Cladistic and Biogeographic Analyses of *Arytera* Blume and *Mischarytera* gen. nov. (Sapindaceae)

with Notes on Methodology and a full Taxonomic Revision

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CONTENTS

SUMMARY

A taxonomic revision of *Arytera* Blume is presented, together with a cladistic analysis. On the basis of this analysis, a new genus is recognised, *Mischarytera* gen. nov., to accommodate the species *A. bullata*, *A. lautereriana*, and *A. macrobotrys*. The necessary new combinations are made. A new classification for *Arytera* at infrageneric level, also based on the cladistic analysis, is given. Two sections are recognised, *Azarytera* and *Arytera*; the latter is further divided into three subsections, *Arytera*, *Distylis* subsect. nov., and *Pacifica* subsect. nov. One new species is described (*A. nekorensis*) and one new combination is made (*A. neoebudensis*). General, regional, and synoptic keys to all taxa are provided, as are detailed descriptions of the species.

Next to macromorphological characters, leaf anatomical characters were studied with SEM and light microscopy. A general leaf anatomical description of *Arytera* is provided, together with data for the individual species.

Several methodological issues pertaining to the practice of cladistic analysis are treated in some detail. These are the coding of polymorphic species, and the choice among multiple equally parsimonious cladograms.

Polymorphic species theoretically should be assigned the locally plesiomorphic character state; because this state is not known in advance, they should be coded as polymorphic when the analysis is carried out with the computer programs PAUP and CAFCA, and as unknown when using Hennig86. In the latter case the resulting cladograms should be checked to ensure that none of the resulting cladograms becomes longer due to species lacking the locally plesiomorphic state for one or more of the characters for which they are polymorphic.

The choice among multiple equally parsimonious cladograms should be based on differential weighting of the characters on the basis of the number of homoplasious (extra) steps they require. Characters with little homoplasy are to be given more weight than characters that display much homoplasy. One of the methods to realise this is to prefer cladograms which have a higher *average* unit retention index.

A historical biogeographic analysis is provided for the region in which *Arytera* occurs, i.e. Australia, Malesia, and the West Pacific. Different methods of analysis (Brooks Parsimony Analysis, Component Compatibility Analysis, Component Analysis *sensu* Page) are carried out and compared. A new method is presented for coding so-called 'missing areas' under Component Compatibility Analysis, which makes use only of the information provided by the taxa that are present in such areas. Attention is also paid to the interpretation of character state changes on areagrams, leading to the conclusion that the nature of chance events (dispersal, extinction, etc.) usually cannot be inferred from the optimisation on the areagram alone.

Next to *Arytera* and *Mischarytera*, six other genera of Sapindaceae were used. Several patterns are apparent in the results. Firstly, New Caledonia, the Loyalty Islands, and Lord Howe Island show a vicariant pattern with respect to the Australian continent, whereas the distributions of taxa on the remaining islands in the West Pacific probably are due to dispersal. Secondly, a dichotomy is apparent between the areas on the Australian craton and areas which geologists assume to have been accreted onto its northern edge. Thirdly, West Malesia was probably reached by some of these genera from the East in a number of dispersal events. Finally, a recent exchange of floristic elements has taken place between Northeast Australia and South and Southeast New Guinea, probably during Pleistocene periods of lowered sea levels.

Key words: *Arytera*, *Mischarytera*, Australia, biogeography, cladogram choice, Malesia, missing areas, New Guinea, Pacific, phylogeny, polymorphism, Sapindaceae.

Chapter 1 — INTRODUCTION

When I embarked upon this study, the treatment of Sapindaceae for Flora Malesiana was already almost completed. *Arytera* Blume was the last genus to be revised, and one of the aims of this study was to provide a treatment for Flora Malesiana. As this study was to serve as my PhD thesis, I did not restrict myself to the Malesian species, but covered the entire genus. The results of this revisionary work are found in Chapter 5.

Another aim was to do a cladistic analysis of *Arytera*, and to use the results thereof in a biogeographic analysis. In order to obtain sufficient characters, next to macromorphological study I chose to perform a leaf anatomical survey. This particular type of data was chosen because previous students of SE Asian Sapindaceae (Van Welzen 1989; Adema 1991; Adema & Van der Ham 1993) had also carried out such analyses, thus allowing for a comparison between their results and mine. The results of the leaf anatomical investigation, together with a general description of the macromorphological features of *Arytera*, are given in Chapter 2.

The cladistic analyses are described in Chapter 3. Because many species showed polymorphism in one or more characters a coding method was needed to accommodate the information from these species in the data set. A literature survey showed that different workers had adopted different methods, so I investigated (together with Prof. Dr. D. J. Kornet, Theoretical Biology Section, EEW, Leiden) the merits of different ways of coding data for polymorphic species from a theoretical point of view (see Sections 3.2.1.1 ff.). The analyses resulted in more than one most parsimonious tree. Therefore, an attempt was made (partly in collaboration with Dr. M. Zandee, Theoretical Biology Section, EEW, Leiden) to provide theoretical grounds for preferring one of these over the others. Different methods of choosing among equally parsimonious trees are described in Sections 3.2.2 ff., and a final choice among the cladograms obtained is made in Section 3.5.1.

The final aim of this study was to provide a biogeographic account of *Arytera*. In order to distinguish between events that affected the entire ecosystem of which *Arytera* has been part (vicariance events) and chance events such as dispersal and (local) extinction, I included in the analysis a number of other monophyletic groups that presumably have been sympatric with *Arytera* for a considerable period of time. The results of the biogeographic analysis (described in Chapter 4) can thus be expected to reflect the biogeographic history of the tropical rainforest ecosystem of Australia, New Guinea, and the West Pacific. In doing this analysis, a new method was developed for a long-recognised problem in historical biogeography, namely how to treat so-called 'missing areas.' This method is described in Section 4.3.2.1. Some thoughts were also given to the way character state changes on areagrams should be interpreted (Section 4.5.3.1), which led to the conclusion that without further information it is unlikely that the nature of chance events can be inferred with certainty from traditional optimisation of distribution data on an areagram.

1.1 – TAXONOMIC HISTORY

The genus *Arytera* was described by Blume in 1849 to accommodate the species *Arytera litoralis* and *A. montana* (the latter transferred to *Lepidopetalum* by Radlkofer [1879b]). In 1859, F. Mueller added the Australian species *A. divaricata* and *A. foveolata*, which were subsequently transferred to the genus *Nephelium* by Bentham in 1863. Bentham also described a number of new species in *Nephelium* which were transferred to *Arytera* by Radlkofer (1879b). Other species of *Arytera* were described in, or moved among, the genera *Cupania*, *Euphoria*, *Ratonia*, and *Zygolepis*, by various authors. The first overviews of the genus were published by Radlkofer (1879a, b). He described eight new species, and included six more from other genera. Over the years he added a number of new species. In 1933, in his posthumously published treatment of the Sapindaceae for Engler's Das Pflanzenreich, Radlkofer mentioned 21 species, of which 14 are retained in this study. Since then, no revision of the genus was undertaken till Van der Ham (1977b) published a short overview. Reynolds (1985a, b) published revisions for Australia in which she recognised three new species, till then the largest single addition to the genus since Radlkofer's work. Finally, Turner (1993) published eight new species from Papua New Guinea and Australia, and in 1994 gave an overview of the genus in the Malesian area.

1.2 – SPECIES CONCEPT

In the past, a variety of species concepts have been used in taxonomy. The oldest one is the morphological species concept. According to this concept, a species is defined by morphological similarity in one form or another. A modern version is Cracraft's (1983a) phylogenetic species concept, based on the sharing of unique (monothetic) sets of character states. Other species concepts are e.g. the biological species concept (Mayr 1942, 1969), the recognition species concept (Paterson 1985), and finally the so-called (Nixon & Wheeler 1990) internodal species concepts, which are based on splits in genealogical networks (Hennig 1950, 1966; Wiley 1981; Ridley 1989). (For more elaborate treatments of different species concepts, see e.g. Kornet [1993a, b] and Otte & Endler [1989].)

