely hairy outside, glabrous inside; pedicel c. 1 mm long, sericeous. *Pistillate flowers* 2–2.5 mm long; sepals 4 or 5, ovate, patent, 0.5–0.7 mm long, thin, sparsely hairy outside, glabrous inside; ovary ellipsoid, 2–2.5 mm long, 3-locular, smooth, sericeous at base, glabrescent towards apex or subglabrous; stigmas sessile, elongated, flattened to the sides of the ovary, apically bifid to near base, straight, 2–2.5 mm long, lowly longitudinally ribbed above, glabrous, beneath smooth, glabrous, style remnant absent. *Infructescences* 9–25 by 1–1.5 mm, sericeous; fruiting pedicel 2–5 mm long, sericeous. *Fruits* ovoid, not



Map 10.36. Distribution of *Aporosa falcifera* Hook.f.

stiped, not beaked, 9–15 by 6–12 mm, punctulate to smooth, drying dark to greyish brown, sparsely hairy, glabrescent; pericarp 0.3–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 3, half-terete, ellipsoid, 5–6 by 3–4 by 2–3 mm.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia, Singapore, Sumatra, Borneo, North Sulawesi.

Habitat & Ecology — Primary forest; low undulating land; on ridges, slopes, and along river banks. Soil: sandy loam, rich, dark or greyish. Altitude: 5–1300 m. Flowering: February, March, September, October; fruiting: February, April to October.

Vernacular names — Peninsular Malaysia: Pisang-pisang (Malay). Borneo: Damak-damak (Kedayan); tambau (Tawau); kayu dusun (Tidong).

39. Aporosa lunata (Miq.) Kurz — Fig. 3.6k, 10.5; Map 10.37

Aporosa lunata (Miq.) Kurz, J. Asiat. Soc. Bengal 42, 2 (1873) 239; Hook.f., Fl. Brit. India 5 (1887) 352; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 279; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 236; Koord., Exkurs.-Fl. Java 2 (1912) 480; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 82; Merr., Enum. Born. Pl. (1921) 330; Ridl., Fl. Malay Penins. 3 (1924) 237; Backer & Bakh.f., Fl. Java 1 (1964) 456; Meijer, Bot. News Bull. Sandakan 7 (1967) 33; Airy Shaw, Kew Bull. 26 (1972) 216; Whitmore, Tree Fl. Malaya 2 (1973) 59; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 38; Kew Bull. 36 (1981) 256. — *Antidesma lunatum* Miq., Fl. Ind. Bat., Suppl. (1860) 467; Müll.Arg. in DC., Prod. 15, 2 (1866) 251. — Type: *Teysmann s.n.* (holo BO; iso K, L), Sumatra, Palembang.

Bridelia? rugosa Miq., Fl. Ned. Ind., eerste bijv. (1860) 178, 445; Jabl. in Engl., Pflanzenr. IV.147.viii (1915) 87. — Type: *Teysmann HB 4544* (holo U, barcode U 0001859), Indonesia, Sumatra, Lampong.

Tree, up to 27 m high, up to 29 cm diam.; buttresses c. 1.5 m by 1.5 cm. *Bark* pale black, dark brown, reddish, greenish or greyish brown, grey mottled, flaking, cracked, shallowly fissured, or smooth; inner bark greenish, pink, bright red, or red-yellowish brown, soft, granular. *Wood* whitish (yellow). Twigs green, tomentose. *Stipules* falcate, 6–9 by 11–15 mm, mostly persistent, black disc-like glands beneath along margin, sparsely hairy. *Petiole* terete, ridged, 6–20 by 2–2.5 mm, hirsute, lower pulvinus 2–3 by 2–3 mm, upper pulvinus 4–7 by 2–3 mm, both distinct. *Leaves* narrowly elliptic to narrowly obovate, 9.5–43 by 3.5–13 cm; base obtuse to emarginate, basal glands absent; margin lowly undulate, marginal glands regular, small, black, in margin; apex acuminate; blade thick, smooth, sometimes slightly bullate, shiny, not brittle, drying bright green to reddish brown above, (light) golden brown beneath, very sparsely hirsute above, midrib (sparsely) hirsute, glabrescent, (sparsely) hirsute beneath; dots irregularly set, fine, grey, fading; disc-like glands present along the margin, many, distinct, black. *Nervation*: midrib flat to prominent in a furrow above, prominent beneath; nerves 10–14 pairs, sunken above, prominent beneath, marginal arches distinct, 1.5–4 mm from the margin; tertiary veins and venation distinct, densely reticulate to slightly scalariform, flat to sunken above, prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 3–6 clustered together, 15–33 by 2–3 mm, puberulous; peduncle 1.5–4 by c. 1 mm; bracts not seen; glomerules indistinct, ellipsoid, dense, consisting of more than 10 flowers, spaced continuously along the rachis; pedicel minute. *Staminate flowers* 1.5–2.5 mm long; sepals 4 or 5, obovate, 0.5–1 mm long, connate to halfway, sparsely hairy outside, glabrous inside; stamens 2 or 3, strongly exserted, 1.2–2 mm long; anthers 0.1–0.2 mm long, connective glabrous;

pistillode cylindrical, c. 0.3 mm long. *Pistillate inflorescences* 2–5 clustered together, 7–27(–45) by 1–1.2 mm, puberulous, flowers up to 15, densely arranged at apical 7/8th of rachis; bracts broadly triangular, 0.4–0.5 mm, sericeous outside, glabrous inside; bracteoles ovate, 0.2–0.3 mm long, sericeous outside, glabrous inside; pedicel 1–1.5 mm long, densely sericeous. *Pistillate flowers* 2–3 mm long; sepals 5 or 6, narrowly elliptic, patent, c. 1 mm long, sparsely hairy outside, glabrous inside; staminodes erratically 2 or 3 present; ovary ellipsoid, 1.8–2.3 mm long, 3- (or 4-)locular, smooth, (densely) sericeous; stigmas sessile, elongated, apically bifid to c. halfway, flattened to the sides of the ovary, straight, 2–3 mm long, lowly longitudinally ribbed above, glabrous, smooth beneath, glabrous, style remnant absent. *Infructescences* 11–33 by 2–4 mm, puberulous; fruiting pedicel 1.5–4 mm long, sericeous. *Fruits* ovoid, sometimes slightly flask-shaped, not stiped, not beaked, 10–16 by 9–14 mm, punctulate to smooth, sparsely hairy, glabrescent, sour; pericarp 0.5–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 3, half-terete, ellipsoid, 8–9 by 7–8 by 3–4 mm.

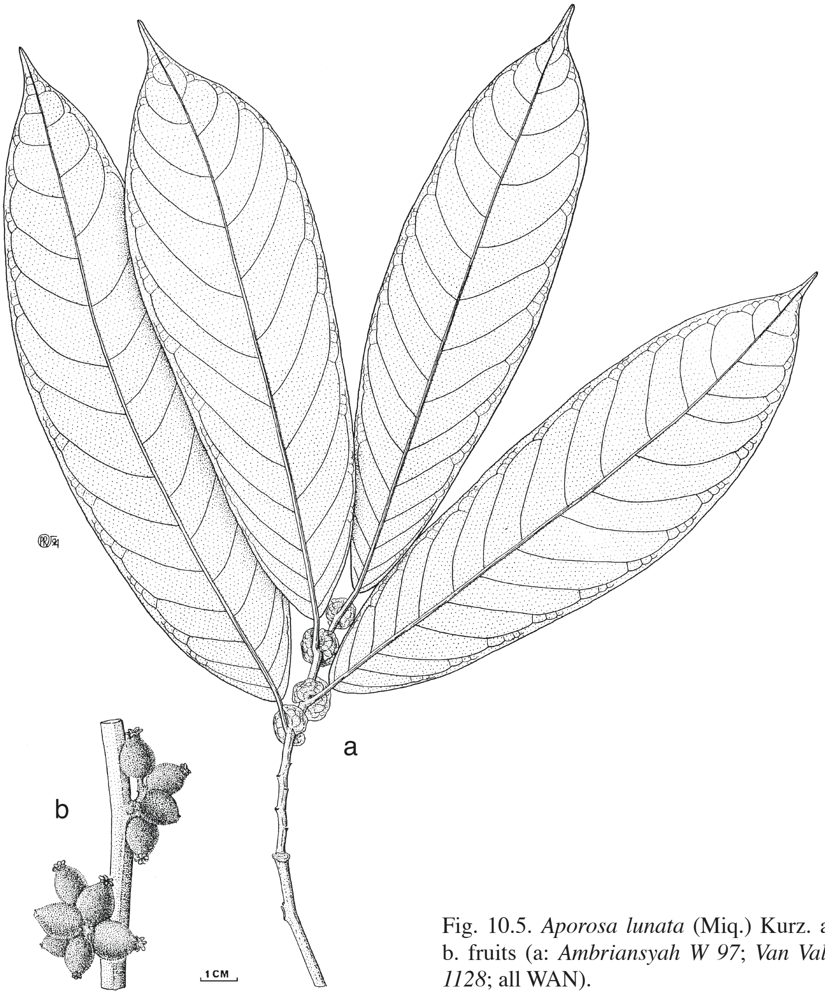
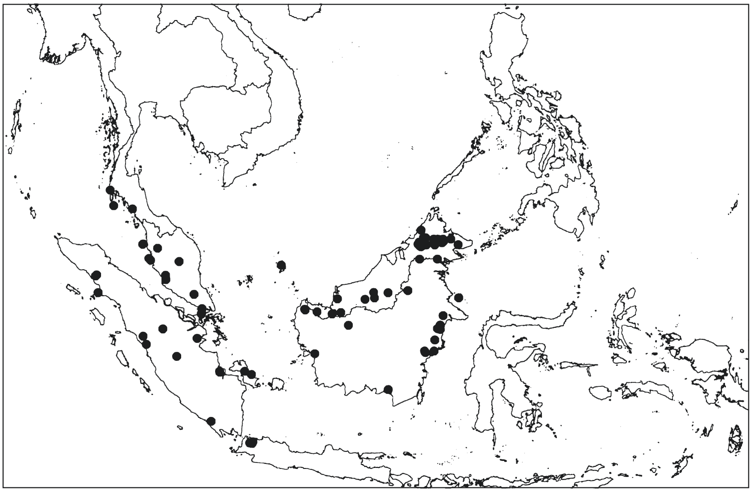


Fig. 10.5. *Aporosa lunata* (Miq.) Kurz. a. Habit; b. fruits (a: *Ambriansyah W 97*; *Van Valkenburg 1128*; all WAN).



Map 10.37. Distribution of *Aporosa lunata* (Miq.) Kurz.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia, Singapore, Sumatra, Java, Borneo.

Habitat & Ecology — Primary and secondary lowland evergreen forest; on hillsides, ridges, and along river banks; in flat, hilly, and moist land. Soil: sandstone, sandy and rich clay, granitic rock, or granodiorite derived. Altitude: low to 1300 m. Flowering: February to April, August to November; fruiting: April to December.

Vernacular names — Sumatra: Semasan (abu) (Palembang). Borneo: Kayu masam (Iban).

Notes — 1. The type, *Teysmann s.n.*, has pistillate flowers. Miquel (1860) wrongly interpreted the erect young smooth stigma lobes as filaments.

2. Some Bornean specimens have branched staminate spikes.

40. Aporosa sylvestri Airy Shaw — Map 10.35

Aporusa sylvestri Airy Shaw, Kew Bull. 32 (1978) 365. — Type: *S (Sylvester) 32813* (holo K; iso BO, L), Sarawak, 5th Division.

Tree, 15 m high, 15 cm diameter. *Bark* chocolate brown, smooth to slightly fissured, pock-marked. *Twigs* brownish grey, tomentose. *Stipules* not seen, caducous [but probably falcate]. *Petiole* terete, smooth, 16–22 by 2.5–3 mm, tomentose, glabrescent, lower pulvinus 3–4 by c. 2 mm, upper pulvinus 5–7 by 3.5–4.5 mm, both distinct. *Leaves* narrowly elliptic, 21–29 by 6.5–10 cm; base rounded to obtuse, basal glands absent; margin lowly undulate, marginal glands few, small, black, in margin; apex acuminate to cuspidate; blade thick, smooth, strongly bullate, shiny, not brittle, drying greenish grey above, brownish beneath, glabrous above, nervation sparsely hairy, hirsute beneath; dots densely set, fine, grey; disc-like glands present along the margin, many, black. *Nervation*: midrib flat to prominent in a furrow above, prominent beneath; nerves 10–12 pairs, flat to sunken above, prominent beneath, marginal arches distinct, 2–5 mm from the margin; tertiary veins and venation distinct, densely reticulate to slightly scalariform, flat to sunken above, prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* and *staminate flowers* not known. *Pistillate inflorescences* 1–3 clustered together, 5–10 by 1.5–2 mm, puberulous, flowers up to 15, densely arranged at apical 3/4th of rachis; bracts triangular, c. 0.4 mm long, sparsely hirsute outside, glabrous inside; bracteoles ovate, c. 0.2 mm long, sparsely hirsute outside, glabrous inside; pedicel 0.1–0.2 mm long, sericeous. *Pistillate flowers* 2–2.5 mm long; sepals 5, narrowly ovate, patent, 0.8–1 mm long, hirsute outside, glabrous inside; staminodes occasionally 3 present; ovary ellipsoid, 2.2–2.8 mm long, 3-locular, smooth, sericeous; stigmas sessile, elongated, apically bifid to c. halfway, flattened to the sides of the ovary, straight, 2–3 mm long, lowly longitudinally ribbed above, glabrous, smooth beneath, style remnant absent. *Infructescence*s, *fruits* and *seeds* not known; septae and column in flower glabrous.

Distribution — Malesia: Borneo (Sarawak).

Habitat & Ecology — Kerangas; hill slopes. Soil: sandy. Altitude: c. 1000 m. Flowering: March.

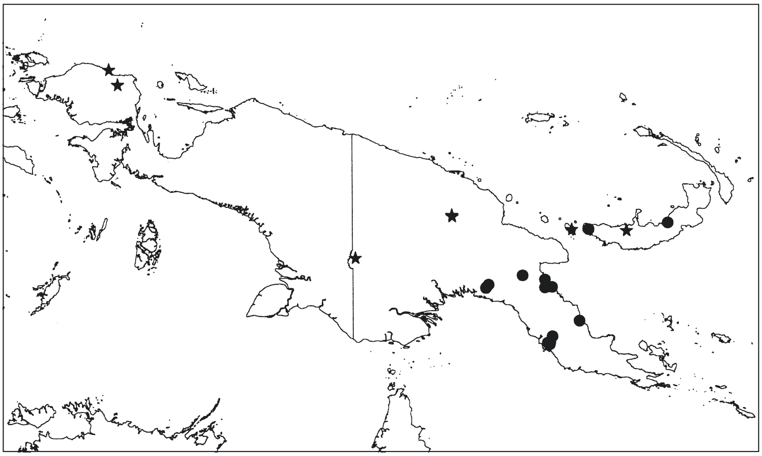
Note — Only known from the type collection. With so little material it remains unclear to me whether *A. sylvestri* is a distinct species or just an extreme – kerangas – form of *A. lunata*.

10.4.4 – *Section Papuanae Schot*

41. Aporosa annulata Schot — Map 10.38

Aporosa annulata Schot, Blumea 40 (1995) 454. — Type: *BW (Van der Sijde) 5556* (holo L; iso BO, LAE), Indonesia, Papua Barat, Vogelkop, Sidei, c. 50 km W of Manokwari.

Tree, up to 20 m high, up to 20 cm diameter. *Bark* grey-brown or brown, flaky; inner bark reddish straw or (light) brown. *Wood* yellow, creamy, or straw. Young branches (red) tomentose. *Stipules* narrowly ovate, oblique, 6–7 by 3–4 mm, margin very sparsely hairy beneath, present in young stages. *Petiole* terete, adaxially lowly grooved, 7–15 by 0.8–1 mm, (red) tomentose, lower pulvinus 1–2 by 1–1.2 mm, upper pulvinus 2–4 by 1.2–1.5 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 8–14.5 by 2.5–5 cm; base rounded to obtuse, basal glands absent; margin subentire, recurved, marginal glands few, small, blackish; apex acuminate to cuspidate; thinnish, slightly shiny, not brittle, smooth, drying greyish or brownish green above and beneath; dots irregularly densely set, very fine, grey; disc-like glands regular, scattered mostly at base within marginal arches; only midrib tomentose above, sparsely tomentose beneath, midrib and nerves tomentose. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 7–10 pairs, slightly prominent to flat above, prominent beneath, marginal arches fading, 1–3 mm from the margin; tertiary veins and venation fading, rather densely reticulate, slightly scalariform, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–6 clustered together, 8–15 by 1.5–2 mm, tomentose; peduncle 0–1 by c. 1 mm; bracts triangular, inconspicuous, 1–1.2 mm long, tomentose outside, hairy at base only inside, margin ciliate; glomerules subglobose, consisting of 8–10 rather densely set flowers, 1.5–2 by 1.2–1.8 mm, spaced at 0.5–1 mm at base of the rachis, decreasing to 0 mm at apex; pedicel 0.3–0.5 mm long. *Staminate flowers* 1.5–2 mm long; sepals 4, obovate, 0.4–0.7 mm long, connate to c. halfway, sparsely tomentose outside, glabrous inside; stamens 3 or 4, exserted,



Map 10.38. Distribution of *Aporosa annulata* Schot (★) and *A. brassii* Mansfield (●).

1.2–2.2 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode minute, sparsely tomentose. *Pistillate inflorescences* 1 or 2 clustered together, 3–10 by 0.5–0.8 mm, tomentose; flowers up to 7, laxly set at base of the rachis, rather densely apically; bracts broadly triangular, 0.8–1 mm long, tomentose outside, hairy at base only inside, margin ciliate; bracteoles ovate, 0.4–0.7 mm long, sparsely tomentose outside, glabrous inside; pedicel 0.5–1 mm long, tomentose. *Pistillate flowers* 2.5–4 mm long; sepals 4, ovate, ascending, 0.5–0.7 mm long, thin, sparsely tomentose outside, tomentose at base only inside; ovary ovoid, 1.5–2.5 mm long, 2- or 3-locular, smooth, tomentose; stigmas raised, elongated, apically bifid to more than halfway, perpendicular to the sides of the ovary, slightly recurved, 2–3 mm long, ribbed and laxly papillate above, margins laxly laciniate, glabrous, smooth beneath, very sparsely hairy, style remnant absent. *Infructescences* 17–31 mm long, 0.5–1 mm diam., sparsely tomentose; fruiting pedicel 2–4 mm long, sparsely tomentose. *Fruits* ellipsoid, not stiped, slightly beaked, 10–12 by 7–9 mm, punctulate, very sparsely puberulous; pericarp 0.3–0.5 mm thick, not fleshy; septae glabrous; column around base with a hairy ring. *Seeds* 1, half-terete, ellipsoid, 7–8 by 4.5–5.5 by 3–4 mm.

Distribution — Malesia: Papua Barat, Papua New Guinea.

Habitat & Ecology — Primary, lowland to lower montane forest; open ground; on gentle slopes. Soil: sandy clay or clay loam, red. Altitude: 5–600 m. Flowering: May, August to October; fruiting: January and March.

Vernacular names — Mofkwa (Amberbaken); mees (Hattam).

42. Aporosa brassii Mansfield — Fig. 3.6w, 3.8h; Map 10.38

Aporosa brassii Mansfield, J. Arnold Arbor. 10 (1929) 77; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 29. — Type: *Brass 1049* (holo A; iso K, P), Papua New Guinea, Vailala river.

(Small or slender) tree, up to 22.5 m high, up to 25 cm diameter. *Bark* blackish brown to brown to light grey, rough, fissured, or striate; inner bark reddish brown to red, orange-brown, or pale pink. *Wood* reddish straw, or creamy brown to white. Young branches densely tomentose. *Stipules* falcate, 2–4 by 8–11 mm, tomentose, present in young stages. *Petiole* terete, adaxially grooved, 6–16 by 1.5–2.2 mm, densely tomentose, lower pulvinus 1.5–2 by 2–3 mm, upper pulvinus 3–6 by 2.5–3.5 mm, both indistinct under indumentum. *Leaves* narrowly ovate to narrowly obovate, 11–21 by 4–9.5 cm; base cordate to rounded, basal glands absent; margin lowly undulate to lowly glandular-crenate, recurved, marginal glands regular, distinct, grey to black; apex acuminate to cuspidate; thickish, smooth, not brittle, dull, drying greyish brown to reddish green above, brown beneath; dots irregularly densely set, very fine, blackish, fading; disc-like glands seldom few at base within marginal arches, hairy; sparsely tomentose above, midrib tomentose, tomentose beneath. *Nervation*: midrib (slightly) prominent above, prominent beneath; nerves 9–15 pairs, slightly prominent to flat above, in older leaves slightly sunken, prominent beneath, marginal arches distinct, 0.5–1.5 mm from the margin; tertiary veins and venation rather distinct, densely reticulate, slightly scalariform, slightly prominent to flat above, in older leaves slightly sunken, (slightly) prominent beneath. *Inflorescences* axillary to just below the leaves or on the upper branches. *Staminate inflorescences* 1–6 clustered together, 16–69 by 2–4 mm, densely tomentose, glabrescent; peduncle 4–17 by 0.8–1 mm; bracts triangular, rather conspicuous, 1.2–2 mm long, (sparsely) villose outside, glabrous inside, ciliate; glomerules ellipsoid, consisting of up to 20 densely set flowers, 2–4 by 1.5–2 mm, spaced at 1–5 mm at base of rachis, decreasing to 0 mm at apex (ramineous ones) to almost continuous (axillary ones); pedicel absent. *Staminate flowers* 1.5–2.5 mm long; sepals 4 (or 5), narrowly elliptic, 0.7–1.5 mm long, connate to c. halfway, sparsely villose outside, glabrous inside, margin ciliate; stamens 2–4, exserted, 1.5–3 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode cylindric, minute, sparsely hairy. *Pistillate inflorescences* 1–3 clustered together, 8–21 by 1.5–2 mm, densely tomentose; flowers up to 13, rather densely set along the rachis; bracts triangular, 1.5–2 mm long, villose outside, very sparsely puberulous inside, margin ciliate; bracteoles triangular, 0.8–1.2 mm long, tomentose outside, very sparsely puberulous inside; pedicel 1–1.5 mm long, densely tomentose. *Pistillate flowers* 4–6 mm long; sepals 4, ovate, ascending, 0.8–1.2 mm long, thin, densely tomentose outside, glabrous inside; ovary ovoid, 2.5–4 mm long, 3- or 4-locular, smooth, densely tomentose; stigmas slightly raised, elongated, apically bifid to near base, perpendicular to the sides of the ovary, straight, 1.5–2.5 mm long, densely laciniate above, glabrous, smooth beneath, sparsely tomentose, style remnant present. *Infructescences* 18–39 by 2–3 mm, densely tomentose; fruiting pedicel 3–7 mm long, tomentose. *Fruits* ovoid, not stiped, beaked, 11–16 by 10–16 mm, (sub)smooth, drying dark (reddish) brown, sparsely tomentose; pericarp 1.5–3 mm thick, not fleshy; septae and column glabrous. *Seeds* 2–4, half-terete, ovoid, 9–12 by 7–10 by 3–5 mm.

Distribution — Malesia: Papua New Guinea.

Habitat & Ecology — In secondary, savannah, gallery, cloud, and rain forest; in substage or regrowth; on rather dry land; on (steep) slopes, hills, gullies, in flat areas, along roads or near creek banks; with *Castanopsis* or *Nothofagus*. Altitude: 6–1260 m. Flowering: August, September; fruiting: May to November.

Vernacular names — Nasake (New Britain).

Notes — 1. There are two forms, one with continuous axillary staminate inflorescences and the other with interrupted staminate inflorescences on the upper branches. Perhaps they represent two species. As yet, I have found no differences in foliage or in fruit (which are all on the upper branches). It may be that they are just two different stages in the development of the tree.

2. Contrary to Mansfield (1929), I do not think that this species is particularly related to *A. reticulata*.

43. **Aporosa brevicaudata** Pax & K. Hoffm. — Fig. 3.5p, 3.8g, 3.11j, 10.6; Map 10.39

Aporosa brevicaudata Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 98; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 29. — Neotype (proposed here): *LAE (Wiakabu & Katik) 73416* (holo K; iso L) Papua New Guinea, Western Highlands.

Aporusa squarrosa Airy Shaw & Gage, Kew Bull. 20 (1966) 25; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 33. — Type: *Eyma 4303* (holo L; iso BO), Indonesia, Papua Barat, Wissel Lakes.

Shrub or tree, up to 18 m high, up to 25 cm diameter. *Bark* brown; inner bark cream-green. *Wood* creamy straw. Young branches sparsely puberulous. *Stipules* narrowly ovate, slightly oblique, 3–3.5 by 0.7–1 mm, sparsely puberulous beneath, caducous.

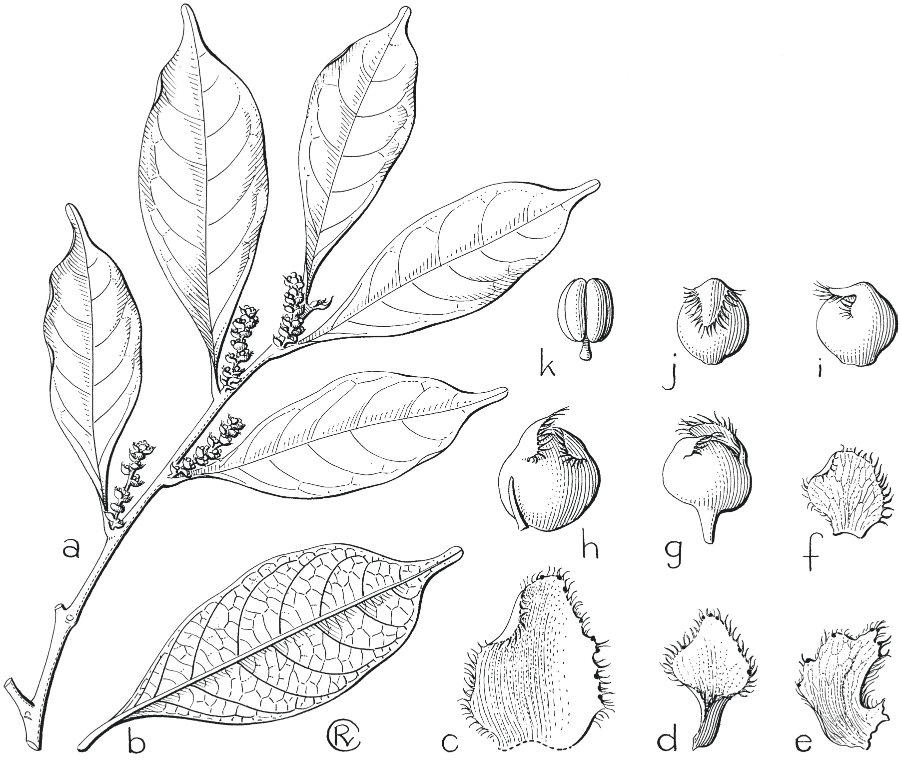
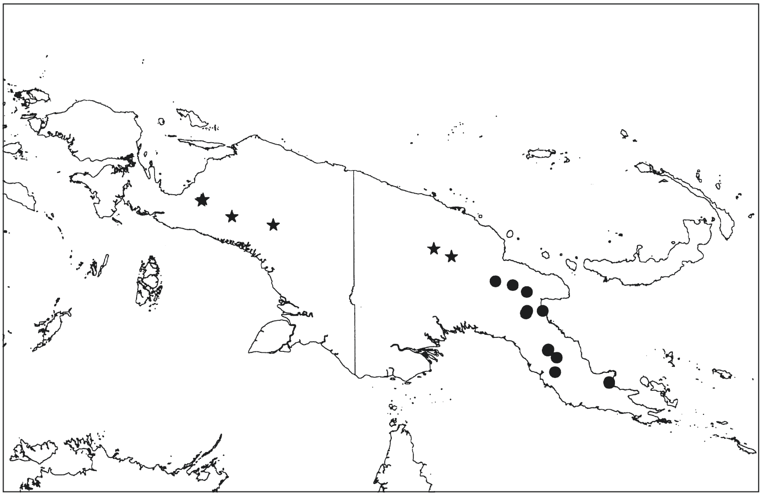


Fig. 10.6. *Aporosa brevicaudata* Pax & K. Hoffm. a. Habit; b. lower surface of leaf; c. bract of glomerule; d–f. bracts of staminate flower; g. staminate bud; h. staminate bud with presume bracteole; i, j: staminate bud, k. stamen (*Pulle 771*, L).

Petiole terete, often adaxially grooved, 3–8 by 1–1.5 mm, often entirely pulvinate, sparsely puberulous. *Leaves* elliptic to (narrowly) obovate, 3–9.5 by 1–4 cm; base attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands few, small, black, often indistinct; apex acuminate; thickish, smooth, brittle, dull, drying dark green above, blackening, (dark) brown beneath; dots densely set, fine, blackish, fading; disc-like glands occasionally few, along margin, large, black; only midrib very sparsely puberulous above, very sparsely puberulous beneath, midrib and nerves sparsely puberulous, glabrescent. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 7–9 pairs, flat above, prominent beneath, marginal arches distinct, 1–2 mm from margin; tertiary veins and venation distinct, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 11–26 by 2–2.5 mm, subglabrous; peduncle 2–4 by 0.5–0.8 mm; bracts (broadly) triangular, conspicuous, 1.4–2.5 mm long, subglabrous outside, glabrous inside, margin sparsely ciliate; glomerules subglobose, consisting of 3 or 4 laxly set flowers, 1.8–2.5 by 1–1.5 mm, spaced at 0.5–1 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 1.5–2.5 mm long; sepals (3 or) 4, elliptic, 1.2–1.8 mm long, connate to c. halfway, very sparsely hairy outside, glabrescent, glabrous inside, margin sparsely ciliate; stamens 2(–4), slightly exserted, 1–2 mm long; anthers 0.6–0.8 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* single, 4–9 by 0.5–0.8 mm, sparsely puberulous; flowers up to 3, laxly arranged at apical end of rachis; bracts triangular, 1.3–1.7 mm long, glabrous, margin ciliate; bracteoles triangular, 0.5–0.8 mm long, sparsely hairy outside, glabrous inside; pedicel 0.3–0.8 mm long, sparsely puberulous. *Pistillate flowers* 2–3.5 mm long; sepals 4, narrowly ovate, subequal, ascending, 1–1.8 mm long, thin, sparsely hairy outside, glabrous inside; occasionally 2 fertile stamens present, as in staminate flowers; ovary narrowly ovoid, 1.2–2.5 mm long, 2-locular, smooth, sericeous at base, glabrescent towards apex; stigmas slightly



Map 10.39. Distribution of *Aporosa brevicaudata* Pax & K. Hoffm. (★) and *A. carrii* Schot (●).

raised, elongated, apically bifid to near base, perpendicular to the sides of the ovary, straight, 1–2 mm long, longitudinally ribbed above, glabrous, smooth beneath, sparsely puberulous, style remnant present. *Infructescences* 13–39 by 0.8–1 mm, sparsely puberulous; fruiting pedicel 2–4 mm long, sparsely puberulous. *Fruits* narrowly ellipsoid, not stiped, beaked, 16–19 by 6–9 mm, punctulate, drying greyish brown, sparsely hairy; pericarp 0.5–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 or 2, half-terete, ellipsoid, c. 9 by 5 by 3 mm.

Distribution — Malesia: Papua Barat, Papua New Guinea.

Habitat & Ecology — Primary, secondary and montane rain forest, undergrowth. Soil sandy or clayey. Altitude: 1650–1800 m. Flowering: December, January, March, May, June; fruiting: June.

Vernacular names — Iekiemoeja, iekomoja, ekiemoja, kiemoja (Kapaukoe); tomalart (Enga); dili (Baliem Valley).

Notes — 1. The selected neotype bears, as the original *Ledermann* collections, "oblique, fusiform, bilocular fruits". The leaf of this specimen is exactly that of Airy Shaw & Gage's *A. squarrosa*, which is staminate. Both fruiting and staminate specimens have characteristic short pulvinate petioles and large distinct bracts.

2. The specimen *Carr 15301* assigned to this species by Airy Shaw (1980a) is *Perrottetia alpestris* (Blume) Loes. subsp. *moluccana* (Blume) Ding Hou (Celastraceae).

3. Though Airy Shaw and Gage (1966) published the species as *A. squarrosa*, the name attached to the type sheet reads *A. macrandra*.

4. See note under *A. parvula*.

44. **Aporosa carrii** Schot — Fig. 3.6z, 3.10d; Map 10.39

Aporosa carrii Schot, Blumea 40 (1995) 454. — Type: *Carr 13285* (holo L; iso BM, K), Papua New Guinea, Boridi.

Tree, up to 24 m high, up to 10 cm diameter. *Bark* (greyish) brown, smooth to slightly fissured, c. 4 mm thick; inner bark pink or pale salmon to light brown. *Wood* white, creamish, pale yellow, or straw, rayed. Young branches very sparsely puberulous, glabrescent. *Stipules* slightly falcate, 5–7 by 3–5 mm, very sparsely puberulous beneath, caducous. *Petiole* terete, adaxially grooved, 8–23 by 0.8–1 mm, very sparsely puberulous, glabrescent, lower pulvinus 1–1.5 by 1–1.2 mm, upper pulvinus 2–3 by 1.2–1.5 mm, both rather distinct. *Leaves* (narrowly) ovate, 5–14.5 by 2–7 cm; base cordate to obtuse, basal glands absent; margin lowly undulate to irregularly lowly glandular-crenate, marginal glands regular, small, greyish, rather indistinct; apex acuminate to cuspidate; thickish, shiny, not brittle, smooth, drying greyish green or brown above and beneath; dots rather densely set, fine, greyish, fading; disc-like glands few, small, scattered at base within marginal arches; glabrous above, midrib and nerves sparsely puberulous beneath, glabrescent. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 5–8 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.5–3 mm from the margin; tertiary veins and venation fading, densely reticulate, slightly scalariform, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–4 clustered together, 13–31 by 1.5–2 mm, sparsely tomentose; peduncle 3–6 by 0.3–0.5 mm; bracts triangular, inconspicuous, 1–1.5 mm long, sparsely puberulous outside, glabrous inside; glomerules subglobose, consisting of 8–12 laxly set flowers, 1.5–2 by 1.2–1.8 mm, spaced at 1.5–3 mm at base of rachis, decreasing to 0 mm at apex; pedicel minute. *Staminate flowers* 1.2–2.5 mm long; sepals 4, elliptic, 0.5–1 mm long, connate to less than halfway, sparsely puberulous outside, glabrous inside; stamens 3, exserted, 1.5–3 mm long; anthers 0.4–0.5 mm long, connective glabrous; pistillode cylindrical, 0.1–0.5 mm long, sparsely tomentose. *Pistillate inflorescences* 1 or 2 clustered together, 17–35 by 0.3–0.5 mm, sparsely tomentose; flowers up to 9, laxly set at base of rachis, more densely at apex; bracts broadly triangular, 0.8–1 mm long, sparsely tomentose at base only outside, sparsely tomentose at base of margins only inside; bracteoles ovate, 0.4–0.6 mm long, sparsely tomentose outside, glabrous inside; pedicel 3–6 mm long, sparsely tomentose. *Pistillate flowers* 3–5 mm long; sepals 4, ovate, ascending, 0.7–1 mm long, thin, sparsely tomentose outside, glabrous inside; staminodes occasionally 1 or 2 present, 0.3–0.4 mm long; ovary ovoid, 2–3.5 mm long, (2- or) 3-locular, smooth, sericeous; stigmas raised, elongated, perpendicular to the sides of the ovary, slightly recurved, apically bifid to c. halfway, 1.8–2.5 mm long, ribbed and laxly laciniate above, glabrous, smooth beneath, sparsely hairy, style remnant absent. *Infructescences* 21–41 by 0.8–1.2 mm, very sparsely tomentose; fruiting pedicel 2–5 mm long, very sparsely tomentose. *Fruits* ovoid, not stiped, young ones beaked, 10–15 by 9–13 mm, almost smooth, drying greyish brown, very sparsely puberulous; pericarp 0.3–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 or 2, half-terete, ellipsoid, 7–9 by 6–8 by 2–4 mm.

Distribution — Malesia: Papua New Guinea.

Habitat & Ecology — Lower montane to montane forest; on ridges, or in gullies; in advanced regrowth. Altitude: 1050–1830 m. Flowering: January to April, September, October; fruiting: June, July, October to January.

Vernacular names — Umatum (Daga).

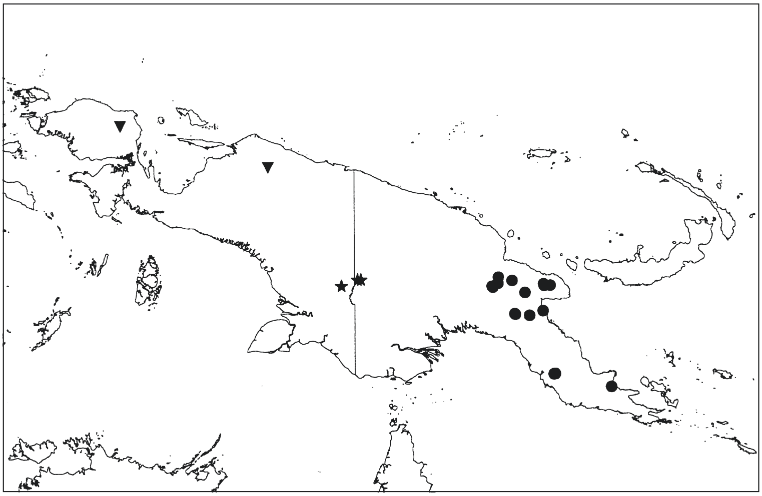
Notes — 1. This species was interpreted as *A. laxiflora* by Airy Shaw, but it has fewer nerves and lacks the disc-like glands along the margin.