The major drawback of all but one of these concepts is that they do not partition the genealogical network fully and unambiguously into mutually exclusive and historically continuous entities, a requirement that must be fulfilled by any sound species concept. The internodal species concept based on permanent splits is the favourable exception (Kornet 1993a, b; Kornet et al. in press), but as shown by her the entities recognised are too short-lived to be acceptable as species. These short-lived entities ('internodons') are grouped by Kornet (1993b) into composite species on the basis of an auxiliary (morphological) criterion, namely the fixation of an evolutionary novelty in an internodon. Internodons that fulfil this requirement are designated originator internodons, and a species is then defined as consisting of an originator internodon and all its descendant internodons, bar those descendant internodons that are also originator internodons themselves and all their descendant internodons. The composite species concept is applied in this study.

The fulfilment of the two criteria for composite species has several implications. Firstly, at least in principle the set of fixed character states for (groups of) populations an be determined exactly, as can a split between them. The permanence of such splits ıust be estimated, however, at least for extant lineages. Thus, two groups of populations with different sets of fixed character states must be assigned to two different composite species if the split between them is estimated to be permanent, else they belong to a single species. Sometimes such groups of distinct, temporarily split populations are given infraspecific rank. Two groups of populations with identical sets of fixed character states on the other hand must be assigned to the same species, unless they are assumed to be permanently split and to have gained the same set of character states through parallel evolution (convergence).

Secondly, it is not necessary that all specimens in a composite species have the fixed evolutionary novelty that defines the species. In the early generations of an originator internodon the character state need not yet be fixed, while during the lifetime of a composite species further evolutionary novelties may arise in that character (and in others) which eventually may increase in frequency till the old character state has become rare. In other words, the possession of the full set of character states characterising a composite species is neither necessary nor sufficient for assigning a specimen to that species. The logical corollary is that deviant specimens are expected to occur. As with other species concepts, with only morphological information at hand it is likely that occasionally such specimens are classified incorrectly.

Chapter 2 — MORPHOLOGY

In this Chapter, a general overview is presented of the various morphological characters of *Arytera*, both macromorphological, leaf anatomical, and pollen morphological. The infrageneric variation is treated. Synapomorphies for particular clades are discussed in detail in Section 3.5.2.

2.1 – MACROMORPHOLOGICAL CHARACTERS

Habit

Small to rather large trees or shrubs, rarely a scrambling climber (*A. miniata*), up to 40 m tall. The large trees are probably always canopy trees, the smaller ones and shrubs substage species. In some species buttresses are reported. The bark is smooth to rough, sometimes flaking. In *A. lautereriana* and *A. macrobotrys* the cambium appears to be wavy, giving a corrugated appearance to the sapwood – hence the vernacular name 'Corduroy Tamarind' for the former species.

Indument

The indument consists of short or long, appressed or patent, straight or crispate, solitary hairs. In *A. arcuata*, *A. brackenridgei*, *A. gracilipes*, and *A. lepidota* peltate scales are present. These are also found in a number of other genera of Sapindaceae. In most species glandular hairs were observed in leaf-anatomical preparations (see Section 2.2). In most species the indument disappears with age; thus it can usually only be observed on young parts.

Varnish

In the species with peltate scales, the young vegetative and reproductive parts are often covered with a resin-like substance, giving them a shiny or 'varnished' appearance. The perfect correlation of this character with the presence of peltate scales leads me to assume that these scales are probably glandular, the more so because no other glandular organs were discovered on these species in the leaf-anatomical study. The same phenomenon was observed by Adema (1991) in *Cupaniopsis* sect. *Mizopetala*.

Leaves

The leaves are arranged spirally. As in many Sapindaceae, they are always paripinnate, the number of jugae varying from one to about eleven. In this study a distinction is made between the petiole and the rachis proper. The latter term here always indicates the central axis of the leaf *from the first leaflet upwards*. The petiole is more or less distinctly swollen into a pulvinus at the base. Both it and the rachis are (hemi)terete to dorsoventrally flattened in transverse section and not (to rarely minutely) winged. The rachis usually hardly extends beyond the terminal leaflet in an apical process or acumen (an exception is formed by *A. nekorensis*, in which the apical process is distinct).

The leaflets are oppositely to alternately arranged along the rachis. They are subsessile to distinctly petioluled. Like the petiole, the petiolule is always swollen into a pulvinus at least at the base; in species with a (very) short petiolule, it is completely swollen, thus consisting of a pulvinus only. Sometimes the petiolule is provided adaxially with one or two grooves.

The shape of the leaflets is rather variable, from (sub)orbicular to elongate, with the greatest width usually below or at, occasionally above, the middle of the leaflet. The consistency of the leaflets varies from thinly chartaceous to very coriaceous. When backlighted, many species display minute bright spots in the lamina (punctation; hand lens!). These bright spots usually occur in species in which secretory idioblasts are found (see Section 2.2), but the correlation is not perfect. Presumably species in which the parenchyma tissue is organised rather irregularly, with many voids, may also appear punctate.

The base of the leaflets may be symmetric or (indistinctly) asymmetric, with either the basi- or acroscopic broader. The shape of the base varies from obtuse to rounded to acute to (slightly) attenuate. The margin of the leaflets is usually entire, sometimes slightly repand; in *A. foveolata* and *A. lautereriana* it may be somewhat dentate to serrate, especially apically. The apex of the leaflets is also variable in shape, from retuse to slightly caudate. The very apex of acute to caudate leaflets may itself be differently shaped, e. g. retuse or rounded. A mucro (apical extension of the midrib beyond the lamina) is only rarely present.

Both the adaxial and abaxial surfaces of the leaflets are always smooth; papillae, which occur on the abaxial sides of leaflets in many Sapindaceae, are always absent in *Arytera*. The two surfaces of the leaflet often are slightly differently coloured, at least in herbarium material, the abaxial surface then lighter than the adaxial surface. The adaxial surface of the leaflets is usually glabrous, with often a slight indument on the basal part of the midrib. The abaxial surface of the leaflets may be glabrous too, but usually carries some indument at least on the major veins.

Domatia may be observed in the axils of the major lateral veins of many species; they are absent in some Australian and all Pacific species. They can take the form of pockets (consisting of a 'roof' between the midrib and the lateral vein only), sacs (like pockets, but with a ridge of tissue on the lamina also), or pits (depressions in the lamina with a wide opening). In *A. litoralis*, *A. miniata*, and *A. pseudofoveolata*, the domatia may

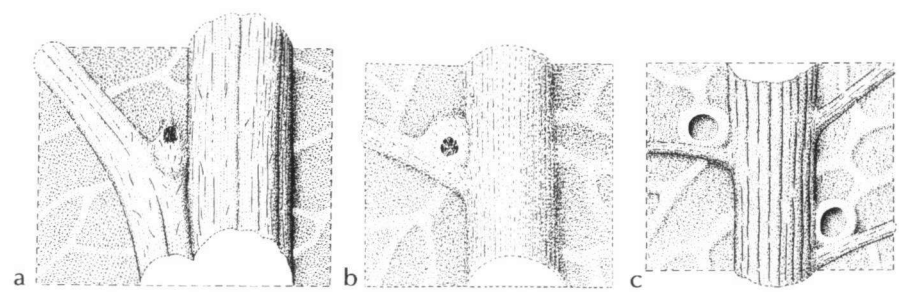


FIGURE 2.1. (a) Pocket domatium (*Arytera litoralis*); (b) sac domatium (*A. brachyphylla*); (c) pit domatia (*A. lautereriana*).

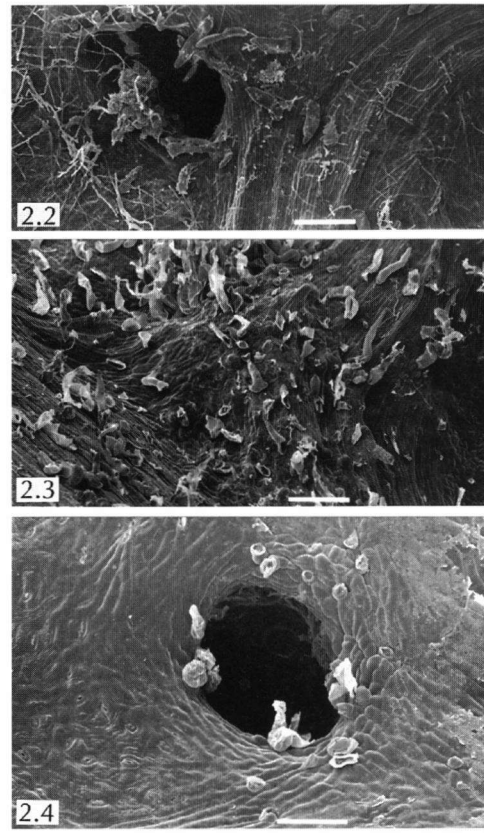


FIGURE 2.2–2.4. — 2.2. Sac-shaped domatium. *Arytera litoralis, SAN 35056.* Scale bar 100 µm. — 2.3. Sac-shaped domatium. *Arytera foveolata, Lam 7673.* Scale bar 100 µm. — 2.4. Pit-shaped domatium. *Arytera lautereriana, Gray 4850.* Scale bar 100 µm.

be pustular. The aperture may be located in front or on top of the domatia (Fig. 2.1–2.4).

The venation of the leaflets is usually not raised above the lamina on the adaxial side, with the exception of the midrib. In *A. bullata* it is more or less distinctly sunken, giving the leaflets a bullate appearance. On the abaxial side the major veins may be raised above the lamina or not; again, the midrib is always raised. Intercalating veins are occasionally encountered; they become indistinguishable from the lateral veins in the apical part of the leaflet. Therefore, the spacing of the lateral veins was always measured in the middle part of the leaf on the abaxial side, where they can be distinguished best. The colour of the venation may be the same as that of the lamina to distinctly different, usually more reddish or yellowish, at least on the adaxial side in herbarium material, but colour differences are also reported in the field notes. The colour difference on the abaxial side is usually much less pronounced or completely absent. The tertiary venation is in some species distinctly scalariform, in others reticulate. It may be distinct or indistinct; it is usually lax, but in some species, particularly *A. dictyoneura*, dense (Fig. 2.5).

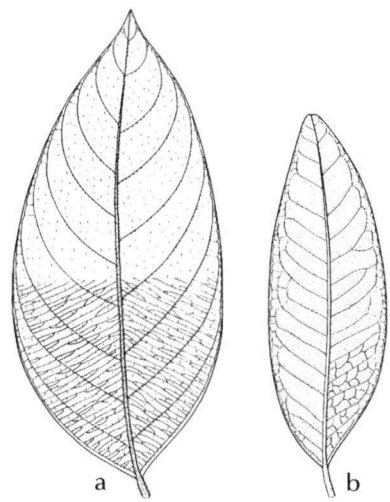


FIGURE 2.5. Venation patterns. (a) Nerves marginally open, veins scalariform (*Arytera lineosquamulata*); (b) nerves marginally looped, veins reticulate (*A. neoebudensis*).

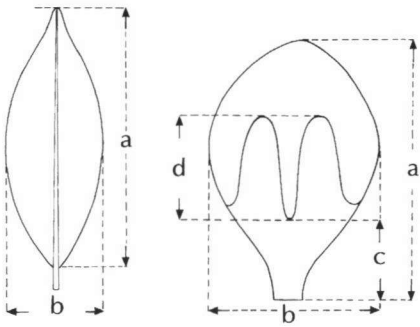


FIGURE 2.6. Measurement schemes of leaflets (left) and petals (right). (a) Total length; (b) total width; (c) length of claw; (d) length of petal scales.

The measurements given for the leaflets are always the greatest length and width (Fig. 2.6).

Inflorescences

The inflorescences of *Arytera* are axillary to pseudoterminal, rarely ramiflorous thyrses: the main axes are racemose, with the flowers arranged in cymose fashion. The inflorescences are mostly branched, usually along the rachis, sometimes at the base, with short to rather long branches.

The cymes are usually dichasial (to monochasial), although cincinnate (*A. densiflora*, *A. dictyoneura*, *A. lautereriana*), pleiochasial (*A. bifoliolata*), and single-flowered ones (*A. microphylla*) also occur. In *A. novaebrittanniae* the cymules are dichasial, but a shift occurs in the position of one of the branches, giving the cymules an irregular appearance.

Bracts and bracteoles

The bracts and bracteoles are usually triangular. Ovate bracts occur in *A. foveolata* and *A. lautereriana*; in *A. densiflora* the bracts and bracteoles are markedly cymbiform. The margin of the bracts and bracteoles is usually entire, but may be dentate in *A. lautereriana*; the abaxial side is usually hairy, the adaxial side glabrous, but in *A. multijuga* hairy.

The bracts and bracteoles are usually subpersistent under the fruits.

Flowers

The flowers in *Arytera* are actinomorphic (sometimes slightly zygomorphic in *A. lineosquamulata*, *A. musca*, and *A. pseudofoveolata*, see below under *petals*, and in *A. multijuga*, see under *calyx*) and usually 5-merous, although 4- or 6-merous examples are occasionally encountered. They are small, diameter up to c. 4 mm. The flowers are seemingly hermaphroditic, but functionally probably unisexual, with female flowers with a well-developed pistil and short indehiscent stamens, and male flowers with a reduced pistil (called pistillode by Adema 1991) and well-developed stamens. Occasionally flowers are found with both well-developed pistils and stamens.

Arytera, like most Sapindaceae, displays the phenomenon of *(duo)dichogamy* (see e.g. Van Welzen 1989 and Adema 1991 for examples). In duodichogamous plants the inflorescence alternates between an initial male phase, followed by a female phase, and finally a male phase again. Flowers in the latter phase usually have both the stamens and the pistil well developed. In dichogamous plants the first or last phase is lacking (see Van Welzen l.c. for a discussion of this phenomenon). Whether *Arytera* is (duo)dichogamous rather than truly dioecious, could not be ascertained with certainty for all species. However, in a number of species male and female flowers were

found in the same inflorescence; thus, dioecy could be excluded as a possibility, at least for these species.

Pedicel — The pedicel is usually hairy, sometimes only slightly so to glabrous in the upper part. An abscission zone can usually be seen at 1/3 to 2/3 from the base.

Calyx — The calyx is usually deeply incised, in some species only dentate. It is early-opening, giving it a cup-like appearance, hence the genus name (Gr. *arytèr* = cup). The calyx teeth are equal, but in *A. multijuga* slightly dimorphic, with the two outer ones slightly smaller than the three inner ones. The calyx is rather coriaceous, rarely with a slightly membranaceous margin on the teeth. The abaxial side is usually hairy, the adaxial side glabrous to hairy.

Petals — There are usually 5 petals, although some of them may be reduced or lacking in *A. lineosquamulata*, *A. musca*, and *A. pseudofoveolata*. In *A. microphylla* the petals are usually completely lacking; if present they are sepal-like. Usually the petals are about as long as or slightly shorter than the calyx. The shape of the petals is rather variable, but in all species they are distinctly to indistinctly clawed. The indument can vary considerably, from almost completely glabrous to densely hairy.

On the adaxial side they are usually provided with scales, which can be free, variably adnate to the margin of the petal, or may be just an enation of the margin. In some species the petal scales may be auricled. The apex of the scales may be broadened or not. In *A. lineosquamulata* the scales are very narrow. The scales are never crested.

Measurements of the petal parts were taken as shown in Fig. 2.6.

Disc — The disc in *Arytera* is annular, without gaps or slits. In *A. chartacea*, *A. collina*, *A. microphylla*, *A. nekorensis*, and *A. neoebudensis* the disc is more or less distinctly five-lobed (Fig. 2.7). It may be glabrous or variably hairy.

Stamens — The number of stamens is usually 8, but can vary between 7 and 10, except in *A. microphylla*, in which the number is always only 5 or 6.

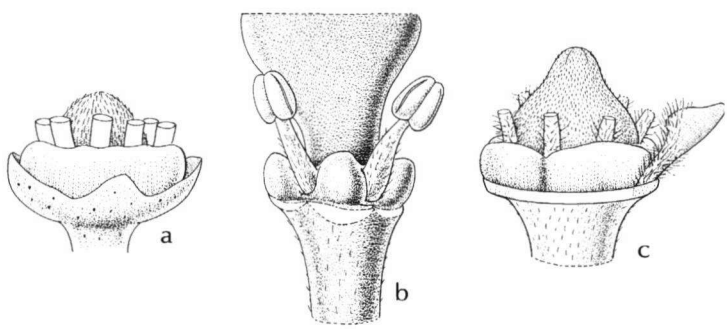


FIGURE 2.7. Disc types. (a) Unlobed disc (*Arytera lepidota*); (b) *microphylla*-type lobed disc, with lobes alternating with stamens (*A. microphylla*); (c) *collina*-type disc, with lobes protruding between petals (*A. neoebudensis*).