2. There is a distinct population near Wau which bear fruits and flowers with shorter pedicels (*Pratt NG-158, Pratt NG 79-1158*, and *Hartley 12945*) or staminate flowers with large pistillodes (*Pratt NG-161* and *NGF 20420*). These staminate flowers can develop small, shortly pedicelled fruits (as found in the LAE specimen of *NGF 20420*)!. A subhermaphrodite specimen? These specimens are inseparable from the common *A. carrii* in vegetative characters. Possibly the hermaphrodite state is developing as a reaction to the higher altitudes (all hermaphrodite specimens occur above 1000 m). The transition to 'normal' staminate specimens is, however, gradual. Also, it is impossible to see whether the staminate specimens with small pistillodes can or cannot develop fruits. The future may show if this variability will become fixed as a new species.

45. **Aporosa decipiens** Pax & K. Hoffm. – Map 10.40

Aporosa decipiens Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 83; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 30. — Neotype (proposed here): *NGF (Ridsdale & Galore) 33470* (holo LAE; iso BO, K, L), Papua New Guinea, Western Prov., Kiunga.

(Small) tree, up to 9 m high, up to 10 cm diameter. *Bark* (dark black) brown, smooth; inner bark light brown to wine red. *Wood* light brown to pale yellow. Young branches densely hirsute. *Stipules* falcate, 5–8 by 9–14 mm, sparsely hirsute beneath, persistent. *Petiole* terete, ridged, 6–10 by 1.2–1.8 mm, densely hirsute, lower pulvinus c. 1.5 by 1.5 mm, upper pulvinus 2–3 by 1.5–2 mm, both indistinct under indumentum. *Leaves* narrowly elliptic, 11–18 by 2.5–5.5 cm; base cordate to rounded, basal glands absent; margin lowly glandular-dentate, recurved, marginal glands many, distinct, black or hairy; apex acuminate to cuspidate; thinnish, dull, rather brittle, smooth, drying bluish or greyish green above, brown beneath; dots absent; disc-like glands absent; only midrib hirsute above, sparsely hirsute beneath, midrib and nerves hirsute, glabrescent. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 12–15 pairs, flat to sunken above, prominent beneath, marginal arches distinct, 1.5–3 mm from margin; tertiary veins and venation distinct, rather laxly reticulate, slightly prominent above, slightly sunken in older leaves, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2 or 3 clustered together, only very young ones seen, 5–8 by 1.5–2.5 mm, densely tomentose; peduncle, bracts, and glomerules not seen. *Staminate flowers* not seen. *Pistillate inflorescences* 1 or 2 clustered together, 3–5 by 1.2–1.5 mm, densely tomentose; flowers 5 or 7, densely set along the rachis; bracts broadly triangular, 0.8–1.2 mm long, densely hirsute outside, sparsely hairy at base only inside; bracteoles narrowly triangular, 0.5–1 mm long, densely hirsute outside, glabrous inside; pedicel absent. *Pistillate flowers* 2–4 mm long; sepals 4, ovate, patent, 1–1.5 mm long, thin, densely hirsute outside, sparsely puberulous inside; ovary ellipsoid, 1.5–2.5 mm long, 3-locular, smooth, densely hirsute; stigmas slightly raised, elongated, apically bifid to near base, perpendicular to the sides of the ovary, straight, 1.5–3 mm long, densely laciniate above, glabrous, smooth beneath, tomentose, style remnant present. *Infructescences* 5–7 mm long, 1.5–2 mm diam., tomentose; fruiting pedicel minute. *Fruits* ovoid, not stiped, slightly beaked, 9–12 by 7–10 mm, punctulate, drying dark brown, (sparsely) hirsute; pericarp 0.5–2



Map 10.40. Distribution of *Aporosa decipiens* Pax & K. Hoffm. (★), *A. egregia* Airy Shaw (▼), and *A. hermaphrodita* Airy Shaw (●).

mm thick, not fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ellipsoid, 6–8 by 4–6 by 2–4 mm.

Distribution — Malesia: Papua New Guinea, Western Province.

Habitat & Ecology — Rain forest, forested hills, swamp forest; lowland. Altitude: 35–60 m. Flowering: August, September; fruiting: July.

Note — Three specimens seen, one very young staminate, a pistillate flowering one, and the neotype, which bears fruits. They agree in most characters with Pax & Hoffmann's description. I have chosen the fruiting specimen as neotype because the fruit is most characteristic for species delimitation in the *papuana*-group.

46. **Aporosa egregia** Airy Shaw — Fig. 3.10c; Map 10.40

Aporusa egregia Airy Shaw, Kew Bull. 29 (1974) 285; Kew Bull., Addit. Ser. 8 (1980) 30. — Type: *Brass 12135* (holo K; iso L, LAE), Indonesia, Papua Barat, Idenburg River.

Tree or shrub, up to 18 m high, up to 30 cm diameter. Young branches very sparsely puberulous. *Stipules* ovate, oblique, 7–10 by 4–9 mm, glabrous, present in young stages. *Petiole* terete, adaxially lowly grooved, 11–26 by 1–1.5 mm, subglabrous, lower pulvinus 1–2 by 1–2 mm, indistinct, upper pulvinus 2–5 by 1.2–2.2 mm, rather distinct. *Leaves* narrowly elliptic to narrowly obovate, 4.5–11.5 by 2–5.5 cm; base obtuse to cuneate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands few, thick, black, distinct; apex acute to acuminate; thick, smooth, brittle, slightly shiny, drying brownish above and beneath; dots irregularly laxly set, fine, blackish, fading; disc-like glands seldom few along the margin, small; glabrous above, very sparsely puberulous beneath, glabrescent. *Nervation*: midrib flat to slightly sunken above, prominent beneath; nerves 6–8 pairs, flat above, prominent beneath, marginal arches distinct, 1–3 mm from the margin; tertiary veins and venation fading, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1 or 2 clustered together, 7–22 by 2–2.5 mm, subglabrous; peduncle 1.5–3 by 0.8–1 mm; bracts broadly triangular, inconspicuous, 0.8–1 mm long, very sparsely puberulous outside, glabrous inside, margin ciliate; glomerules subglobose, consisting of 4–6 laxly set flowers, 2–2.5 by 1.5–1.8 mm, spaced at 0.5–1 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Young staminate flowers* 0.8–1 mm long; sepals 4, obovate, 0.6–0.8 mm long, connate to almost halfway, very sparsely puberulous outside, glabrous inside; stamens 2 (or 3), young ones not exserted, 0.5–0.7 mm long; anthers 0.4–0.5 mm long, connective sparsely hairy; pistillode absent. *Pistillate inflorescences* not seen, induced from infructescence to be ?single, sparsely puberulous; flowers up to 9, rather laxly set at base of rachis, densely apically; bracts broadly triangular, 0.7–1 mm long, sparsely puberulous outside, glabrous inside, margin ciliate; bracteoles not seen, ?absent; pedicel 0.5–1 mm long, sparsely puberulous. *Pistillate flowers* 3–4.5 mm long; sepals 4, ovate, ascending, 0.5–1 mm long, very sparsely puberulous outside, glabrous inside; occasionally 2 stamens present, as in staminate flower; ovary narrowly ovoid, 2-locular, smooth, sparsely puberulous at base, glabrescent towards apex; stigmas slightly raised, elongated, perpendicular to or sometimes slightly ascending from the ovary, apically bifid to near base, straight, 1.5–2 mm long, lowly papillate above, glabrous, smooth beneath, very sparsely puberulous, style remnant present. *Infructescences* 19–24 by

0.8–1.2 mm, very sparsely puberulous; fruiting pedicel 2–4 mm long, very sparsely puberulous. *Fruits* narrowly ellipsoid to fusiform, not stiped, not beaked, 16–19 by 7–9 mm, punctulate, drying dark brown, very sparsely puberulous at base; pericarp 1–2 mm thick, ?rather fleshy; septae and column glabrous. *Seeds* 1, half-terete, ellipsoid, c. 10 by 5 by c. 4 mm.

Distribution — Malesia: Papua Barat.

Habitat & Ecology — Mossy forest; on slope. Altitude: 1800–2000 m. Flowering: October; fruiting: January, October.

47. Aporosa flexuosa Pax & K. Hoffm. — Map 10.41

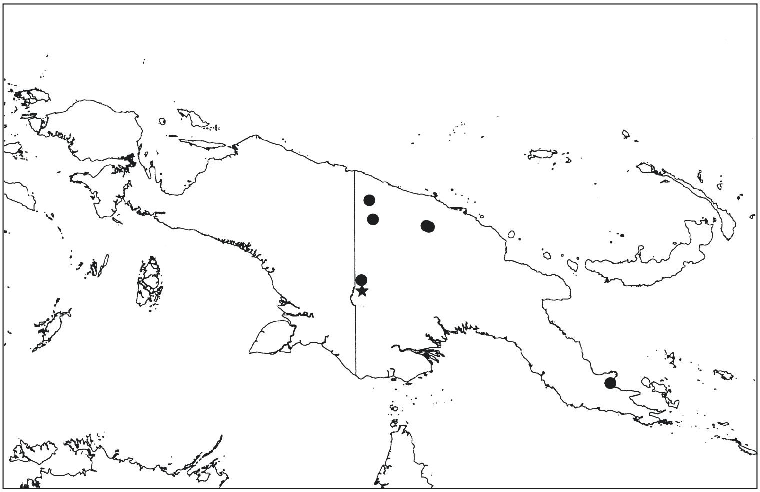
Aporosa flexuosa Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 91; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 30. — Neotype (proposed here): *Pullen 7470* (holo LAE; iso K, L), Papua New Guinea, Western Prov., June River, northern Lake Murray Area.

Slender tree, up 5 m high. Young branches very sparsely tomentose. *Stipules* narrowly ovate, slightly oblique, 2–3 by c. 1 mm, very sparsely puberulous outside, caducous. *Petiole* terete, lowly ribbed, 8–13 by 0.5–0.9 mm, very sparsely tomentose, glabrescent, lower pulvinus c. 1 by 1 mm, upper pulvinus 2–3 by 1–1.2 mm, both rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 6.5–11 by 2.5–3.5 cm; base rounded to obtuse, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands few, small, grey; apex acuminate to cuspidate; blade thin, smooth, slightly shiny, not brittle, drying yellow-green to brown above, (dark) brownish beneath, glabrous above, only midrib and nerves very sparsely tomentose beneath; dots densely set, fine, grey, fading; disc-like glands along the margin, many small, black. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 5–7 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.5–3 mm from the margin; veins and venation distinct, rather laxly reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* and *staminate flowers* not seen. *Pistillate inflorescences* 1 or 2 clustered together, 4–7 by 0.3–0.5 mm, very sparsely puberulous; flowers up to 4, laxly arranged at base of rachis, rather densely apically; bracts broadly triangular, 0.4–0.6 mm long, glabrous, margin ciliate; bracteoles ovate, 0.2–0.3 mm long, glabrous, margin ciliate; pedicel 0.5–1.5 mm long, subglabrous. *Pistillate flowers* 2.5–3.5 mm long; sepals 5 (or 6), ovate, patent, 0.4–0.6 mm long, thin, glabrous; ovary ovoid, 1.5–2.5 mm long, 3-locular, smooth, glabrous; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, slightly recurved, lowly bifid apically, 1–1.5 mm long, laxly papillate to laciniate above, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences*, *fruits* and *seeds* not seen; septae and column in flower glabrous.

Distribution — Malesia: Papua New Guinea.

Habitat & Ecology — Rain forest, low undulating terrain. Altitude: c. 23 m. Flowering: October.

Notes — 1. Known only from *Pullen 7470*, which agrees best with Pax & Hoffmann's description (1922) in vegetative characters. Two other collections referred by Airy Shaw (1980a) to this species do not match, nor are they conspecific. The leaves show a strong likeness to *A. misimana*, and less to *A. leptochrysandra*. Both differ, however, in their inflorescence type.



Map 10.41. Distribution of *Aporosa flexuosa* Pax & K. Hoffm. (★) and *A. ledermannii* Pax & K. Hoffm. (●).

2. Pax & Hoffmann's specimen was staminate, yet they placed this species in their sect. Gymnogynae because of the resemblance to the Philippine *A. banahaensis* (*A. similis*). The fact that *Pullen 7470* also has glabrous ovaries is purely coincidence, the reference to *A. flexuosa* is only based on vegetative characters!

3. There is one staminate specimen, which agrees to Pax & Hoffmann's staminate description. However, the leaves of this one are larger and have more nerves (see *A. spec. B*).

48. **Aporosa hermaphrodita** Airy Shaw — Fig. 3.10a; Map 10.40

Aporusa hermaphrodita Airy Shaw, Kew Bull. 25 (1971) 478; Kew Bull., Addit. Ser. 8 (1980) 30. — Type: *Brass 32401* (holo K; iso A, BO, L), Papua New Guinea, E Highlands Prov., Kassam.

Tree, up to 30 m high, up to 35 cm diameter. *Bark* pale reddish brown, brown, or grey, pocked and flaking, rough to smooth; inner bark very light brown, pinkish straw, or red. *Wood* dark cream. Young branches sparsely puberulous. *Stipules* not seen, early caducous. *Petiole* terete, adaxially lowly grooved, 8–18 by 0.5–1.2 mm, sparsely puberulous, lower pulvinus 1.5–2 by 0.8–1.2 mm, upper pulvinus 2–5 by 0.8–1.5 mm, both rather distinct. *Leaves* (narrowly) ovate to (narrowly) elliptic, 5.5–17 by 2–10 cm; base obtuse to slightly attenuate, basal glands absent; margin lowly crenate to lowly undulate, marginal glands often indistinct, few, small, greyish; apex acuminate to cuspidate; blade thickish, smooth, dull, not brittle, drying greyish green or yellowish green above, (dark) brown beneath, glabrous above, very sparsely puberulous beneath, midrib sparsely puberulous; dots densely set, fine, blackish; disc-like glands absent. *Nervation*: midrib flat to raised in a furrow above, prominent beneath; nerves 6–10 pairs, slightly prominent to flat above, prominent beneath, marginal arches often distinct, sometimes fading, 1–2 mm from margin; tertiary veins and venation fading, rather densely reticulate, sometimes slightly scalariform, slightly prominent to flat. *Inflorescences* axillary or just below the leaves, 1–4 clustered together, 5–28 by 0.3–0.5 mm, (sparsely) puberulous; flowers bisexual, up to 6, laxly arranged at base of rachis, more densely apically; bracts broadly triangular, 1–1.8 mm long, sparsely puberulous outside, glabrous inside, margin ciliate; bracteoles narrowly ovate, 0.3–0.7 mm long, puberulous outside, glabrous inside; pedicel 1–3.5 mm long, (very sparsely) puberulous. *Flowers* 3–4.5 mm long; sepals 4 (or 5), ovate, ascending, 1–1.5 mm long, thin, sparsely puberulous outside, glabrous inside; stamens 4 (or 5), subepisepalous, exserted, 1.2–2.2 mm long; anthers 0.4–0.5 mm long, connective sparsely hairy; ovary ovoid, 1.5–3.5 mm long, 2- (or 3-)locular, smooth, sparsely puberulous at base, glabrescent towards apex; stigmas raised, elongated, apically bifid, perpendicular to the sides of the ovary, slightly recurved, 1.5–2.5 mm long, longitudinally ribbed above, margins lowly papillate, glabrous, smooth beneath, glabrous, style remnant absent. *Infructescences* 11–38 by 0.8–1.2 mm, (sparsely) puberulous; fruiting pedicel 2–7 mm long, sparsely puberulous. *Fruits* ellipsoid to ovoid, not stiped, slightly beaked, 8–13 by 8–13 mm, punct(ul)ate, drying brownish, very sparsely puberulous at base; pericarp 0.3–0.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 or 2 (seldom 3), half-terete, ellipsoid, 6.5–8 by 5.5–6.5 by 3–4 mm.

Distribution — Malesia: Papua New Guinea.

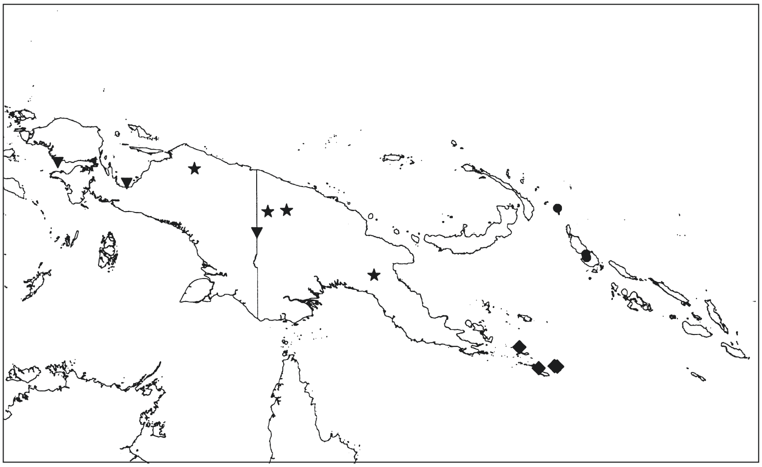
Habitat & Ecology — Primary, secondary, or mid-mountain rain forest, mossy forest, or oak forest; on ridges, slopes, (steep) hills, or in river gorges. Soil: loamy. Altitude: 1070–2100 m. Flowering: September, October; fruiting: June to September, December, January. Seed aril recorded to be extremely bitter.

Vernacular names — Bepu (Naho).

49. **Aporosa heterodoxa** Airy Shaw — Fig. 3.10b; Map 10.42

Aporusa heterodoxa Airy Shaw, Kew Bull. 25 (1971) 479; Kew Bull., Addit. Ser. 8 (1980) 31, in obs. — Type: *Schodde (& Craven) 3762* (holo K; iso BO, L), Papua New Guinea, Bougainville, Lake Loloru.

(Small) tree, up to 17 m high, up to 12 cm diameter. *Bark* mid brown to red brown, smooth, striate, to rather rough pustular or nodular; inner bark pale chestnut. *Wood* (pale) cream to creamy brown. Young branches very sparsely puberulous. *Stipules* not seen, early caducous. *Petiole* (half-)terete, adaxially grooved, 8–15 by 1.2–2 mm, very sparsely puberulous, glabrescent, lower pulvinus 1.5–3 by 1.5–2 mm, upper pulvinus 3–6 by 1.8–2.2 mm, both rather distinct. *Leaves* narrowly ovate to (narrowly) elliptic, 8–16 by 3.5–9 cm; base rounded to slightly attenuate, basal glands absent; margin lowly undulate to lowly crenate, marginal glands few, grey, indistinct; apex acuminate; blade thickish, smooth, dull, sometimes brittle, drying bluish or yellowish green to brown above, brown beneath, glabrous above, only midrib and nerves very sparsely puberulous beneath, glabrescent; dots patchy densely set, fine, grey to black; disc-like glands seldom few present, small, along margin. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 6–9 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 2.5–5 mm from the margin; tertiary veins and venation fading, laxly reticulate, flat above, (slightly) prominent beneath. *Inflores-*



Map 10.42. Distribution of *Aporosa heterodoxa* Airy Shaw (●), *A. lamellata* Airy Shaw (★), *A. longicaudata* Kaneh. & Hatus. ex Schot (▼), and *A. misimana* Airy Shaw ex Schot (◆).

cences axillary or just below the leaves, 3–8 clustered together, 12–37 by 0.5–1 mm, (sparsely) puberulous; flowers bisexual, up to 15, laxly set at base of rachis, sometimes more densely set apically; bracts broadly triangular, 0.5–1 mm long, sparsely puberulous outside, glabrous inside, margin sparsely ciliate; bracteoles broadly triangular, 0.3–0.8 mm long, sparsely puberulous outside, glabrous inside, margin sparsely ciliate; pedicel 0.5–1 mm long, (sparsely) puberulous. *Flowers* 2.5–4 mm long; sepals 4, ovate, ascending, 0.5–1.2 mm long, thin, sparsely puberulous outside, glabrous inside; stamens 4, slightly exerted, 0.5–0.7 mm long; anthers 0.4–0.5 mm long, connective glabrous; ovary ovoid, 1.5–2.5 mm long, 2- or 3-locular, smooth, sparsely puberulous at base, glabrescent towards apex; stigmas slightly raised, elongated, apically bifid to c. halfway, perpendicular to the sides of the ovary, slightly recurved, 0.8–1.2 mm long, laxly papillate above, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 25–44 by 1–1.2 mm, sparsely puberulous; fruiting pedicel 3–5 mm long, sparsely puberulous. *Fruits* globose, not stiped, slightly beaked, 12–13 by 11–14 mm, punctulate, drying (dark) brown, very sparsely hairy; pericarp 0.5–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 2 or 3, only immature ones seen.

Distribution — Malesia: Papua New Guinea, Bougainville.

Habitat & Ecology — Primary montane, cloud or rain forest; on slopes. Altitude: 660–1200 m. Flowering: August; fruiting: August, October.

Note — I have seen two specimens in flower, *Schodde (& Craven) 3762* (type) and *Schodde (& Craven) 3875*. The first one has young flowers, the second old ones. They differ in that the first often has 2 or 3 (!) flowers clustered together in one bract, no bracteoles, and very short pedicels. The second specimen has single flowers, bracteoles, and a distinct pedicel. These differences may be explained by assuming that *Schodde (& Craven) 3762* has inflorescences derived from staminate inflorescences, and *Schodde (& Craven) 3875* inflorescences derived from pistillate ones. But before accepting this hypothesis, a comparison with more material is essential.

50. **Aporosa lamellata** Airy Shaw — Fig. 3.9e, f; Map 10.42

Aporusa lamellata Airy Shaw, Kew Bull. 33 (1978) 26; Kew Bull., Addit. Ser. 8 (1980) 31. — Type: *Brass 13469* (holo BRI; iso BO, L), Indonesia, Papua Barat, Idenburg River.

(Slender) tree, up to 20 m high, up to 20 cm diameter. *Bark* dark brown, with reddish sap; inner bark dull pink. *Wood* yellowish straw. Young branches tomentose. *Stipules* falcate, 6–12 by 14–18 mm, sparsely tomentose beneath, often persistent. *Petiole* terete, adaxially grooved, 11–37 by 2–2.5 mm, tomentose, lower pulvinus 2–3 by 2–3 mm, upper pulvinus 3–5 by 2.5–3.5 mm, both rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 20–32.5 by 6.5–10 cm; base subcordate to rounded, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular to many, distinct, black; apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, drying (dark) bluish or greyish green above, brown beneath, only midrib tomentose above, very sparsely tomentose beneath, midrib and nerves tomentose, glabrescent; dots irregularly patchy densely set, very fine, black, fading; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 12–15 pairs, flat to slightly sunken above, prominent beneath, marginal arches distinct, 1–3 mm from margin; tertiary veins and venation distinct, densely reticulate, slightly scalariform, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* borne on the upper branches. *Staminate inflorescences* and *staminate flowers* not seen. *Pistillate inflorescences* 1–3 clustered together, 12–78 by 0.8–1.2 mm, densely tomentose; flowers up to 19, rather densely set along the rachis; bracts broadly triangular, 1.8–2.2 mm long, densely tomentose outside, glabrous inside; bracteoles triangular, 0.8–1.2 mm long, thin, densely tomentose outside, glabrous inside; pedicel minute. *Pistillate flowers* 3–4 mm long; sepals 5, ovate, patent, 0.5–1.2 mm long, tomentose outside, sparsely puberulous inside; ovary ellipsoid to globose, 1.5–2.5 mm long, 3–5-locular, with 6, 8 or 10 lamellae, tomentose; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, straight, apically bifid to near base, 1.8–3 mm long, densely laciniate above, glabrous, smooth beneath, tomentose, style remnant present. *Infructescences* 38–51 by 2.5–3 mm, tomentose; fruiting pedicel 1.5–3 mm long, tomentose. *Fruits* broadly ellipsoid, not stiped, not beaked, 11–16 by 18–23 mm, striate, with 6, 8, or 10 lamellae, drying reddish brown, (sparsely) tomentose; pericarp 1–2 mm thick, not fleshy; septae and column glabrous. *Seeds* 3–5, half-terete, ovoid, 8–10 by 5–8 by 3–5 mm.

Distribution — Malesia: Papua Barat, Papua New Guinea.

Habitat & Ecology — Secondary forest; on hillsides or ridges. Soil: copper rich. Altitude: 450–1200 m. Flowering: June; fruiting: March, April.

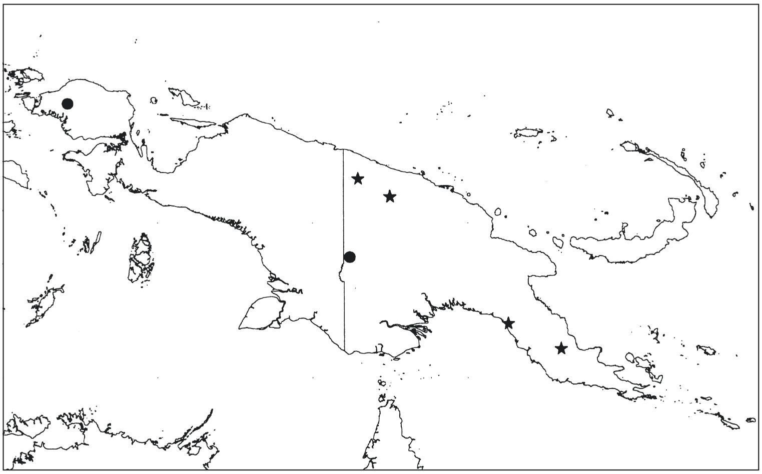
Notes — 1. Specimen *Ledermann 9557*, cited by Pax & K. Hoffmann (1922) to be near *A. papuana* but differing in its lobed 3- or 4-locular ovary is *A. lamellata*.

2. In view of the strong resemblance in leaves between *A. lamellata*, *A. papuana*, *A. brassii*, and to a lesser degree also *A. vagans* and *A. decipiens*, it will be quite difficult to find specimens with staminate inflorescences which match *A. lamellata*.

51. **Aporosa laxiflora** Pax & K. Hoffm. — Map 10.43

Aporosa laxiflora Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 95; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 31. — Lectotype (proposed here): *Ledermann 8010* (K), Papua New Guinea, Sepik Prov., Malu.

(Small) tree, up to 10 m high, up to 20 cm diameter. *Bark* grey, vertically cracked; inner bark straw brown, 6 mm thick. Young branches sparsely puberulous. *Stipules* falcate, 5–7 by 11–14 mm, glabrous above, very sparsely puberulous beneath, present in young stages. *Petiole* terete, adaxially grooved, 11–28 by 1–2 mm, very sparsely puberulous, glabrescent, lower pulvinus 2–4 by 1.5–2.5 mm, upper pulvinus 4–7 by 1.8–3 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 17–27 by 4–10 cm; base subcordate to obtuse, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular to many, distinct, black; apex acuminate; blade thickish, smooth, shiny, not brittle, drying greenish grey to brownish grey above and beneath, glabrous above, only midrib and nerves very sparsely puberulous beneath, glabrescent; dots laxly set, fine, greyish, mostly indistinct; disc-like glands often present, along the margin, blackish, distinct. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 10–14 pairs, slightly prominent to flat above, prominent beneath, marginal arches often fading, 3–6 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 14–36 by 0.7–1.5 mm, sparsely puberulous; peduncle 1–3 by 0.5–0.8 mm; bracts broadly triangular, inconspicuous, 0.5–0.8 mm long, sparsely puberulous outside, sparsely puberulous at base only inside, margin ciliate; glomerules globose, 1–1.5 by 1–1.5 mm, consisting of 7–12 densely set flowers, spaced at 1–5 mm along the rachis; pedicel 0.2–0.3 mm long. *Staminate flowers* 0.8–1.5 mm long; sepals (4 or) 5, narrowly obovate, 0.4–0.7 mm long, connate at base only, sparsely puberulous outside, glabrous inside, margin ciliate; stamens 3 or 4, exserted, 1–1.5 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode a minute hair tuft. *Pistillate inflorescences* 1 or 2 clustered together, 13–24 by 0.8–1 mm, (sparsely) puberulous; flowers up to 11, rather laxly set along the rachis; bracts broadly triangular, 0.4–0.6 mm long, sparsely puberulous outside, sparsely puberulous at base only inside; bracteoles ovate, 0.3–0.5 mm long, sparsely puberulous outside, puberulous at base only inside; pedicel 1–3 mm long, (sparsely)



Map 10.43. Distribution of *Aporosa laxiflora* Pax & K. Hoffm. (★) and *A. spec. C* (●).

puberulous. *Pistillate flowers* 4–6 mm long; sepals 4, ovate, patent, 0.8–1.2 mm long, thin, sparsely puberulous outside, glabrous inside; ovary ovoid, 3–4.5 mm long, 3- (or 4-)locular, smooth, (sparsely) puberulous; stigmas raised, elongated, apically bifid to c. halfway, perpendicular to the sides of the ovary, slightly recurved, 1.2–2 mm long, longitudinally ribbed above, papillate, glabrous, smooth beneath, sparsely puberulous, style remnant present. *Infructescences* 13–23 by 1–1.8 mm, sparsely tomentose; fruiting pedicel 2–11 mm long, sparsely tomentose. *Fruits* ovoid to subglobose, not stiped, not beaked, 13–15 by 13–15 mm, punctate, drying reddish to dark brown, sparsely tomentose; pericarp 0.3–0.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ellipsoid, 8–11 by 6.5–8.5 by 3–3.5 mm.

Distribution — Malesia: Papua New Guinea.

Habitat & Ecology — In rain forest, on ridges. Altitude: 50–550 m. Flowering: October; fruiting: September.

Vernacular names — Akaia-naeku (Mekeo language, Maipa dialect).

Note — In addition to the only surviving *Ledermann* collection, I refer to this species *NGF 3935*, from the Yellow River Hills, *Paijmans 167*, from the Northern Prov., and tentatively *Darbyshire 870*, from Maipa, Central Province.

52. Aporosa ledermanniana Pax & K. Hoffm. — Fig. 3.5q, 3.7m, 3.8d; Map 10.41

Aporosa ledermanniana Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 84; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 32 (p.p.). — Type: *Ledermann 7270* (holo B†; iso K), Papua New Guinea, Sepik river.

Tree, up to 10 m high, up to 25 cm diameter. *Bark* dark brown to pale grey, smooth; inner bark brown or pink, fibrous. *Wood* pale yellow. Young branches sparsely tomentose. *Stipules* falcate, 3–5 by 6–8 mm, rather persistent, glabrous above, at base sparsely tomentose beneath, scattered round black glands beneath. *Petiole* terete, adaxially lowly grooved, 7–13 by 0.8–1.2 mm, sparsely tomentose, glabrescent, lower pulvinus 1–1.5 by 1–1.2 mm, upper pulvinus 2–4 by 1–1.5 mm, both rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 9–17.5 by 3.5–7 cm; base rounded to obtuse, basal glands absent; margin lowly glandular-crenate, marginal glands many, small, grey, often indistinct; apex acuminate to cuspidate; blade thin, smooth, dull, not brittle, drying greyish green to dark brownish above, greyish or dark brown beneath, only midrib sparsely tomentose above, midrib and nerves sparsely tomentose beneath, glabrescent; dots densely set, fine, grey, fading in older leaves; disc-like glands irregularly scattered within the marginal arches, many, black. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 10–12 pairs, slightly prominent to flat above, prominent beneath, marginal arches fading, 1.5–4 mm from the margin; tertiary veins and venation indistinct, rather laxly reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–4 clustered together, 10–19 by 1.5–2 mm, (sparsely) tomentose; peduncle 2–6 by 0.3–0.5 mm; bracts broadly triangular, inconspicuous, 0.8–1.2 mm long, sparsely puberulous outside, hairy at base only inside, margin ciliate; glomerules subglobose, 2–2.5 by 1–2 mm, consisting of more than 10 rather densely set flowers, spaced at 3–5 mm at base of rachis, decreasing to 0.5 mm at apex; pedicel 0.2–0.3 mm long. *Staminate flowers* 1.5–2 mm long; sepals 4, narrowly obovate, 0.5–0.9 mm long, connate to c. halfway, glabrous, ciliate;

stamens 2 or 3, exserted, 1.2–2 mm long; anthers 0.3–0.4 mm long, glabrous; pistillode absent. *Pistillate inflorescences* 1–4 clustered together, 7–11 by 0.5–0.8 mm, (sparsely) tomentose; flowers up to 9, laxly arranged at base of rachis, rather densely apex; bracts broadly triangular, 0.5–1 mm long, sparsely puberulous outside, glabrous inside, margin ciliate; bracteoles triangular, 0.3–0.5 mm long, puberulous outside, glabrous inside; pedicel 0.5–1.5 mm long, (sparsely) tomentose. *Pistillate flowers* 2–3.5 mm long; sepals 4, ovate, patent, 0.4–0.8 mm long, sparsely puberulous outside, glabrous inside; ovary ovoid, 1.5–2.5 mm long, 2- or 3-locular, smooth, sparsely puberulous; stigmas slightly raised, elongated, ?undivided, perpendicular to the sides of the ovary, slightly recurved, 1.2–2 mm long, laxly laciniate above, glabrous, smooth beneath, sparsely puberulous, style remnant present. *Infructescences* 7–17 by 0.5–0.8 mm, sparsely tomentose; fruiting pedicel 2–4 mm long, sparsely tomentose. *Fruits* ellipsoid, not stiped, not beaked, 9–11 by 7–8 mm, punctulate, subglabrous; pericarp 0.3–0.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 or 2, half-terete, ovoid, c. 7 by 4 by c. 2 mm.

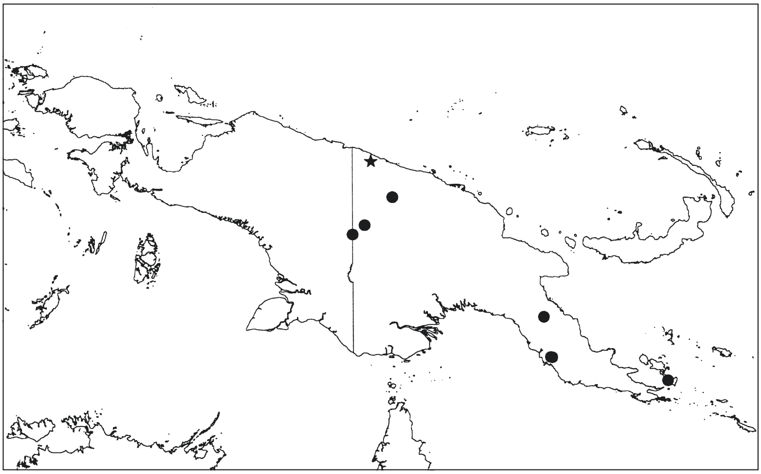
Distribution — Malesia: Papua New Guinea: Northern Province.

Habitat & Ecology — Swamp forest; on swampy ground, subject to flooding; along rivers. Altitude: 30–75 m. Flowering: May, July, September; fruiting: October.

53. **Aporosa leptochrysandra** Airy Shaw — Fig. 3.5m, 3.7o; Map 10.44

Aporusa leptochrysandra Airy Shaw, Kew Bull. 20 (1966) 381 (type only); Kew Bull., Addit. Ser. 8 (1980) 32. — Type: *Darbyshire & Hoogland 8375* (holo K; iso L, LAE), Papua New Guinea, Sepik Prov., Wantapi.

Small tree. Young branches ?glabrous. *Stipules* not seen, early caducous. *Petiole* terete, adaxially lowly grooved, 8–17 by 0.8–1.2 mm, glabrous, lower pulvinus 1–1.5 by 1–1.5 mm, upper pulvinus 3–5 by 1.2–2 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 10–15 by 4–7.5 cm; base cuneate to attenuate, basal glands absent;



Map 10.44. Distribution of *Aporosa leptochrysandra* Airy Shaw (★) and *A. nigropunctata* Pax & K. Hoffm. (●).

margin subentire, marginal glands few, grey, indistinct; apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, drying greyish to bluish green above, brownish beneath, ?glabrous; dots densely set, fine, grey; disc-like glands along the margin, occasionally present, black. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 6–8 pairs, slightly prominent to flat above, prominent beneath, marginal arches rather distinct, 2–4 mm from the margin; tertiary veins and venation fading, laxly reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 11–27 by 0.5–1 mm, very sparsely puberulous; peduncle absent; bracts broadly triangular, 0.4–0.6 mm long, inconspicuous, very sparsely puberulous outside, glabrous inside; glomerules indistinct, consisting of 2–5 flowers, spaced continuously along the rachis; pedicel absent. *Staminate flowers* 1–1.5 mm long; sepals 4, elliptic, 0.5–0.7 mm long, connate to c. halfway, glabrous, margin sparsely ciliate; stamens 2, exserted, 1–1.8 mm long; anthers 0.2–0.3 mm long; pistillode absent. *Pistillate inflorescences*, *pistillate flowers*, *infructescences*, *fruits*, and *seeds* not seen.

Distribution — Malesia: Papua New Guinea: Sepik Province.

Habitat & Ecology — In tall foothill forest. Altitude: c. 275 m. Flowering: August.

Vernacular name — Pohruru (Orne language, Wantipi dialect).

Note — Only truly known from the type. Airy Shaw (1966) lists a couple of fruiting specimens, but these belong to *A. hermaphrodita* or *A. carrii*.

54. Aporosa leytensis Merr. — Fig. 3.6n, 3.8e; Map 10.45

Aporosa leytensis Merr., Philipp. J. Sci., Bot. 9 (1914) 368; Enum. Philipp. Flow. Pl. 2 (1923) 410; Schot, Blumea 40 (1995) 452. — Type: *Wenzel 614* (iso A, BM, L), Philippines, Leyte.

Aporosa alvarezii Merr., Philipp. J. Sci., Bot. 9 (1914) 470; Enum. Philip. Fl. Pl. 2 (1923) 409. — Type: *FB (Alvarez) 21245* (iso K), Philippines, Luzon.

?*Aporusa grandistipula* auct. non Merr.: Airy Shaw, Kew Bull. 37 (1982) 7.

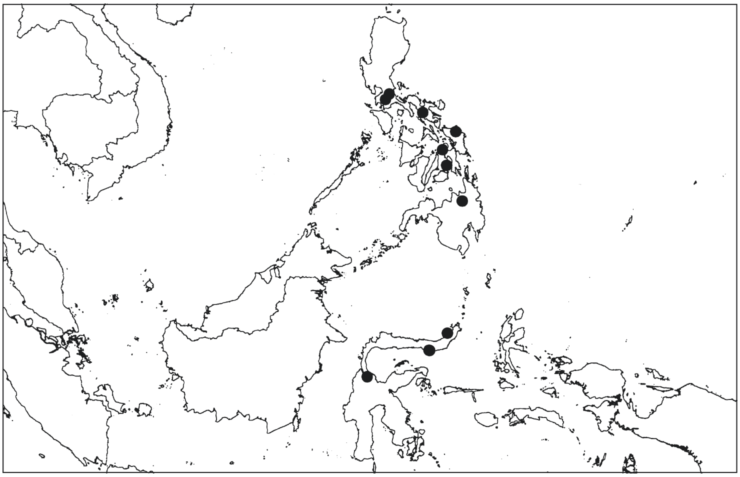
(Small or slender) tree, up to 20 m high, up to 18 cm diameter. *Bark* rufous brown or greyish brown, with scattered small adherent scales; inner bark brown. *Wood* pale ochre. Young branches tomentose to hirsute. *Stipules* falcate, 5–9 mm by 8–16 mm, sparsely hirsute, glabrescent, often persistent. *Petiole* terete, adaxially grooved, 7–16 by 1.2–2 mm, tomentose to hirsute, glabrescent, pulvinate at both ends, lower pulvinus 1.5–3 by 1.5–2.5 mm, sometimes indistinct, upper pulvinus 2–5 by 1.5–2.8 mm, distinct. *Leaves* narrowly ovate to narrowly elliptic, 10–26.5 by 4–9.5 cm; base rounded to subcordate, basal glands absent; margin lowly undulate to lowly glandular-crenate or glandular-serrate, marginal glands regular to many, distinct, greyish to black, young ones hairy; apex acuminate to cuspidate; blade thinnish, smooth, mostly dull, not brittle, drying greyish or bluish green to reddish brown above, greyish brown beneath, sparsely tomentose to hirsute, glabrescent, midrib tomentose to hirsute above, midrib and nerves tomentose to hirsute beneath; dots laxly set, fine, greyish to black, fading; disc-like glands occasionally few, small at base within marginal arches. *Nervation*: midrib slightly prominent to flat above, sometimes sunken, prominent beneath; nerves 9–13 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1–4 mm from the margin; tertiary veins and venation fading, rather densely reticulate, slightly scalariform, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–6 clustered together, 14–59 by 2–3 mm, densely (reddish) tomentose; peduncle 2–6 mm long, 0.8–1 mm diam.; bracts broadly triangular, inconspicuous, 0.8–1 mm long, sparsely hirsute outside, glabrous inside; glomerules ellipsoid, 2–4 by 1.2–2 mm, consisting of 9–13 densely set flowers, spaced at 1–2 mm at the base of the rachis, decreasing to 0 mm at apex; pedicel 0.2–0.3 mm long, sparsely hirsute. *Staminate flowers* 1–1.5 mm long; sepals 4 (or 5), obovate, connate at base, 1.2–1.4 mm long, sparsely hirsute outside, glabrous inside; stamens 4, exserted, 1.2–1.8 mm long; anthers 0.3–0.4 mm long, connective ?glabrescent; pistillode 0.2–0.3 mm long, lumpy, apex hairy. *Pistillate inflorescences* 1–4 clustered together, 18–35 by 1–1.5 mm, (reddish) tomentose; flowers up to 11, mostly rather densely set along the rachis; bracts broadly triangular, 1–1.2 mm long, sparsely hirsute outside, glabrous inside; bracteoles triangular, 0.8–1 mm long, sparsely hirsute outside, glabrous inside; pedicel 1–3 mm long, (reddish) tomentose. *Pistillate flowers* 3–5 mm long; sepals 4, ovate, patent, 0.8–1.2 mm long, thin, sparsely hirsute outside, glabrous inside; ovary ovoid, 2–3 mm long, (2- or) 3-locular, smooth, sericeous; stigmas raised, elongated, perpendicular to the sides of the ovary, slightly recurved, apically bifid to c. halfway, 1–1.5 mm long, papillate above, glabrous, smooth beneath, sparsely sericeous, style remnant present. *Infructescences* 15–54 by 1.5–2 mm, (sparsely) tomentose; fruiting pedicel 2–5 mm long, (sparsely) tomentose. *Fruits* (broadly) ovoid, not stiped, slightly beaked, 12–17 by 10–19 mm, punctulate to smooth, drying (light) brownish, sparsely puberulous; pericarp 0.5–3 mm thick, not fleshy; septae and column glabrous. *Seeds* 1–3, (half-)terete, ovoid, 8–11 by 7–8 by 3–5 mm.

Distribution — Malesia: Philippines, Sulawesi.

Habitat & Ecology — Primary, (un)disturbed rain forest; in lowland, on hillsides, hill ridges, along paths or rivers. Soil: clayey volcanic. Altitude:250–750 m. Flowering: February, March, September; fruiting: March, June, September.

Uses — Fruit said to be edible.

Notes — 1. The specimen *Johansson, Nyboom & Riebe 198* from Central Sulawesi has subglabrous leaves with relatively more nerves and smaller fruits with a lesser



Map 10.45. Distribution of *Aporosa leytensis* Merr.

indumentum. Two other collections from North Sulawesi have sparsely tomentose leaves, but have the smaller, less hairy fruits with pericarp 0.5–1 mm thick like the Central Sulawesian collection. Staminate specimens found in North Sulawesi have also a smaller, less hairy rachis in their inflorescences. This might indicate a geographical variation, but whether these differences are on forma, variety, or even species level is impossible to say on the base of so few collections.

2. *Aporosa grandistipula* is to my knowledge restricted to Borneo.

55. Aporosa longicaudata Kaneh. & Hatus. ex Schot — Map 10.42

Aporosa longicaudata Kaneh. & Hatus. ex Schot, Blumea 40 (1995) 456. — Type: *Kanehira & Hatusima 12343* (holo FU; iso A, BO), Indonesia, Papua Barat, Nabire.

Tree or shrub, up to 10 m high. Young branches sparsely tomentose. *Stipules* (narrowly) ovate, oblique, 9–14 by 3–6 mm, at base very sparsely hirsute beneath, present in young stages. *Petiole* terete, adaxially grooved, 3–8 by 0.8–1 mm, sparsely tomentose, lower pulvinus c. 1 by 1 mm, upper pulvinus 1.5–3 by 1–1.2 mm, both rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 6.5–14 by 1.5–4.5 cm; base cuneate to slightly attenuate, basal glands absent; margin irregularly lowly glandular-crenate to subentire, marginal glands few, small, indistinct; apex cuspidate to caudate; blade thin, smooth, dull, not brittle, drying dark greyish green above, blackening, (dark) brown beneath, only midrib sparsely tomentose above, glabrescent, midrib and nerves sparsely tomentose beneath, glabrescent; dots densely set, fine, black, fading; disc-like glands seldom present, along margin, black. *Nervation*: midrib flat to slightly sunken above, prominent beneath; nerves 10–13 pairs, flat to slightly sunken above, prominent beneath, marginal arches distinct, 2–4 mm from the margin; tertiary veins and venation fading, rather densely reticulate, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* clustered 3 or 4 together, 4–7 by 1–1.5 mm, sparsely tomentose; peduncle 0.5–1 by 0.5–0.8 mm; bracts broadly triangular, inconspicuous, 0.5–0.8 mm long, (sub)glabrous outside, glabrous inside, margin ciliate; glomerules globose, rather indistinct, consisting of 5–7 rather densely set flowers, set continuously along the rachis or slightly interrupted at base; pedicel absent. *Staminate flowers* 0.3–0.6 mm long; sepals 4, obovate, 0.5–0.7 mm long, connate at base only, sparsely puberulous outside, glabrous inside; stamens 2, not to slightly exserted, 0.3–0.5 mm long; anthers c. 0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* clustered 1 or 2 together, c. 6 by 0.8 mm, tomentose; flowers up to 11, rather laxly set at base of rachis, more densely apically; bracts broadly triangular, 0.5–0.8 mm long, sparsely hirsute outside, glabrous inside, margin ciliate; bracteoles triangular, 0.4–0.6 mm long, sparsely sericeous outside, glabrous inside; pedicel minute. *Pistillate flowers* c. 4 mm long; sepals in young fruit 4, ovate, patent, 0.4–0.7 mm long, thin, sparsely hirsute outside, glabrous inside; ovary ovoid, c. 3 mm long, 3-locular, smooth, sparsely tomentose, glabrescent towards apex; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, recurved, apically bifid to c. halfway, 1–1.5 mm long, papillate to laciniate above, glabrous, ribbed beneath, sparsely hairy, style remnant absent. *Infructescences* 14–47 by 0.8–1.2 mm, sparsely tomentose; fruiting pedicel less than 0.5 mm long, sparsely tomentose. *Fruits* ovoid, not stiped, not beaked, 10–11 by 9–10 mm, punctulate to smooth, drying dark brown, sometimes mottled, sparsely puberulous; pericarp 0.5–1.2 mm thick, not fleshy; septae and column glabrous. *Seeds* 3, half-terete, ovoid, 7–8 by c. 6 by 2–3 mm.

Distribution — Malesia: Papua Barat, Papua New Guinea.

Habitat & Ecology — Broken forest, on hillsides. Altitude: 10–400 m. Flowering: April, May, August; fruiting: March, June.

56. Aporosa misimana Airy Shaw ex Schot — Fig. 3.6x, 3.8i; Map 10.42

Aporosa misimana Airy Shaw ex Schot, Blumea 40 (1995) 457. — Type: *Brass 27800* (holo K; iso L, LAE), Papua New Guinea, Sudest Island.

Tree, up to 15 m high, up to 20 cm diameter. *Bark* black; inner bark (light) green or dark red, thinly fibrous. *Wood* white or orange-brown Young branches sparsely puberulous. *Stipules* slightly falcate, 2–4 by 4–6 mm, at margin sparsely hairy beneath, caducous. *Petiole* terete, adaxially lowly grooved to smooth, 6–14 by 0.8–1.2 mm, sparsely puberulous, lower pulvinus 1–2 by 1–1.2 mm, upper pulvinus 1.5–2.5 by 1–1.5 mm, both distinct. *Leaves* (narrowly) elliptic, 8–18 by 2.5–7 cm; base cordate to cuneate, basal glands absent; margin subentire, marginal glands few, grey, indistinct; apex acuminate to cuspidate; blade thin, smooth, slightly shiny, not brittle, drying grey-green to brown above, darkening, (dark) brown beneath, ?glabrous above, midrib and nerves sparsely puberulous beneath; dots densely set, fine, black; disc-like glands occasionally present, along the margin, black. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 7–9 pairs, slightly prominent to flat above, (slightly) prominent beneath, marginal arches distinct, 1–3 mm from the margin; tertiary veins and venation distinct, rather densely reticulate, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 8–16 by 1–1.5 mm, sparsely puberulous; peduncle absent; bracts broadly triangular, inconspicuous, 0.5–0.7 mm long, sparsely puberulous outside, glabrous inside; glomerules indistinct, consisting of 4–6 flowers, spaced rather continuously along the rachis; pedicel absent. *Staminate flowers* 1.2–1.8 mm long; sepals 4, elliptic, 0.5–0.7 mm long, connate to halfway, sparsely puberulous outside, glabrous inside; stamens 2, exserted, 1–1.8 mm long; anthers 0.2–0.3 mm long, glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 3–6 by 0.5–1 mm, tomentose; flowers up to 9, densely arranged along the rachis; bracts broadly triangular, 0.4–0.7 mm long, puberulous outside, glabrous inside; bracteoles narrowly ovate, 0.2–0.4 mm long, puberulous outside, glabrous inside; pedicel minute, 0–0.3 mm long. *Pistillate flowers* 3–4.5 mm long; sepals 4 (or 5), ovate (the 5th narrowly ovate), patent, 0.5–0.8 mm long, sparsely puberulous outside, glabrous inside; ovary ovoid, 2–3.5 mm long, 2-locular, smooth, very sparsely puberulous, glabrescent; stigmas slightly raised, elongated, apically bifid to slightly more than halfway, perpendicular to the sides of the ovary, recurved, 1.5–2.5 mm long, laxly papillate to laciniate above, glabrous, smooth beneath, very sparsely puberulous, style remnant present. *Infructescences* 3–18 by 0.8–1.2 mm, (sparsely) tomentose; fruiting pedicel minute. *Fruits* (broadly) ellipsoid, not stiped, not beaked, 8–10 by 7–10 mm, punctate, subglabrous; pericarp 0.5–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 or 2, (half-)terete, ellipsoid, c. 6.5 by 4.5 by 3 mm.

Distribution — Malesia: Papua New Guinea: Eastern Papuan Islands.

Habitat & Ecology — Rain forest; in low land, on hills and ridges. Altitude: 60–300 m. Flowering: August; fruiting: March, July, August.

57. **Aporosa nigropunctata** Pax & K. Hoffm. — Fig. 3.6y; Map 10.44

Aporosa nigropunctata Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 98; Airy Shaw, Kew Bull. 20 (1966) 382, excl. var. *antennifera*; Kew Bull., Addit. Ser. 8 (1980) 32. — Lectotype (proposed here): *Ledermann 9698* (holo B†; iso L), Papua New Guinea, Sepik Prov., April river.

Tree or shrub, up to 8 m high, up to 6 cm diameter. *Bark* reddish brown, coppery brown, or pale grey brown, vertically cracked; inner bark reddish or straw brown. *Wood* pinkish brown. Young branches (sparsely) tomentose. *Stipules* narrowly ovate, slightly oblique, 1.5–2 by 0.5–0.8 mm, sparsely puberulous beneath, caducous. *Petiole* terete, adaxially lowly grooved, 5–13 by 0.5–0.8, (sparsely) tomentose, lower pulvinus 1–1.5 by 0.8–1 mm, upper pulvinus 1.5–3 by 0.8–1.2 mm, both rather distinct. *Leaves* (narrowly) elliptic, 5–12.5 by 1.5–4.5 cm; base rounded to slightly attenuate, basal glands absent; margin lowly crenate to subentire, marginal glands few, black, indistinct; apex cuspidate to caudate; blade thin, smooth, dull, not brittle, drying greyish brown or greenish brown above, blackening, (dark) brown beneath, ?glabrous above, only midrib and nerves (sparsely) tomentose beneath; dots densely set, fine, black, fading; disc-like glands often present, small, along the margin. *Nervation*: midrib flat to raised in a furrow above, prominent beneath; nerves 6–9 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1–3 mm from the margin; tertiary veins and venation distinct, rather densely reticulate, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–5 clustered together, 10–21 by 1–1.5 mm, puberulous; peduncle 1–4 by c. 0.5 mm; bracts broadly triangular, inconspicuous, 0.5–0.8 mm long, sparsely puberulous outside, glabrous inside, margin ciliate; glomerules globose, 1.5–1.8 by 1.2–1.8 mm, consisting of 6–10 densely set flowers, set at 2–4 mm along the rachis; pedicel minute. *Staminate flowers* 1–1.5 mm long; sepals 4, obovate, 0.5–0.8 mm long, connate to c. halfway, sparsely puberulous outside, glabrous inside, margin ciliate; stamens 2 or 3, slightly exserted, 0.8–1.2 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode cylindric, minute, hairy. *Pistillate inflorescences* 1–3 clustered together, 7–14 by 0.5–0.8 mm, (sparsely) puberulous; flowers up to 8, rather laxly set at base of rachis, more densely apically; bracts broadly triangular, 0.5–0.8 mm long, sparsely puberulous outside, glabrous inside, margin ciliate; bracteoles ovate, 0.3–0.5 mm long, sparsely puberulous outside, glabrous inside; pedicel 1–1.7 mm long, puberulous. *Pistillate flowers* 2.5–3.5 mm long; sepals 4, ovate, patent, 0.7–2 mm long, thin, sparsely puberulous outside, glabrous inside; ovary ovoid, 1.5–2 mm long, 3-locular, smooth, sparsely sericeous; stigmas raised, elongated, perpendicular to the sides of the ovary, slightly recurved, apically bifid to near base, lobes sometimes lowly divided, 1.2–2.2 mm long, longitudinally ribbed above, margins laciniate, glabrous, smooth beneath, sparsely puberulous, style remnant absent. *Infructescences* 8–38 by 0.8–1 mm, (sparsely) puberulous; fruiting pedicel 3–5 mm long, puberulous. *Fruits* ovoid to globose, slightly lobed, not stiped, beaked, 9–11 by 8–12 mm, punctulate, drying (dark) brownish, sparsely puberulous; pericarp 0.5–1.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ovoid, 7–7.5 by 6–6.5 by c. 2 mm.

Distribution — Malesia: Papua New Guinea.

Habitat & Ecology — Secondary and lower montane forest; on hillsides; in undulating country, moderately dry. Altitude: 30–900 m. Flowering: May, June, September to November; fruiting: June, July, December.

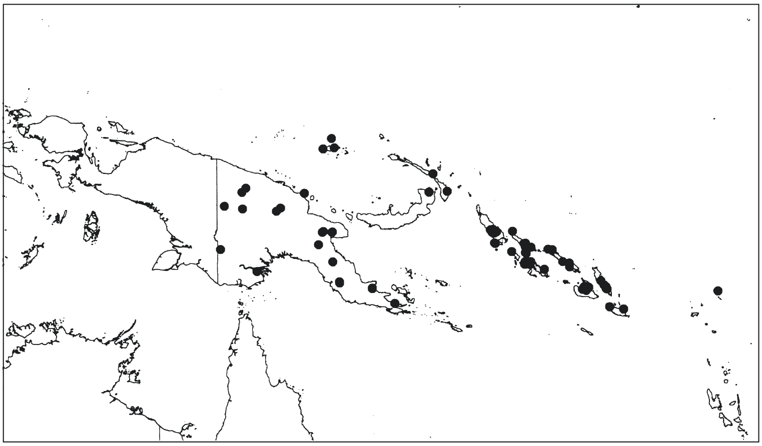
Uses — Firewood, larvae harvest, and construction.

Vernacular names — As sanglomas (Mianmin).

58. **Aporosa papuana** Pax & K. Hoffm. — Fig. 3.5n, 3.71, 4.6e, f; Map 10.46

Aporosa papuana Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 83; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 32. — Lectotype (proposed here): *Ledermann 6996* (holo K), Papua New Guinea, Sepik Prov., Malu.

(Small) tree or shrub, up to 25 m high, up to 35 cm diameter. *Bark* black to brown to grey, fissured, scaly, with furrows or craters, or smooth, thin; inner bark brown, pink, or reddish brown, salmon-streaked. *Wood* yellowish or cream or light brown to white, hard. Young branches densely tomentose. *Stipules* falcate, 4–8 by 6–14 mm, tomentose beneath, mostly persistent. *Petiole* terete, often adaxially grooved, 5–27 by 1–1.8 mm, densely tomentose, glabrescent, lower pulvinus 1–3 by 1.2–2 mm, upper pulvinus 2–6 by 1.2–2 mm, both distinct. *Leaves* narrowly ovate, narrowly elliptic, or narrowly obovate, 7–31 by 3–11 cm; base subcordate to obtuse, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands many, distinct, black; apex acuminate to slightly cuspidate; blade mostly thinnish, smooth, dull, not brittle, drying bluish or greyish green above, (light) brown beneath, very sparsely tomentose above, midrib tomentose, glabrescent, sparsely tomentose beneath, midrib and nerves tomentose, glabrescent; dots indistinct, irregular, greyish, fading in older leaves; disc-like glands occasionally few, small, along the margin at the end of nervules. *Nervation*: midrib prominent above, prominent beneath; nerves 11–14 pairs, slightly prominent to flat above, prominent beneath, marginal arches often fading, 1–3 mm from the margin; tertiary veins and venation fading, densely reticulate, slightly scalariform, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–4 clustered together, 14–46 by 2.5–4 mm, densely tomentose; peduncle 0–3 by 1.5–1.8 mm; bracts broadly triangular, often conspicuous, 1–1.8 mm long, densely tomentose outside, (sub)glabrous inside; glomerules ellipsoid, consisting of much more than 10 densely set flowers, 2–3 by 1.5–2 mm, slightly spaced at base of rachis, rather continuously set apically; pedicel 0.1–0.5 mm long. *Staminate flowers* 1.5–3 mm long; sepals 4, narrowly obovate, 0.5–1 mm long, connate to almost halfway, (sparsely) tomentose outside, glabrous inside; stamens 2 or 3, strongly exserted, 1.5–3 mm long; anthers 0.2–0.3 mm long; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 7–18 by 0.8–1.2 mm, densely tomentose; flowers up to 13, rather densely set along the rachis; bracts broadly triangular, 0.8–1 mm long, (sparsely) tomentose outside, glabrous inside; bracteoles narrowly ovate, 0.5–0.8 mm long, (sparsely) tomentose outside, glabrous inside; pedicel 0.5–1.5 mm long, tomentose. *Pistillate flowers* 3–5 mm long; sepals (3 or) 4, ovate, patent, 0.5–1 mm long, thin, tomentose outside, glabrous inside; ovary ovoid, 2–3.5 mm long, 3- (or 2- or 4-)locular, smooth, densely tomentose; stigmas raised, elongated, perpendicular to the sides of the ovary, recurved, apically bifid to



Map 10.46. Distribution of *Aporosa papuana* Pax & K. Hoffm.

near base, 2–3 mm long, densely laciniate above, glabrous, smooth beneath, sparsely tomentose, style remnant present. *Infructescences* 13–22 by 1.2–1.8 mm, tomentose; fruiting pedicel 2–5 mm long, tomentose. *Fruits* (broadly) ovoid, not stiped, beaked, 12–18 by 12–19 mm, almost smooth, young ones irregularly ridged, drying (light) brownish, sparsely tomentose; pericarp 1–1.2 mm thick, not fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ovoid, 9–10 by 5–6 by 3–4 mm.

Distribution — Malesia: Papua New Guinea, Solomon Islands.

Habitat & Ecology — Primary, secondary, or montane rain forest, sometimes monsoon forest; on ridges, ridge tops, slopes, hillsides, or stony plateaus; in lowland or flat plains. Soil: stiff clay or limestone. Altitude: 15–1500 m. Flowering: June to February; fruiting: throughout the year.

Uses — Construction and firewood.

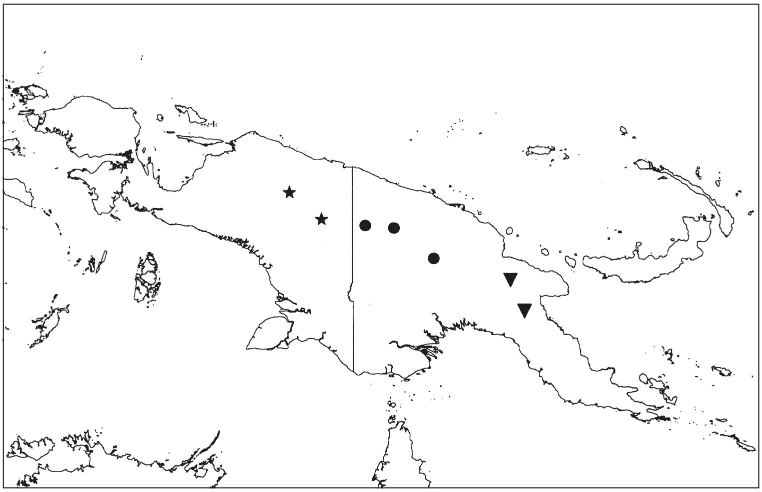
Vernacular names — Papua New Guinea: As kiluwanas (Mianmin). Solomons: Aisalin(g)a, aisale (Kwara'ae); napanirung (Bor Petats).

Note — Specimen *Ledermann 9557* cited by Pax & Hoffmann (1922) as "cum *A. papuana* optime convenit", is *A. lamellata*.

59. **Aporosa parvula** Schot — Map 10.47

Aporosa parvula Schot, Blumea 40 (1995) 457. — Type: *Milliken 1368* (holo L; iso K), Indonesia, Papua Barat, Baliem Valley.

Shrub or tree, up to 6 m high. Young branches sparsely tomentose. *Stipules* narrowly ovate, sometimes slightly oblique, 1.8–2 by 0.5–0.8 mm, caducous. *Petiole* terete, adaxially grooved, 2–5 by 0.8–1 mm, often entirely pulvinate, sparsely tomentose, glabrescent. *Leaves* elliptic to obovate, 2.5–5 by 1.5–2 cm; base cuneate to slightly attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands few, small, grey; apex acute to acuminate; blade thickish, smooth, dull, not brittle, drying green-grey or bluish grey above, (light) brown beneath, glabrous above, only midrib and nerves very sparsely tomentose beneath, glabrescent; dots rather densely set, fine, black, distinct; disc-like glands seldom present, along the margin. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 5–7 pairs, flat above, prominent beneath, marginal arches distinct, 1–2.5 mm from the margin; tertiary veins and venation fading, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* single, 5–8 by 1.5–2 mm, sparsely tomentose; peduncle 1–2 by c. 0.5 mm; bracts triangular, inconspicuous, 0.8–1 mm long, subglabrous outside, glabrous inside, margin sparsely ciliate; glomerules subglobose, indistinct, consisting of 3 or 4 laxly set flowers, c. 1 by 1 mm, sometimes slightly spaced at base of rachis, mostly continuously set along the rachis; pedicel absent. *Staminate flowers* 1–1.5 mm long; sepals 3 or 4, narrowly elliptic, 0.8–1.2 mm long, connate to c. halfway, very sparsely hairy outside, glabrous inside, margin ciliate; stamens 2, exserted, 1.2–1.8 mm long; anthers 0.4–0.5 mm long, connective very sparsely hairy at apex; pistillode absent. *Pistillate inflorescences* not seen, induced from young inflorescences to be single, sparsely tomentose; flowers up to ?5, rather laxly arranged at base of rachis, more densely at apex; bracts in young fruit (broadly) triangular, 1–1.5 mm long, ?glabrescent outside, glabrous inside, margin sparsely ciliate; bracteoles ovate, 0.4–0.5 mm long, glabrous; pedicel 1.5–2 mm long, sparsely puberulous. Old *pistillate flowers* c. 4 mm long; sepals 3 or 4, narrowly ovate, ascending, 0.9–1.2 mm long, thin, subglabrous outside, glabrous inside, margin sparsely ciliate; ovary ovoid, c. 3 mm long, 2-locular, smooth, sparsely puberulous; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, slightly recurved, apically bifid to near base, 1.2–1.5 mm long, longitudinally ribbed above, margins lowly papillate, glabrous, smooth beneath, subglabrous, style remnant present. *Infructescences* 7–10 by 0.8–1 mm, sparsely tomentose; fruiting pedicel 1–1.5 mm long, sparsely puberulous. Young *fruits* ellipsoid, not stiped, not beaked, c. 8 by 7 mm, punctate, drying (light) brown, sparsely puberulous; pericarp 0.5–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 or 2, only immature ones seen.



Map 10.47. Distribution of *Aporosa parvula* Schot (★), *A. reticulata* Pax & K. Hoffm. (▼), and *A. sclerophylla* Pax & K. Hoffm. (●).

Distribution — Malesia: Papua Barat.

Habitat & Ecology — Primary (lower) montane rain forest, on ridges and slopes. Soil: clayey. Altitude: 1805–2100 m. Flowering: March, May; fruiting: October.

Vernacular names — Ikiemoeja (Kapaukoe).

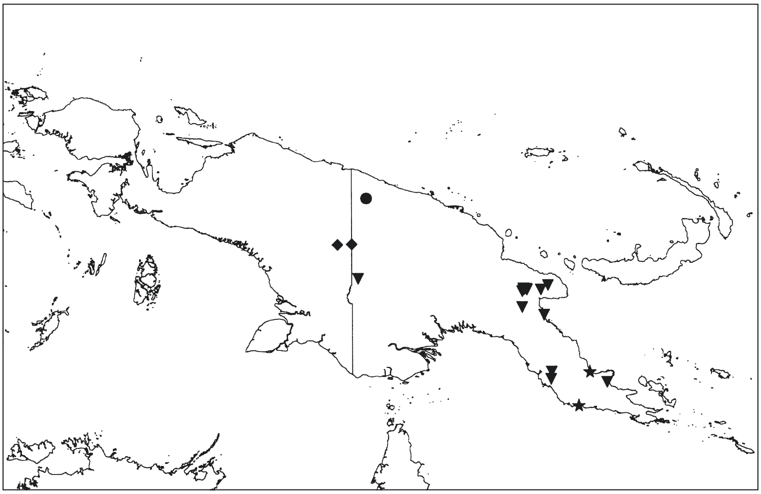
Note — *Aporosa brevicaudata*, *A. sclerophylla*, and this species can be distinguished by the 'persistence' of the stipules, the different shape of the leaves, the size of the staminate inflorescences, and the shape of the fruit. *Aporosa brevicaudata* and *A. parvula* share the leaf shape and caducous stipules, whereas *A. parvula* and *A. sclerophylla* agree in small staminate inflorescences with small bracts, and probably in the small ellipsoid fruits. Presently, the combination of these characters is enough to distinguish the three entities on the species level. However, it is possible that future material will bridge these small gaps, and reduce one or more species to variety level.

60. **Aporosa praegrandifolia** (S. Moore) Schot, *comb. nov.* — Map 10.48

Antidesma praegrandifolium S. Moore in H.O. Forbes, J. Bot. 61, Suppl. (1923) 46. — Type: *H.O. Forbes 250* (holo BM; iso K, L, MEL), Papua New Guinea, Sogeri Region.

Aporusa petiolaris Airy Shaw, Kew Bull. 25 (1971) 474; Kew Bull., Addit. Ser. 8 (1980) 32. — Type: *NGF (Henty) 14384* (holo K; iso L), Papua New Guinea, Sogeri.

(Small) tree or shrub, up to 18 m high, up to 15 cm diameter. *Bark* greyish, greenish, or reddish brown, brown, blackish, or grey and brown blotched, slightly vertically scaly to smooth; inner bark greenish brown, red(dish) brown, brown, pink, or whitish. *Wood* pale yellow, straw, or white. Young branches (sub)glabrous. *Stipules* falcate, 6–10 by 9–18 mm, sparsely puberulous beneath, often persistent. *Petiole* terete, shortly grooved to smooth, 18–42 by 1.5–2.5 mm, (sub)glabrous, lower pulvinus 2–3 by 2.5–3 mm, upper pulvinus 6–9 by 3–4 mm, both distinct. *Leaves* narrowly ovate, narrowly elliptic, or narrowly obovate, 17–34 by 7–13 cm; base rounded to cuneate, basal glands absent; margin lowly undulate to lowly crenate, marginal glands regular, distinct, black; apex acuminate; blade thickish, smooth, often shiny, not brittle, drying greyish, reddish, or brownish green above, (dark) brown beneath, glabrous, midrib sometimes very sparsely puberulous beneath; dots irregularly, laxly set, fine, blackish; disc-like glands occasionally present, along the margin, black. *Nervation*: midrib flat above, prominent beneath; nerves 14–17 pairs, slightly prominent to flat above, prominent beneath, marginal arches often fading, 2–4 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly scalariform, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1 or 2 clustered together, 24–41 by 3–3.5 mm, (densely) tomentose; peduncle 0–3 by 1–1.5 mm; bracts broadly triangular, 1.2–1.5 mm long, conspicuous, tomentose outside, sparsely tomentose at base only inside; glomerules ellipsoid, 3–4 by 2–3 mm, consisting of much more than 10 densely set flowers, slightly spaced at base of rachis, continuous apically; pedicel 0.1–0.3 mm long. *Staminate flowers* 1.5–3 mm long; sepals 4 or 5, narrowly obovate, 0.5–0.9 mm long, connate to c. halfway, sparsely sericeous outside, glabrous inside; stamens 2–8, exserted, 1.5–2.5 mm long; anthers 0.2–0.3 mm long, connective sparsely hairy; pistillode cylindric, small, hairy. *Pistillate inflorescences* clustered 1–3 together, 2–8 by 1.2–1.5 mm, (densely) tomentose; flowers up to 9, rather densely set along rachis; bracts broadly triangular, 1.5–2.2 mm long, tomentose outside, very sparsely puberulous inside; bracteoles not seen; pedicel absent. *Pistillate flowers*



Map 10.48. Distribution of *Aporosa praegrandifolia* (S. Moore) Schot (▼), *A. spec. A* (●), *A. spec. B* (★), and *A. spec. D* (◆).

2–3.5 mm long; sepals 5, ovate, ascending, 0.8–1.2 mm long, thin, puberulous outside, sparsely puberulous inside; ovary ovoid, 1.5–3 mm long, 3- (or 4-)locular, slightly lobed, tomentose; stigmas sessile, elongated, perpendicular to the sides of the ovary, straight, apically bifid to near base, 0.8–1 mm long, laxly laciniate above, glabrous, smooth beneath, sparsely tomentose, style remnant absent. *Infructescences* 12–38 by 2–3 mm, tomentose; fruiting pedicel 9–17 mm long, tomentose. *Fruits* subglobose, not stiped, not beaked, 12–15 by 13–16 mm, punctulate, drying (dark) brown, sparsely tomentose; pericarp 0.5–1.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 3 (or 4), half-terete, ellipsoid, 9–11 by 7–9 by 3–5 mm.

Distribution — Malesia: Papua New Guinea: East Papua.

Habitat & Ecology — Rain, cloud, or mountain forest, or in forest-grassland transition; in low, sloping, or flat country; on ridges and slopes. Altitude: 45–900 m. Flowering: November to January; fruiting: March to August, October, December.

61. Aporosa reticulata Pax & K. Hoffm. — Map 10.47

Aporosa reticulata Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 100; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 33. — Neotype (proposed here): *Hartley 12005* (holo A; iso K, L), Papua New Guinea, Eastern Highlands Prov.

Tree, up to 20 m high, up to 25 cm diameter. *Bark* brown or grey-brown, smooth, flaking in thin flat plates; inner bark red or pale salmon. Young branches (sparsely) tomentose. *Stipules* not seen, early caducous. *Petiole* terete, adaxially grooved, 9–16 by 1–1.2 mm, sparsely tomentose, lower pulvinus 1–2 by 1.2–1.5 mm, indistinct, upper pulvinus 2–4 by 1.5–1.8 mm, rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 8–15 by 2.5–5 cm; base obtuse to cuneate, basal glands absent; margin lowly undulate to lowly glandular-crenate, slightly revolute, marginal glands many, small, greyish black; apex acuminate; blade thinnish, smooth, rather shiny, not brittle, drying greenish grey to greenish brown above, brown beneath, sparsely tomentose above, glabrescent, sparsely tomentose beneath, midrib and nerves tomentose, glabrescent; dots densely set, fine, grey, fading; disc-like glands absent. *Nervation*: midrib flat above, prominent beneath; nerves 7–10 pairs, flat above, prominent beneath, marginal arches often fading, 1–3 mm from the margin; tertiary veins and venation densely reticulate to slightly scalariform, flat above, fading, slightly prominent beneath, distinct. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, young ones 12–15 by 1–1.5 mm, tomentose; peduncle 1–4 by c. 1 mm; bracts broadly triangular, conspicuous, c. 1 mm long, sparsely hairy outside, glabrous inside, margin ciliate; immature glomerules subglobose, c. 1.5 by 1 mm, consisting of ?7–9 laxly set flowers, spaced at 0.5–2 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. Young *staminate flowers* 0.5–0.7 mm long; sepals 4, narrowly elliptic, c. 0.8 mm long, connate to c. halfway, sparsely hairy outside, glabrous inside, margin ciliate; stamens 3 or 4, immature not exserted, c. 0.5 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode cylindric, 3-lobed, c. 0.4 mm long, sparsely hairy. *Pistillate inflorescences* 1 or 2 clustered together, only old ones seen, densely tomentose; flowers up to 9, rather laxly arranged at base of rachis, densely apically; bracts broadly triangular, 0.9–1.1 mm long, tomentose to villose outside, sparsely tomentose at base inside; bracteoles ovate, 0.7–0.9 mm long, villose outside, sparsely tomentose at base inside; pedicel 0.5–1 mm long, densely tomentose. *Pistillate flowers* 2.5–3.5 mm long; sepals 4 or 5, ovate, patent, 0.8–1.2 mm long, tomentose outside, subglabrous inside; ovary ovoid, 1.5–2.5 mm long, 2- (or 3-)locular, smooth, densely tomentose; stigmas slightly raised, elongated, apically bifid to near base, perpendicular to the sides of the ovary, curving downwards, 2.5–3.5 mm long, papillate to laciniate above, glabrous, ribbed and papillate beneath, sparsely tomentose, style remnant absent. *Infructescences* only young ones seen, 8–33 by 1–1.5 mm, (densely) tomentose; fruiting pedicel 1–2 mm long, tomentose. *Young fruits* ovoid, not stiped, slightly beaked, 9–11 by 7–9 mm, punctate, patchy densely tomentose, glabrescent; pericarp c. 1 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 or 2, only immature ones seen.

Distribution — Malesia: Papua New Guinea: North.

Habitat & Ecology — Mid montane forest, disturbed bush, on slopes. Altitude: 1300–1650 m. Flowering: April, July; fruiting: July, November.

Note — I refer to this species a single specimen, *Hartley 12005*, from the Eastern Highlands, alt. 1650 m, because it matches best with Pax & Hoffmann's (1922) description. It resembles *A. annulata* and *A. carrii* very closely, but contrary to these two it combines a high altitude with reddish brown tomentose branches and leaves. The ovary, contrary to Pax and Hoffmann's description, is mostly 3-locular, but some 2-locular ones also occur. Two other specimens are tentatively added to *A. reticulata*: a young staminate one (*Hartley 11548*), from which the description of the flowers has been drawn, and one with small fruits (*Hartley 12321*). They differ in the fainter nervation and the much lesser indumentum of the leaves, and, in the latter case, of the fruits.

62. **Aporosa sclerophylla** Pax & K. Hoffm. — Map 10.47

Aporosa sclerophylla Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 98; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 33. — Lectotype (proposed here): *Ledermann 10255* (K, L), Papua New Guinea, Sepik Prov., Lordberg.