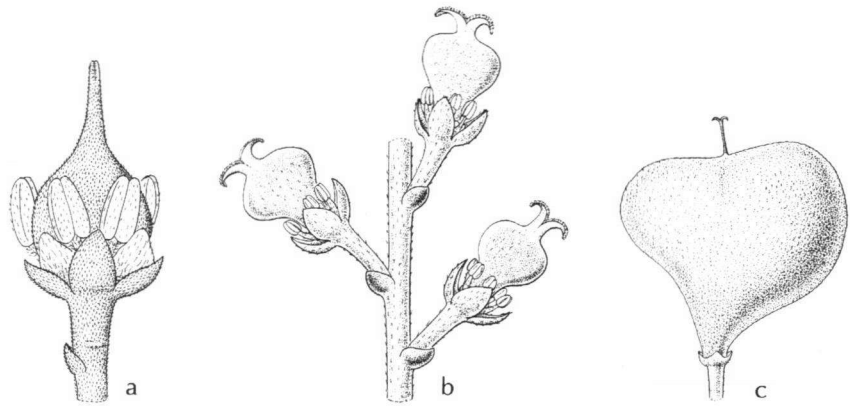


FIGURE 2.8. Stigma types. (a) Unlobed stigma (*Arytera morobeana*); (b) sessile deeply lobed stigma (*A. microphylla*); (c) minutely lobed stigma with distinct style (*A. brackenridgei*).

The filaments are usually filiform, decreasing slightly in diameter towards the anthers, but in *A. neoebudensis* slightly flattened dorsoventrally. They are at least basally hairy.

The anthers are basifixed and open latrorsely with longitudinal slits. They are variable in size and shape. In some species they are rather small (less than 1 mm in length), in others larger (up to 1.7 mm). Their shape is mostly ellipsoidal to ovoidal, rarely almost globose. The anthers are usually straight, but in some Australian and New Guinean species distinctly curved inward. Mostly they are slightly hairy.

In some species the connective protrudes slightly beyond the thecae in a gland-like fashion, although no exudate was ever observed.

Pistil — The ovary is two- or three-locular, indistinctly lobed, mostly sessile, smooth, hairy. In *A. neoebudensis* the ovary appears to be grooved in the lower half.

Each locule contains one ovule.

The style and stigma are distinct, elongating and subpersistent in fruit. In *A. bifoliolata*, *A. dictyoneura*, *A. distylis*, and *A. microphylla* the stigma is almost sessile, deeply lobed, with the lobes distinctly recurving in fruit. In the remaining species the style is distinct. In the Pacific species and in *A. bullata*, *A. lautereriana*, and *A. macrobotrys* the stigma is very small, minutely recurved in fruit. Elsewhere the stigma consists of two or three stigmatic lines descending along the sides of the style and corresponding to the two or three locules of the ovary; in these species the stigma is not, or only minutely, apically lobed, even in fruit (Fig. 2.8).

Fruits

The fruits of *Arytera* are capsules, opening loculicidally, but in *A. bullata*, *A. lautereriana*, and *A. macrobotrys* usually loculifragally. They are variable in shape, usually obcordate, but sometimes obovoid, and always more or less distinctly lobed. In some species the septa between the locules are more or less distinctly developed (i.e. seen from above the central axis seems to increase in thickness as the fruit matures),

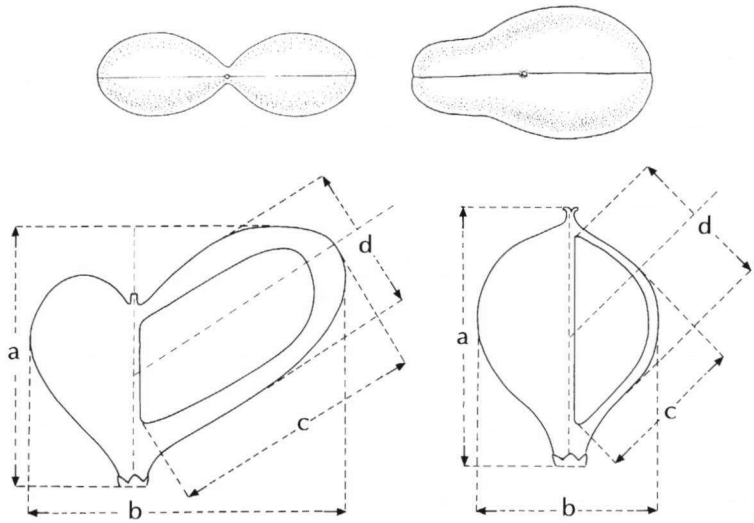


FIGURE 2.9. Schematic top views of fruits with slender and thickened central axis (top), and measurement schemes for fruits (bottom). (a) Total height; (b) total width, (c) valve length; (d) valve height.

in others these septa, although always complete, do not increase in width as the fruit matures, i.e. the central axis remains slender. In the three species mentioned above the septa may broaden so much that the fruits appear almost globose. As often in Sapindaceae, one or more locules of the ovary may not develop fully.

Measurements of the fruits are taken as shown in Fig. 2.9.

Stipe — All species have more or less distinctly stiped fruits. The stipe may be slender or broadly cuneate.

Lobes — The lobes are ellipsoid to obovoid, often somewhat flattened laterally, not winged, but at most slightly keeled along the sutures of the carpels.

Fruit wall — The fruit wall is smooth to rugose or verrucose on the outside, and glabrescent when mature (densely hairy in *A. foveolata*). The inside is usually hairy at least on the sutures between the carpels, but glabrous in *A. bullata*, *A. lautereriana*, and *A. macrobotrys*. The exocarp is thick, coriaceous; the mesocarp thick, coriaceous to woody; the endocarp usually thin, chartaceous.

In *A. bullata*, *A. lautereriana*, and *A. macrobotrys* the endocarp is provided with an extra sclerenchymatic layer which radiates from the attachment of the seeds outwards, leaving the axis and sutures between the carpels free, and reaching up to 1/3 to 2/3 of the height of the lobes. This sclerenchymatic layer detaches from the fruit wall at maturity. The only other genus of Sapindaceae in which an extra layer occurs on the inside of the fruit is *Dimocarpus*, but here the layer is smooth, not notably radiating, and does not detach from the fruit wall at maturity. The two situations therefore do not seem to be homologous.

Seeds

The seeds are orbicular to (ob)ovoid to ellipsoid, often somewhat flattened laterally, shiny dark brown to blackish when dry, and always surrounded by an arilloid (*sensu* Van Welzen 1989).

Arilloid — Two types of arilloid are encountered in *Arytera*: In the Pacific species and in *A. bifoliolata*, *A. dictyoneura*, *A. distylis*, *A. microphylla*, *A. bullata*, *A. lautereriana*, and *A. macrobotrys*, it consists of a single layer, in the latter three species rather spongy and thicker than in the others; in the remaining species there are two layers, a rather thin outer one which is pale yellow and soft, and an inner, thicker one which is chocolate-coloured and rather firm (at least in herbarium material; in the very few live specimens I could observe the inner layer was not distinguishable with a hand lens). Often the arilloid is basally folded on the inside in both types, but particularly in the second one. The arilloid is always open apically, and covers the seed entirely or up to about half-way.

Testa — The testa is always glabrous and thin. It consists of two layers: The exotesta is coriaceous to almost woody, the endotesta more membranaceous. On the outward facing side, the endotesta is provided with a small pocket pointing toward the micropyle into which the radicle of the embryo is inserted. Sometimes pleurograms (fracture lines) emanating from this pocket towards the apex of the seed can be distinguished on the testa.

Hilum — The hilum is orbicular to (transversely) elliptic. A distinction can be made between the true hilum (the scar of the placenta) and the pseudohilum (the hilum plus the scar tissue of the arilloid) (Van Welzen 1989). According to Van der Ham (1977b), a difference between the two types of arilloid is that the two-layered arilloid has a micropylar slit, whereas in the one-layered type, a micropylar cap overlays the micropyle and the region between the micropyle and the placenta. However, this observation could not be confirmed by me.

Measurements of the hilum are always for the pseudohilum.