Small tree. *Bark* light brown; inner bark deep red. Young branches sparsely tomentose. *Stipules* falcate, 1.2–2 by 2–4 mm, sparsely tomentose, present in young stages. *Petiole* (half-)terete, adaxially grooved, 2–4 by 0.8–1.2 mm, (sparsely) tomentose, often entirely pulvinate. *Leaves* ovate to (narrowly) elliptic, 2.5–6 by 1–2.5 cm; base rounded to cuneate, basal glands absent; margin subentire to very lowly glandular-crenate, marginal glands few, small, black, indistinct; apex acuminate to cuspidate; blade thickish, smooth, dull, rather brittle, drying greyish green above, blackening, brown beneath, only midrib very sparsely tomentose above, midrib and nerves sparsely tomentose beneath; dots densely set, fine, black, mostly distinct; disc-like glands regularly present, black, distinct, along margin. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 6–9 pairs, flat above, (slightly) prominent beneath, marginal arches distinct, 1–2 mm from the margin; tertiary veins and venation distinct, densely reticulate, flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* single, young ones 2–4 by c. 1.5 mm, (sparsely) tomentose; peduncle 0.5–0.8 by c. 0.5 mm; bracts broadly triangular, inconspicuous, 0.8–1 mm long, very sparsely hairy outside, glabrous inside, margin ciliate; glomerules subglobose, indistinct, consisting of 3–5 laxly set flowers, mostly continuously set along the rachis, seldom slightly interrupted at base; pedicel absent. *Staminate flowers* 1–1.5 mm long; sepals 4, narrowly obovate, 0.8–1.1 mm long, connate to more than halfway, subglabrous outside, glabrous inside, margin sparsely ciliate; stamens 2, young ones slightly exserted, 1–1.2 mm long; anthers 0.4–0.5 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* single or 2 clustered together, 6–12 by 0.3–0.5 mm, sparsely puberulous; flowers up to 8, rather laxly set at base of rachis, more densely so apically; bracts broadly triangular, 0.4–0.8 mm long, sparsely puberulous outside, glabrous inside; bracteoles ovate, 0.3–0.5 mm long, puberulous outside, glabrous inside; pedicel 1–1.5 mm long, puberulous. *Pistillate flowers* 1.5–2 mm long; sepals 4 or 5, ovate, patent, 0.3–0.8 mm long, thin, sparsely puberulous outside, glabrous inside; ovary ovoid, 0.8–1.5 mm long, 2-locular, smooth, sparsely puberulous; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, slightly recurved, apically bifid to c. halfway, 0.5–1 mm long, longitudinally ribbed above, margins laxly papillate, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences*, *fruits* and *seeds* not seen; septae and column in flower glabrous.

Distribution — Malesia: Papua New Guinea.

Habitat & Ecology — Sub-alpine grassland. Altitude: ?1000–2692 m. Flowering: December (*Ledermann 9897* and *10255* according to literature collected in December at 1000 m altitude).

Note — Known only from two young pistillate flowering collections. I have also tentatively placed the young staminate specimen *Vinas 125* here – see note under *A. parvula*.

63. **Aporosa vagans** Schot — Fig. 3.5o, 3.7k; Map 10.49

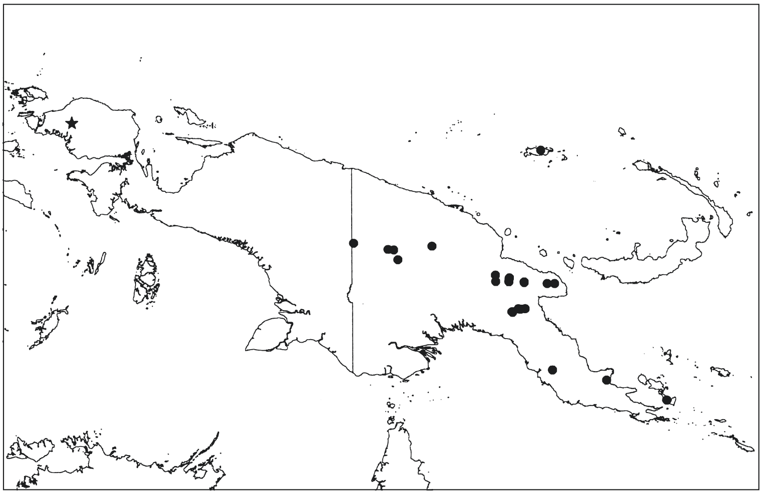
Aporosa vagans Schot, Blumea 40 (1995) 459. — Type: *Brass 32296* (holo A; iso K, L, LAE), Papua New Guinea, Eastern Highlands Prov., Kassam Gap.

(Small) tree, up to 21 m high, up to 45 cm diameter. *Bark* greyish or red to brown, smooth to scaly or pustular; inner bark green, straw, cream, red, or reddish brown. *Wood* red, brown to yellowish white, or cream. Young branches tomentose. *Stipules* falcate, 8–9 by 12–17 mm, sparsely tomentose, often black disc-like glands beneath along upper margin, mostly caducous. *Petiole* terete, adaxially grooved, 5–28 by 0.8–2.2 mm, (sparsely) tomentose, glabrescent, lower pulvinus 1–3 by 1.2–2.5 mm, upper pulvinus 2–7 by 1.5–3 mm, both rather distinct. *Leaves* narrowly ovate to (narrowly) elliptic, 9–26 by 3–12 cm; base rounded to cuneate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular to many, often distinct, grey to blackish; apex acuminate to cuspidate; blade thickish, smooth, dull, not brittle, drying (dark) bluish to greyish brown above, brown beneath, very sparsely tomentose above, midrib tomentose, glabrescent, sparsely tomentose beneath, midrib and nerves tomentose, glabrescent; dots densely set, fine, blackish grey, fading; disc-like glands irregularly present at base along the margin, black. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 9–12 pairs, slightly prominent to flat above, prominent beneath, marginal arches rather distinct, 2–5 mm from the margin; tertiary veins and venation distinct, densely reticulate to slightly scalariform, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 9–29 by 2.5–4 mm, tomentose; peduncle 3–6 by 1–1.5 mm; bracts broadly triangular, inconspicuous, 1.2–1.8 mm long, sparsely tomentose outside, very sparsely tomentose hairy at base only inside, margin ciliate; glomerules globose, 1.5–3 by 1.5–2.5 mm, consisting of 9–15 densely set flowers, spaced at 2–4 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 1.5–3 mm long; sepals 4, obovate, 1–1.5 mm long, connate to c. halfway, very sparsely tomentose outside, glabrous inside, margin ciliate; stamens (2 or) 3 (or 4), exserted, 1.5–3 mm long; anthers 0.3–0.4 mm long, connective glabrous; pistillode cylindric, minute, sparsely hairy. *Pistillate inflorescences* 1–5 clustered together, 5–32 by 0.5–1.8 mm, (sparsely) tomentose; flowers up to 11, rather laxly set throughout the rachis; bracts broadly triangular, 0.5–1 mm long, sparsely tomentose outside, glabrous inside, margin ciliate; bracteoles ovate, 0.3–0.5 mm long, sparsely tomentose outside, glabrous inside; pedicel 0.5–4 mm long, (sparsely) tomentose. *Pistillate flowers* 2.5–5 mm long; sepals 4 or 5, ovate, patent, 0.7–1.2 mm long, thin, sparsely tomentose outside, very sparsely tomentose at base inside; ovary ovoid, 2–3.5 mm long, 3-locular, smooth, (sparsely) tomentose; stigmas raised, elongated, perpendicular to the sides of the ovary, recurved, apically bifid to near base, 1.2–2.5 mm long, laxly laciniate above, glabrous, smooth beneath, sparsely tomentose, style remnant present. *Infructescences* 9–48 mm long, 0.8–2 mm diam., (sparsely) tomentose; fruiting pedicel 4–9 mm long, (sparsely) tomentose. *Fruits* ovoid to globose, not stiped, not beaked, 11–15 by 10–16 mm, punctulate, drying light to dark brown, sparsely tomentose; pericarp 0.5–2.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ovoid, 9–11 by 7–9 by 3–4 mm.

Distribution — Malesia: Papua New Guinea.

Habitat & Ecology — In understorey of secondary, fagaceous, or lowland to montane rain forest; in advanced regrowth, in moderately dry, and/or strongly shaded places; on hills, slopes, flats, in ravines, and beside rivers. Soil: latosol or sandstone. Altitude: 450–760 m. Flowering: February, June, July, October; fruiting: March, April, June to January.

Uses — Firewood.



Map 10.49. Distribution of *Aporosa vagans* Schot.

Vernacular names — Sakindoot (Enga); wak'eni (Kassam); tuwoi (Koroba); womekant (Maring); pukong (Nako); tomkuri (Oksapmin).

Notes — 1. The epithet means 'the wandering', and stems from the fact that the species was interpreted as *A. papuana* by Airy Shaw, *A. reticulata* by Mansfield (probably), and at first as *A. laxiflora* by myself.

2. There seem to be two forms of this species: the more common, (sub)montane, typical form and a lowland form. The lowland form has a much lesser indumentum on all parts, which gradually changes into the tomentose montane form. The inflorescences/infructescences are also more slender in the lowland form, which gives it a superficial likeness to *A. ledermanniana*. No other differences have been found.

64. Aporosa spec. A (aff. *Aporosa nigropunctata* Pax & K. Hoffm.) — Map 10.48

Specimen: *NGF (Womersley) 3936* (BM, K, L, LAE), Papua New Guinea, Sepik Province.

Small tree. *Bark* pale grey brown, vertically cracked, brown on the back; inner bark straw brown, c. 6 mm thick. *Wood* white. Young branches sparsely puberulous. *Stipules* not seen, early caducous. *Petiole* terete, rather smooth, 8–14 by 0.5–1 mm, sparsely puberulous, glabrescent, lower pulvinus c. 1 by 0.8–1 mm, indistinct, upper pulvinus 1.5–2 by c. 1 mm, rather distinct. *Leaves* (narrowly) ovate, 5–11 by 2–5 cm; base obtuse to cuneate, basal glands absent; margin lowly glandular-crenate, marginal glands few, small; apex acuminate to cuspidate; blade thin, smooth, dull, not brittle, drying grey-green above, grey-brown beneath, glabrous above, only midrib very sparsely puberulous beneath, glabrescent; dots absent; disc-like glands distinct, scattered within the arches, small, black. *Nervation*: midrib flat above, prominent beneath; nerves 5–7 pairs, flat above, prominent beneath, marginal arches distinct, 2–3 mm from the margin; tertiary veins and venation distinct, rather densely reticulate, flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* and *staminate flowers* not seen. *Pistillate inflorescences* 1–4 clustered together, 6–18 by 0.5–0.8 mm, puberulous; flowers up to 7, laxly arranged below, more densely at apical end of the rachis; bracts broadly triangular, 0.7–1 mm long, sparsely hairy outside, glabrous inside, margin ciliate; bracteoles ovate, 0.4–0.7 mm long, sparsely hairy outside, glabrous inside; pedicel 1–1.5 mm long, sparsely puberulous. *Pistillate flowers* 3–4 mm long; sepals 4 or 5, ovate, 0.6–1 mm long, thin, sparsely hairy outside, glabrous inside; ovary ovoid, 1.7–2 mm long, 3-locular, smooth, sparsely puberulous; stigmas raised, elongated, perpendicular to the sides of the ovary, recurved, apically bifid to c. halfway, 1.5–2.5 mm long, longitudinally ribbed and laxly laciniate above, glabrous, smooth beneath, sparsely puberulous, style remnant present. *Infructescences* one remnant seen, c. 11 mm long, c. 1 mm diam., sparsely puberulous; fruiting pedicel c. 1.2 mm long, sparsely puberulous. *Fruits* one remnant seen, probably globose, not stiped, not beaked, c. 8 by 8 mm, smooth, sparsely puberulous; pericarp 0.8–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 seen, half-terete, broadly ellipsoid, c. 5 by 6 by 4 mm.

Distribution — Malesia: Papua New Guinea, Sepik Province.

Habitat & Ecology — In second storey of foothill forest. Flowering and fruiting: October.

Note — Known only from the *NGF 3936* collection. The pistillate inflorescences resemble closely those of *A. nigropunctata*, but the leaves lack the caudate apex and the distinct dots. The disc-like glands differ also in their placement.

65. **Aporosa spec. B** (aff. *Aporosa flexuosa* Pax & K. Hoffm./less so with *Aporosa laxiflora* Pax & K. Hoffm.) — Map 10.48

Specimens: *NGF (Henty & Lelean) 41835* (K, L, LAE), Papua New Guinea, Central Prov., Mori, originally identified and distributed as *Baccaurea papuana*; *Paijmans 43* (LAE) Papua New Guinea, Northern District, Musa Basin.

(Small) tree, c. 15 m high, 25 cm diameter. *Bark* grey-brown, fibrous; inner bark light brown, thin. *Wood* brownish straw. Young branches sparsely puberulous. *Stipules* not seen, early caducous. *Petiole* (half-)terete, adaxially grooved, 9–16 by 1–1.2 mm, glabrescent, lower pulvinus 1–1.5 by 1–1.5 mm, indistinct, upper pulvinus 3–4 by 1.5–2 mm, rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 12–18.5 by 4–6.5 cm; base rounded to cuneate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands few, small, black; apex acuminate; blade thin, smooth, dull, not brittle, drying greenish grey above, brownish grey beneath, ?glabrous; dots absent; disc-like glands along the margin, regular to many, small, black. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 7–11 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 2–4 mm from the margin; veins and venation distinct, rather densely reticulate, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* mostly born on the trunk, some just below the leaves. *Staminate inflorescences* 5–12 clustered together (1 or 2 just below the leaves), 19–69 by 1–1.5 mm, (sparsely) puberulous; peduncle 4–17 by 0.5–1 mm; bracts broadly triangular, 1–1.2 mm long, sparsely hirsute outside, hairy at base only inside; glomerules ellipsoid to subglobose, consisting of more than 10 rather densely packed flowers, sometimes a few sterile flowers present, 1.5–4 by 1.5–2 mm, spaced at 2–9 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 1–1.8 mm long; sepals 4 (or 5), elliptic, 0.7–1 mm long, connate to almost halfway, sparsely hirsute outside, hairy at base only inside; stamens 2 (or 3), exserted, 1.2–2 mm long; anthers 0.2–0.4 mm long, connective glabrous; pistillode minute, cylindric, hairy. *Pistillate inflorescences*, *pistillate flowers*, *infructescences*, *fruits*, and *seeds* not seen.

Distribution — Malesia: Papua New Guinea.

Habitat & Ecology — Hill or light ridge forest, on low limestone hills. Altitude: 250–300 m. Flowering: February, August.

Note — Known from 2 specimens: *NGF 41835* and *Paijmans 43*. Both characterized by the elongated, interrupted, mostly cauliflorous inflorescences. These inflorescences bear a strong resemblance with Pax & Hoffmann's description of *A. flexuosa*, but the leaves are larger and they have more nerves, more like, e.g., those of *A. laxiflora*. A true species or a luxuriant form of *A. flexuosa*?

66. Aporosa spec. C[1] (aff. *Aporosa papuana* Pax & K. Hoffm./*Aporosa brassii* Mansfield/less so *Aporosa lamellata* Airy Shaw) — Map 10.43

Specimens: *Pleyte 738* (BO, L, SING), Indonesia, Papua Barat, Sorong; *Pullen 7318* (L, LAE), Papua New Guinea, Western Prov., upper Fly River, SW of Kiunga.

(Small) tree, up to 15 m high, up to 10 cm diameter. *Bark* slightly rough, blaze pink. *Wood* pale orange-straw. Young branches tomentose. *Stipules* not seen, early caducous. *Petiole* terete, adaxially grooved, 7–16 by 2–2.5 mm, tomentose, lower pulvinus 2–3 by 2.5–3 mm, indistinct, upper pulvinus 3–5 by 2.5–3 mm, rather distinct. *Leaves* narrowly ovate to narrowly obovate, 11–21 by 4–7 cm; base rounded to cuneate, basal glands absent; margin subentire to lowly undulate, marginal glands few, grey, indistinct, in margin; apex acuminate; blade thickish, smooth, sometimes slightly shiny, not brittle, drying light grey-green to red-brown above, (light) brown beneath, only midrib and nerves tomentose-hirsute above, sparsely hirsute beneath, midrib and nerves tomentose-hirsute; dots irregularly laxly set, fine, grey, often indistinct; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 9–11 pairs, flat above, prominent beneath, marginal arches distinct, 1.5–2 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly scalariform, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* mostly just below the leaves. *Staminate inflorescences* 2–5 clustered together, 27–92 by 1.5–3 mm, tomentose; peduncle (0–)2–5 by 0.8–1 mm; bracts broadly triangular, inconspicuous, 1–1.2 mm long, hirsute outside, glabrous inside, margin ciliate; glomerules indistinct, consisting of 3–5 laxly set flowers, mostly continuously set along the rachis, sometimes lower ones spaced at 1–2 mm; pedicel absent. *Staminate flowers* 1.5–2.5 mm long; sepals 4, narrowly elliptic, 0.8–1.2 mm long, connate to c. halfway, sparsely hirsute outside, glabrous inside, margin ciliate; stamens 2 (or 3), exserted, 1.5–2.5 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences*, *pistillate flowers*, *infructescences*, *fruits*, and *seeds* not seen.

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1) Lately new material has been collected from Ayawasi (near Sorong, Bird's Head, Papua Barat), including pistillate specimens, indicating spec. C is a true species. The species will be named later.

Distribution — Malesia: Papua Barat (Sorong), Papua New Guinea (Kiunga).

Habitat & Ecology — Primary or thinned out rain forest. Altitude: c. 60 m. Flowering: September.

Note — Only two staminate specimens seen. The vegetative characters almost fit those of *A. papuana* and *A. brassii*, and maybe also of *A. lamellata*, but not quite. The delimitation of these three species is mainly based on fruiting characters, therefore, I cannot identify the non-fruiting specimens *Pleyte 738* or *Pullen 7318* positively with any of them. They may belong to one of the three, or represent a new species.

67. Aporosa spec. D (aff. *Aporosa vagans* Schot) — Map 10.48

Specimens: *NGF (Ridsdale & Galore) 33177* (LAE), Indonesia, Papua Barat, Okwalimkam River Headwaters; *NGF (Ridsdale & Galore) 33154* (BO, K, L, LAE), Indonesia, Papua Barat, Okwalimkam River Headwaters; *NGF (Henty, Ridsdale & Galorer) 33082* (BO, K, L, LAE), Indonesia, Papua Barat, headwaters of Ok Denim River; *Soegeng Reksodihardjo 567* (BO, L), Indonesia, Papua Barat, below Okdenan – Oksibil River, Star Mountains.

Tree, up to 10 m high, up to 10 cm diameter. *Bark* red brown, pustular; inner bark cream. *Wood* cream. Young branches tomentose. *Stipules* falcate, 8–9 by 12–14 mm, sparsely tomentose, often caducous, margin with black disc-like glands beneath. *Petiole* terete, apically grooved adaxially, 12–28 by 1.8–2.2 mm, lower pulvinus 1.5–3 by 2–2.5 mm, upper pulvinus 4–7 by 2.5–3 mm, both rather distinct, sparsely tomentose. *Leaves* (narrowly) elliptic, 14–24.5 by 6.5–12 cm; base rounded to obtuse, basal glands absent; margin subentire, marginal glands few, at base, indistinct; apex acuminate to slightly cuspidate; blade thickish, smooth, dull, not brittle, drying red-brown to black above, (dark) brownish beneath, sparsely tomentose above, midrib tomentose, glabrescent, tomentose beneath, glabrescent; dots densely set, fine, black; disc-like glands occasionally few at base within marginal vein arches. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 9–11 pairs, flat to sunken above, prominent beneath, marginal arches distinct, 2–5 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly scalariform, flat to sunken above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 18–47 by 1.5–2.5 mm, tomentose; peduncle 3–6 by 0.8–1 mm; bracts triangular, 1–1.5 mm long, sparsely hairy outside, with hairy patch at base inside, margin ciliate; glomerules (sub)globose, 2–2.5 by 2–2.5 mm, consisting of 8–10 laxly set flowers, spaced at 3–8 mm along the rachis, except sometimes apically; pedicel absent. *Staminate flowers* 1.2–2 mm long; sepals 4, narrowly obovate, 1–1.5 mm long, thin, connate to less than halfway, sparsely hairy outside, glabrous inside, margin ciliate; stamens 2–6, exserted, 1–1.8 mm long; anthers 0.3–0.5 mm long, connective glabrous; pistillode a hair tuft. *Pistillate inflorescences* 2–5 clustered together, 24–32 by 1.2–1.5 mm, densely tomentose; flowers up to 11, rather laxly arranged along the rachis; bracts triangular, 1.5–2 mm long, sparsely hairy outside, glabrous inside, margin ciliate; bracteoles ovate, 0.8–1.2 mm long, sparsely hairy outside, glabrous inside, margin ciliate; pedicel 0.5–1.5 mm long, tomentose. *Pistillate flowers* 2–3 mm long; sepals 4 or 5, ovate, patent, 1–1.5 mm long, thin, sparsely hairy outside, with hairy patch at base inside; ovary ovoid, 1.5–2.5 mm long, 3-locular, smooth, tomentose; stigmas sessile, elongated, perpendicular to the sides of the ovary, apically bifid to c. halfway, straight to slightly recurved, 1.2–1.8 mm long, ribbed and papillate above, glabrous, rather papillate beneath, sparsely tomentose, style remnant absent. *Infructescences*, *fruits*, and *seeds* not seen; septae and column in flower glabrous.

Distribution — Malesia: Papua Barat.

Habitat & Ecology — Montane rain forest or broken forest, on lower slopes, ridges, or hillsides. Soil: sandstone. Altitude: 1300–1570 m. Flowering: June.

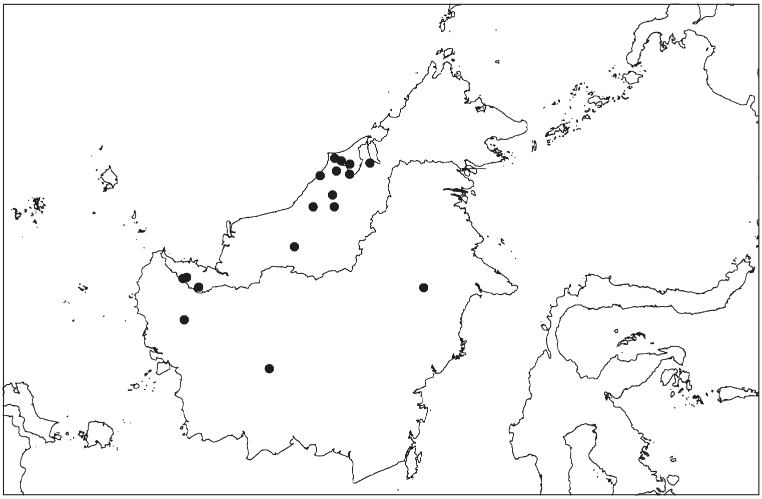
Note — This entity closely resembles *A. vagans*, but differs in the more interrupted staminate inflorescences (like the less hairy lowland form of *A. vagans*) and the sunken nervation of the leaves. Perhaps a variety of *A. vagans*?

10.4.5 – ***Section Sundanenses Schot***

68. Aporosa alia Schot — Fig. 10.7; Map 10.50

Aporosa alia Schot, Blumea 40 (1995) 453. — *Aporusa granularis* forma: Airy Shaw, Kew Bull. 29 (1974) 283. — Type: *Fuchs 21230* (holo L; iso BO, K), Sarawak, 4th Division.

Tree, up to 18 m high, up to 20 cm diameter. *Bark* greyish brown, greyish, yellowish, or whitish, smooth. Young branches sparsely tomentose. *Stipules* narrowly ovate, slightly oblique, 3–7 by 1–2 mm, sparsely hairy outside, glabrescent, caducous. *Petiole* terete, ridged, 7–19 by 0.7–1.2 mm, sparsely tomentose, glabrescent, lower pulvinus 1.5–2.5 by 1–1.5 mm, indistinct, upper pulvinus 2–5 by 1–2 mm, rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 6–21 by 2–7 cm; base cuneate to slightly attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, distinct, brownish, hairy in young leaves; apex cuspidate to caudate; blade thin, smooth, rather shiny, not brittle, drying (bright) greyish green above and beneath, glabrous above, only midrib and nerves sparsely tomentose beneath, glabrescent; dots irregularly laxly set, fine, greyish, often indistinct; disc-like glands absent. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 7–10 pairs, slightly



Map 10.50. Distribution of *Aporosa alia* Schot.

Fig. 10.7. *Aporosa alia* Schot. a. Habit; b. leaf margin; c. staminate inflorescence (a, b: *S (A.E. Wright) 23954*; c: *S (Yii) 43134*; all L).

prominent to flat above, prominent beneath, marginal arches distinct, 2–5 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly scalariform, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–5 clustered together, 5–12 by 0.5–1 mm, sparsely tomentose; peduncle 1–3 by 0.5–0.8 mm; bracts broadly triangular, inconspicuous, 0.2–0.4 mm long, sparsely hairy outside, glabrous inside; glomerules subglobose, consisting of 5–7 laxly set flowers, 0.5–1 by 0.3–0.5 mm, spaced at 0.3–1 at base of the rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 0.3–0.5 mm long; sepals 5, ovate, 0.5–0.7 mm long, connate at base only, sparsely hairy outside, glabrous inside; stamens 2 or 3, slightly exserted, 0.4–0.6 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–4 clustered together, 6–15 by 0.5–1 mm, sparsely tomentose; flowers up to 9, rather densely set at apical end of the rachis, laxly below; bracts broadly triangular, 0.6–0.8 mm long, sparsely hairy at base outside, glabrous inside; bracteoles not seen; pedicel absent. *Pistillate flowers* 1.2–2 mm long; sepals 4 or 5, ovate, patent, 0.6–1 mm long, fleshy at base, sparsely hairy at base outside, glabrous inside; staminodes erratically present; ovary ellipsoid, 1–1.5 mm long, 2-locular, smooth, sparsely puberulous; stigmas sessile, elongated, apically bifid to near base, perpendicular to the sides of the ovary, straight, 0.5–1 mm long, smooth above, apex laxly laciniate, glabrous, smooth beneath, style remnant absent. *Infructescences* 8–27 by 0.7–1.2 mm, puberulous; fruiting pedicel absent. *Fruits* (narrowly) ovoid, lowly stiped, not beaked, 11–16 by 6–9 mm, (lowly) granulate, sparsely hairy, glabrescent; pericarp 0.2–0.3 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 or 2, (half-)terete, ellipsoid, 7.5–9 by 5–6.5 by 3–4 mm.

Distribution — Malesia: Borneo.

Habitat & Ecology — In primary or secondary (mixed dipterocarp) forest, kerangas, or peat swamps; on hills, ridges, gentle or steep slopes, in open spaces, and near streams. Soil: clayey or loamy, yellow, rather wet. Altitude: 30–400 m. Flowering: April, June to Oct.; fruiting: April, August to December.

Vernacular names — Jangau, kayu masam (Iban).

69. **Aporosa antennifera** (Airy Shaw) Airy Shaw — Fig. 3.6r, 3.8r, 3.11i, 4.6a, 10.8; Map 10.51

Aporusa antennifera (Airy Shaw) Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 32; Kew Bull. 36 (1981) 253. — *Aporusa nigropunctata* Pax & K. Hoffm. var. *antennifera* Airy Shaw, Kew Bull. 20 (1966) 382; Meijer, Bot. News Bull. Sandakan 7 (1967) 34; Whitmore, Tree Fl. Malaya 2 (1973) 61. — Type: *J. & M.S. Clemens 40437* (holo K; iso BM, L), Sabah, Mt Kinabalu.

Shrub or tree, up to 30 m high, up to 60 cm diameter. *Bark* dark, reddish, pinkish brown, dark to light grey, with reddish patches, smooth, cracked, or slightly rugose; inner bark dark, reddish to light orangish, or yellowish brown to pale pink, firmly fibrous. *Wood* yellow to white, hard, finely radially striate. Young branches dark brown sparsely puberulous, hairs brown pilose. *Stipules* not seen, early caducous. *Petiole* terete, adaxially lowly grooved, 4–8 by 1–1.2 mm, sparsely puberulous, lower pulvinus 0.7–1 by c. 1 mm, indistinct, upper pulvinus 2–3 by 1–1.2 mm, distinct. *Leaves* narrowly ovate to narrowly elliptic, 6.5–14 by 2.2–6 cm; base cuneate to slightly attenuate, basal glands absent; margin lowly undulate to irregularly glandular-crenate, marginal glands regular, distinct, blackish, hairy in young leaves; apex cuspidate; blade thinnish, smooth, dull, not brittle, drying (dark) greenish blue above, greyish brown beneath, glabrous above, only midrib and nerves sparsely puberulous beneath; dots irregularly laxly set, very fine, black, often indistinct; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 4–6 pairs, slightly prominent to flat above, prominent beneath, marginal arches often rather fading, 0.5–1.5 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly scalariform, flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Stami-*

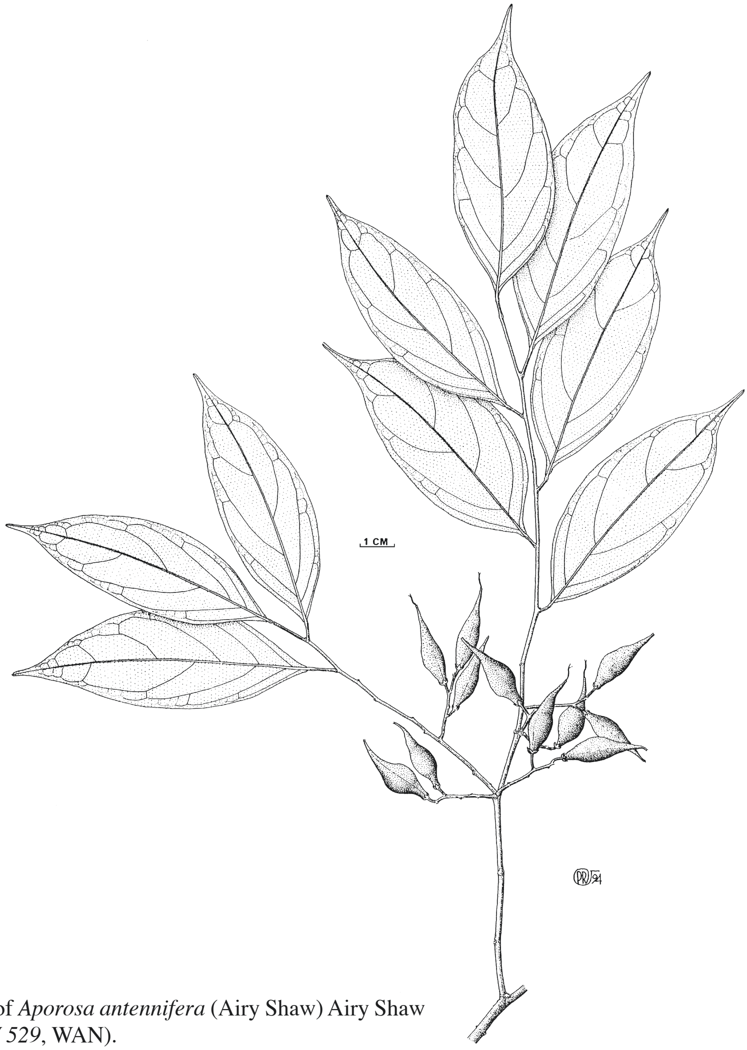
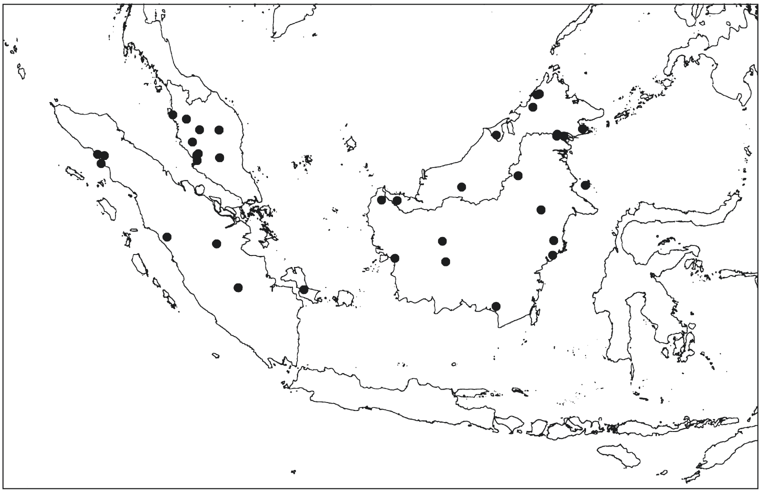


Fig. 10.8. Habit of *Aporosa antennifera* (Airy Shaw) Airy Shaw (*Ambriansyah W 529*, WAN).

nate inflorescences 2–5 clustered together, 9–25 by 1–1.3 mm, sparsely puberulous; peduncle 0.5–2 by 0.2–0.4 mm; bracts broadly triangular, inconspicuous, 0.2–0.3 mm long, sparsely hairy outside, glabrous inside; glomerules subglobose, consisting of 5–8 laxly set flowers, 0.7–1.2 by c. 0.5 mm, spaced at 0.1–1 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 1–1.5 mm long; sepals 4, obovate, connate at base, 0.3–0.5 mm long, sparsely hairy outside, glabrous inside; stamens 2, 1–1.5 mm long, exserted; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 5–13 by 0.5–1 mm, puberulous; flowers up to 7, laxly set along the rachis; bracts broadly triangular, 0.3–0.5 mm long, very sparsely hairy outside, glabrous inside, ciliate; bracteoles ovate, 0.3–0.4 mm long, glabrous, ciliate; pedicel 1–3 mm long, puberulous. *Pistillate flowers* 3–4



Map 10.51. Distribution of *Aporosa antennifera* (Airy Shaw) Airy Shaw.

mm long; sepals 4, ovate, subequal, patent, 0.3–0.8 mm long, thin, sparsely hairy outside, glabrous inside; ovary flask-shaped to slightly fusiform, 2-locular, 3–3.5 mm long, punctulate, sparsely puberulous at base, glabrescent towards apex; stigmas raised, elongated, apically bifid to c. halfway, lobes divided, perpendicular to the sides of the ovary, recurved, 2.5–5.5 mm long, papillate above, glabrous, lowly papillate beneath, style remnant absent. *Infructescences* 9–23 by 0.8–1 mm, sparsely puberulous; fruiting pedicel 2–4 mm long, sparsely puberulous. *Fruits* ellipsoid, shortly stiped, beaked, 7–10(–15) by 5–8 mm, punctulate to smooth, sparsely hairy at base, glabrescent; pericarp 0.5–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 (or 2), half-terete, ellipsoid, 7–8 by 4–5 by c. 2 mm.

Distribution — Malesia: Peninsular Malaysia, Sumatra, Borneo.

Habitat & Ecology — Primary, secondary, or logged dipterocarp forest; on hill sides, ridges, and along rivers. Soil: clay, sandy loam, granitic sand, or basalt, yellow-red brownish or greyish. Altitude: 20–1050 m. Flowering: March, April, July to November; fruiting: April to June, August to December.

Vernacular names — Peninsular Malaysia: Semasam lanang, kelat jambu (Malay). Sumatra: Bangka rambei. Borneo: Manyi (Bukit Baka); kasingan tahatung (Dayak); kayu masam (Iban).

Note — Specimen *KEP-FRI 786* shows the same galled bunchy inflorescences as regularly found in *A. subcaudata*.

70. **Aporosa arborea** (Blume) Müll.Arg. — Fig. 3.8a, 3.11b, 4.1c; Map 10.52

Aporosa arborea (Blume) Müll.Arg. in DC., Prod. 15, 2 (1866) 470; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 232; Koord., Exkurs.-Fl. Java 2 (1912) 480; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 95; Ridl., Fl. Malay Penins. 3 (1924) 239; Backer & Bakh.f., Fl. Java 1 (1964) 456; Airy Shaw, Kew Bull. 26 (1972) 214; Whitmore, Tree Fl. Malaya 2 (1973) 61; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975), in obs.;

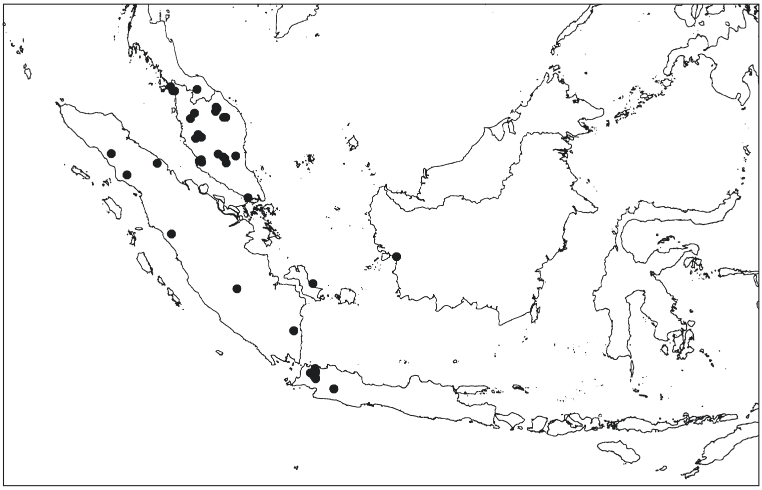
Kew Bull. 36 (1981) 254. — *Leiocarpus arboreus* Blume, Bijdr. (1825) 582; Miq., Fl. Ind. Bat. 1, 2 (1859) 362. — Type: *Blume s.n.* (L, barcode L 0062743), Java, Salak.

Leiocarpus arborescens Hassk., Hort. Bogor. Descr. (1858) 59; Bull. Soc. Bot. France 6 (1859) 715. — *Aporosa arborescens* (Hassk.) Müll.Arg. in DC., Prod. 15, 2 (1866) 470; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278. — Type: *Teysmann s.n.* (n.v.), Sumatra.

Daphniphyllum kingii Hook.f., Fl. Brit. India 5 (1887) 354. — Syntypes: *Scortechini s.n.*, *King's Collector s.n.* (K?, n.v.), Peninsular Malaysia: Perak.

Baccaurea forbesii Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) . — Type: *Forbes 3165* (holo BM; iso L), Sumatra.

Shrub or tree, up to 25 m high, up to 30 cm diameter. *Bark* brown to grey, reddish, or greenish, with white patches, smooth to scaly, fissured, cracking; inner bark (pale) brown to reddish, (pale) pink, or yellow. *Wood* brown-white, cream-yellow, or pale orange. Young branches brown, sparsely puberulous. *Stipules* not seen, early caducous, recorded falcate. *Petiole* terete, adaxially grooved, 14–51 by 1.5–2.5 mm, very sparsely hairy, glabrescent, upper pulvinus 4–11 by 2–5 mm, lower pulvinus 3–5 by 2–4 mm, both distinct. *Leaves* (narrowly) elliptic to narrowly obovate, 13.5–35 by 4.5–15 cm; base rounded to acute, basal glands absent; margin lowly undulate, marginal glands regular, small, blackish to greyish brown, variably distinct; apex acuminate to cuspidate; blade thin, smooth, dull, sometimes brittle, drying bluish or greenish above, blackening with age, greyish brown beneath, only midrib at base sparsely puberulous above, only midrib and nerves sparsely puberulous beneath, glabrescent; dots irregularly densely set, rather fine, black, fading in older, darker leaves; disc-like glands often few present, along the margin. *Nervation*: midrib flat to slightly sunken above, prominent beneath; nerves 12–16 pairs, flat to slightly sunken above, prominent beneath, marginal arches distinct, 2–6 mm from the margin; tertiary veins and venation distinct, rather densely reticulate, slightly scalariform, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* below the leaves or borne on the upper branches. *Staminate inflorescences* 1–6 clustered together, 16–55 by 0.5–1 mm, (sparsely) tomentose; peduncle 0.5–4 by 0.5–1 mm; bracts broadly triangular, inconspicuous, 0.3–0.5 mm long, sparsely puberulous outside, glabrous inside; glomerules ellipsoid, 1.5–2 by c. 1 mm, consisting of up to 20 densely set flowers, spaced at 0–4 mm at base of rachis, decreasing to 0 mm at apex; pedicel minute. *Staminate flowers* 0.4–0.8 mm long; sepals 4 or 5, narrowly obovate, connate at base, 0.5–0.8 mm long, sparsely puberulous outside, glabrous inside; stamens 2, slightly exserted, 0.3–0.4 mm long; anthers c. 0.2 mm long, connective glabrous; pistillode minute, lumpy, glabrous. *Pistillate inflorescences* 1–6 clustered together, 12–36 by 0.9–1.2 mm, (sparsely) tomentose; flowers up to 11, laxly set along the rachis; bracts triangular, 0.3–0.5 mm long, sparsely puberulous outside, glabrous inside; bracteoles ovate, 0.2–0.3 mm long, puberulous outside, glabrous inside; pedicel 1.5–3 mm long, (sparsely) tomentose. *Pistillate flowers* 2–5 mm long; sepals 5, ovate, patent to slightly reflexed, 0.6–1 mm long, sparsely puberulous outside, glabrous inside; ovary globose, 3- (or 4-)locular, 2–3.5 mm long, smooth, sparsely puberulous, glabrescent; stigmas slightly raised, elongated, apically bifid to c. halfway, perpendicular to the sides of the ovary, (slightly) recurved, 0.7–1.5 mm long, ribbed and lowly papillate above, glabrous, smooth beneath, style remnant absent. *Infructescences* 15–82 by 1.2–1.5 mm, (sparsely) tomentose; fruiting pedicel 5–12 mm long, sparsely tomentose. *Fruits* ellipsoid to globose, not stiped, young ones slightly beaked, 13–17 by 10–13 mm, approximately smooth, drying (dark) brown,



Map 10.52. Distribution of *Aporosa arborea* (Blume) Müll. Arg.

glabrous; pericarp 0.8–1.5 mm thick, slightly fleshy; septae and column glabrous. *Seeds* 1–3, half-terete, ovoid, 9–11 by 5.5–7.5 by 2–4 mm.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia, Sumatra, West Java, Borneo.

Habitat & Ecology — Primary or secondary evergreen forest; lowland, undulating country; on hill sides, ridges, and river sides. Soil: granitic sand, brown. Altitude: 20–1000 m. Flowering: March to May, July to October; fruiting: March, May to January.

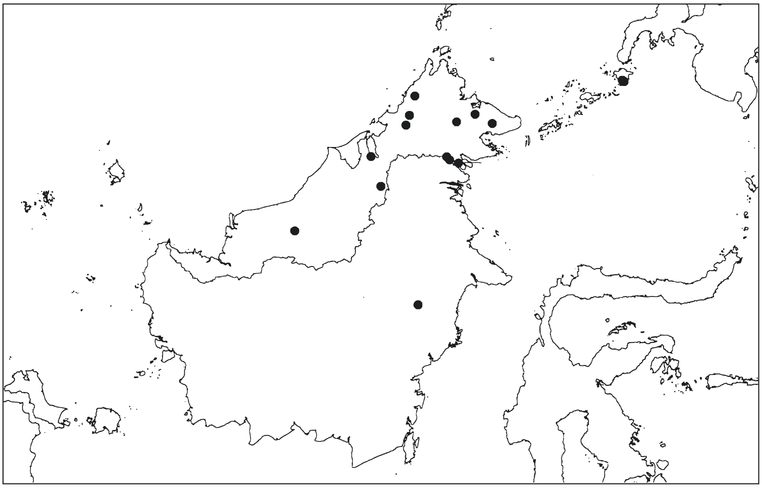
Vernacular names — Peninsular Malaysia: Sebasah, bulu-bulu (Malay); rambai ajam, rambai hantu (Temuan). Sumatra: Kayu djahut-djahut. Java: Huru pasgeng.

Note — Only two collections from Borneo, Gunung Palung National Reserve (*Van Balgooy & Van Setten 5353, 5564*) have the long petioles and large bluish leaves that are characteristic of *A. arborea*. Other collections from Borneo belong to *A. illustris*.

71. Aporosa basilanensis Merr. — Fig. 3.6o, 3.8f, 4.5b; Map 10.53

Aporosa basilanensis Merr., Philipp. J. Sci., Bot. 9 (1914) 471; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 94; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 410; Airy Shaw, Enum. Philipp. Flow. Pl. (1983). — Type: *BS (Reillo) 16168* (holo K; iso BM, P; photo A), Philippines, Basilan.

Tree, up to 25 m high, up to 30 cm diameter. *Bark* greenish, greyish, or brownish, smooth to scaly, sometimes flaking; inner bark pinkish, yellowish, orange-brown, or brownish (grey). *Wood* yellow to pale white. Young branches tomentose. *Stipules* not seen, early caducous. *Petiole* terete, adaxially sometimes lowly grooved, 6–17 by 1.2–2 mm, tomentose, lower pulvinus 1.5–2 by 1.5–2 mm, indistinct, upper pulvinus 2.5–6 by 2–3 mm, distinct. *Leaves* narrowly elliptic to narrowly obovate, 12–21 by 3.5–7 cm; base rounded to cuneate, basal glands absent; margin (very) lowly undulate, marginal glands few, small, black, indistinct; apex acuminate; blade thinnish, smooth, dull, not brittle, drying greenish brown to reddish brown above, (light) brownish beneath, glabrous above, sparsely hirsute beneath, midrib tomentose; dots irregularly laxly set, greyish, often indistinct; disc-like glands seldom few present, small, along the margin. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 10–12 pairs, slightly prominent to flat above, prominent beneath, marginal arches rather distinct, 1–2.5 mm from the margin; tertiary veins and venation fading, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 18–47 by 1.5–2.2 mm, tomentose; peduncle 2.5–10 by 0.5–0.8 mm; bracts broadly triangular, 0.7–1 mm long, inconspicuous, hairy outside, sparsely hairy inside, margin ciliate; glomerules approximately ellipsoid, consisting of 9–13 rather densely set flowers, 1.5–2 by 1–1.5 mm, spaced at 2–3 mm at base of rachis, decreasing to 0 mm at apex; pedicel minute. *Staminate flowers* 0.5–0.8 mm long; sepals 4 (or 5), narrowly obovate, 0.8–1 mm long, connate at base, scarious, sparsely hairy outside, glabrous inside, margin ciliate; stamens (2 or) 3, not to slightly exserted, 0.8–1 mm long; anthers c. 0.3 mm long, connective glabrous; pistillode minute, lumpy, resembling an undeveloped anther. *Pistillate inflorescences* 1–4 clustered together, 23–41 by 0.8–1 mm, tomentose, the flowers up to 11, laxly set along the rachis; bracts triangular, 1.5–1.7 mm long, hairy outside, hairy at base only inside, margin ciliate; bracteoles ovate, 0.5–0.8 mm long, hairy outside, hairy at base only inside; pedicel 1–1.5 mm long, tomentose. *Pistillate flowers* 2.5–3 mm long; sepals 4, ovate, patent, 1–1.5 mm long, thin, hairy outside, sparsely hairy near base inside; ovary ovoid, 2–2.5 mm long, 2-locular, smooth, (sparsely) sericeous; stigmas slightly raised, elongated, perpendicular to the sides of the ovary, slightly recurved, apically bifid to near base, 2–2.5 mm long, ribbed above, margins papillate, glabrous, lowly papillate beneath, style remnant absent. *Infructescences* 27–58 by 1–1.5 mm, (sparsely) tomentose; fruiting pedicel 2–6 mm long, (sparsely) tomentose. *Fruits* ovoid to slightly flask-shaped, not stiped, beaked, 13–19 by 10–13 mm, punctulate, drying orangish brown, sparsely puberulous; pericarp 0.8–1.5 mm thick, slightly fleshy; apex



Map 10.53. Distribution of *Aporosa basilanensis* Merr.

of endocarp caudate; septae and column glabrous. *Seeds* 1–3, half-terete, ellipsoid, 10–11 by 6–8 by 3–4 mm.

Distribution — Malesia: Borneo, Philippines.

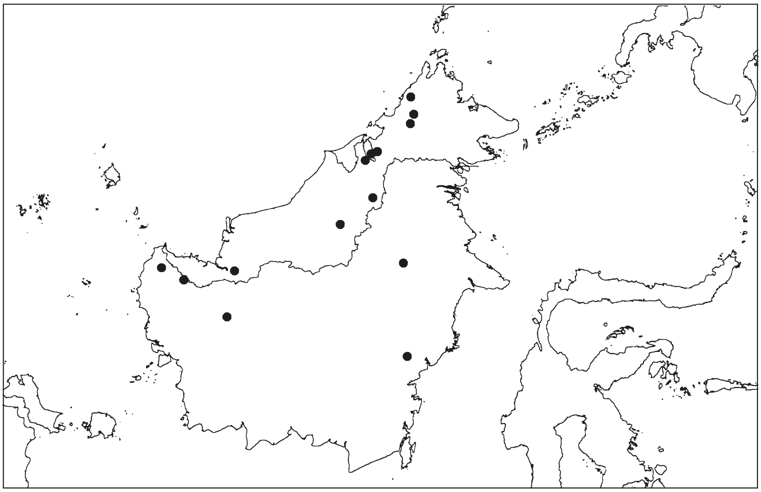
Habitat & Ecology — Primary, mixed dipterocarp forest and in logging areas; on hill sides, hill tops, flat land, and along river banks. Soil: basalt or clayish, yellow. Altitude: 30–1450 m. Flowering: March to May; fruiting: February to December.

Vernacular names — Borneo: Janggau, kayu ma(s)sam (Iban).

72. Aporosa caloneura Airy Shaw — Map 10.54

Aporusa caloneura Airy Shaw, Kew Bull. 23 (1969) 5; Kew Bull., Addit. Ser. 4 (1975) 34. — Type: *J. & M.S. Clemens 40625* (holo K; iso A, BM, L), Sabah, Mt Kinabalu.

Tree, up to 30 m high, up to 35 cm diameter. *Bark* brown(ish) or grey(ish) or whitish, smooth; inner bark reddish (orange) or reddish brown. *Wood* light brown or grey-white to yellowish. Young branches whitish brown, very sparsely puberulous. *Stipules* not seen, early caducous. *Petiole* terete, smooth, 11–31 by 1.5–2 mm, very sparsely puberulous, lower pulvinus 1.5–2.5 by 2–2.5 mm, indistinct, upper pulvinus 3–5 by 2–3 mm, distinct. *Leaves* (narrowly) elliptic to narrowly obovate, 7–20 by 3–8 cm; base rounded to slightly attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, distinct, black; apex acuminate; blade thickish, smooth, often shiny, older ones brittle, drying greenish brown above, brownish beneath, glabrous above, only midrib and nerves at base very sparsely puberulous beneath, glabrescent; dots irregularly laxly set, distinct, black, fading; disc-like glands seldom few present, small, along the margin. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 7–11 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 2–4 mm from the margin; tertiary veins and venation distinct, rather densely reticulate, slightly scalariform, slightly prominent to flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 9–26 by 2–3 mm, sparsely puberulous; peduncle 1.5–4 by 0.8–1.2 mm; bracts broadly triangular, 0.8–1 mm long, inconspicuous, sparsely hairy outside, glabrous inside; glomerules subglobose, 2–3 by 1.5–2 mm, consisting of 8–10 laxly set flowers, spaced at 1–5 mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 1.5–2 mm long; sepals 4, narrowly obovate, 1–1.5 mm long, connate at base only, sparsely hairy outside, glabrous inside; stamens 2 or 3, exserted, 1.2–1.5 mm long; anthers 0.3–0.4 mm long, connective glabrous; pistillode cylindrical, c. 0.2 mm long, apically hairy. *Pistillate inflorescences* 1–3 clustered together, 14–40 by 1–1.2 mm, sparsely puberulous; flowers up to 9, rather laxly set along the rachis; bracts broadly triangular, 1–1.5 mm long, glabrous, margin ciliate; bracteoles triangular, 0.8–1 mm long, sparsely hairy outside, glabrous inside; pedicel 1–2 mm long, sparsely puberulous. *Pistillate flowers* 3–4 mm long; sepals 3 or 4, ovate, subequal, patent, 0.8–1.5 (0.3–0.5) mm long, thin, sparsely hairy outside, glabrous inside; ovary ovoid, 2.5–3 mm long, 2- or 3-locular, rugose, subglabrous; stigmas raised, elongated, perpendicular to the sides of the ovary, recurved, apically bifid to near base, 1.5–2.5 mm long, rather smooth above, margins lowly laciniate, glabrous, lowly papillate beneath, glabrous, style remnant absent. *Infructescences* 19–41 by c. 1.5 mm, very sparsely puberulous; fruiting pedicel 3–5 mm long, sparsely puberulous. *Fruits* (narrowly) ovoid to ellipsoid, young ones slightly



Map 10.54. Distribution of *Aporosa caloneura* Airy Shaw.

stiped and beaked, 15–22 by 9–14 mm, punctulate to smooth, drying dark brown to black, glabrous; pericarp 1–1.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 1–3, half-terete, ovoid, 10–13 by 4–7 by 3–4 mm.

Distribution — Malesia: Borneo.

Habitat & Ecology — Primary, secondary forest, kerangas; on hill sides, ridges, slopes, and along river sides. Soil: sandy or sandstone. Altitude: 30–1460 m. Flowering: March, May, September to November; fruiting: March, April, September to November.

Notes — 1. Some specimens smell like fenugreek.

2. Specimen *S (Pickles) 2943* from high kerangas has extremely thick leaves, but equals in other characters *A. caloneura*.

73. **Aporosa dendroidea** Schot — Fig. 3.8b, 3.11h, 10.9; Map 10.55

Aporosa dendroidea Schot, Blumea 40 (1995) 455. — Type: *Van Balgooy 4634* (holo L; iso K), Moluccas, N Buru.

Aporosa sphaeridiophora auct. non Merr.: Airy Shaw, Kew Bull. 37 (1982) 8.

?Aporosa nervosa auct. non Hook.f.: Airy Shaw, Kew Bull. 37 (1982) 8.

Tree, up to 12 m high, up to 15 cm diameter. Young branches very sparsely puberulous, glabrescent. *Stipules* not seen, early caducous. *Petiole* terete, smooth, 7–12 by 0.8–1.2 mm, glabrescent, lower pulvinus 1–1.5 by 1–1.2 mm, upper pulvinus 4–6 by 1–1.5 mm, both rather distinct. *Leaves* (narrowly) elliptic, 7–16 by 3–5.5 cm; base acute to slightly attenuate, basal glands absent; margin very lowly undulate, marginal glands few, indistinct; apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, drying (dark) greenish grey above, (dark) brownish grey beneath, completely glabrous; dots rather densely set, rather large, distinct, grey to black; disc-like glands scattered near base along margin and within marginal arches, often distinct. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 7–9 pairs, slightly

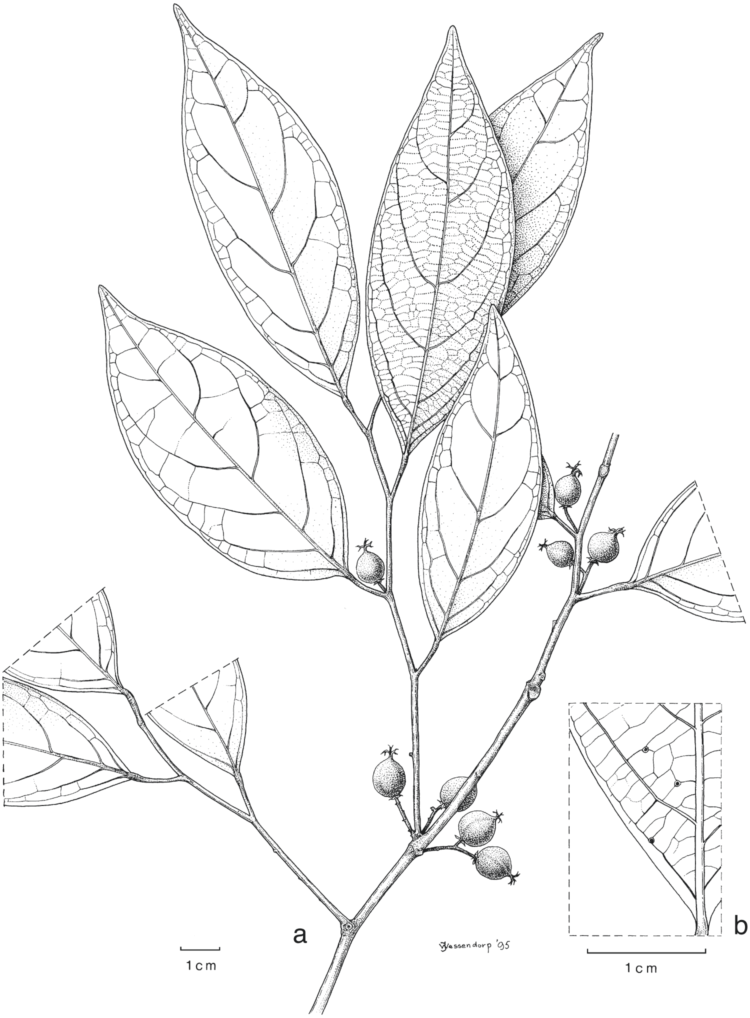
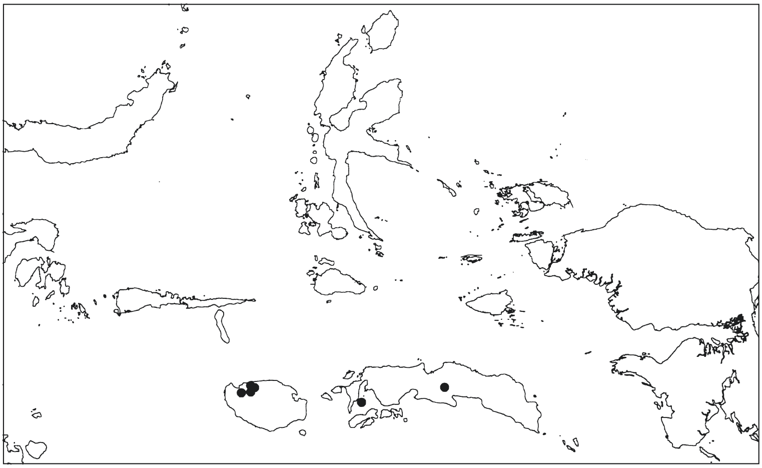


Fig. 10.9. *Aporosa dendroidea* Schot. a. Habit; b. lower surface of leaf showing disc-like glands (*Van Balgooy 4634*, L).

prominent to flat above, prominent beneath, marginal arches distinct, 2–4 mm from the margin; tertiary veins and venation fading, rather laxly reticulate, slightly prominent to flat. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* and *staminate flowers* not seen. *Pistillate inflorescences* 1 or 2 clustered together, 7–14 by 0.5–0.8 mm, (sparsely) puberulous, flowers up to 6, laxly set at base of rachis, more densely apically; bracts broadly triangular, c. 0.5 mm long, sparsely puberulous outside, glabrous inside; bracteoles ovate, c. 0.5 mm long, sparsely sericeous outside, glabrous inside; pedicel 0.5–1.5 mm long, puberulous. *Pistillate flowers* 2.5–3.5 mm long; sepals 4, patent, ovate, 0.5–0.8 mm long, thin, sparsely puberulous outside, glabrous



Map 10.55. Distribution of *Aporosa dendroidea* Schot.

inside; ovary ovoid, 1.5–3 mm long, 3-locular, smooth, very sparsely puberulous at base, glabrescent towards apex; stigmas raised, elongated, perpendicular to the sides of the ovary, recurved, apically bifid to slightly more than halfway, lobes apically bifid or trifid, 1–2.5 mm long, papillate above, margins laxly laciniate, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 3–26 by 0.8–1.5 mm, sparsely puberulous, glabrescent; fruiting pedicel 1.5–5 mm long, sparsely puberulous. *Fruits* ovoid to subglobose, not stiped, beaked, 9–13 by 9–13 mm, punct(ul)ate, drying light brown, glabrous; pericarp 0.5–1.2 mm thick, not fleshy; septae and column glabrous. *Seeds* 3 (seldom 4), half-terete, ellipsoid, 7–8 by 5–7 by 2–3 mm.

Distribution — Malesia: Moluccas (Ambon, Buru, Seram).

Habitat & Ecology — Primary, logged over forest; on steep mountainous land; on ridges. Altitude: 200–650 m. Fruiting: February, November. The seed is said to be eaten by birds.

Vernacular names — Buru: Bisugebe, belui `epe.

Note — Airy Shaw (1982) lists both *A. nervosa* and *A. sphaeridiophora* for the Moluccas. The specimens identified as *A. sphaeridiophora* from the Moluccas (left under this name in the Kew Herbarium by Airy Shaw) are *A. dendroidea*. I have not seen any specimens from the Moluccas identified as *A. nervosa*, but they very likely belong to *A. dendroidea*.

74. **Aporosa duthieana** King ex Pax & K. Hoffm. — Map 10.56[1]

Aporosa duthieana King ex Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922). — Type: *Meebold 14290* (holo B†; ?iso CAL), Burma, Mergui.

Tree, up to 13 m high, up to 17 cm diameter. Young branches very sparsely puberulous. *Stipules* not seen, early caducous. *Petiole* terete, adaxially grooved, 7–16 by 1–1.5

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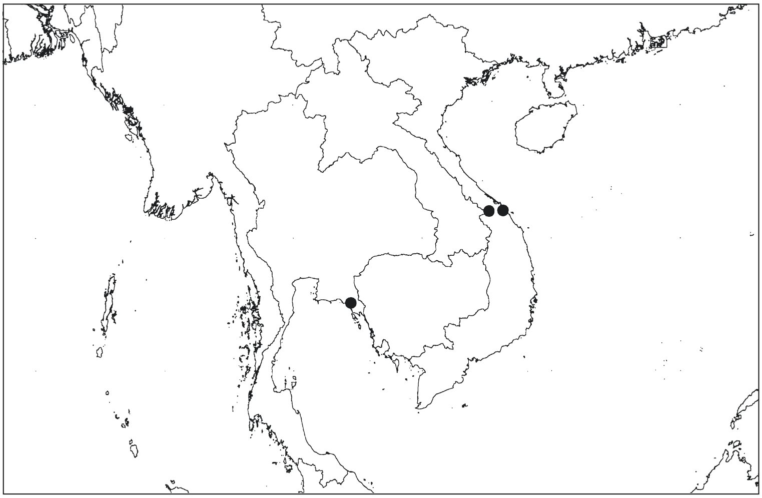
[1] Staminate inflorescences and staminate flowers as observed by P.C. van Welzen from a specimen at Bangkok, Thailand.

mm, very sparsely puberulous, glabrescent, lower pulvinus 1.5–2 by 1.2–1.8 mm, often indistinct, upper pulvinus 2–5 by 1.5–2 mm, rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 7–13 by 2–5 cm; base obtuse to cuneate, basal glands absent; margin lowly undulate to irregularly lowly glandular-crenate, marginal glands few, black, distinct; apex acuminate; blade thickish, smooth, rather shiny, not brittle, drying greenish to reddish brown above, light greenish grey to greyish brown beneath, glabrous above, midrib and nerves very sparsely puberulous beneath, glabrescent; dots laxly set, fine, distinct, blackish, fading; disc-like glands few to regular, distinct, along the margin, often at the end of venules. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 5–7 pairs, slightly prominent to flat above, prominent beneath, marginal arches fading, 1–2.5 mm from the margin; tertiary veins and venation indistinct, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–4 clustered together, 25–50 by 0.7–0.9 mm, sparsely puberulous; peduncle 0–10 by 0.7–0.9 mm; bracts approximately triangular, inconspicuous, c. 0.6 mm long, glabrescent; glomerules subglobose, 3.5–4 by 3–3.5 mm, consisting of up to 15 (or more?) densely set flowers, spaced at 5(–11) mm at base of rachis, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 2.2–3.8 mm long; sepals 4 (or 5), elliptic, 0.9–1.3 mm long, connate at base, puberulous outside and along margin, puberulous at base only inside; stamens 2–4, long exserted, 2.2–3.8 mm long; anthers c. 0.5 mm long; connective glabrous; pistillode absent. *Pistillate inflorescences* not seen, induced from infructescences to be single, tomentose; flowers up to 9, rather densely arranged at apical end; bracts broadly triangular, 0.5–0.8 mm long, sparsely puberulous outside, hairy at base inside, margin ciliate; bracteoles ovate, 0.3–0.5 mm long, sparsely puberulous outside, puberulous at base inside, margin ciliate; pedicel small, tomentose. *Pistillate flowers* not seen; sepals in fruit 3 or 4, ovate, patent, 0.8–1.2 mm long, thin, sparsely puberulous; ovary probably ovoid, 2-locular, punctulate, sparsely puberulous; stigmas in fruit slightly raised,



Map 10.56. Distribution of *Aporosa duthieana* King ex Pax & K. Hoffm.

elongated, perpendicular to the sides of the ovary, apically bifid to c. halfway, slightly recurved, 2–2.5 mm long, above papillate to laciniate, glabrous, ribbed and papillate beneath, sparsely puberulous, style remnant absent. *Infructescences* 7–18 by 0.8–1 mm, sparsely tomentose; fruiting pedicel 1–2 mm long, sparsely puberulous. *Fruits* ellipsoid, not stiped, slightly beaked, 10–12 by 7–8 mm, punctate, drying brown to black, sparsely puberulous at base, glabrescent; pericarp 0.3–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 1, terete, ellipsoid, c. 8 by 5–5.5 by c. 4 mm.

Distribution — Burma, Thailand, Vietnam.

Habitat & Ecology — Evergreen forest. Altitude: 800–1000 m. Fruiting: February, July, September.

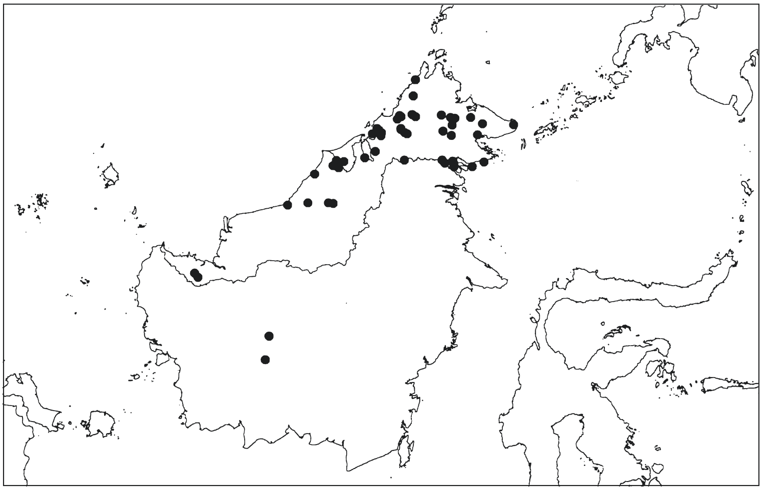
Notes — 1. Airy Shaw (1972) included *A. duthieana* tentatively under *A. microstachya*. I have seen specimens that were like *A. microstachya*, but differed in the thicker leaves, which is exactly the character by which Pax & Hoffmann (1922) separated their *A. duthieana* from *A. maingayi* (synonymised by Airy Shaw with *A. microstachya*, but reinstated here). Another vegetative difference between both species are the glands, more than 1 mm from the margin in *A. duthieana*, always less than 1 mm in *A. microstachya*. The two species differ dramatically in the staminate inflorescences and, less so, in the length of the fruit pedicel.

2. Chakrabarty & Gangopadhyay (1993), following the synonymy with *A. microstachya*, cite an isotype of the *Meebold 14290* collection of *A. duthieana* under their *A. microstachys*, but I have not seen this CAL specimen.

75. Aporosa elmeri Merr. — Fig. 3.5l, 3.6q, 3.7d, 3.8m, 3.11e, 4.7c; Map 10.57

Aporosa elmeri Merr., Pl. Elmer. Born. (1929) 142; Meijer, Bot. News Bull. Sandakan 7 (1967) 35 (excl. fig. = *A. illustris* Airy Shaw); Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 35. — Type: *Elmer 20954* (iso BM, BO, L, P), Sabah, Tawau.

Tree, up to 12 m high, up to 20 cm diameter. *Bark* pale or dark (red-)brown(ish), whitish, or grey to greenish, smooth, c. 2 mm thick; inner bark brownish, (pale) reddish, pale green, pink, or yellowish. *Wood* orange to yellow-white. Young branches brown, densely tomentose. *Stipules* (narrowly) ovate, 6–13 by 4–6.5 mm, (densely) tomentose, present in young stages. *Petiole* terete, rather smooth, older ones adaxially lowly grooved, 8–19 by 2–3 mm, (densely) tomentose, lower pulvinus c. 3 by 3 mm, upper pulvinus 4–7 by 3–3.5 mm, both indistinct under indumentum. *Leaves* (narrowly) elliptic to (narrowly) obovate, 11–25 by 5–11 cm; base emarginate to cuneate, basal glands absent; margin (lowly) undulate to glandular-crenate, marginal glands few, small, indistinct; apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, drying dark brownish green above, blackening, light to golden brown beneath, sparsely tomentose above, midrib and nerves tomentose, sparsely tomentose beneath, nervation tomentose, glabrescent; dots irregularly laxly set, fine, grey, often indistinct; disc-like glands absent. *Nervation*: midrib flat to raised in a furrow above, prominent beneath; nerves 8–11 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.5–2.5 mm from the margin; tertiary veins and venation distinct, rather densely reticulate, slightly scalariform, slightly prominent to flat above, sometimes near the margins slightly sunken, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 10–20 clustered together, 11–47 by 0.3–0.5



Map 10.57. Distribution of *Aporosa elmeri* Merr.

mm, sparsely puberulous; peduncle 2–3 by 0.5 mm; bracts triangular, inconspicuous, 0.2–0.5 mm long, sericeous outside, glabrous inside; glomerules globose, lax, 0.8–1.2 by 0.5–0.8 mm, consisting of 7–10 densely set flowers, spaced at 1–3 mm along the rachis; pedicel minute. *Staminate flowers* 0.3–0.8 mm long; sepals (3 or) 4, narrowly obovate, 0.3–0.6 mm long, connate at base, sparsely sericeous outside, glabrous inside; stamens 2, slightly exserted, 0.5–1 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode minute, lumpy. *Pistillate inflorescences* 5–10 clustered together, 6–54 by 0.5–0.8 mm, puberulous; flowers up to 21, rather densely set mostly at apical 3/4 of the rachis; bracts triangular, 0.3–0.5 mm long, sericeous outside, glabrous inside; bracteoles triangular, 0.1–0.2 mm long, sericeous outside, glabrous inside; pedicel minute, up to 0.3 mm long. *Pistillate flowers* 1.3–2 mm long; sepals 4 (or 5), narrowly ovate, patent, 0.6–0.9 mm long, thin, sparsely sericeous outside, sparsely puberulous at base only inside; ovary ellipsoid, 1.2–1.5 mm long, 2-locular, densely sericeous; stigmas sessile, elongated, flattened on top and to the sides of the ovary, almost completely divided, straight, 0.8–1.5 mm long, densely laciniate above, glabrous, smooth beneath, (sparsely) puberulous, style remnant absent. *Infructescences* 9–57 by 0.8–1.5 mm, sparsely tomentose; fruiting pedicel 0.5–1 mm long, puberulous. *Fruits* ellipsoid, not stiped, not beaked, 9–12 by 6–9 mm, punctate, drying dark (reddish) brown, sparsely sericeous; pericarp 0.5–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 (or 2), (half-)terete, ovoid, 7–9 by 5–6 by 3–4 mm.

Distribution — Malesia: Borneo (mostly Sabah).

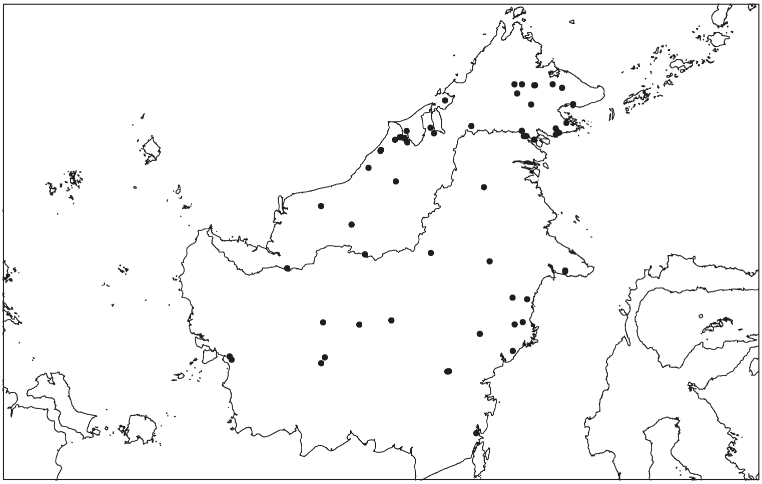
Habitat & Ecology — Primary, old logged, heath forest; on hill sides, hill tops, ridges, mountain ranges, valley bottoms, or flat land. Soil: sandy clay, black or yellow. Altitude: sea level to 750 m. Flowering: January, March to May, August to October; fruiting: February to December.

Vernacular names — Panatan, penatan (Dusun); tarinis (Dusun Kinabatangan); kayu mas(s)am (Iban); pahi (Kayan).

76. Aporosa grandistipula Merr. — Fig. 3.7b; Map 10.58

Aporosa grandistipula Merr., Philipp. J. Sci. 21 (1922) 521; Pl. Elmer. Born. (1929) 142; Meijer, Bot. News Bull. Sandakan 7 (1967) 33; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 37. — Type: *Agama 579* (iso A, K, P), Sabah.

Tree, up to 20 m high, up to 18 cm diameter. *Bark* (dark to pale) greyish or brownish, reddish, chocolate, or red-brown, smooth, c. 1.5 mm thick; inner bark brown(ish), greenish, reddish, pink, or yellowish. *Wood* (pale) brownish, reddish, or yellowish to white. Young branches sparsely puberulous. *Stipules* falcate, 6–14 by 12–24 mm, often persistent, glabrous, often black disc-like glands along margin beneath. *Petiole* terete, adaxially or around grooved, 8–47 by 1–2 mm, sparsely puberulous, lower pulvinus 1.5–4 by 1.5–3 mm, upper pulvinus 3–9 by 1.5–3 mm, both distinct. *Leaves* narrowly elliptic to narrowly obovate, 12–35 by 3.5–10.5 cm; base emarginate to truncate, basal glands absent; margin lowly glandular-crenate to lowly glandular-serrate, marginal glands many, small, black, distinct; apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, drying greenish greyish to greyish blue above, (dark) brown-grey beneath, glabrous above, only midrib and nerves sparsely puberulous beneath, glabrescent; dots irregularly laxly set, fine, greyish black, fading; disc-like glands few, small, indistinct, along the margin. *Nervation*: midrib (slightly) prominent above, prominent beneath; nerves 14–23 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 2–4 mm from the margin; tertiary veins and venation distinct, rather densely reticulate, slightly scalariform, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 3–6 clustered together, 13–61 by 0.3–0.5 mm, subglabrous; peduncle 1–3 by 0.3–0.5 mm; bracts broadly triangular, inconspicuous, 0.8–1.2 mm long, glabrous, margin sparsely ciliate; glomerules globose, 0.8–1.5 by 0.8–1.5 mm, consisting of 7–12 densely set flowers, spaced at 1.5–6 mm along the rachis; pedicel minute. *Staminate flowers* 0.5–1 mm long; sepals 4 (or 5), (narrowly) obovate, subequal, 0.5–0.8 mm long, connate at base, glabrous, margin sparsely ciliate; stamens 3 (or 4), 0.5–0.9 mm long, slightly



Map 10.58. Distribution of *Aporosa grandistipula* Merr.

exserted; anthers 0.2–0.3 mm long, connective glabrous; pistillode minute, lumpy. *Pistillate inflorescences* 1–3 clustered together, 13–24 by 0.5–0.8 mm, subglabrous; flowers up to 11, laxly arranged along the rachis; bracts broadly triangular, 0.3–0.5 mm long, glabrous, margin sparsely ciliate; bracteoles triangular, 0.2–0.3 mm long, glabrous, margin ciliate; pedicel 3–5 mm long, sparsely puberulous. *Pistillate flowers* 2.5–4 mm long; sepals 5, ovate, subequal, patent, 0.6–1.2 mm long, thin, glabrous, margin sparsely ciliate; ovary ovoid, 2–3 mm long, 3-locular, smooth, glabrous; stigmas slightly raised, elongated, apically bifid to near base, perpendicular to the sides of the ovary, recurved, 1–1.5 mm long, laxly papillate above, glabrous, slightly ribbed to smooth beneath, glabrous, style remnant absent. *Infructescences* 10–41 by 0.8–1.2 mm, glabrous; fruiting pedicel 4–9 mm long, glabrous. *Fruits* ovoid, not stiped, not beaked, 11–16 by 10–14 mm, punctate, young ones slightly ridged on sutures, drying (dark) brown, glabrous; pericarp 0.5–1 mm thick, slightly fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ovoid, 7–11 by 6.5–9 by 3–4 mm.