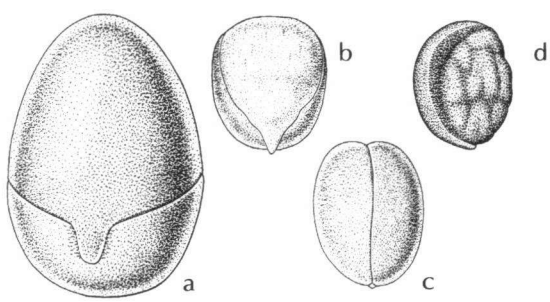


FIGURE 2.10. Embryo types. (a) Cotyledons dorsoventrally above each other, margin of radicle hairy (*Arytera novaebrittanniae*); (b) cotyledons obliquely dorsoventrally above each other (*A. foveolata*); (c) cotyledons laterally beside each other (*A. miniata*); (d) cotyledons with knobby surface (*A. bullata*).

Embryo

Cotyledons — The cotyledons are usually placed dorsoventrally above each other. In many species the cotyledons are positioned more or less distinctly obliquely with respect to each other, in *A. bifoliolata*, *A. bullata*, *A. dictyoneura*, *A. lautereriana*, *A. microphylla*, and *A. miniata* they are laterally beside each other (Fig. 2.10). The cotyledons are always straight. In *A. bullata* and *A. macrobotrys*

their surface is irregular, in the other species it is smooth. The apices of the cotyledons are not elongated, except for *A. macrobotrys*, in which they are slightly elongated.

Radicle—The radicle is always positioned at right angles to the suture between the cotyledons (notorrhizal embryo). It may be small or rather long with respect to the cotyledons, and is always inserted into a pocket in the endotesta (see above). In *A. novae-brittanniae*, and in *A. chartacea*, *A. collina*, *A. nekorensis*, and *A. neoebudensis* the margin of the radicle is (at least basally) hairy; in the remaining species glabrous (Fig. 2.10).

2.2 – LEAF ANATOMICAL CHARACTERS

2.2.1 – **Introduction**

In order to obtain additional characters for the cladistic analysis (and to allow comparison with Van Welzen's [1989] results on *Guioa* and Adema's [1991] on *Cupaniopsis*), a leaf anatomical survey of the genus was undertaken. Radlkofer (1933) gave only cursory notes on the presence of hypoderm, secretory idioblasts, and scale hairs. Solereder (1899) noted many other details, including most of the particulars presented here. He did not mention the presence of transcurrent veins or glandular hairs other than scale hairs. Van Welzen (1989) published a general survey of leaf anatomy in Cupanieae, and included *A. arcuata*.

2.2.2 – **Material**

As far as possible, at least two samples were taken of each species; for the widespread species *A. brackenridgei* and *A. litoralis* more samples were taken, in order to cover their distributional range more completely. Next to material of *Arytera*, samples were prepared for the species of *Mischocarpus* used as the outgroups; for the other outgroup, *Cupaniopsis anacardioides*, samples prepared by Adema for his work on that genus were used (Adema 1991, see there for his methods). A list of the specimens examined is given in Table 2.1.

2.2.3 – **Methods**

Two analytical methods were employed to study the leaf samples: light microscopy and scanning electron microscopy. For both, mature leaflets were taken from herbarium material, rehydrated in boiling water, and temporarily stored in 50% alcohol.

2.2.3.1 – *Light microscopy*

Two types of preparations were made: transverse sections and leaf macerations. For both, samples were taken from the middle part of the stored leaflets; care was taken to include the margin and the midrib with domatia, if present, in the samples.

The transverse sections were prepared on a sledge microtome and mounted without staining. They were observed under both unpolarised and polarised light, the latter in order to observe more clearly the presence of sclerenchyma and crystals.

TABLE 2.1. List of leaf and pollen samples for *Arytera* and species used as outgroups in the cladistic analysis. The collections are kept in L, unless indicated otherwise (abbreviations as in Index Herbariorum). Samples from which only a pollen or a leaf sample was taken are indicated by a superscript P or L, respectively.

Arytera arcuata	*MacKee 25149, 41368*
A. bifoliolata	*Godwin s.n.* (BRI)^{P}, *Hyland 10854* (BRI), *Perzietz 87* (MEL)^{P}, *Sharpe 4171* (CANB)^{P}, *4184* (CANB)^{P}, *L.S. Smith 10638*^{P}, *Webb & Tracey 13247*
A. brackenridgei	*BSIP 5645, 5727*^{P}, *14968*^{P}, *Cabalion 1520, Crosby 32* (K), *Greenwood 478* (K), *A. C. Smith 4562*
A. bullata	*Hartley 12077* (K)
A. chartacea	*MacKee 41134, 42449, Vieillard 2381*^{P}
A. collina	*MacKee 22074, 33563, McMillan 5049*^{P}
A. densiflora	*Jacobs 9509, Ledermann 9555*^{P}, *Schodde 2438*
A. dictyoneura	*W.J.F. McDonald 3439*^{L}
A. distylis	*Jessup 266* (BRI), *Schodde 5594* (K)
A. divaricata	*Brass 19157, Hyland 1353*
A. foveolata	*Lam 7631, 7673, Williams s.n.* (BRI)^{P}
A. gracilipes	*MacKee 20384, 38028, Vieillard 2403* (M)^{P}
A. lautereriana	*Bailey s.n.* (M)^{P}, *Gray 4850* (BRI), *Hyland 4168*^{P}, *4218*^{P}, *McDonald et al. 3183, Pearson s.n.*^{P}, *Schodde 3255*^{P}
A. lepidota	*MacKee 23434, McPherson 5667, 4252*^{P}
A. lineosquamulata	*Carr 14969, Webb & Tracey 13258*
A. litoralis	*d'Alleizette 1458, s.n.*^{P}, *Backer 74, s.n.*^{P}, *Van Beusekom & Phengklai 2929, NGF 15490, PNH (Sulit) 15708, SAN 35056*
A. macrobotrys	*Brass 7464* (A), *Dockrill 467* (BRI)
A. microphylla	*Clemens s.n., Michael 3029* (K)^{P}, *Randall & Young 630*^{P}, *L.S. Smith 4110*^{L}
A. miniata	*Carr 11080*^{L}, *11554*^{L}
A. morobeana	*LAE 74816*
A. multijuga	*Flenley ANU 2846*
A. musca	*Brass 7620, 7743*^{P}, *Pullen 7229*
A. nekorensis	*Veillon 6905*^{L}, *7380* (P)
A. neoebudensis	*Bernardi 13030*^{P}, *13367, MacKee 18973*
A. novaebrittanniae	*NGF 26789, 26856*
A. pauciflora	*Brass 20251, Graham 2488* (BRI), *Sankowsky & Sankowsky 594*^{P}
A. pseudofoveolata	*Brass 5560* (A), *Jones 2551, L.S. Smith 12579*^{L}
Cupaniopsis anacardioides	*Van Balgooy & Byrnes 1304*^{L}, *Boorman s.n.*^{L}, *Brass 19836*^{L}, *Forbes & Kennealy 2453*^{L}, *Hubbard 3715*^{L}, *Lam 7681*^{L}, *Martensz AE 169*^{L}, *Van Royen 4634*^{L}, *Schodde & Hayes 3554*^{L}, *L.S. Smith & Webb 3124*^{L}
Mischocarpus anodontus	*P.I. Forster 3464*^{L}
M. exangulatus	*L.S. Smith 14441*^{L}
M. pentapetalus	*Danser 6076*^{L}
M. pyriformis	*Hoogland 8552*^{L}
M. sundaicus	*Buwalda 3017*^{L}

The cuticular macerations were prepared by incubating the samples overnight in a mixture of equal volumes of glacial acetic acid and 30% hydrogen peroxide and staining the remaining cuticulas with Sudan IV.

Both types of preparations were mounted in glycerin jelly.

2.2.3.2 – *Scanning electron microscopy*

Samples were taken from the middle part of the stored leaflets; as far as possible, the midrib, at least one lateral vein, and a domatium if present were included in the sample. Samples were first critically point dried in a Balzers Critical Point Dryer CPD030, then mounted on stubs and sputter-coated with gold using a Polaron SEM coating unit E5100. They were studied and photographed with a JEOL JSM-35 scanning electron microscope.

2.2.4 – **Description**

In this Section, a general leaf anatomical description is given of *Arytera*. Table 2.2 presents the same and additional data in tabular form, and includes data on the species used as outgroups in the cladistic analysis (see Chapter 3).

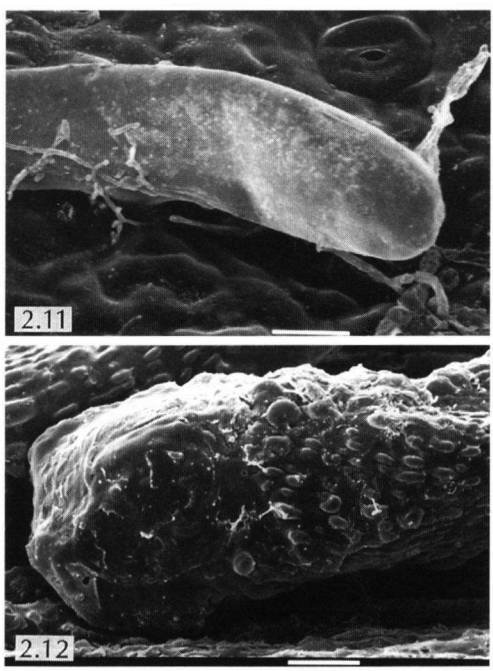


FIGURE 2.11 & 2.12. — 2.11. Smooth, very subbasally attached hair. *Arytera foveolata, Lam 7673*. Scale bar 10 µm. — 2.12. Warty, subbasally attached hair. *Arytera novaebrittanniae, NGF 26789*. Scale bar 5 µm.

In surface view: *Non-glandular hairs* usually unicellular (some pluricellular cells observed in *A. densiflora*), absent to present on both surfaces, usually more abundant over veins and abaxially, usually all approx. the same length; base constricted, then attachment of hairs subbasal (in *A. foveolata* almost up to T-shaped, Fig. 2.11), walls usually thin, striate to warty (Fig. 2.12), rarely smooth, or base not constricted (*A. arcuata, A. brackenridgei, A. gracilipes, A. lepidota*, and *A. multijuga*), then attachment basal, wall usually thick (thin in *A. brackenridgei*), and smooth (striate in *A. multijuga*). *Glandular hairs* usually present, three types distinguished; type A (Fig. 2.13): stalk cells 1–3(–4) small, flat, uniseriate, head large, ovoid, unicellular; type B: small, unicellular, approx. dome-shaped; type C: stalkcells 5–7, small, flat, uniseriate, head small, ovoid, unicellular (in one sample of *A. distylis* only [*Jessup*

TABLE 2.2. Anatomical characters of *Arytera*, *Mischocarpus* species, and *Cupaniopsis anacardioides*.
Legend: ( ) = sometimes present; / = and; ? = unknown; ++ = abundant or very distinct; + = present; – = absent (unless indicated otherwise below).

Column:

1 Species name
2 Distribution of hairs on adaxial surface (e: entire surface; v: over venation)
3 Distribution of hairs on abaxial surface (e: entire surface; v: over venation)
4 Attachment of hairs (b: basally; s: subbasally)
5 Walls of hairs (+: thick; –: thin)
6 Type of glandular hairs on adaxial surface (see Section 2.2.4)
7 Type of glandular hairs on abaxial surface (see Section 2.2.4)
8 Thin areas in adaxial cuticle (usually between loops of undulations of anticlinal walls)
9 Thin areas in abaxial cuticle (usually between loops of undulations of anticlinal walls)
10 Adaxial cuticle striate (v: over venation)
11 Abaxial cuticle striate (v: over venation)
12 Anticlinal walls of adaxial epidermis cells undulating
13 Anticlinal walls of abaxial epidermis cells undulating
14 Thickness of anticlinal walls of adaxial epidermis cells (v: very thick; +: thick; –: thin)
15 Thickness of anticlinal walls of abaxial epidermis cells (v: very thick; +: thick; –: thin)
16 Extra anticlinal divisions present in adaxial epidermis cells
17 Stomata present on adaxial surface (e: over entire surface; v: along venation pattern)
18 Giant stomata present on abaxial surface
19 Size of stomata on adaxial surface (in µm)
20 Size of stomata on abaxial surface (in µm)
21 Size of giant stomata on abaxial surface (in µm)
22 Ridge around stomata on abaxial surface
23 Hypodermis present adaxially (v: over venation)
24 Hypodermis present abaxially (v: over venation)
25 Number of layers in palisade tissue (+ transition layers)
26 Veins embedded in mesophyll
27 Large veins transcurrent to adaxial epidermis
28 Large veins transcurrent to abaxial epidermis
29 Bundle sheath extension sclerified
30 Sclerenchyma present around domatia (a: adaxially of domatia only)
31 Crystals present around sclerenchymatic sheath of midrib
32 Crystals present in phloem
33 Crystals present in pith of midrib
34 Crystals present around domatia
35 Crystals present around major veins
36 Crystals present in adaxial epidermis
37 Crystals present in abaxial epidermis
38 Crystals present in adaxial hypodermis
39 Crystals present in abaxial hypodermis
40 Crystals present in palisade tissue
41 Crystals present in sponge tissue
42 Frequency of secretory idioblasts (f: few; r: regular; m: many)
43 Secretory idioblasts present in hypodermis
44 Secretory idioblasts present in palisade tissue
45 Secretory idioblasts present in sponge tissue
46 Lamina thickness in cross section (between major veins) (in µm)
47 Height × width of midrib in cross section (in µm)

(Table 2.2, continued)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Arytera arcuata	v	–/v	b	+	–	–	+/–	+/–	–	–	–	–	+	+/–	+/–	–	+
A. bifoliolata	–	e	s	–	AB	–	+	+	(v)	+(–)	+	+	+/–	+/–	–(+)	v	+
A. brackenridgei	–/v	–	b	–	–	–	+	+	–	–	+	+	–	–	+/–	–/e	+
A. bullata	–	v	b/s	–	–	A	–	–	–	–	–	–	+(–)	–	–	v	+
A. chartacea	–	e	s	–	B	B	+	+	–	–(+)	+(–)	+	v	+	+	v/e	+
A. collina	v	e	s	–	B	B	–	–	+(–)	+/–	–	–	v	v	+	–	+
A. densiflora	–	e	b/s	–(+)	AB	A	+	+	–	–	+	+	+(–)	–	+	e	+
A. dictyoneura	v	v	b	–	AB	A	+	+	–	–	–	–	+(–)	+(–)	(+)	v	+
A. distylis	–	e	s	–	A/–	AC	+	+	–(+)	+(–)	+(–)	+(–)	+(–)	+/–	(+)	v	+
A. divaricata	–	v(e)	s	–	A	A	+	+	–	–	+	+	–	–	+	v	+
A. foveolata	–	e	s	–	A/–	–	+	+	–	–	+	+	–	–	+	e	+
A. gracilipes	–	–	?	?	–	–	+	+	–	–	+	+(–)	+(–)	+(–)	–(+)	(v)	+
A. lautereriana	–	v/e	b	–	B(A)	AB	+(–)	+	–	+(–)	+(–)	+(–)	+/–	+/–	–	v	+
A. lepidota	v	v	b	+	–	–	–(+)	+/–	–	–	–(+)	+/–	+(–)	+(–)	–	v	+
A. lineosquamulata	–(v)	v	s	–	A	A	+	+	–	–	+	+	–	–	+/–	e	+
A. litoralis	–(v)	e	s	–	A	A	+	+	–	–	+	+	–	–	+	e	+
A. macrobotrys	–	v	b/s	–	A	A	+	+	–	–	+(–)	–	–	–	–	v	+
A. microphylla	–	–/v	s	–	–	A/–	+	+	+	+	+	+	–	–	–	v/e	+
A. miniata	–	v(e)	s	–	–	A	+	+	–	(v)	+	+	+/–	+/–	+	e	+
A. morobeana	(e)	v(e)	s	–	A	A	+	+	–	–	+	+	–	–	–	e	+
A. multijuga	v	v	b	+	A	A	–	–	(v)	+	–	–	+	–	–	–	+
A. musca	–	e	s	–	A	A	–	+(–)	–	–	+(–)	+	v(+)	+(–)	–	e	+
A. nekorensis	–	e	s	–	–(A)	B(A)	+	+	+(–)	+	+(–)	++	v(+)	v	+	–	+
A. neoebudensis	–	v/e	s	–	(B)	(B)	+(–)	+(–)	–	–	+/–	–	+(–)	+(–)	+	v/–	+
A. novaebrittanniae	–	v/e	s	–	–	A	+	+	–	–	+/++	++	–	–	+	v/e	+
A. pauciflora	–	v(e)	s	–	A	AB	+	+	–	–	+	+	–	–	–(+)	v/e	+
A. pseudofoveolata	v	v(e)	s	–	A	A	+	+	–	–	+	+	–	–	+/–	e	+
Cupaniopsis anacardioides	–	v/e	s	+	A	A	–	–	+	+	–	–	+	–	?	v	+
Mischocarpus anodontus	–	v	b	–	–	M	+(–)	–	+(–)	–	+(–)	–	–	–	+	v	+
M. exangulatus	v	e	b	–	M	M	–	+(–)	++	–	–	+(–)	v(+)	+(–)	(+)	v	+
M. pentapetalus	–	v	s	–	M	M	–(+)	–	+	++	–	–	+(–)	–	–	–	+
M. pyriformis	–	e	s	–	M	M	+	+	+(–)	+	+	+	v(+)	–	–	–	+
M. sundaicus	v	e	s	–	(M)	M	++	+	+(–)	+(–)	+	+(–)	v(+)	–	+	–	+