Distribution — Malesia: Borneo.

Habitat & Ecology — Primary, (old) secondary, disturbed, logged, alluvial, or riverine forest; in flat, low undulating, hilly, moist, or swampy country, sometimes subject to flooding; on ridges, hills, or along streams. Soil: sandy, clayey, clay-loam, sandstone, limestone, rich yellow to blackish, stony. Altitude: 5–500 m. Flowering: March, April, July to December; fruiting: March to January.

Vernacular names — Ketune (Dayak); ulas, mantus (Dusun-Kinabatangan); galang-galang (Dusun, Sungei Kinabatangan); kayu mas(s)am (Iban); bua ba-ee (Kenyah); boata (Sungei).

Note — All collections from Sulawesi that I saw identified as *A. grandistipula* belong to *A. leytensis* Merr.

77. **Aporosa granularis** Airy Shaw — Fig. 3.5d, 3.6e; Map 10.59

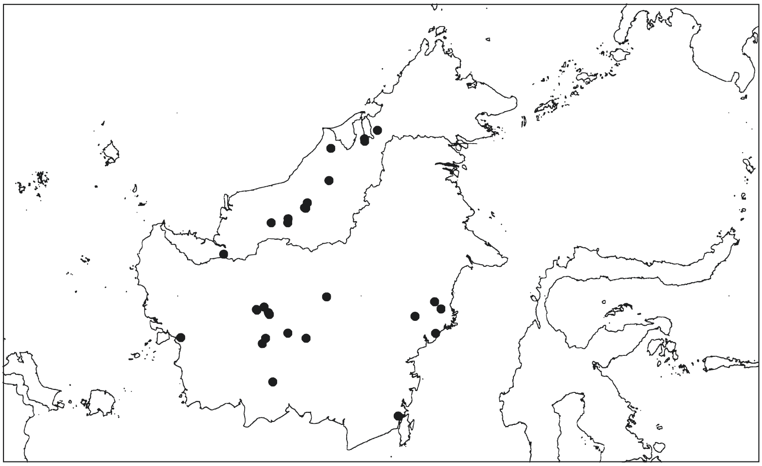
Aporusa granularis Airy Shaw, Kew Bull. 29 (1974) 283; Kew Bull., Addit. Ser. 4 (1975) 37. — *Aporusa microstachya* (Tul.) Müll.Arg. forma ?: Airy Shaw, Kew Bull. 23 (1969) 3, in obs. — Type: *S (Ismawi) 29658* (holo K; iso L, SING), Sarawak, 3rd Division.

Shrub or tree, up to 9 m high, up to 11 cm diameter. *Bark* greyish or light brown, smooth to rugose; inner bark pale brown. Young branches (pale) brown, (sparsely) tomentose. *Stipules* narrowly ovate, slightly oblique, 6–8 by 1.5–2.5 mm, very sparsely sericeous beneath, present in young stages. *Petiole* terete, adaxially lowly grooved, 7–12 by 0.5–1 mm, tomentose, glabrescent, lower pulvinus 1–1.5 by c. 1 mm, indistinct, upper pulvinus 2–3 by 1–1.2 mm, rather distinct. *Leaves* narrowly elliptic, 6–16 by 1.8–5 cm; base obtuse to attenuate, basal glands absent; margin very lowly undulate to lowly glandular-crenate, marginal glands few, small, grey, indistinct; apex cuspidate to caudate; blade thin, smooth, dull to slightly shiny, not brittle, drying (dark) greenish grey to greenish brown above, greyish brown beneath, only midrib and nerves puberulous above, glabrescent, sparsely puberulous beneath, midrib and nerves puberulous, glabrescent; dots irregularly set, fine, blackish, mostly indistinct; disc-like glands absent. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 6–8 pairs, flat to slightly sunken above, prominent beneath, marginal arches distinct, 1–3 mm from the margin; tertiary veins and venation distinct, laxly reticulate, slightly scalariform, flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 5–9 by 1–1.5 mm, puberulous; peduncle 0.5–1.5 by c. 0.8 mm; bracts broadly triangular, inconspicuous, 0.3–0.5 mm long, very sparsely puberulous outside, glabrous inside, margin ciliate; glomerules subglobose, c. 1 by 0.5 mm, indistinct, consisting of 3–5 laxly set flowers, some spaced at 0.1–0.5 mm at base of rachis, mostly continuous at apex; pedicel minute. *Staminate flowers* 0.3–0.5 mm long; sepals 4, obovate, connate at base, 0.4–0.6 mm long, sparsely hairy at base only outside, glabrous inside, margin ciliate; stamens 2, slightly exserted, 0.5–0.7 mm long; anthers 0.1–0.2 mm long; pistillode minute, lumpy. *Pistillate inflorescences* 1 or 2 clustered together, 2–4 by 0.5–0.8 mm, (sparsely) puberulous; flowers up to 7, mostly densely set at apical part of the rachis; bracts broadly triangular, 0.3–0.5 mm long, sparsely hairy outside, glabrous inside; bracteoles ovate, c. 0.3 mm long, sparsely hairy outside, glabrous inside; pedicel absent. *Pistillate flowers* 1.5–2 mm long; sepals 4, ovate, patent, 0.7–1 mm long, thin, sparsely hairy outside, glabrous inside; ovary ellipsoid, 2-locular, 1.5–2 mm long, smooth, sparsely sericeous at base, glabrescent; stigmas sessile, elongated, flattened to the sides of the ovary, apically bifid to near base, straight, 1–2 mm long, lowly papillate to laciniate above, glabrous, smooth beneath, glabrous, style remnant absent. *Infructescences* 3–5 by 0.5–1 mm, sparsely puberulous; fruiting pedicel absent. *Fruits* ellipsoid, not stiped, not beaked, 7–9 by 6–8 mm, granular, drying (dark) brownish, very sparsely hairy, glabrescent; pericarp 0.3–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 1, half-terete, ellipsoid, 6–7 by 4–5 by 2–3 mm.

Distribution — Malesia: Borneo (mostly Sarawak).

Habitat & Ecology — Primary, disturbed, old secondary mixed dipterocarp lowland forest, peat swamp, kerangas; on undulating country, steep or gentle slopes, and along river banks. Soil: sandstone or sandy (clay), yellow, rich. Altitude: 50–700 m. Flowering: June, August to October; fruiting: May to February.

Vernacular names — Ganjii (Bukit Baka); jangau, kayu masam, kayu matalio (Iban).

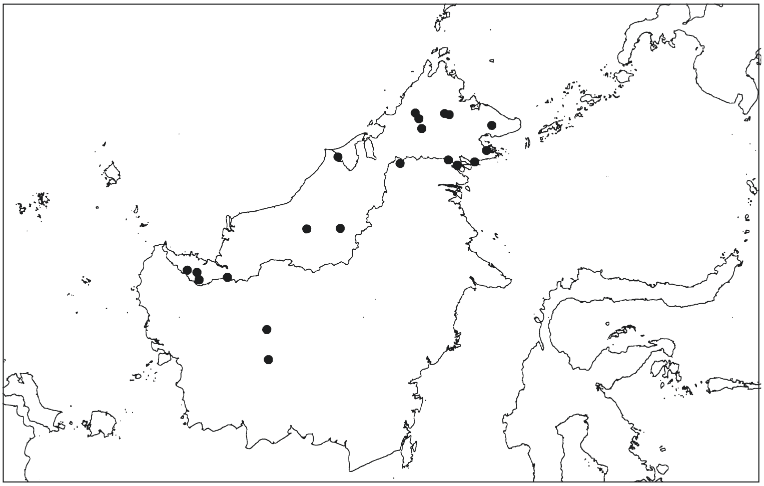


Map 10.59. Distribution of *Aporosa granularis* Airy Shaw.

78. Aporosa illustris Airy Shaw — Map 10.60

Aporusa illustris Airy Shaw, Kew Bull. 29 (1974) 181; Kew Bull., Addit. Ser. 4 (1975) 37. — *Aporusa nervosa* Hook.f. forma: Airy Shaw, Kew Bull. 23 (1969) 5, in obs. — Type: *S (Paie) 17026* (holo K; iso BO, L), Sarawak, Serian.

Tree, up to 30 m high, up to 30 cm diam.; buttresses c. 60 cm high, 5 cm thick, 120 cm long. *Bark* greyish brown, pale brown, or red, smooth, c. 0.5 cm thick; inner bark dark to light brown, yellowish, or pale red, c. 0.5 cm thick. *Wood* white brown, (light) yellowish, or whitish. Young branches greyish brown, tomentose. *Stipules* falcate, 4–12 by 8–22 mm, sparsely tomentose beneath, often early caducous. *Petiole* half-terete, ridged, 8–38 by 1.2–3 mm, tomentose to hirsute, glabrescent, lower pulvinus 2–6 by 2–3 mm, upper pulvinus 4–10 by 2–4 mm, both distinct. *Leaves* (narrowly) ovate to narrowly elliptic, 13–28 by 4.5–12 cm; base rounded to cuneate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands many, large, distinct, black, hairy in young leaves; apex acuminate to cuspidate; blade thickish, smooth, dull, not brittle, drying greyish green to greenish brown above, brownish beneath, glabrous above, sparsely tomentose beneath, midrib and nerves tomentose, glabrescent; dots irregularly densely set, black, fading; disc-like glands seldom few, small, along the margin. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 8–13 pairs, slightly prominent to slightly sunken above, prominent beneath, marginal arches distinct, 1.5–5 mm from the margin; tertiary veins and venation distinct, rather laxly reticulate, slightly scalariform, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–4 clustered together, 18–33 by 0.8–1.5 mm, (sparsely) tomentose; peduncle 2.5–10 by 0.5–0.8 mm; bracts triangular, 0.8–1 mm long, inconspicuous, sparsely tomentose outside, sparsely tomentose at base only inside; glomerules globose, 1.5–2.5 by 1.5–2.5 mm, consisting of more than 10 densely set flowers, spaced at 1–3 mm throughout; pedicel minute. *Staminate flowers* 0.5–1 mm long; sepals 4, narrowly obovate, 0.8–1.2



Map 10.60. Distribution of *Aporosa illustris* Airy Shaw.

mm long, connate at base, sparsely puberulous outside, glabrous inside; stamens 3 or 4, slightly exserted, 0.3–0.8 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode a minute hair tuft. *Pistillate inflorescences* clustered 1–3 together, 12–29 by 0.5–0.8 mm, (sparsely) tomentose; flowers up to 11, laxly set along the rachis; bracts broadly triangular, 0.5–0.8 mm long, sparsely puberulous outside, glabrous inside; bracteoles ovate, 0.3–0.5 mm long, sparsely puberulous outside, glabrous inside; pedicel 1–2.5 mm long, (sparsely) tomentose. *Pistillate flowers* 3.5–5 mm long; sepals 3, ovate, 1.2–1.5 mm long, sparsely puberulous outside, sparsely puberulous at base only inside; ovary ovoid, 2.5–4 mm long, 3- (or 4-)locular, smooth, very sparsely puberulous at base; stigmas raised, elongated, perpendicular to the sides of the ovary, slightly recurved or straight, apically bifid to near base, 1–2.2 mm long, ribbed and papillate to laciniate above, glabrous, ribbed beneath, glabrous, style remnant absent. *Infructescences* 10–76 by1–2.5 mm, sparsely tomentose, glabrescent; fruiting pedicel 2–6 mm long, sparsely tomentose, glabrescent. *Fruits* ovoid to globose, not stiped, not beaked, 12–19 by 10–16 mm, punctulate to smooth, drying brownish, sparsely puberulous, glabrescent; pericarp 1–4 mm thick, slightly fleshy; septae and column glabrous. *Seeds* 2 or 3, half-terete, ellipsoid, 9.5–13 by 7–9 by 3–5 mm.

Distribution — Malesia: Borneo.

Habitat & Ecology — Primary forest, logged forest; in swampy areas, on hills, ridges, flat land, near paths, and along riversides. Soil: sandy clay; black. Altitude: 25–1500 m. Flowering: March, April, September; fruiting: February, June to November.

Vernacular names — Kayu masam (Iban); kata (Kayan); damak-damak, limpuang (Tawau).

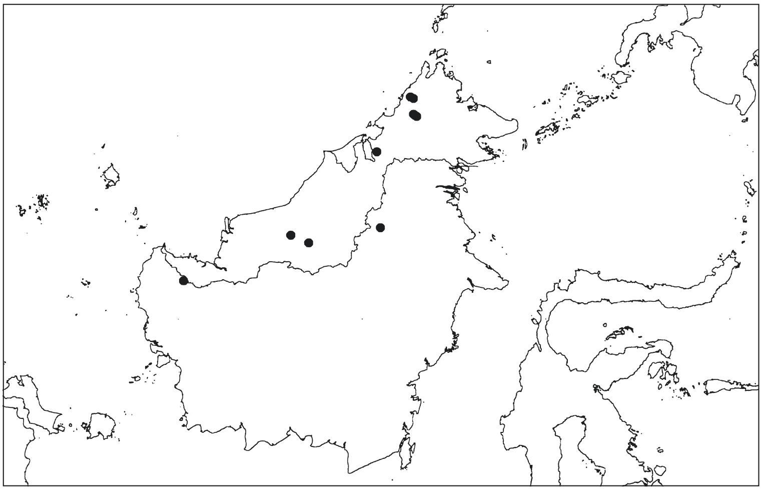
Note — Two forms occur: one, common in Sabah, with often rather persistent stipules, a lesser indumentum on the leaves and the rachis, and subglabrous ovaries or fruits. This form is often mistaken for *A. grandistipula*, but differs in its thicker leaves with a cuneate base and fewer nerves. The second, 'typical' form, is more common in Sarawak, has caducous stipules, tomentose leaves, and sparsely puberulous ovaries and fruits. It is also often distinct by its long petiole. The distinction between the two forms is rather gradual, and since I have not been able to find any constant differences, I am not willing to describe them as varieties.

79. Aporosa lagenocarpa Airy Shaw — Fig. 3.5h, 3.6f, 3.8s, 3.11k; Map 10.61

Aporusa lagenocarpa Airy Shaw, Kew Bull. 21 (1968) 355; Meijer, Bot. News Bull. Sandakan 10 (1968) 229; Airy Shaw, Hook. Ic. Pl. (1974) 38, t. 3701; Kew Bull., Addit. Ser. 4 (1975) 37. — Type: *S (Sibat ak Luang) 21918* (holo K; iso BO, L, SING), Sarawak, Bt. Mersing.

Tree, up to 25.5 m high, up to 20 cm diameter. *Bark* green grey; inner bark red, scaly. *Wood* white. Young branches tomentose. *Stipules* narrowly ovate, strongly oblique, 7–10 mm wide, 2–4 mm high, sparsely hirsute beneath, present in young stages. *Petiole* terete, smooth, 8–16 by 1–1.5 mm, densely tomentose, glabrescent, lower pulvinus 1.5–2 by 1–1.2 mm, upper pulvinus 3–5 by 1–1.5 mm, both indistinct under indumentum. *Leaves* narrowly elliptic to narrowly obovate, 6–16.5 by 1.5–5.5 cm; base rounded to acute, basal glands absent; margin lowly undulate to subentire, marginal glands indistinct; apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, drying brownish grey above and beneath, nervation lighter beneath, sparsely hirsute, glabrescent, midrib and nerves hirsute beneath; dots laxly set, fine, brownish, often indistinct; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 6–9 pairs, slightly prominent above, prominent beneath, marginal arches distinct, 0.8–1.2 mm from the margin; tertiary nerves and venation distinct, laxly reticulate, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–4 clustered together, 8–23 by 1–1.5 mm, tomentose; peduncle 3–7 by 0.5–0.8 mm; bracts broadly triangular, c. 0.5 mm long, rather conspicuous, villose outside, glabrous inside; glomerules subglobose, indistinct, consisting of 3–5 laxly set flowers, spaced continuously along the rachis; pedicel absent. *Staminate flowers* 1–1.5 mm long; sepals 4, obovate, connate to more than halfway, 0.6–0.9 mm long, sparsely villose outside, glabrous inside; stamens 2, exserted, 1.2–2 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 3–8 by 1–1.2 mm, densely tomentose; flowers up to 7, mostly densely set at apical end of rachis; bracts broadly triangular, 0.3–0.4 mm long, densely villose outside, glabrous inside; bracteoles ovate, 0.2–0.3 mm long, densely villose outside, glabrous inside; pedicel absent. *Pistillate flowers* 2.5–5 mm long; sepals 4, ovate, patent, 0.8–1.1 mm long, thin, densely villose outside, glabrous inside; ovary narrowly ovoid to flask-shaped, 2–4 mm long, 2-locular, densely tomentose; stigmas sessile, elongated, perpendicular to the sides of the ovary, slightly recurved to straight, apically bifid to near base, 4.5–6 mm long, ribbed and laciniate above, glabrous, smooth beneath, glabrous, style remnant absent. *Infructescences* 7–23 by 0.8–1.2 mm, densely tomentose; fruiting pedicel minute, less then 0.5 mm. *Fruits* narrowly ovoid to flask-shaped, not stiped, beaked, 15–21 by 6–9.5 mm, slightly punctulate to smooth, drying (dark) brownish, sparsely tomentose; pericarp 0.3–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 1, half-terete, ellipsoid, 8–9 by 4–5 by 3–4 mm.

Distribution — Malesia: Borneo.



Map 10.61. Distribution of *Aporosa lagenocarpa* Airy Shaw.

Habitat & Ecology — Primary or submontane mixed dipterocarp forest; on hill sides, ridges, mountain tops, or high river terraces. Soil: basalt or sandstone. Altitude: 200–1000 m. Flowering: August, September; fruiting: June to October.

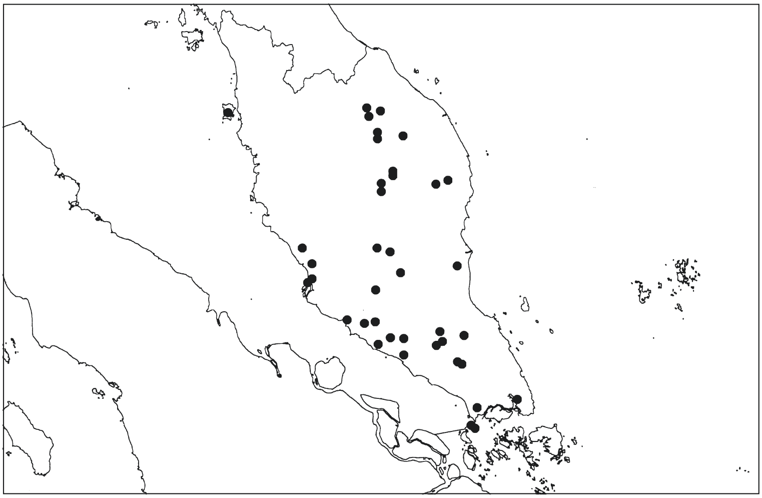
Vernacular names — Kayu masam (Iban).

80. Aporosa maingayi Hook.f. — Fig. 3.61, 4.3a, c; Map 10.62

Aporosa maingayi Hook.f., Fl. Brit. India 5 (1887) 348; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 278; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 99; Ridl., Fl. Malay Penins. 3 (1924) 241; Corner, Wayside Trees Malaya (1940) 237. — Lectotype (proposed here): *Maingay KD 1418* (holo BM; iso L), Malacca.

Aporusa isabellina Airy Shaw, Kew Bull. 25 (1971) 475; Whitmore, Tree Fl. Malaya 2 (1973) 61. — Type: *KEP (Cockburn) 115985*, (holo K; iso L), Peninsular Malaysia, Kelantan.

Shrub or tree, up to 10 m high, up to 17.5 cm diameter. *Bark* (light) grey to blackish brown or fawn, smooth or scaly with papery, elongated, adpressed scales; inner bark cream-yellow to brown. *Wood* pale yellow-orange to brown or white. Young branches sparsely tomentose. *Stipules* narrowly ovate, often oblique, 4–12 by 1–4 mm, sparsely sericeous near base outside, glabrous inside, present in young stages. *Petiole* terete, adaxially shallowly grooved, 6–9 by 0.5–0.8 mm, puberulous, glabrescent, lower pulvinus 0.5–1.5 by c. 1 mm, upper pulvinus 1–3.5 by 0.8–1.2 mm, both rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 6.5–13 by 1.5–5 cm; base cuneate to attenuate, basal glands absent; margin lowly undulate to subentire, marginal glands few, small, indistinct, black; apex caudate; blade thin, smooth, dull, not brittle, drying orcheous-grey to green-grey above, brownish grey beneath, only midrib puberulous above, sparsely puberulous beneath, midrib and nerves puberulous, glabrescent; dots irregularly densely set, fine, greyish, fading; disc-like glands seldom present, few, minute, black, along the margin. *Nervation*: midrib prominent above, prominent beneath; nerves 6–8 pairs, flat to slightly sunken above, prominent beneath, marginal arches distinct, 1.5–2.5 mm from the margin; tertiary nerves and venation fading, rather densely reticulate, slightly scalariform, flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–4 clustered together, 5–8 by 1–1.5 mm, puberulous; peduncle 0–1.5 by 0.8 mm; bracts broadly triangular, inconspicuous, 0.5–0.6 mm long, sparsely hairy outside, glabrous inside; glomerules subglobose, 0.5–1 by 0.5–0.7 mm, often indistinct, consisting of 4–8 densely set flowers, spaced at less than 0.1 mm along the rachis; pedicel absent. *Staminate flowers* 0.3–0.5 mm long; sepals 4 (or 5), elliptic, connate at base, 0.4–0.6 mm long, hairy outside, glabrous inside; stamens 2, slightly exserted, 0.4–0.7 mm; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 3–7 by 1–1.5 mm, puberulous; flowers up to 7, of rachis, densely set along the rachis, sometimes rather laxly set at base, densely apically; bracts broadly triangular, 0.5–0.7 mm long, sericeous outside, glabrous inside; bracteoles ovate, 0.3–0.5 mm long, sericeous outside, glabrous inside; pedicel absent. *Pistillate flowers* 1–2 mm long; sepals 4 (or 5), ovate, patent, 0.5–1.1 mm long, thin, sparsely hairy outside, glabrous inside; ovary ellipsoid, 1.5–1.7 mm long, 2-locular, densely sericeous; stigmas sessile, broad, flattened to the top and sides of the ovary, straight, apically bifid to near base, 0.3–0.5 mm long, densely laciniate above, glabrous, smooth beneath, glabrous, style remnant absent. *Infructescences* 3–7 by 1–1.5, puberulous; fruiting pedicel absent.



Map 10.62. Distribution of *Aporosa maingayi* Hook.f.

Fruits ellipsoid, not stiped, not beaked, 8–10 by 5–8 mm, punctate, drying brownish, sparsely hairy; pericarp 0.5–0.8 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 (or 2), (half-)terete, ellipsoid, 6–8 by 4.5–6 by 2–3.5 mm.

Distribution — Malesia: Peninsular Malaysia, Singapore.

Habitat & Ecology — In primary, secondary, disturbed and logged forest; low undulating country; on hill sides, ridges and near streams. Soil: granitic or sandy, white. Altitude: 15–900 m. Flowering: January, March to July, October; fruiting: May to September.

Vernacular names — Sebasah, nipis kulit (Malay).

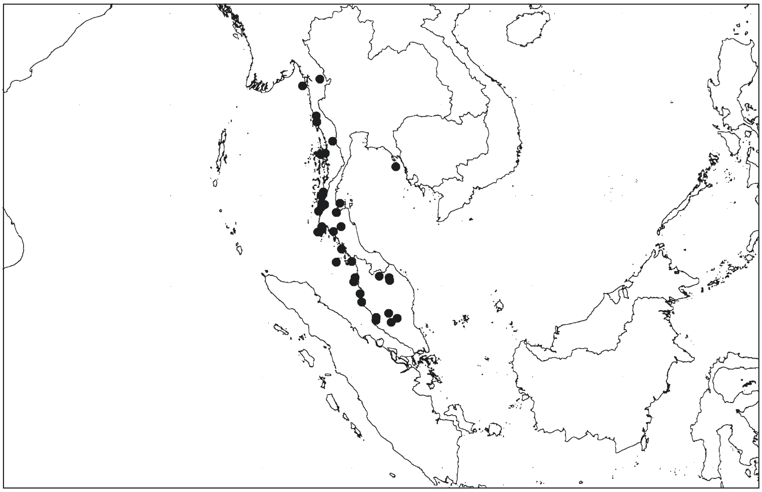
Note — *Aporosa maingayi* was united by Airy Shaw (1969) with *A. microstachya*. Three years later, he described a new species for Peninsular Malaysia, *A. isabellina* (Airy Shaw, 1971). *Aporosa isabellina* resembles *A. microstachya*, but Airy Shaw associated it with *A. subcaudata* and *A. elmeri*. However, the syntypes of *A. maingayi* (*Maingay KD 14128* and *Cantley s.n.*) also represent *A. isabellina*. Even though they lack, probably through their age, the typical orcheous-grey colour, the nervation of the leaves, the flowers, and the fruits are unmistakably those of *A. isabellina*. This means that *A. maingayi* needs to be reinstated with *A. isabellina* as synonym.

81. Aporosa microstachya (Tul.) Müll.Arg. — Map 10.63

Aporosa microstachya (Tul.) Müll.Arg. in DC., Prod. 15, 2 (1866) 474; Hook.f., Fl. Brit. India 5 (1887) 349; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 102; Henderson, Gard. Bull. Straits Settlem. 7 (1933) 124; Hundley & Ko, List Trees, Shrubs, Burma, ed. 3 (1961) 229; Airy Shaw, Kew Bull. 23 (1969) 2, excl. *A. maingayi*; Kew Bull. 26 (1972) 217; Whitmore, Tree Fl. Malaya 2 (1973) 61; Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 166. — *Scepa microstachya* Tul., Ann. Sci. Nat. Ser. 3 (1851) 255. — *Aporosa tulasneana* Baill., Étude Gén. Euphorb. (1858) 645, nom. illig. — Type: *Wallich 7985* (holo P, sub no. *Wallich 591*; iso K-WALL), Burma, Tavoy.

Aporosa maingayi Hook.f. var. *penangensis* auct. non Ridl.: Ridl., Fl. Malay Penins. 3 (1924) 2, p.p., tantum spec. *Haniff s.n.*

Shrub or tree, up to 10.5 m high, up to 12.5 cm diameter. *Bark* (reddish) brown, grey(ish), or blackish, smooth or finely roughened, thin; inner bark red, thin. *Wood* white. Young branches (sparsely) tomentose. *Stipules* narrowly ovate, very slightly oblique, 3–4 by 1–1.5 mm, hairy beneath, present in young stages. *Petiole* terete, adaxially grooved, 6–8 by 0.5–0.8 mm, tomentose, glabrescent, lower pulvinus 1–1.5 by 0.8–1 mm, upper pulvinus 2–3 by 0.9–1.1 mm, both rather distinct. *Leaves* narrowly ovate to narrowly elliptic, 6–12 by 2–3.5 cm; base cuneate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, small, blackish grey; apex cuspidate to caudate; blade thin, smooth, dull, not brittle, drying blue-green above, blackening, (light) brown beneath, only midrib puberulous above, very sparsely puberulous beneath, midrib and nerves puberulous, glabrescent; dots irregularly patchy densely set, fine, greyish, fading; disc-like glands seldom present, few, minute, blackish, along the margin. *Nervation*: midrib prominent; nerves 5–7 pairs, flat above, prominent beneath, marginal arches distinct, 1–2.5 mm from the margin; tertiary nerves and venation fading, laxly reticulate, flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 6–14 by 1–1.5 mm-, sparsely puberulous; peduncle 0–0.5 by c. 0.8 mm; bracts not seen, inconspicuous; glomerules subglobose, 0.7–1 by 0.5–0.7 mm, mostly indistinct, consisting of 7–10 densely set flowers, often continuously set along the rachis, sometimes slightly interrupted at base; pedicel absent. *Staminate flowers* 0.4–0.6 mm long; sepals 4, obovate, connate at base only, 0.3–0.5 mm long, puberulous; stamens 2, slightly exserted, 0.4–0.6 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1–3 clustered together, 2–5 by 1–1.5 mm, puberulous; flowers up to 5, often densely set along the rachis, sometimes laxly set at base; bracts broadly triangular, 0.4–0.6 mm long, puberulous outside, glabrous inside; bracteoles ovate, 0.2–0.3 mm long, densely puberulous outside, glabrous inside; pedicel 0–0.5 mm long, puberulous. *Pistillate flowers* 1.5–2.5 mm long; sepals 4, ovate, patent, 0.5–0.7 mm long, thin, puberulous; ovary ovoid to slightly flask-shaped, 1.5–2 mm



Map 10.63. Distribution of *Aporosa microstachya* (Tul.) Müll.Arg.

long, 2-locular, punctulate, puberulous; stigmas slightly raised, elongated, flattened to the sides of the ovary, rather straight, apically bifid to near base, 1.5–2.5 mm long, densely laciniate above, glabrous, smooth beneath, sparsely hairy, style remnant absent. *Infructescences* 3–4 by 0.8–1 mm, puberulous; fruiting pedicel 0–0.5 mm long, puberulous. *Fruits* (narrowly) ovoid, not stiped, slightly beaked, 9–12 by 5–6.5 mm, punctulate, drying dark brown to black, sparsely hairy; pericarp 0.3–0.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 (or 2), half-terete, ellipsoid, 6–7.5 by 4.5–5 by 2.5–3.5 mm.

Distribution — Burma (Tenasserim); Malesia: Peninsular Thailand, Peninsular Malaysia.

Habitat & Ecology — Primary, degraded, or disturbed (dipterocarp), evergreen forest; sometimes dry; lowland, hill sides, ridges. Soil: shale & granitic or limestone bedrock. Altitude: 10–480 m. Flowering: December to April; fruiting: January to July, November.

Vernacular names — Thailand: Krim kao (Thai); rzip, reb (Bazek).

Notes — 1. Tulasne (1851) cited as type *Wallich 591*, and this is also the number under which it is labelled in P. However, the only specimen in Wallich's herbarium that matches it is *Wallich 7985*.

2. See also note under *A. duthieana*.

82. Aporosa nervosa Hook.f. — Fig. 3.6m, 3.7a, 3.11a, 4.2a; Map 10.64

Aporosa nervosa Hook.f., Fl. Brit. India 5 (1887) 350; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 279; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 97; Ridl., Fl. Malay Penins. 3 (1924) 238; Meijer, Bot. News Bull. Sandakan 7 (1967) 34; Airy Shaw, Kew Bull. 23 (1969) 4; Whitmore, Tree Fl. Malaya 2 (1973) 61; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975); Kew Bull. 36 (1981) 256; ?Kew Bull. 37 (1982) 8. — Type: *Maingay KD 1365* (holo K), Peninsular Malaysia.

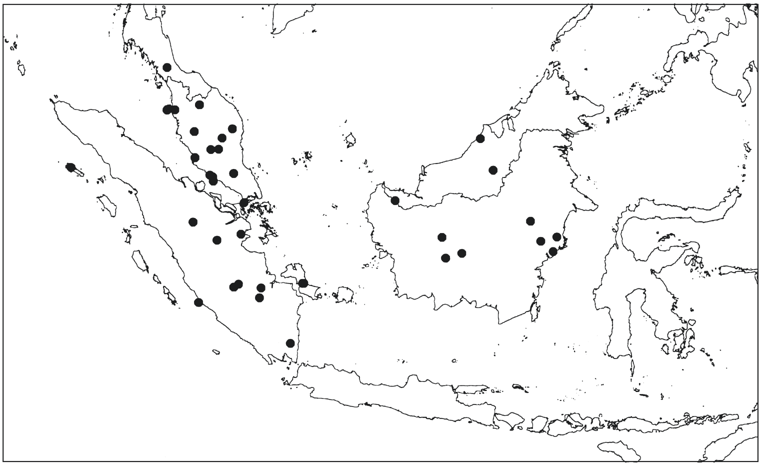
Aporosa sphaeridiophora Merr. var. *pubescens* J.J. Sm., Bull. Jard. Bot. Buitenzorg III, 6 (1924) 109; Airy Shaw, Kew Bull. 23 (1969) 4, nomen.

Aporosa penangensis auct. non (Ridl.) Airy Shaw: Airy Shaw, Kew Bull. 36 (1981) 256.

Tree, up to 30 m high, up to 45 cm diameter. *Bark* dark chocolate brown to reddish brown to light brown or grey, smooth, slightly fissured and flaking, 4–5 mm thick; inner bark pink, or dull or reddish brown, c. 5 mm thick. *Wood* cream, yellow, or pale to dull orange-brown. Exudate watery, resinous, sticky. Young branches (sparsely) puberulous. *Stipules* narrowly ovate, slightly oblique, 7–10 by 3–5 mm, (sparsely) tomentose, caducous. *Petiole* terete, smooth, 8–21 by 0.8–1.2 mm, (sparsely) puberulous, lower pulvinus 1.5–3 by 1.2–1.8 mm, upper pulvinus 2–5 by 1.2–2 mm, both distinct. *Leaves* (narrowly) elliptic, 8.5–21 by 2.5–8 cm; base obtuse to attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, large, black; apex acuminate to cuspidate; blade thickish, smooth, dull, older leaves brittle, drying greenish grey to greenish blue above, greyish brown beneath, only midrib at base very sparsely puberulous above, very sparsely hirsute beneath, glabrescent, midrib and nerves (sparsely) hirsute; dots densely set, large, black, distinct, fading; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 6–9 pairs, slightly prominent to flat above, prominent beneath, marginal arches often distinct, 1–3 mm from the margin; veins and venation fading, rather laxly reticulate, slightly scalariform, flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 14–57 by 1.5–2 mm, puberulous; peduncle 2–4 by 0.8–1 mm; bracts inconspicuous, triangular, 1.2–1.5 mm long, sparsely hairy outside, glabrous inside, margin ciliate; glomerules subglobose, lax, consisting of 6–10 flowers, 1.5–2 by c. 1.5 mm, spaced at 2–3 mm at base, decreasing to 0 mm at apex; pedicel minute. *Staminate flowers* 2–3 mm long; sepals 4, obovate, ridged, 1.2–1.5 mm long, connate to c. halfway, sparsely hairy outside, glabrous inside, margin ciliate; stamens 3 or 4, exserted, 2–3 mm long; anthers 0.3–0.4 mm long, connective sparsely hairy; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 5–9 by 0.8–1.2 mm, (sparsely) puberulous, the flowers up to 9, rather densely arranged throughout, more densely so apically; bracts triangular, 0.7–0.9 mm long, sparsely hairy outside, glabrous inside, margin ciliate; bracteoles triangular to ovate, 0.4–0.6 mm long, sparsely hairy outside, glabrous inside; pedicel 0.8–1 mm long, (sparsely) puberulous. *Pistillate flowers* 2–3 mm long; sepals 4, ovate, patent, 0.8–1.2 mm long, at base sparsely hairy outside, glabrous inside; ovary ellipsoid, 1.5–2.5 mm long, 2-, 3- (or 4-)locular, smooth, (sparsely) puberulous, glabrescent towards apex; stigmas sessile, elongated, apically bifid to near base, perpendicular to the sides of the ovary, slightly recurved, 0.8–1.2 mm long, smooth above, margins lowly laciniate, glabrous, smooth beneath, sparsely hairy, style remnant present. *Infructescences* 7–32 by 1–1.8 mm, (sparsely) puberulous; fruiting pedicel 2–8 mm long, (sparsely) puberulous. *Fruits* ellipsoid to globose, not stiped, not beaked, 10–22 by 9–13 mm, rather smooth, sparsely hairy; pericarp 0.8–1.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 1–3, half-terete, ellipsoid, 7–9 by 5–6 by 2–3 mm.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia, Singapore, Sumatra, Borneo.

Habitat & Ecology — Primary and secondary mixed dipterocarp forest; lowland, high, or alluvial forest; flat or undulating land, on hill sides, ridges, near swamps, along river banks. Soil: clay, sandy loam, granitic sand, black or red. Altitude: 20–800 m. Flowering: January to May, August; fruiting: May to February.



Map 10.64. Distribution of *Aporosa nervosa* Hook.f.

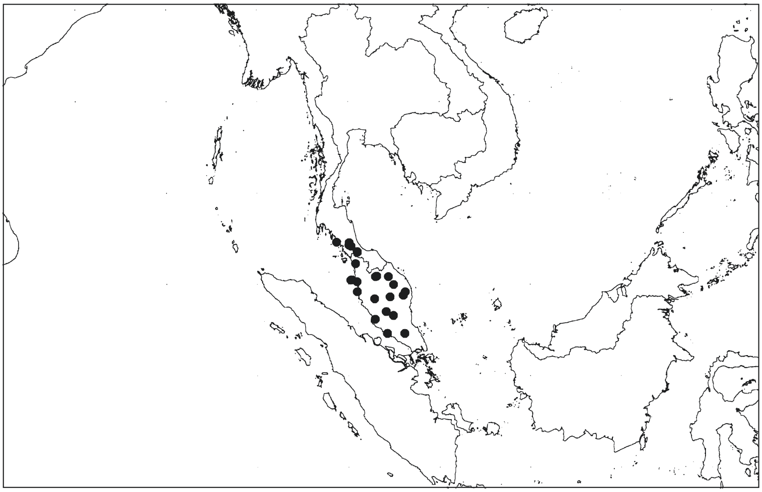
Vernacular names — Sumatra: Rangkap (Tamuk); semasan lanang, semasan betino (Palembang).