(Table 2.2, continued)

1	19	20	21	22	23	24	25	26	27	28	29	30
Arytera arcuata	–	14–19 × 13–17	33–46 × 17–24	–	+	–	1–2(+1)	+	–	–	?	?
A. bifoliolata	19–26 × 14–21	14–21 × 13–21	24–32 × 13–21	–	+/–	–	1–2(+1)	+	–	–	?	?
A. brackenridgei	–	14–24 × 9–17	33–50 × 19–29	–(+)	+/–	+/–	1–2(+1–2)	+	–	–	?	?
A. bullata	19–24 × 12–14	14–17 × 14–17	29–34 × 17–24	–	–	–	3–5(+1–2)	+/–	+(–)	–	+(adx)	?
A. chartacea	17–22 × 17–19	17–25 × 17–24	36–41 × 14–22	+	+	+	1–2(+1)	+	–	–	?	?
A. collina	–	17–24 × 19–24	31–43 × 14–19	–	+	+	3	+	–	–	?	?
A. densiflora	19–29 × 17–22	19–24 × 14–19	29–41 × 19–25	–	–	–	1–2(+1)	+	–	–	?	?
A. dictyoneura	22–26 × 19–24	17–19 × 14–19	29–41 × 17–26	–	–	–	2(+1)	+	–	–	?	?
A. distylis	17–26 × 17–22	14–20 × 17–22	26–31 × 17–22	–	–	–	1–3(+1)	+	–	–	?	–
A. divaricata	17–24 × 14–19	14–17 × 12–16	26–34 × 14–22	–	–	–	1–3(+1)	+	–	–	?	?
A. foveolata	16–22 × 14–17	12–19 × 12–14	26–34 × 14–26	–	–	–	2	+	–	–	?	?
A. gracilipes	21–24 × 12–17	14–19 × 12–14	36–53 × 19–24	–	–	–	2(+1)	+	–	–	?	?
A. lautereriana	14–22 × 13–19	13–23 × 13–19	26–36 × 16–22	–	–	–	2(+1)	+/–	+	–(+)	+(adx)	?
A. lepidota	13–19 × 10–12	13–17 × 8–12	24–31 × 14–19	–	–	–	1–3	+	–	–	?	?
A. lineosquamulata	18–26 × 15–26	14–17 × 13–17	33–50 × 19–26	–	–	–	2–3	+	–	–	?	?
A. litoralis	14–24 × 14–21	13–19 × 12–17	29–42 × 18–25	–	–	–	(1)2–4	+	–	–	?	?
A. macrobotrys	17–26 × 10–22	12–14 × 12–17	29–41 × 17–24	–	–	–	2–3(+1–2)	+/–	+	–	+/–(adx)	+/–
A. microphylla	17–26 × 14–23	17–24 × 14–19	26–31 × 14–19	–	–	–	2–3	+	–	–	?	?
A. miniata	17–21 × 15–21	15–24 × 15–19	33–38 × 19–26	–	+	+	2–3	+	–	–	?	?
A. morobeana	19–24 × 15–19	14–17 × 14–15	31–41 × 17–19	–	–	–	3	+	–	–	?	?
A. multijuga	–	17–24 × 13–17	26–33 × 17–24	+	–	–	2(+1)	+/–	+	–	–	?
A. musca	19–24 × 15–20	13–21 × 14–17	26–33 × 17–26	–	–	–	3	+	–	–	?	?
A. nekorensis	–	14–24 × 19–26	34–67 × 19–26	+	+	+	2–3	+/–	+/–	+/–	+	?
A. neoebudensis	19–26 × 17–22	17–22 × 14–19	36–53 × 14–29	+	+	+	2	–	+(–)	+/–	+	?
A. novaebrittanniae	13–31 × 14–19	12–14 × 12–14	33–43 × 17–21	–	(v)	(v)	1(+1)	+	–	–	?	a
A. pauciflora	13–25 × 13–22	13–19 × 13–17	28–43 × 11–22	–	–	–	1–2(+1)	+	–	–	?	?
A. pseudofoveolata	14–20 × 12–19	12–19 × 12–17	24–33 × 14–24	–	–	–	3–4	+	–	–	?	?
Cup. anacardioides	–	–	–	–	–	–	1	+/–	+/–	+/–	+	?
Misch. anodontus	19–24 × 13–22	17–19 × 17–18	36–41 × 17–24	–	–	–	1	–	+	+	+	?
M. exangulatus	13–19 × 11–13	16–17 × 13–17	34–46 × 26–31	–	–	–	1	–	+	+	+(adx)	?
M. pentapetalus	–	17–19 × 14–17	29–41 × 20–26	–	–	–	1–2(+1)	–	+	+	+	?
M. pyriformis	–	14–20 × 13–18	29–48 × 12–24	–	–	–	1	–	+	+	+	?
M. sundaicus	–	24–26 × 20–24	34–50 × 24–34	–	–	–	1(+1)	–	+	+	+	?

(Table 2.2, continued)

1	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Arytera arcuata	+	+	+	?	+	(+)	(+)	–	?	+	+	–	–	–	–	168–204	545– 827 × 649– 884
A. bifoliolata	+	+	+/–	?	+	–	–	–	?	(+)	+/–	r	–	+	+/–	98–180	611–1099 × 658–1052
A. brackenridgei	+	+	+/–	?	+	–	–	–	–	+/–	(+)	–fr	–	+/–	+/–	65–185	507– 639 × 592– 883
A. bullata	+	(+)	+	?	+	–	+	?	?	–	+	m	?	+	+	218–240	1128 × 1184
A. chartacea	+	+/–	+/–	?	+	(+)	(+)	–(+)	–	+	+	–	–	–	–	154–209	649– 752 × 752– 780
A. collina	+	+	+	?	+	–	–	–	+/–	+	+	–f	–	+/–	+/–	269–372	987–1786 × 752–1175
A. densiflora	+	+	+	?	+	–	–	?	?	+	+	–f	?	+/–	–	77–154	808–1006 × 827– 978
A. dictyoneura	+	–	–	?	+	–	–	?	?	–	+	–	?	–	–	166–199	489 × 564
A. distylis	+	+	+	+	+/–	–	–	?	?	+	+	–	?	–	–	120–154	508– 583 × 526– 602
A. divaricata	+	+	+/–	?	+	–	–	?	?	+	+	–(f)	?	(+)	–	98–139	592– 724 × 827– 865
A. foveolata	+	+	+	?	+	–	–	?	?	+	+	fr	?	+/–	+/–	110–146	545– 555 × 714– 808
A. gracilipes	+	+/–	+	?	+	–	–	?	?	–	+	frm	?	+	+	122–293	902– 940 × 893– 977
A. lautereriana	+	–	–	?	+	–	+	?	?	–	–	m	?	+	+	180–278	686–1024 × 601–1006
A. lepidota	+	+	+	?	+	(+)	–	?	?	(+)	+/–	f	?	+(–)	+	127–235	752– 958 × 723– 884
A. lineosquamulata	+	+	+	?	+	–	–	?	?	+	+	fr	?	+	–	101–137	667– 742 × 470– 686
A. litoralis	+	+/–	+/–	?	+	–	–	?	?	+/–	+/–	rm	?	+/–	+/–	58–106	498– 902 × 582– 911
A. macrobotrys	+	+/–	–	–	+	–	+/–	?	?	+/–	+/–	m	?	+	+	149–163	611– 733 × 630– 658
A. microphylla	+	+	+	?	+	(+)	(+)	?	?	+	+	f	?	+	–	130–175	338– 526 × 385– 818
A. miniata	+	+	+	?	+	–	–	+	+	+	+	rm	–	+	+/–	77–156	770– 808 × 620– 630
A. morobeana	+	+	+	?	+	–	–	?	?	+	+	f	?	+	–	60– 65	620 × 733
A. multijuga	+	+	+	?	+	–	–	?	?	–	+	f	?	+	–	86–115	1090 × 1664
A. musca	+	+	+/–	?	+	–	–	?	?	+	+	r(f)	?	+	+	98–139	752– 902 × 592– 911
A. nekorensis	+	+	+/–	?	+	–	–	+	–	+	+	m	+	+	+	118–283	695– 771 × 592– 761
A. neoebudensis	+	+	+	?	+	–	–	–	–	+/–	+	f(r)	–	+	+/–	161–213	790– 931 × 799– 837
A. novaebrittanniae	+	+	+	+	+	–	–	–	–	+	+	f	–	+/–	+	84–134	718–1086 × 436– 582
A. pauciflora	+	(+)	+	?	+	–	–	?	?	+	+	r	?	+	+	58–108	555– 696 × 639– 790
A. pseudofoveolata	+	+	+/–	?	+	–	–	?	?	+	+	f	?	+	+/–	86–122	817– 883 × 620– 752
Cup. anacardioides	+	(+)	(+)	?	+	?	?	?	?	+/–	+/–	rm	?	+	+	87–118	–
Misch. anodontus	+	–	+	?	+	(+)	+	?	?	–	–	–	?	–	–	158–197	592 × 592
M. exangulatus	+	–	–	?	+	–	–	?	?	–	–	–	?	–	–	122–139	498 × 564
M. pentapetalus	+	+	+	?	+	–	+	?	?	–	–	fr	?	+	+	84–134	620 × 582
M. pyriformis	+	+	–	?	+	–	+	?	?	–	–	–	?	–	–	86–122	677 × 649
M. sundaicus	+	–	–	?	+	–	+	?	?	–	–	rm	?	–	+	226–240	761 × 564