Note — Airy Shaw (1982) records *A. nervosa* from the Moluccas, but I have not seen these collections. They probably represent, as the *A. sphaeridiophora* collections from these islands, *A. dendroidea* Schot.

83. Aporosa penangensis (Ridl.) Airy Shaw — Fig. 3.8n; Map 10.65

Aporosa penangensis (Ridl.) Airy Shaw, Kew Bull. 23 (1969) 3; Whitmore, Tree Fl. Malaya 2 (1973) 61. — *Aporosa maingayi* Hook.f. var. *penangensis* Ridl., Fl. Malay Penins. 3 (1924) 242. — Type: *Curtis KD 1466* (holo K), Peninsular Malaysia, Penang, Moniots Road.

Tree, up to 21 m high, up to 30 cm diameter. *Bark* brown to grey, fawn, or pink-grey, vertically cracked, scaly, flaking, fissured, or smooth; inner bark (orange- or yellow-) brown, or pale pink, thin. *Wood* brown to yellow to orange, hard. Young branches (sparsely) hirsute. *Stipules* narrowly ovate, slightly oblique, 5–11 by 1.5–4 mm, caducous. *Petiole* half-terete, ridged, 6–13 by 0.8–1.5 mm, (sparsely) hirsute, lower pulvinus 1–2 by 1–1.5 mm, upper pulvinus 2–4 by 1.2–2 mm, both distinct. *Leaves* narrowly ovate to narrowly elliptic, 7–20 by 2–7 cm; base obtuse to slightly attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, indistinct, greyish; apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, drying brownish green to brownish grey above, light brownish beneath, only midrib at base sparsely hirsute above, nervation sparsely hirsute beneath; dots irregularly set, greyish, fading; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 7–9 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1–2 mm from the margin; tertiary veins and venation fading, rather laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–4 clustered together, 9–18 by 1.5–3 mm, tomentose; peduncle 0.5–1.5 by 0.8–1.2 mm; bracts broadly triangular, 0.8–1 mm long, inconspicuous, very sparsely puberulous outside, glabrous inside, margin ciliate; glomerules subglobose, lax, consisting of less than 10 flowers, 1.5–2.2 by 1.2–1.8 mm, spaced at 1–2 mm at base of rachis, decreasing to 0 mm at apex; pedicel minute. *Staminate flowers* 0.5–1 mm long; sepals 4, narrowly obovate, ridged, 1–1.5 mm long, connate at base, sparsely puberulous outside, glabrous inside, margin ciliate; stamens 3, slightly exserted, 0.6–0.8 mm long; anthers 0.2–0.3 mm long, connective glabrous; pistillode a minute lump. *Pistillate inflorescences* 1–4 clustered together, 5–11 by 0.8–1.5 mm, tomentose; flowers up to 9, rather densely arranged along the rachis; bracts triangular, 0.8–1.2 mm long, sparsely sericeous outside, hairy at base only inside, margin ciliate; bracteoles triangular, 0.5–0.8 mm long, sparsely sericeous outside, hairy at base only inside, margin ciliate; pedicel minute, tomentose. *Pistillate flowers* 2.5–3 mm long; sepals 4, ovate, subequal, patent, 1–1.5 mm long, sericeous outside, glabrous inside, papillate; ovary ellipsoid, 1.8–2.2 mm long, 2-locular, smooth, (sparsely) sericeous; stigmas sessile, broad, apically bifid to near base, flattened on top of the ovary, straight, 1–1.2 mm long, ribbed and laxly laciniate above, glabrous, smooth beneath, very sparsely sericeous, style remnant present. *Infructescences* 7–11 by 1.2–1.5 mm, tomentose; fruiting pedicel 0.2–1 mm long, tomentose. *Fruits* ellipsoid, young ones slightly stiped, not beaked, 10–15 by 6–10



Map 10.65. Distribution of *Aporosa penangensis* (Ridl.) Airy Shaw.

mm, punctulate to smooth, sparsely puberulous; pericarp 0.5–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 1, subterete, ovoid, 7–10 by 5–6 by 3–4 mm.

Distribution — Malesia: Peninsular Thailand, Peninsular Malaysia.

Habitat & Ecology — Primary, logged, and evergreen forest, or seraya; in lowland, on hill sides, gentle slopes, ridges, flat land, near rivers, along roads. Soil: sandstone, granite, or granitic bedrock. Altitude: 50–780 m. Flowering: March to June; fruiting: April to August.

Notes — 1. This species resembles *A. subcaudata*, but differs in the less persistent stipules, the tomentose indumentum of only the lower leaf surface, less nerves, and shortly pedicelled fruits. It differs from *A. nervosa* in the (sub)sessile and always 2-locular pistillate flowers and fruits.

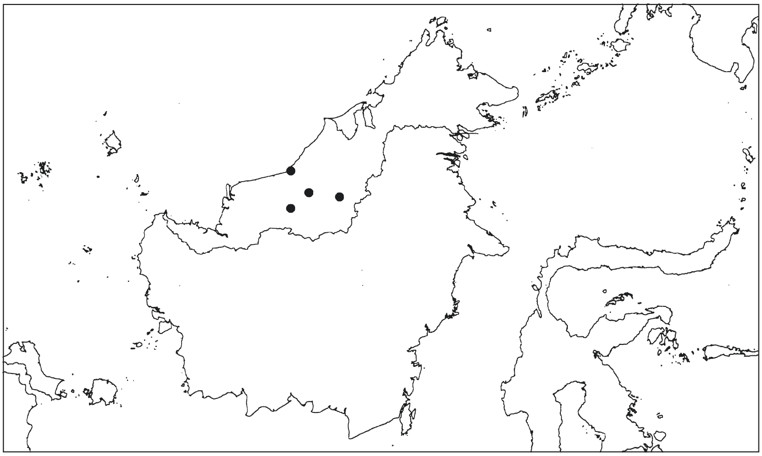
2. Many of the Peninsular Malaysian specimens of this species have been distributed as '*A. acuminatissima* Merr.'.

84. **Aporosa rhacostyla** Airy Shaw – Fig. 3.6p; Map 10.66

Aporusa rhacostyla Airy Shaw, Kew Bull. 29 (1974) 282; Kew Bull., Addit. Ser. 4 (1975) 40. — Type: *S (Paie) 28797* (holo L; iso K), Sarawak, Kapit.

Tree, up to 10 m high, up to 10 cm diameter. *Bark* dark or greyish brown with greenish brown patches, smooth, with twisted square fissures; inner bark creamy orange. *Wood* creamy orange. Young branches tomentose. *Stipules* narrowly ovate, sometimes slightly oblique, 6–9 by 2–3 mm, glabrous above, (sparsely) sericeous beneath, present in young stages. *Petiole* terete, about smooth, 5–11 by 1–1.5 mm, tomentose, lower pulvinus c. 1.5 by 1.5 mm, upper pulvinus 1–2 by c. 1.5 mm, both indistinct under indumentum. *Leaves* narrowly elliptic, 5.5–13 by 2–4.5 cm; base obtuse to acute, basal glands absent; margin lowly undulate to subentire, marginal glands few, small, indistinct; apex acuminate to cuspidate; blade thinnish, smooth, dull, not brittle, drying dark green or brown above, blackening, (dark) brown beneath, sparsely tomentose above, midrib tomentose, sparsely tomentose beneath, midrib and nerves densely tomentose; dots indistinct; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 6–9 pairs, flat above, prominent beneath, marginal arches distinct, 1–1.5 mm from margin; tertiary veins and venation fading, rather laxly reticulate, slightly scalariform, flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 2–5 clustered together, 7–12 by 0.3–0.5 mm sparsely puberulous; peduncle 1.5–2 mm long, c. 0.4 mm diam.; bracts triangular, inconspicuous, 0.5–0.8 mm long, sparsely sericeous outside, glabrous inside; glomerules subglobose, 0.5–0.7 by 0.3–0.5 mm, consisting of 5–8 densely set flowers, spaced at 0.3–0.5 mm along the rachis; pedicel minute. *Staminate flowers* (young) 0.2–0.4 mm long; young sepals 4, narrowly obovate, connate at base, 0.3–0.5 mm long, sparsely sericeous outside, glabrous inside; young stamens 2, not exserted, 0.2–0.4 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode not seen. *Pistillate inflorescences* 2–5 clustered together, 10–23 by 0.5–0.8 mm, puberulous; flowers up to 15, rather laxly arranged along the rachis; bracts triangular, 0.3–0.4 mm long, sparsely sericeous outside, glabrous inside; bracteoles triangular, c. 0.1 mm long, sericeous outside, glabrous inside; pedicel minute, up to 0.2 mm long, sericeous. *Pistillate flowers* 1.5–2 mm long; sepals 4, narrowly ovate, patent, 0.6–0.8 mm long, thin, sparsely puberulous outside, glabrous inside; ovary ellipsoid, 1–1.5 mm long, 2-locular, (sparsely) puberulous; stigmas sessile, elongated, at first ascending from the top of the ovary to an apical bunch and then bending downwards to the sides of the ovary, straight, apically bifid to near base, 1–1.5 mm long, ribbed and papillate above, margins laciniate, glabrous, smooth beneath, sparsely hairy, style remnant absent. *Infructescences* 12–33 by 1–1.5 mm, tomentose; fruiting pedicel c. 0.5 mm, puberulous. *Fruits* ellipsoid, not stiped, not beaked, 10–12 by 7–9 mm, punctate, drying (dark) reddish brown, sparsely puberulous; pericarp 0.8–1.2 mm thick, not fleshy; septae and column glabrous. *Seeds* 1, (half-)terete, ovoid, 7–8 by 6–6.5 by 2–3 mm.

Distribution — Malesia: Borneo (Central Sarawak).



Map 10.66. Distribution of *Aporosa rhacostyla* Airy Shaw.

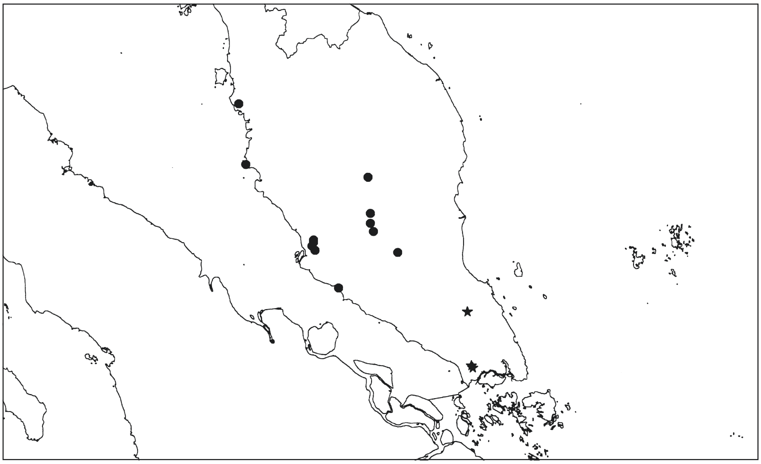
Habitat & Ecology — Primary or old secondary forest; on hill sides. Soil: clay, rich. Altitude: 200–575 m. Flowering: April, October; fruiting: October.

Note — *Aporosa rhacostyla* is only really distinct from *A. elmeri* in the curious bunching of the stigmas. The other differentiating characters, length of the leaves and inflorescences, overlap. I have no idea why most (not all!) flowers of the type specimen have such curious bunched stigmas, but it might be artificial, and then *A. rhacostyla* should be merged into *A. elmeri*.

85. **Aporosa selangorica** Pax & K. Hoffm. — Fig. 3.9c, d; Map 10.67

Aporosa selangorica Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 105; Airy Shaw, Kew Bull. 25 (1971) 480; Whitmore, Tree Fl. Malaya 2 (1973) 59. — Type: *Ridley 13385* (iso K, SING), Peninsular Malaysia, Selangor.

Shrub or tree, up to 9 m high, up to 10 cm diameter. *Bark* (light) brown, smooth. Young branches (sparsely) tomentose. *Stipules* (narrowly) ovate, often slightly oblique, 6–14 by 3–6 mm, glabrous above, sparsely sericeous beneath, rather persistent. *Petiole* terete, adaxially lowly grooved, 6–12 by 0.8–1.2 mm, sparsely hirsute, lower pulvinus 1.5–2 by 1–1.5 mm, upper pulvinus 1.5–4 by 1.5–2 mm, both distinct. *Leaves* narrowly elliptic to narrowly obovate, 10–25.5 by 3.5–8.5 cm; base truncate to emarginate, basal glands absent; margin lowly undulate to lowly glandular-crenate, marginal glands regular, brownish, distinct; apex acuminate to cuspidate; blade thin, smooth, not brittle, slightly shiny, drying (dark) greenish to greenish grey above, (dark) brownish to greyish beneath, only midrib and nerves at base sparsely tomentose above, sparsely tomentose beneath, midrib and nerves tomentose, glabrescent; dots laxly set, fine, greyish, indistinct; disc-like glands absent. *Nervation*: midrib slightly prominent above, prominent beneath; nerves 12–16 pairs, slightly prominent to flat above, prominent beneath, marginal arches distinct, 1.5–4 mm from the margin; tertiary veins and venation distinct or fading, rather densely reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–5 clustered together, 6–12 by 1.2–1.8 mm, tomentose; peduncle 0–1 by 0.5–1 mm; bracts broadly triangular, inconspicuous, 0.5–0.7 mm long, sparsely puberulous outside, glabrous inside; glomerules subglobose, indistinct, consisting of 5–7 rather laxly set flowers, continuously spaced along the rachis, seldom slightly interrupted at base; pedicel minute. *Staminate flowers* 0.6–1 mm long; sepals 4, obovate, 0.5–0.8 mm long, connate at base, glabrous, margin ciliate; stamens 2, slightly exserted, 0.6–1 mm long; anthers 0.1–0.2 mm long, connective glabrous; pistillode minute, lumpy. *Pistillate inflorescences* 1 or 2 clustered together, 7–10 by 0.8–1.2 mm, tomentose, flowers up to 9, mostly densely set at apical end of the rachis; bracts broadly triangular, 0.8–1 mm long, sparsely puberulous outside, glabrous inside; bracteoles ovate, 0.6–0.8 mm long, sparsely puberulous outside, glabrous inside; pedicel absent. *Pistillate flowers* 3.5–5 mm long; sepals 4, ovate, patent, 1–1.5 mm long, thin, sparsely puberulous outside, glabrous inside; ovary globose, 2.5–4 mm long, 2- or 3-locular, ruminate-verrucate, puberulous; stigmas slightly raised, elongated, flat to the top of the ovary, recurved, apically bifid to near base, 2–2.5 mm long, ribbed and papillate above, glabrous, smooth beneath, sparsely puberulous, style remnant absent. *Infructescences* 3–11 by 1.5–2 mm, sericeous; fruiting pedicel 0.5–1 mm long. *Fruits* globose or ovoid, not



Map 10.67. Distribution of *Aporosa selangorica* Pax & K. Hoffm. (●) and *A. spec. F* (★).

stiped, not beaked, 13–16 by 13–16 mm, ruminate-verrucate, drying light to reddish brown, sparsely puberulous; pericarp 0.5–1.5 mm thick, not fleshy; septae and column glabrous. *Seeds* 1–3, half-terete, ovoid, 9–10.5 by 6–8 by 3–5 mm.

Distribution — Malesia: Peninsular Malaysia.

Habitat & Ecology — Primary dipterocarp forest; in shaded valleys, on hills, or near streams. Altitude: 150–600 m. Flowering: March, August; fruiting: April to September.

Uses — Seed aril recorded edible.

Vernacular names — Meruai, tamun mas (Temuan).

86. Aporosa sphaeridiophora Merr. — Fig. 3.7j, 3.8j; Map 10.68

Aporosa sphaerid[i]ophora Merr., Philipp. J. Sci. 1, Suppl. (1906) 76[1]; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 86 (excl. *A. sphaeridiophora* Merr. var. *campanulata* (J.J. Sm.) Pax & K. Hoffm.); Merr., Enum. Philipp. Flow. Pl. 2 (1923) 410. — Lectotype (proposed here): *FB (Barnes) 146* (holo A; iso BO, K), Philippines, Luzon, Bataan.

Aporosa acuminatissima Merr., Philipp. J. Sci. 16 (1920) 546. — Type: *FB (Amarillas) 26185* (holo A; iso K, P), Philippines, Luzon, Laguna.

Tree, up to 20 m high, up to 30 cm diameter. Young branches sparsely puberulous. *Stipules* not seen, early caducous. *Petiole* terete, adaxially grooved, 8–24 by 1–1.5 mm, very sparsely puberulous, glabrescent, lower pulvinus 1.5–2 by 1.5–2 mm, upper pulvinus 3–6 by 1.5–2.5 mm, both distinct. *Leaves* (narrowly) ovate to (narrowly) elliptic, 6.5–20 by 2.5–9.5 cm; base cuneate to attenuate (occasionally slightly cordate), basal glands absent; margin very lowly undulate to crenate, marginal glands regular, large, black; apex acuminate to cuspidate; blade thickish, smooth, dull, not brittle, drying greyish green to brownish green above, brownish beneath, glabrous above, only midrib and nerves at base very sparsely puberulous beneath, glabrescent; dots distinct,

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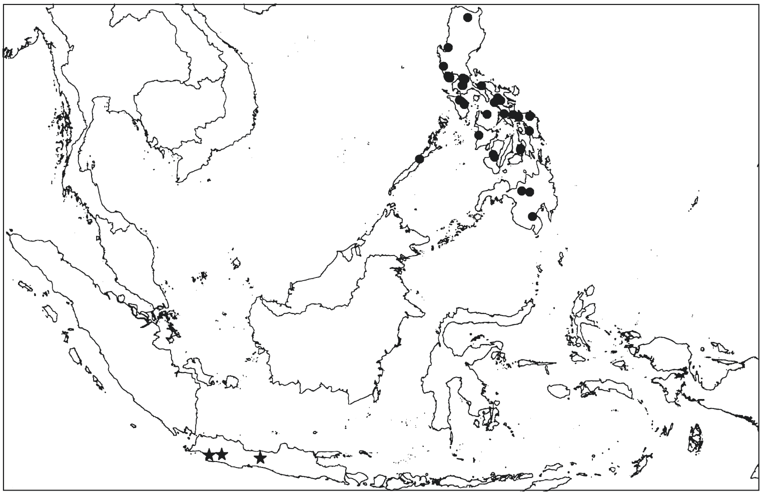
[1] Specific epithet corrected from original *sphaeridophora* to *sphaeridiophora* by Airy Shaw, Kew Bull. 23 (1969) 4.

densely set, black; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 6–9 pairs, slightly prominent to flat above, prominent beneath, marginal arches mostly distinct, 2–4 mm from the margin; veins and venation indistinct, laxly reticulate, flat above, slightly prominent to flat beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* single, 28–74 by 1.5–2.5 mm, sparsely puberulous; peduncle 3–5 by 0.7–1 mm; bracts broadly triangular, conspicuous, 0.8–1.5 mm long, very sparsely hairy outside, glabrous inside, margin ciliate; glomerules subglobose, lax, consisting of 6–10 flowers, 2.5–3 by 1.2–1.5 mm, spaced at 1–3 mm at base, decreasing to 0 mm at apex; pedicel absent. *Staminate flowers* 2–3.5 mm long; sepals 4, obovate, 0.8–1.5 mm long, connate to more than halfway, ridged, sparsely hairy outside, hairy at base only or glabrous inside; stamens 2–4, exserted, 1.5–4 mm long; anthers 0.5–0.6 mm long, connective glabrous; pistillode absent. *Pistillate inflorescences* 1 or 2 clustered together, 7–16 by 1–1.2 mm, puberulous; flowers up to 15, rather densely arranged below, densely arranged apically; bracts broadly triangular, 0.5–0.9 mm long, sparsely hairy outside, glabrous inside, margin ciliate; bracteoles ovate, 0.3–0.5 mm long, sparsely hairy outside, glabrous inside, margin ciliate; pedicel 1–2 mm long, puberulous. *Pistillate flowers* 2.5–3.5 mm long; sepals 4, ovate, patent, fleshy, 1–1.5 mm long, sparsely hairy at base outside, glabrous inside; ovary ovoid, 2–3 mm long, 2- or 3-locular, smooth, glabrous; stigmas sessile, elongated, almost completely divided, perpendicular to or slightly ascending from the sides of the ovary, slightly recurved, 0.8–1.2 mm long, ribbed above, margins papillate, glabrous, smooth beneath, glabrous, style remnant present. *Infructescences* 22–33 by 0.8–1.2 mm, sparsely puberulous; fruiting pedicel 4–6 mm long, sparsely puberulous. *Fruits* globose to ellipsoid, not stiped, not beaked, 8.5–12 by 8.5–11 mm, smooth or slightly punctulate, glabrous; pericarp 0.7–1.5 mm thick, not fleshy; septae and column glabrous. *Seeds* (1 or) 2, half-terete, suborbicular, 7–8 by 6–7 by 2–4 mm.

Distribution — Malesia: Java, Philippines.



Map 10.68. Distribution of *Aporosa sphaeridiophora* Merr.: var. *sphaeridiophora* (●) and var. *campanulata* (J.J. Sm.) Pax & K. Hoffm. (★).

Key to the varieties

1a. Leaves (sub)glabrous. Fruits ellipsoid, slightly punctulate . **b.** var. **campanulata**
b. Leaves with only midrib and nerves at base very sparsely puberulous beneath, glabrescent. Fruits globose, smooth .... **a.** var. **sphaeridiophora**

a. var. **sphaeridiophora**

Nomenclature see under species.

Leaves only midrib and nerves at base very sparsely puberulous beneath, glabrescent, glabrous above. *Staminate flowers* 2–3.5 mm long; sepals 4, narrowly obovate, 0.8–1 mm long, connate to c. halfway, sparsely hairy outside, only hairy at base inside, ciliate; stamens 2 or 3, exserted, 1.5–3.5 mm long, anthers 0.5–0.6 mm long, connective sparsely hairy; pistillode absent. *Fruit* globose, 8–10 by 8–10 mm, smooth.

Distribution — Philippines

Habitat & Ecology — Lowland primary or secondary rain forest, lower montane forest, disturbed or logged over areas; in cloud zone; on steep slopes. Soil: (rocky or volcanic) clay, dark. Altitude: 200–1200 m. Flowering: January to April, November; fruiting: January, April to November.

Vernacular names — Sono-sono (Cebuano).

Notes — 1. The material identified as *A. sphaeridiophora* from the Moluccas, belongs to *A. dendroidea*.

2. *Aporosa sphaeridiophora* var. *sphaeridiophora* is variable in texture and indumentum of the branchlets and leaves: a couple of specimens from Luzon have thick, leathery leaves and fruits of 15–19 by 14–20 mm with the pericarp 1.5–2 mm thick [distributed as '*Aporosa (sphaeridiophora* var.*) mirandae* Merr.']. Two collections from Samar have (sparsely) tomentose branchlets, petioles and nerves beneath. However, all these characters are gradual, and in addition there is one specimen from Mindanao which has both tomentose and leathery leaves. With so few collections and so little consistency in the characters I cannot designate any of these Philippine forms as different varieties.

b. var. **campanulata** (J.J. Sm.) Pax & K. Hoffm.

Aporosa sphaeridiophora Merr. var. *campanulata* (J.J. Sm.) Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 86; Backer & Bakh.f., Fl. Java 1 (1964) 456, ?457. — *Aporosa campanulata* J.J. Sm., Ic. Bog. 3 (1907) 71, t. 224; Meded. Dept. Landb. Ned.-Indië 10 (1910) 237. — *Aporosa sphaeridiophora* auct. non Merr.: Koord., Exkurs.-Fl. Java 2 (1912) 480. — Lectotype (proposed here): *Koorders 26274* (holo BO; iso L, P), Java, Preanger, Tjigenteng.

Leaves (sub)glabrous. *Staminate flowers* 2–3.5 mm long; sepals 4, narrowly obovate, 1–1.5 mm long, connate to c. halfway, sparsely hairy outside, glabrous inside, ciliate; stamens 2–4, exserted, 2–4 mm long, anthers 0.5–0.6 mm long, connective sparsely hairy; pistillode absent. *Fruits* ellipsoid, c. 12 by 11 mm, slightly punctulate.

Distribution — Malesia: W Java.

Vernacular names — W Java: ki endang

Note — Directly after describing his *A. campanulata* J.J. Smith (1907) mentioned that the specific status was in doubt. It should probably be reduced to a variety of the

Philippine *A. sphaeridiophora*. This view has been followed by subsequent authors. At present, however, I am not so sure of this. The leaves are undoubtedly similar, but then, so are the leaves of the Bornean *A. caloneura*. *Aporosa sphaeridionphora* var. *campanulata* has (sub)glabrous leaves, *A. caloneura* also, *A. sphaeridiophora* very sparsely puberulous ones, but variable. All three species have the same type of nervation. The also similar *A. nervosa* differs in the stronger nervation on the lower side, and in the indumentum, but this is also variable. The staminate inflorescence of all three is similar, but again variable. The three, *A. caloneura*, *A. nervosa*, and *A. sphaeridiophora* differ mostly in their pistillate inflorescence: *A. caloneura* has distinctly pedicelled flowers with subglabrous ovaries; *A. nervosa* has subsessile flowers with sparsely sericeous ovaries; *A. sphaeridiophora* has subsessile flowers with glabrous ovaries. The infructescence of all three species, however, is quite similar, though *A. nervosa* has ellipsoid or ovoid sparsely puberulous fruits, *A. caloneura* (narrowly) ovoid, slightly beaked, glabrous ones, and *A. sphaeridiophora* globose glabrous ones. The infructescence of *A. sphaeridiophora* var. *campanulata* is in accordance with all of them, but the ellipsoid glabrous fruits do not fit particularly one or other. As the pistillate inflorescence of *A. campanulata* is unknown, the true position of this species is doubtful. It is to hope there will be still some specimens left in West Java to solve this question in the (near) future, but I doubt it.

87. Aporosa subcaudata Merr. — Fig. 3.5e, 3.6j, 10.10; Map 10.69

Aporosa subcaudata Merr., Philipp. J. Sci., Bot. 11 (1916) 64; Enum. Born. Pl. (1921) 330; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 95; Merr., Pl. Elmer. Born. (1929) 142; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 41; Kew Bull. 36 (1981) 257. — Type: *Hose 204* (holo A; iso BM, L), Sarawak, Baram.

Aporosa bracteosa Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.xv (1922) 95; Ridl., Fl. Malay Penins. 3 (1924) 237; S. Moore, J. Bot. Brit. & For. 63, Suppl. (1925) 34; Meijer, Bot. News Bull. Sandakan 7 (1967) 34 (+ fig.); Whitmore, Tree Fl. Malaya 2 (1973) 60; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 33; Kew Bull. 36 (1981) 254. — Lectotype (proposed here): *Forbes 3132* (holo BM; iso L, P), Sumatra, Nepal Litjin.

Aporusa penangensis auct. non (Ridl.) Airy Shaw: Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 39.

Tree, up to 30 m high, up to 25 cm diameter. *Bark* (dark, pale, or reddish) brown, or dark green to (light) grey, smooth, slightly fissured, flaking; inner bark dark or pale brown to reddish or pinkish, yellowish, or whitish, scaly. *Wood* light brown, reddish, orange, or yellow to whitish. Young branches brown, tomentose. *Stipules* (narrowly) ovate, 5–6 by 1.5–3 mm, sparsely sericeous, present in young stages. *Petiole* terete, adaxially lowly grooved, 5–13 by 1–2 mm, densely hirsute, glabrescent, lower pulvinus c. 2 by 2 mm, indistinct, upper pulvinus 2.5–4 by 2–3 mm, distinct. *Leaves* narrowly elliptic to narrowly obovate, 7–26 by 2–7.5 cm; base obtuse to cuneate, basal glands absent; margin lowly undulate to subentire, marginal glands many, in margin, small, black; apex cuspidate to caudate; blade thinnish, smooth, dull, not brittle, drying greyish green to almost black above, (light) brown beneath, only midrib and nerves tomentose above, glabrescent, sparsely tomentose beneath, midrib and nerves tomentose, glabrescent; dots laxly set, greyish, fading in older leaves; disc-like glands absent. *Nervation*: midrib flat to raised in a furrow above, prominent beneath; nerves 8–15 pairs, flat to slightly sunken above, prominent beneath, marginal arches distinct, 0.5–2 mm from margin;

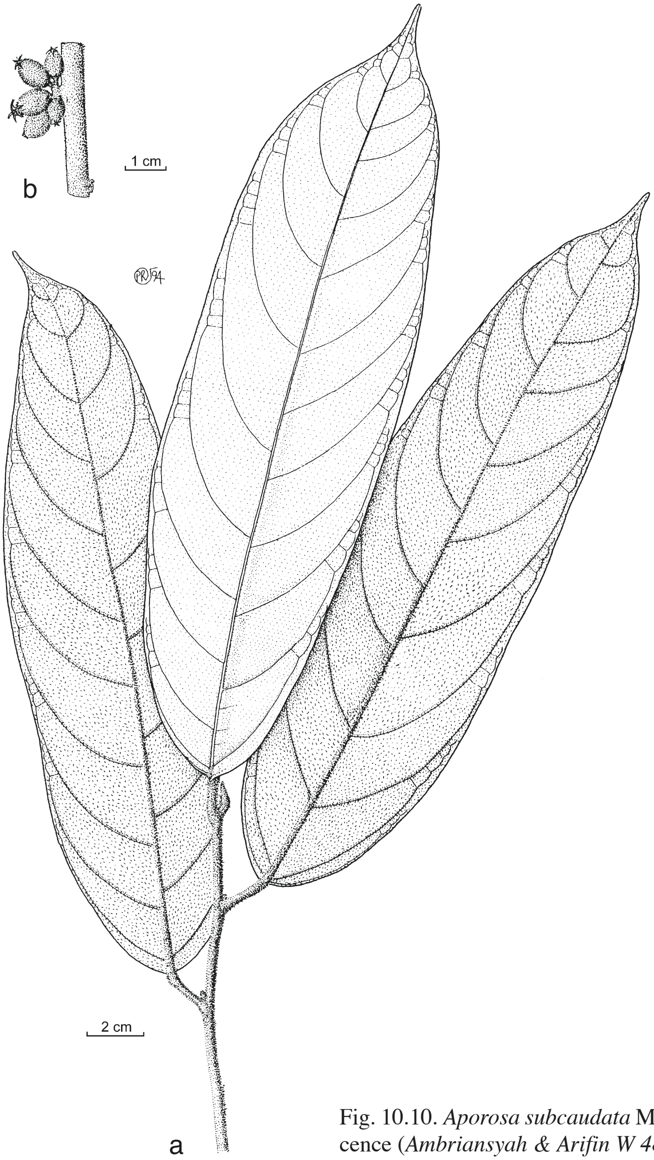


Fig. 10.10. *Aporosa subcaudata* Merr. a. Habit; b. infructescence (*Ambriansyah & Arifin W 483*, WAN).

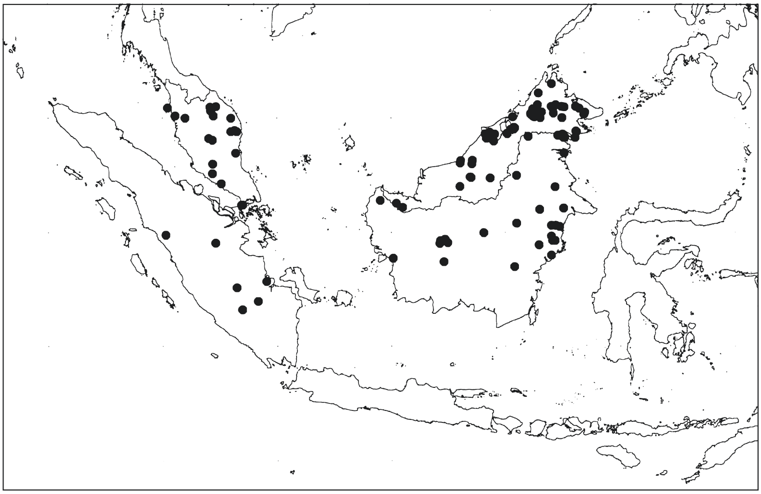
tertiary veins and venation often distinct, (slightly) scalariform, flat above, prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–7 clustered together, 9–23 by 1–2 mm, sericeous to tomentose; peduncle 2–4 by c. 1 mm; bracts broadly triangular, 0.5–1.5 mm long, inconspicuous, densely hairy outside, glabrous inside; glomerules subglobose, 1–2.5 by 1–1.5 mm, spaced at 0.5–1.5 mm at base of rachis, decreasing to 0 at apex; pedicel minute. *Staminate flowers* 0.3–0.5 mm long; sepals 4, narrowly obovate, 0.3–1 mm long, connate at base only, hairy outside, glabrous inside; stamens 2, not to slightly exserted, 0.3–0.6 mm; anthers 0.1–0.2 mm long, connective glabrous; pistillode a minute lump. *Pistillate inflorescences* 1–3 clustered together, 2–9 by 1.5–2 mm, sericeous; flowers up to 13, densely arranged along the rachis; bracts broadly triangular, 0.3–0.6 mm long, sericeous outside, glabrous inside; bracteoles ovate, 0.2–0.3 mm long, sericeous outside, glabrous inside; pedicel absent. *Pistillate flowers* 1.5–2.2 mm long; sepals 4, ovate, patent, 0.5–1.2 mm long, hairy outside, hairy at base only inside, margin ciliate; ovary ellipsoid, 1.2–2 mm long, 2-locular, densely sericeous; stigmas sessile, elongated, completely divided, flattened to the sides of the ovary, straight, 1.2–1.5 mm long, densely laciniate above, glabrous, smooth beneath, sericeous, style remnant absent. *Infructescences* 3–15 by 1.5–2.5 mm, sericeous; fruiting pedicel 0.5–1 mm long. *Fruits* ellipsoid, occasionally globose, 8–12 by 4–6(–10) mm, not stiped, not beaked, punctate, (sparsely) sericeous; pericarp 0.5–1 mm thick, not fleshy; septae and column glabrous. *Seeds* 1 (or 2), half-terete, ovoid, 6–8 by 4–5 by 2–4 mm.

Distribution — Malesia: Peninsular Malaysia, Singapore, Sumatra, and Borneo.

Habitat & Ecology — Primary, secondary, disturbed, logged forests; flat or low undulating country; on ridges, hill sides, hill tops, (steep) slopes, valleys, near riverbanks. Soil: clay, sandy clay, sandy loam, or sandstone, yellow or red. Altitude: 10–1200 m. Flowering: April to June, August to November; fruiting throughout the year.

Vernacular names — Peninsular Malaysia: Kaum tebasa, sebasah (Malay). Borneo: Panatan (Dusun); murok, kayu masam (Iban).

Notes — 1. An extremely variable species: the leaves can be densely or sparsely tomentose beneath; the nervation can be distinctly scalariform with the marginal arches very close to the margin or only slightly scalariform with marginal arches farther from the margin; the arrangement of the staminate glomerules or pistillate flowers can be lax below, with a bare peduncle, to almost continuous, densely set throughout; the bracts can be large and conspicuous or small; and there are even some specimens from Sarawak with globose, sericeous fruits. Thus, Pax & K. Hoffmann's *A. bracteosa* is a



Map 10.69. Distribution of *Aporosa subcaudata* Merr.

form which has leaves with an indistinct reticulate venation and a short inflorescence rachis with conspicuous bracts and densely arranged flowers. Merrill's *A. subcaudata* is one with leaves with a dense scalariform venation and inflorescences with interrupted flowers below and small bracts. There is, however, no consistent combination of the variable characters to justify distinction even on variety level, thus even less so on species level.

2. A third species often placed in this complex, *A. acuminatissima* of Merrill (1929), was a mixture: the type is *A. falcifera*, but the staminate specimen used in the description was *A. subcaudata* (*A. bracteosa*). The same name, *A. acuminatissima*, was already used earlier by Merrill (1920) and is a synonym of *A. sphaeridiophora*.

3. Pax & Hoffmann (1922) give for *A. bracteosa* as syntype *Ridley 6484*, but this number as preserved in BM and K is unmistakably *A. confusa*. Regarding the fact that they wrongly cited a couple of other specimens, I feel no guilt stating that *Ridley 6484a*, from the same place as the foregoing, but definitely representing *A. subcaudata*, is their originally intended syntype, and is here designated the paratype.

4. Two types of galls are found in this species: a gall that deforms the inflorescence into a panicle-like bushy structure, and one that aborts the flowers in the glomerule into finger-like strings.

5. Some specimens show signs of ant-habitation, because on the leaves hairy nests can be present which are made along the midrib below, and once I have seen ant-holes in the upper branchlets.

88. Aporosa spec. F (aff. *A. subcaudata* Merr./*A. selangorica* Pax & K. Hoffm.) — Map 10.67

Aporosa spec. nov.: Whitmore, Tree Fl. Malaya 2 (1973) 60. — Specimens: *SF (Corner) 29425* (L), Malaysia, 13.5 miles Mawai – Jemaluang Road; *SF (Kiah) 31999* (L), Malaysia, Sungai Kayu; *KL (Teo & P.) 3348* (K, L) Malaysia, Johore, Mersing, Compt. 129 Hutan Simpanan, Lenggor.

Small tree, up to 3 m high, up to 2 cm diameter. *Bark* pale. Young branches tomentose. *Stipules* narrowly ovate, slightly oblique, 9–14 by 2.5–6 mm, sparsely tomentose, present in young stages. *Petiole* terete, smooth, 6–12 by 1.5–2.5 mm, tomentose, lower pulvinus 1–2 by 1.5–2 mm, indistinct, upper pulvinus 2.5–5 by 2–3 mm, distinct. *Leaves* narrowly ovate to narrowly obovate, 9–24 by 4–8.5 cm; base emarginate to subcordate, basal glands absent; margin subentire to lowly undulate, marginal glands few, small, distinct; apex acuminate to cuspidate; blade thinnish, smooth, dull to slightly shiny, not brittle, drying greenish or brownish above, brownish beneath, only midrib tomentose above, sparsely tomentose beneath, midrib and nerves tomentose; dots laxly set, fine, grey, fading; disc-like glands occasionally present, few, minute, along the margin. *Nervation*: midrib slightly prominent to raised in a furrow above, prominent beneath; nerves 12–15 pairs, flat to slightly sunken above, prominent beneath, marginal arches distinct, 1–4 mm from the margin; tertiary veins and venation distinct, densely reticulate, slightly scalariform, slightly prominent to flat above, (slightly) prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* 1–3 clustered together, 11–22 by 1.5–2 mm, tomentose; peduncle 1–4 by 0.8–1 mm; bracts broadly triangular, 0.5–0.8 mm long, inconspicuous, puberulous outside, glabrous inside, margin ciliate; glomerules ellipsoid, 2–2.5 by 1–1.5 mm, consisting of densely set flowers, spaced at 1–2 mm at base, decreasing to 0 mm at apex; pedicel minute. *Staminate flowers* 0.7–0.9 mm long; sepals 4, (narrowly) obovate, 0.5–0.9 mm long, connate at base, sparsely puberulous outside, glabrous inside, margin ciliate; stamens 2, slightly exserted, 0.6–0.8 mm long; anthers c. 0.2 mm long, connective glabrous; pistillode minute, lumpy. *Pistillate inflorescences* single, 4–14 by 1.2–1.8 mm, densely tomentose; flowers up to 9, mostly densely set at apical end of the rachis; bracts broadly triangular, 0.8–1 mm long, sparsely tomentose outside, glabrous inside; bracteoles ovate, 0.5–0.7 mm long, sparsely tomentose outside, glabrous inside, margin ciliate; pedicel absent. *Pistillate flowers* 3–3.5 mm long; sepals 4, ovate, patent, 1–1.5 mm long, thin, sparsely tomentose outside, glabrous inside, margin ciliate; ovary ellipsoid, 2.5–3 mm long, 2-locular, smooth, tomentose; stigmas sessile, elongated, perpendicular to the sides of the ovary, straight, almost completely divided, 0.8–1.2 mm long, longitudinally ribbed and papillate above, glabrous, smooth beneath, sparsely tomentose, style remnant absent. *Infructescences, fruits*, and *seeds* unknown; column and septae in flower glabrous; pericarp thickish.

Distribution — Malesia: Peninsular Malaysia: Johore

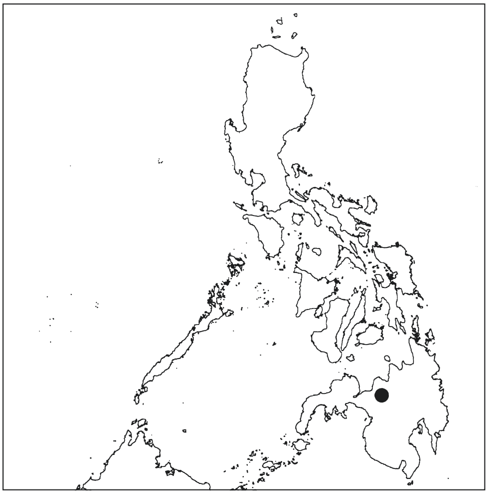
Habitat & Ecology — Forest, on swampy ground. Altitude: low. Flowering: May.

Note — This species closely resembles *A. subcaudata* and *A. selangorica*. The staminate specimen *KL 3348* has dried a greener shade than the other collections. The leaves are also smaller and less bullate.

89. **Aporosa spec. G** (aff. *A. caloneura* Airy Shaw/*A. sphaeridiophora* Merr.) — Map 10.70

Specimens: *PNH (Sulit) 10029* (staminate) (A, BM, L), Philippines, Mindanao, Bukidnon Prov., Mt Katanglad; *PNH (Sulit) 9899* (pistillate) (A, L), idem.

Young branches sparsely tomentose. *Stipules* not seen, early caducous. *Petiole* half-terete, 9–17 by 1.5–2.5 mm, sparsely tomentose, glabrescent, lower pulvinus 1–2 by 2 mm, indistinct, upper pulvinus 3–5 by 2–3 mm, distinct. *Leaves* narrowly ovate to narrowly elliptic, 11–20 by 4.5–9 cm; base obtuse to slightly attenuate, basal glands absent; margin lowly undulate to lowly glandular-crenate, recurved, marginal glands regular, in margin, distinct, brownish to black; apex acuminate to cuspidate; blade thick, smooth, dull, not brittle, drying grey-greenish to brownish above and beneath, only midrib sparsely hirsute above, glabrescent, midrib and nerves sparsely hirsute beneath, glabrescent; dots irregularly, rather laxly set, fine, greyish, fading in older leaves; disc-like glands absent. *Nervation*: midrib slightly prominent to flat above, prominent beneath; nerves 6–9 pairs, slightly prominent to flat above, prominent beneath, marginal arches fading, 1.5–3.5 mm from margin; tertiary veins and venation rather distinct, lax, slightly scalariform, flat above, slightly prominent beneath. *Inflorescences* axillary or just below the leaves. *Staminate inflorescences* single, 36–64 by 2–3.5 mm, sparsely tomentose; peduncle 0.5–2 by 0.8–1.1 mm; bracts broadly triangular, 1.8–2 mm long, inconspicuous, sparsely puberulous outside, glabrous inside; glomerules consisting of 12–15 laxly set flowers, globose, 2.5–3.5 by 2.5–3.5 mm, spaced at 0.5–3 mm at base of rachis, decreasing to 0 at apex; pedicel 0.5–1 mm long. *Staminate flowers* 1.8–2.5 mm long; sepals 3 or 4, ovate, 1–1.4 mm long, connate at base only,



Map 10.70. Distribution of *Aporosa spec. G.*

sparsely puberulous outside, glabrous inside; stamens 3 or 4, exserted, 1.8–2.7 mm long; anthers 0.5–0.6 mm long, connective glabrous; pistillode cylindric, 0.3–0.6 mm long. *Pistillate inflorescences* 1–3 clustered together, 24–58 by 1–1.5 mm, sparsely tomentose; flowers up to 21, rather densely arranged along the rachis; bracts broadly triangular, 1.8–2 mm long, at base very sparsely hairy outside and inside; bracteoles ovate, 0.8–1.2 mm long, sparsely hairy outside, glabrous inside; pedicel 2–3.5 mm long. *Pistillate flowers* 1–3 per bract, 5–6.5 mm long; sepals 4 or 5, ovate, patent, 0.7–1 mm long, subequal, sparsely hairy outside, hairy at base only inside, ciliate; petal-like organs occasionally present, 0.4–0.6 mm long, sparsely hairy; ovary ellipsoid, 2.5–3.5 mm long, 3-locular, sparsely hairy at base, glabrescent towards apex; stigmas raised, elongated, completely divided, perpendicular to the sides of the ovary, straight, 2.5–3 mm long, ribbed and lowly papillate above, glabrous, ribbed beneath, glabrous, style remnant absent. *Infructescences*, *fruits*, and *seeds* unknown; septae and column in flower glabrous.

Distribution — Malesia: Philippines.

Note — A strange species: the thick leaves are reminiscent of *A. caloneura* and *A. sphaeridiophora*, but the sometimes higher number of up to 3 clustered pistillate flowers in one bract and the relatively distinct petal-like organs and relatively large pistilloid are almost not *Aporosa*-like.

10.5 – **Excluded and dubious species**

Excluded species

Aporosa aberrans Gagnep., Bull. Soc. Bot. France 70 (1923) 232. = **Antidesma** sp.; Schot, Blumea 40 (1995) 450.

Aporosa billitonensis Pax & K. Hoffm., in Engl., Pflanzenr. IV.147.xv (1922) 97. = **Baccaurea minor** Hook.f.; Airy Shaw, Kew Bull. 16 (1963) 342.

Aporosa dolichocarpa Pax & K. Hoffm., in Engl., Pflanzenr. IV.147.xv (1922) 98. = **Baccaurea minutiflora** Müll.Arg.; Airy Shaw, Kew Bull. 36 (1981) 255.

Aporosa griffithii Hook.f., Fl. Brit. India 5 (1887) 353. = **Antidesma coriaceum** Tul.; Ridl., Fl. Malay Penins. 3 (1924) 233.

Aporosa incisa Airy Shaw, Kew Bull. 25 (1971) 477. = **Prunus arborea** (Blume) Kalkman var. **montana** (Hook.f.) Kalkman; Airy Shaw, Kew Bull. 29 (1974) 287.

Aporosa ineaqualis Pax & K. Hoffm., in Engl., Pflanzenr. IV.147.xv (1922) 104. = ?**Drypetes roxburgii** (Wall.) Hurosawa; Airy Shaw, Kew Bull., Addit. Ser. 8 (1980) 31.

Aporosa minahassae Koord., Meded. Lands Plantentuin 14 (1898) 580, 625. = **Shorea assamica** Dyer var. **koordersii** (Brand) Symington.

Dubious species

Aporosa wallichii Hook.f. var. *russellii* Chakrab. & Gangop., J. Econ. Tax. Bot. 17 (1993) 190. — Type: *P.T. Russell 1929* (holo CAL; iso CAL), Myanmar, Tavoy, Heinze No. 1 camp, 1700 ft, 2 April 1921.

The type specimen contains fragments of fruits without infructescences; solely on base of the characteristic and distinct scalariform venation of the leaf I can say nothing about which species and genus it might belong to; it is certainly not *A. wallichii*.

10.6 – **Identification list**

Species abbreviations as in the synoptical key (paragraph 10.3.8).

Abbe, Abbe, Smitinand, Nang & Dau 9539: octc — Achmad 15: nerv; 369: quad; 373: falc; 513: nerv; 522: prai; 757, 943: nerv; 1017: falc; 1217: luci; 1249: quad; 1250: prai; 1253: falc; 1284: prai; 1286: nerv; 1307: quad; 1314: nerv; 1334: prai; 1355: falc; 1357: quad; 1369: nerv; 1370: prai; 1396: nerv; 1402: luci; 1411: quad; 1413: falc; 1431: whit; 1440: falc; 1451: nerv; 1465: prai; 1490: luci; 1508: nerv; 1516: whit; 1551: falc; 1558: symco; 1636: whit; 1649: symcc; 1710: nerv — Aet 104, 683: long — Afriastini 126, 203: luc; 604: luna; 850a: grand — Agama 579: grand; 7655: frut — Alleizette 6429: fici — Alston 13260: conf; 13299: granu — Ambri & Arifin 66: frut; 97: grand; 104: ante; 134: nit; 218: luci; 250: nit; 253: subc; 345: falc; 397: nit; 399: luna; 410: falc; 529: ante; 530: grand; 548: conf; 655: falc; 659: nerv; 664: luci; 862: falc — Ambriansyah & Arifin AA 22: nit; 33: luna; 157: granu; 269, 788: subc; 869: falc; 917: sara; 983: grand; 1983: frut — Amdjah 46: conf; 73, 74: subc — Anta & Kostermans 1377: arbo — ANU series 1653: spha; 2861: vaga; 2876, 10931, 10932: brev — Argent 94108: conf — Argent et al.: 9160, 9161 sara; 93185 granu — Argent & Saridan 9386: frut — Atjih 226: lucp — Axelius 180: frut.

Baccon 129: frut — Backer 2219, 2748: octm — Bakhuizen van den Brink f. 1602, 2730: oct; 3137: frut; 4092: oct; 5800, 6262: arbo; 7468: oct; 7750: frut; 7791: arbo — Balajadia 2577: subc; 3715: frut; 3739: nit; 3762: octm; 7083: grand — Balakrishnan NBK 221: lati; 717, 768, 988: octa 1162: card; 1170: lanc — Balakrishnan & Bhargava 3449: oct — Balansa 3277: vill; 3278, 3279, 32780: oct; 3281, 3282, 4676: octc; 4689: oct — Barber 5733, 5827: acum; 5881: card — Barnard 40: frut — Bartlett 7602: frut; 8293: symco; 14081: symci — bb series 725: octm; 1822: luci; 2173, 2339, 2473: octm; 2488: ante; 2824: sp; 2832: falc; 2843: octm; 3059: arbo; 3970: ante; 5851, 8093, 8364, 9076, 9395: octm; 9585: nerv; 13647: octm; 13922: bent; 14341, 14543: leyt; 16333: octm; 20603: sp; 20746: falc; 20890: sp; 21612, 24974: octm; 25938: frut; 26096:

nerv; 26181: luna; 26349, 26451: calo; 28873: lucp; 29805: lucp; 30284, 30384: sp; 31679: nerv; 34115: luna; 34133: prai; 35721: subc — J.H. Beaman 6785: lage; 6998: bent; 7106: ante; 7597: sp; 7933: basi — Beccari PB 309: prai; PB 736: alia; PB 1213: luna; PB 2516: subc; PB 2811: bent; PB 2959: sara; PB 3739: falc — Beddome 26: acum; 7163: acum; 7164: micr; 7165: octy; 7167: vill; 7169, 7170: macr — Bejaud 171: octc; 541: plan — Berkhout 1311: frut — Beumée 6739: octm — Bicknell 728: octm — Bisla 3685: octa — Blicher-Mathiesen & Rantai Jawa 45: nit — Bloembergen & Kostermans 280: octm — Blume 63: octm; 215: frut; 470, 476, 779, 859: arbo; 1530: frut; 1699: lucp; 1704, 2136, 2223a, 2233a: frut — (B)NBFD A series 506: nit; 635: luci; 1225: elme; 1870: frut; 1876: luc; 2839: conf; 2845: elme; 2945: grand; 3417: subc; 3437, 3964: frut; 4268: grand; 4273: frut; 4393: elme — Bodinier 999: octc — Bogor Botanical Garden VIII.C-60: luna; VIII.F-5a: arbo; VIII.F-6, VIII.F-6a, VIII.F-20, VIII.F-20a: frut; VIII.F-72: nerv — Bon 266, 267: oct; 380, 429: octc; 1682, 2653, 4282, 4294, 4327, 9674: oct — Bordeneuve 36814: fici — Boschproefstation 135.T3.P376: nerv; 139.E1.P1018: subc; 139.E3.P817: nerv; 139.T3.P817: subc; 141.E3.P811: nerv; 78.T1.P148: luc; 146.T1.P189: luna; 244.T3.P828: arbo; T.189: luna; T.486: falc; T.673: frut; T.795: subc; T.828: arbo; T.931: nerv; T3.1073: luna; T3.P509: symco — Bourdillon 9: bour; 14, 50, 128, 197: acum; 221: fusi; 544, 1568: bour — Boutreau 18: oct — Brass 1049, 1062: bras; 7460: papu; 12110, 12135: egre; 13469: lame; 23142, 23377: herm; 27498, 27800: misi; 32296, 32343: vaga; 32401: herm — Brooke 9953, 10168: sara — Bruinier 5: falc; 28: quad – BRUN series 57, 65: subc; 430: chon; 750: sara; 866: grand; 5678: luct; 5934: subc; 15116: luc — BS series 797: symci; 1364: conf; 1486: spha; 1681: octm; 1900, 2125, 2678: symci; 5088: spha; 13519: frut; 15112: bana; 16168: basi; 17499: spha; 18641: leyt; 20514: bana; 20567: leyt; 20595, 23611, 24163: spha; 24218, 24281: leyt; 25460, 28563, 28563: spha; 29210: frut; 30808: spha; 30860, 31248: bana; 33122, 38325, 39425: symci; 40857: bana; 40997: spha; 41076: bana; 42471: octm; 46485, 79531, 79559, 79887: symci — BSIP series 142, 297, 931, 1390, 2062, 2258, 2338, 2723, 2816, 3161, 3538, 3571, 3839, 4157, 5361, 5408, 5558, 5812, 6063, 6613, 7075, 7554, 7809, 7817, 8314, 8655, 8805, 8924, 9825, 9924, 10110, 10133, 10419, 10772, 10996, 11287, 11323, 11430, 11616, 12082, 12562, 12897, 13048, 13437, 13504, 13653, 14113, 16015, 16372, 16963, 16990, 17332, 17425, 17559, 18350, 18907, 19411: papu — Buapheng 637: vill — Bunchuai 1047: plan; 1587, 1883: vill — Bunchuai & Nimanong 1373: octm — Bünnemeyer 1508: octm — Burkill 1850: falc; 2043: pena; 2049: aur; 2781: sela; 3253: aur; 3392, 4959: octm; 6386: main — Burkill & Shah 1069: aur — Burley & Ismail 4610: parv — Burley & Lee 297: subc — Burley, Tukirin et al. 701: conf; 732: frut; 825: grand; 1079: prai; 1400: glob; 1505: prai; 1567: subc; 1608: glob; 1689: nerv; 1707: stel; 1722: whit; 1727: nerv; 1728: ante; 1749, 1786: prai; 3520, 3556, 3730, 3840: frut — Burn-Murdoch 262: aur — Burut Ho 1775: nigc; 1892: frut — Buwalda 2902, 3023: octm — BW series 4933: sp; 5169, 5556, 6792: annu; 8657, 8708, 8874, 8936: brev — Bygrave 40: falc.

Callery 258, 285: octc — E.G. Campbell 129: nit — E.J.F. Campbell 130: frut — J.L. Campbell 18: luna; 75, 80: frut; 114, 140: subc — Cantley 92: main; 167: bent — Carr 12801: bras; 13024, 13073, 13258, 13285: carr; 13491: cf. papu; 14323: carr; 14996: vaga; 15576: carr; 16270: (mixture) — Castro 4421, 4499: conf; 4443: frut; 4489: subc — C.C.C. 756: yunn; 960, 1210, 2018, 2323, 2710, 6337, 8977: octc — Champion 180: octc — Chan 1012: octc — Chand 1459, 2981: oct — Chantaranothai, Middleton, Parnell, Simpson & Simpson 1341, 1346: aur; 1509: octm — Charmsirivathana 1356: aur — Charoenphol 73: octa; 446: yunn — Chatterjee 80: oct — Chevalier 30123: oct; 30206: plan; 30247, 30587: vill; 30927: octy; 31722: fici; 31732: plan; 31941: fici; 31996, 32008, 32091: plan; 32387: oct; 35822: macr; 36600: tetr; 36614: plan; 36814: fici; 37664, 37689, 37834, 41233: oct — Chew 169: octm; 229: stel; 284: aur; 604, 611: ante; 640 nigc; 1143 sara — Chew & Corner 4428, 4532, 4992, 7098: fulv — Chew, Corner & Stainton 72: fulv; 136: frut; 221: falc — Chin 2612: sten — Chow 217: octc — K.S. Chow & P.P. Wan 80118: yunn — Chun & Tso 44687: octc — Church 15, 45: granu; 68: luct; 80: sara; 103: ante; 125: sara; 148: luct; 359: frut; 364: ante; 378a: granu; 388: luct; 432: granu; 461: luct; 464: nerv; 566: nit; 622: subc — Church & Mahyar 1021: luci; 1175: subc; 1407b, 1425: sara; 1431: subc; 1432: granu; 1476: nit; 1655: conf; 1665: nit; 1750: grand; 1769: illu; 1832: sara; 1880: nit; 1886: subc; 1909: bent; 1929: luct — Church, Mahyar & Afriastini 1446: sara; 1638:

nit — Clarke 19544: wall — J. & M.S. Clemens 3525: oct; 3785, 3843: tetr; 9541: octm; 10784: falc; 20077: conf; 20088, 20246: nit; 22238: sara; 22276: nit; 26245: chon; 26276, 26276a: luna; 26540, 26966: chon; 29221, 29374, 29458, 29458a: fulv; 32146: falc; 32606: fulv; 40107, 40382: falc; 40387: fulv; 40414: chon; 40437: ante; 40476: lage; 40495: fulv; 40586, 40598: chon; 40625: calo; 40782: ante; 50090: falc; 50223: frut; 51339: falc — M.S. Clemens 972: prae; 1819, 2974: vaga; 4786: herm; 8060, 8628 vaga; 9000: herm; 41829: vaga — Collett 367: vill — Collins 334, 816, 1131, 1955: plan — Coode 3756: papu; 6329: grand; 6905: bent; 6911: luct — Cramer 4399: lanc; 4713: acum — Craven (& Schodde) 44: papu; 305: hete — Cuming 860, 1724: octm — Curtis 1460: aur; 1464: nerv; 1466: pena; 1469: bent; 1470: pena; 1472: stel; 1476, 1477: prai; 1482: nerv; 1483: subc; 1555: conf; 1570: nigc; 1583: pseu; 2434: frut; 2738: stel; 3003: nerv; 3047: subc; 3585, 3595: prai.

Dachlan 1169: prai; 2421: octm — Danser 5436: arbo — Darbyshire 870: laxi — Darbyshire & Hoogland 8375: lept — Davidson 1368: aur — W. de Jong 402: alia; 457: luct — De Vogel 1418: whit; 1427: quad; 1452, 1549: whit; 1591: sara; 1673: grand; 1675: subc; 1693: frut; 1742a: grand; 1876, 2028: falc; 9803: spC — De Vogel & Vermeulen 6770: leyt; 7506: luna — De Voogd 1192: octm — De Wilde & De Wilde-Duyfjes 12028: luce; 12474: whit; 12500, 12607: quad; 12642: whit; 12773, 12817: luce; 12913: luna; 13446: whit; 13477: quad; 13568: luce; 13641: luna; 13828: luce; 13880: whit; 13881: luce; 15478: ante; 15485, 15517: quad; 15619: ante; 15621: arbo; 15632: quad; 15710: whit; 15713: quad; 15881: conf; 16539: ante; 16958: quad; 16968: ante; 18015: luce; 18677: luci; 18889, 18900: aur; 19288: prai; 19381: conf; 19395: quad; 19493: prai; 19513: symco; 20000: ante; 20216: bent; 20232: luc; 20375: prai; 20383: bent; 20391: prai; 20400: bent; 20603: prai; 20630: frut; 20632: luna; 20655, 20664: quad; 20717: luc; 20756: prai; 20761, 20787, 21213: quad; 21285: whit; 21317: prai — De Wit 11: octm — Delmaar 1339: octm — Den Berger 364: luna — Derry 5: aur — Dirksen 18: octm; 26: sp — J. Dransfield 1016: luna; 1164: lucp; 6650: sara; 6676: grand; 6714: alia; 6841: subc; 6865: luct; 6894, 6899: sara; 6972: elme; 7059: subc; 7107: falc; 7349: luct; 7371: alia; 7399: granu; 7445: luna — Dumas 1508: octm; 1516, 1518: nerv; 1646: ante; 1653: whit; 1655: ante; 1668: octm — Duthir 6429: octa — Dwivedi 7877: octa.

Ebalo 1075, 1168: bent — Eberhardt 2691, 2693, 2763, 3112, 3922, 3928, 3938, 3954, 4015, 4538, 4577: oct; 4596: yunn; 4802, 4834, 9092: oct — Elmer 6101, 6225: spha; 9106, 13415: bana; 13474, 14042: bent; 15563: spha; 15652: bana; 15654: spha; 15744: frut; 15913, 16400: spha; 16987: bana; 17237: spha; 20243, 20245: nit; 20760: grand; 20826: elme; 20944: bent; 20954: elme; 20978: nit; 20987: grand; 21048: falc; 21084: nit; 21087: grand; 21120: subc; 21142: grand; 21146: nit; 21219: subc 21233: bent; 21243: subc; 21255: elme; 21278: subc; 21286: nigc; 21420: subc; 21450: frut; 21765: conf; 21773: nit; 21805: bent — Endert 55, 78: octm; 2332: bent; 2544: elme; 3045: conf; 3345: chon; 3374: luna; 3583: bull; 3797: chon; 3851: calo; 4298: conf; 4695: lage; 4696: luna; 4700: conf; 4706: chon; 4710: ante; 4770: basi; 4781: grand; 4813: subc; 4826: prai; 4877: luci; 4886: alia; 4931: nit; 4985: ante; 5044: subc; 5067: prai; 5070: luci; 5118: grand; 5144: bent; 5157: subc; 5205: grand — Enggoh 7319, 10667: grand — Engler-Julius 16: symco — Esquirol 1208: octc — Evrard 2039, 2181: vill — Eyma 4303: brev.

Falconer 908: octa; 954: vill; 956: octa — FB series 133, 146, 198: spha; 202, 394, 403: symci; 732, 818, 834: spha; 1099, 1187: symci; 1451: spha; 2361, 2541, 2657, 2745, 2894, 3086, 5767, 5988, 6764: symci; 7279: bana; 13603, 16885: spha; 21245: leyt; 21673: symci; 21698: spha; 22048: symci; 24829: spha; 25438, 25598: symci; 26185: spha; 26745, 26958: symci; 27148: spha; 28389: symci; 29591: spha; 30317: bana — Fernandes 81, 153: card; 237, 282: acum; 2009, 2036, 2234: card — Forbes 194: nigp; 250: prae; 411: frut; 412: octm; 899: nigp; 1783: whit; 2409a: prai; 2912: luci; 2937, 2938: octm; 2955: ante; 2956: conf; 2958: prai; 2962: conf; 2999a: symco; 3047: luci; 3064, 3084: conf; 3115: falc; 3122: symco; 3132: subc; 3165, 3177: arbo; 3221: symco; 3247: nigc — Ford 586: octc — Foret 21, 22: octc — L.L. Forman 426: grand; 449, 487, 882: nit; 908: sara; 987, 1057, 1147: grand — Forrest 12192: octa — Foster & Puasa 3473: calo — FRDU & Van Welzen 10: octy — Frodin 2148: symco — Frodin & Ismawi 2024: nit — Frodin & Mornen 3138: nigp; 3449: papu — Frodin, Mornen & Gabir 2461: nigp — Fuchs 21230: alia; 21264: sara; 21271: grand; 21287: sara.

Gage 98: micr — Gallatly 478: octa; 742: vill — Galoengi 482: prai — Gamble 393a, 460a, 460d, 6795a, 6859a: octa; 15484: card — Gardner 804: card; 805: lanc — Gaudichaud 247: octc — Geesink 9094: basi; 9099: chon — Geesink, Hattink & Charoenphol 7378: aur — Geesink, Hattink & Phengkhlai 6456: plan — Geesink, Phanichapol & Santisuk 5796, 6038: vill — Geesink & Santisuk 4927: aur; 5011: octm; 5026: plan; 5093: micr; 5374, 5387: aur; 5412: micr — Gentry & LaFrankie 66943: micr — Geollogue 112: frut — Gilbert Rogers 132: octa — Goklin 2397: luci — Grashoff 238: nerv; 969: subc; 981: prai; 1134: frut — Gressit 876: octc; 5860: oct — Griffith 892: octa; 1095a: plan; KD 4950: micr; 4952: octa; 4956: plan; 4957: yunn; 4958: octa; 4959: aur — Guierson & Long 3588, 3799: oct — Guigonis 302: ante — Guinet 119: plan — Guoliang 15455: octc — Gusdorf 102, 158: octm.

Hallé 1950: prae — Hallier 344: octm; 4236, 4236a: symci — Hance 1082: octc; 7810: yunn — Haniff 374, 4296: octm; 13140: aur — Hansen 603: sara; 684: nit; 787: conf; 823: subc; 865: sten; 885: granu; 903: bent; 1015: sara; 1070: nit — Hansen, Seidenfaden & Smitinand 11229: yunn — Hansen & Smitinand 11976, 11996: micr; 12245: aur — Hardial 169: pena; 342: prai — Hardial & Samsuri 144: prai; 172: luna — Harmand 259: vill; 280: plan; 332: vill; 383: serr; 438: vill — Hartley 10068: papu; 10488: prae; 10708, 10739: bras; 10912: vaga; 11346: papu; 11548: reti; 11917: prae; 11959: vaga; 12005: reti; 12043: herm; 12081: vaga; 12253: prae; 12321: reti; 12531: herm; 12945: carr; 13117, 13130: herm — Haselfoot-Haines 350, 3831, 4093, 4583: octa; 5821: vill — Haviland 732, 733: falc; 1605: bull; 2195: frut — Haviland & Hose 722: frut; 3236: nigc — Heinig 376: octa — Helfer KD 4951, 4953: octa; 4954: vill; 4956: plan — A.N. Henry 52402: acum — Henry 8495, 8519: octc; 11638, 11638a, 11638b, 11638c, 11638d: octy; 11638e, 11638f, 12828: yunn – HFP series 1250, 1371: card — Hiepko & Schultze-Motel 1379: parv – Hohenacker 352, 860: card — Hoogland 11428, 11569: lanc — Horsfield 114: octm — Hose 40, 92: falc; 204: subc; 238: nit; 278: falc — Hotta 12592: alia; 12594: nigc; 12625: sara — Ding Hou 199: grand; 328, 343: luc — How 70486, 71704: octc — How & Chun 70006, 70007: oct; 70102, 70113: octc — Huq & Mia 10266: wall

Indrapong 81: oct — Indrapong et al. 196: vill — Iwatsuki, Murata, Dransfield & Saerudin S-1666: quad.

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Valera 4745: bana — Van Balgooy 4545: frut; 4598, 4634: dend; 5861: frut — Van Balgooy & Kessler 5892: nit; 5924: luci — Van Balgooy & Van Setten 5294: frut; 5337a: ante; 5344: grand; 5350: arbo; 5355: subc; 5360: sara; 5507: frut; 5521: granu; 5533: falc; 5564: arbo; 5565: luna — Van Balgooy & Stone 2035: sela — Van Beusekom & Phengkhlai 227: yunn; 319: oct; 654: octm; 674: plan; 1091: vill; 2963: oct — Van Beusekom, Phengkhlai, Geesink & Wongwan 4271: vill; 4319: octy — Van Beusekom & Santisuk 2850, 3157: oct; 3172: plan — Van der Maesen 4905: card — Van Slooten 2241: granu — Van Steenis 1231: luna; 5388: oct; 9309: aur — Van Valkenburg 513, 516: sp; 1047, 1048: chon — Van Welzen 906: grand — Veldkamp 8036: granu; 8242: conf; 8274, 8302, 8386, 8421: sara; 8441: nerv; 8458: conf; 8475: luct; 8499: granu; 8550: sara — Verhoef 93: grand — J.E. Vidal 837b: serr; 1236: plan; 1236b?: serr; 1449: oct; 1574: vill; 2232: plan; 2611b: oct; 4426: plan — J.E. Vidal, Y. Vidal & Niyomdham 6119, 6211: vill — Vidal y Soler 185, 185bis, 874: symci; 901, 1738: octm; 1774: symci; 2391: bana; 3752: octm — Villamil 258, 390: frut — Vinas 125: scle — Vu Van Cuong 1178: vill.

Waas 694: card; 905, 931: lanc; 1178 card; 1439, 1440, 1489: lanc; 1531: card; 1603, 1723: acum; 1893, 1939, 1940: lanc — Waas & Paeris 449: acum — Walker 47: fusi/lati — Wallich 6816a, 6816b, 6816c, 6816d, 6816d, 6816e: octa; 7298a, 7298b: vill; 7299: octa; 7985: micr; 7991: octa; 8017: pseu; 8019: wall — C. W. Wang 33249, 36052, 36159: octc; 39071: yunn; 74772: oct; 74787: octa — Y.K. Wang 1850: yunn — Waterhouse 105, 298b, 461(b): papu — Watt 12176: octa — Wenzel 587, 614: leyt; 637: bent; 687, 716, 776: bana; 969: leyt; 1387: octm; 2504: bana — Whitford 53, 99, 1055, 1073: symci — Whitmore & Kalima 3304: whit — Whitmore & Sidiyasa 3206: aur; 3472, 3493: leyt — Whitmore & Sutisna 3354: whit — Widjaja 486, 816: octm — Wight KD 2653: card — Wilford 399: octc — Wilkie 9547: nit; 93357: ante; 94286, 94341: sara — Wilkie & Armstrong 94129: grand — Wilkie & Latupeirisse 94345: grand — Williams 282: octa; 366: symci; 412: spha; 498: symci; 548, 581, 689: spha; 697: symci; 3010: frut — Hubert Winkler 3356: grand; 3401: octm; 3412: luc — Winit 29, 678: vill; 1250: octa; 1418, 1432, 1760: vill — Wirawan 419: octm — Wiriadinata 325: frut; 617: granu; 873: lucp; 1089, 1124: nit; 1191: luci; 1314: nit; 1320: grand; 3235, 3413: prai; 3602: luci — Wong WKM 1068: luct; 1082: bent; 1170: grand; 1250: subc; 1465: calo; 1498: falc; 1531: luci; 1628: nit; 1948: granu; 1974, 1984: sara — Wongprasert 19: vill — Woo 244, 266: octc — Wood 2087: subc — Worthington 12: card; 114: fusi; 154, 355: card; 901: fusi; 902: lati; 1523, 1524, 1760: card; 2236: lati; 2533: lanc; 2548: lati; 2551: lanc; 2763: fusi; 2847: card; 3198: lanc; 6595: lati; 6957, 7172: card — Wray Jr. 1421: nigc; 2683: pseu; 3483: aur; 3686: glob — Wright 423: octc.

Yamada K-9521: falc; K-9539: luct — Yates 1796: arbo — Yin Yin Kyi 12283: vill — Yip 377: octc — Yulita & Wilkie 93406: subc.

Zainudin 1743: oct; 2626: conf; 2685: micr; 2730: prai; 2874: sela; 2890: arbo; 2893: whit; 3606: pena; 4542: nit; 4549: conf; 4606: sara; 5058: frut; 5160: micr; 5529: pena; 5545: arbo; 5548: stel; 5556, 5722: aur — Zhang Jian-Hou 18536: vill — Zoefri Hamrah 18: nit — Zollinger 39, 645, 654: octm; — Zulkarnain & Giesen 362: conf 365: luna.

10.7 – **Index**

Accepted names are in roman, new names in **bold**, and synonyms, excluded and dubious names in *italics*. Numbers refer to the species numbers used in this revision.

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CURRICULUM VITAE

Anne Marketta Schot werd geboren op 20 september 1966 te Leidschendam. Na in 1984 op het Stedelijk Gymnasium te Leiden het diploma behaald te hebben, begon zij in 1985 met haar studie Biologie aan de Rijksuniversiteit Leiden. In augustus 1991 werd het doctoraal behaald met doctoraalonderwerpen in de evolutiebiologie en plantenbiogeografie, te weten:

1. 'Een kwantitatieve analyse van de schutkleur bij *Melanitis leda* (Fabricius) (Lepidoptera: Satyridae)' onder leiding van Prof. Dr. P. Brakefield en Dr. J. Windig op het Instituut voor Evolutionaire en Ecologische Wetenschappen;
2. 'Phylogenetic relations and historical biogeography of *Fordia* and *Imbralyx* (Papilionaceae: Millettieae)' onder leiding van Dr. R. Geesink en Dr. J.W.A. Ridder-Numan op het onderzoeksinstituut Rijksherbarium / Hortus Botanicus.

Tijdens haar studie heeft zij student-assistentschappen gedaan bij de eerste-jaars biologie onderwerpen 'Overzicht Dierenrijk'en de binnenlandse excursie.

Vanaf 1 juni 1992 tot en met 31 mei 1996 was zij als Assistent in Opleiding in dienst van het onderzoeksinstituut Rijksherbarium / Hortus Botanicus te Leiden, tegenwoordig de Leidse Universitaire vestiging van het Nationaal Herbarium Nederland, alwaar zij onderzoek deed aan het geslacht *Aporosa*.

Vanaf juni 1996 werkte zij als freelance vertaler voor het vertaalbureau Bothof, en in april 1997 werd haar eerste dochter geboren. Op 1 maart 1998 trad zij in dienst van het toenmalige ICT bedrijf Roccade Civility in Rotterdam als Applicatieontwerper Cobol op de afdeling Salarissen en HR, welke per 1 januari 2004 opgegaan is in de nieuwe opgerichte divisie PinkRoccade Payroll en HR Services van de werkmaatschappij PinkRoccade Public sector. Gedurende haar diensttijd bij PinkRoccade werden in maart 1999 en februari 2003 een tweede en derde dochter geboren.

Als parttime gastmedewerker vanaf 1 juni 1996 is zij verbonden geweest aan het Nationaal Herbarium Nederland, Universiteit Leiden branch, in welke hoedanigheid zij, tussen alle overige werkzaamheden door, uiteindelijk het tot stand komen van dit proefschrift heeft gerealiseerd.

Publicaties:

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NAWOORD

Het is in Leidse proefschriften traditie geworden om te eindigen met een nawoord, waarin iedereen die maar enigszins een constructieve bijdrage heeft geleverd aan het tot stand komen van het boekwerk in positieve terminologie wordt omschreven, om hiermee het artikel 35, vierde lid, van het promotiereglement, te kunnen omzeilen. Ook ik wil mij niet aan deze traditie onttrekken.

Peter, vooruit dan maar, als eerste. Mijn erkentelijkheid voor de discussies die wij in een vorig leven nog met elkaar voerden. Zou dat over 20 jaar weer wat worden? Haai, ga maar weer lekker spelen en doe de groeten aan Elgoog.

Margit, Britta, Lilan. Jullie zijn op dit moment nog te klein om hier ook maar iets van te begrijpen, maar er komt een dag dat… Geniet nu nog maar lekker!

Mijn ouders en schoonouders, voor de morele steun en de vrijwillige oppas.

Voor de echte constructieve bijdragen aan dit proefschrift kan ik natuurlijk de onmisbare hulp van Bertie Joan van Heuven bij het maken van de anatomische preparaten niet ongenoemd laten, en evenmin de nauwgezetheid, goede smaak en grote vakkunde van Connie Baak bij de opmaak van de tekst. Joop Wessendorp en Priyono maakten een aantal mooie tekeningen en Anita Walsmit Sachs verfraaide de door mij geleverde primitieve schetsen. Ben Kieft verzorgde het scannen van de foto's, tekeningen en verspreidingskaarten. Peter van Welzen stak veel tijd in het maken van de verspreidingskaartjes en het omzetten van de cladogrammen in een door de computer leesbaar formaat.

Dit proefschrift was er ook niet geweest zonder de inspirerende werking die uitging van de immer gezellige sfeer onder de collega's van het Nationaal Herbarium, met name de staf van de toenmalige onderzoeksgroep Tropische Fanerogamen en mijn mede AiO's en OiO's.