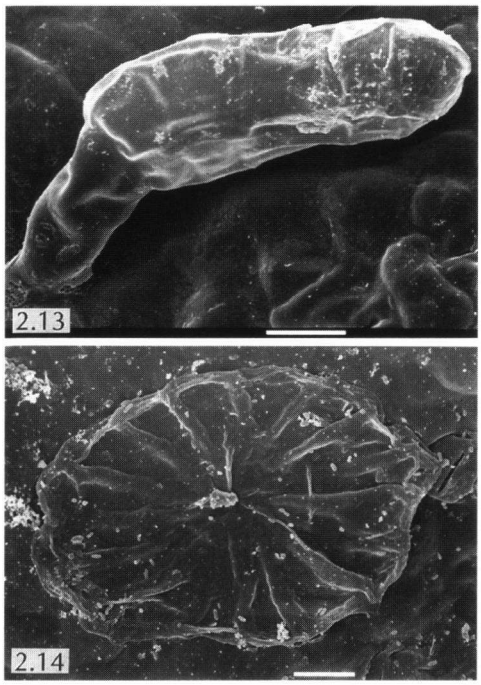


FIGURE 2.13 & 2.14. — 2.13. A-type glandular hair. *Arytera nekorensis, Veillon 7380.* Scale bar 10 μm. — 2.14. Scale hair. *Arytera arcuata, MacKee 25149.* Scale bar 10 μm.

266]). *Glandular scales* (Fig. 2.14) present in *A. arcuata*, *A. brackenridgei*, *A. gracilipes*, and *A. lepidota* only: stalk cell 1, scale cells numerous, radiating. *Cuticle* smooth to striate (usually more so over venation; Fig. 2.15), if anticlinal walls sinuate (Fig. 2.16) (but occasionally also in species with approx. straight anticlinal walls) thin areas in loops of undulations. *Unspecialised epidermal cells* polygonal, anticlinal walls thin to (very) thick, sinuate or straight, often adaxially with extra anticlinal divisions; around hairs, glandular hairs, and stomata in a radiating pattern; over midrib and major veins rectangular, elongate, in rows parallel to venation pattern. *Stomata* predominantly anomocytic, not sunken, often present on both surfaces, more abundant abaxially, sometimes completely absent from adaxial surface or present only over and along venation, rather small, up to approx. 30 μm long, usually somewhat smaller on abaxial side; giant stomata always present at least over or along midrib, up to 50 μm long; outer stomatal rim distinct in *A. chartacea*, *A. nekorensis*, *A. neoebudensis*, and in *A. multijuga* (Fig. 2.17, 2.18).

In transverse section: *Lamina* dorsiventral. *Unspecialised epidermal cells* square to flatly rectangular, to erect over midrib and along margin of leaflet. *Hypodermis* present as a usually uniseriate layer of square, thin-walled cells both ad- and abaxially in *A. chartacea*, *A. collina*, *A. nekorensis*, *A. neoebudensis*, and in *A. miniata*, adaxially only in *A. arcuata* and some samples of *A. bifoliolata* and *A. brackenridgei*, in *A. novae-brittanniae* locally over venation. *Mesophyll:* palisade tissue composed of 1–3(–4) regular, compact to irregular, rather loose layers of usually long, erect, rarely almost isodiametric cells, often with a transition layer of shorter, less compact cells towards spongy tissue; spongy tissue rather compact to rather loose. *Midrib* flat to distinctly raised adaxially, raised abaxially; ground tissue of isodiametric cells, more developed on abaxial side; sclerenchyma sheath present around vascular system; vascular system collateral, with flat to arched adaxial strand and arched abaxial strand, in *A. multijuga* with an additional flat vascular strand in pith; pith consisting of large, round parenchyma cells. *Major veins* sometimes raised abaxially; bundles usually fully embedded in meso-

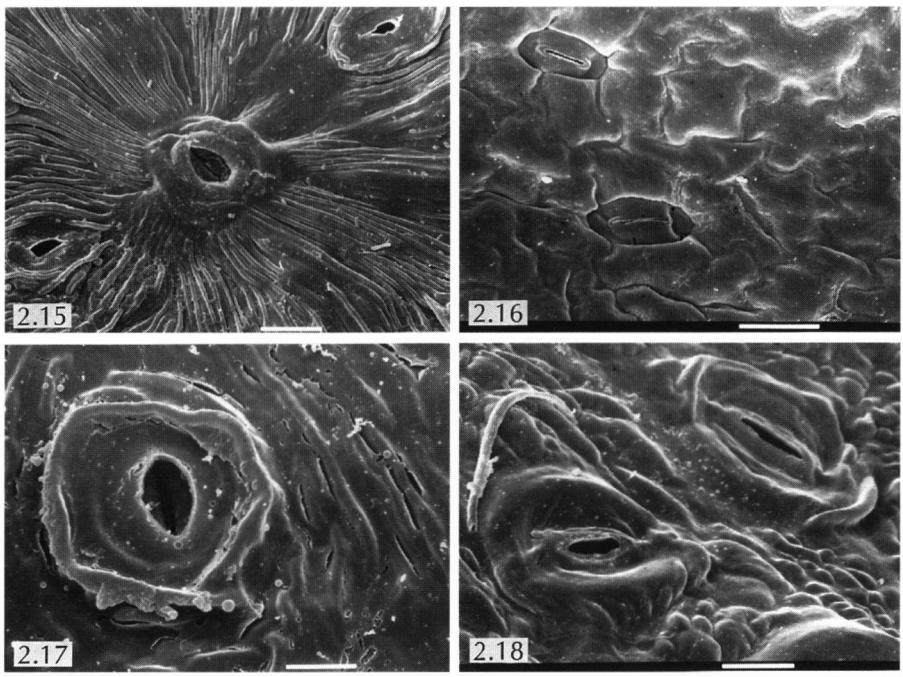


FIGURE 2.15–2.18. — 2.15. Stomata and striate epidermis. *Arytera distylis, Jessup 266.* Scale bar 10 µm. — 2.16. Stomata and sinuate anticlinal walls. *Arytera brackenridgei, BSIP 5645.* Scale bar 10 µm. — 2.17. Stoma with cuticular ridge. *Arytera nekorensis, Veillon 7380.* Scale bar 5 µm. — 2.18. Stoma with cuticular ridge. *Arytera multijuga, Flenley ANU 2846.* Scale bar 5 µm.

phyll, in *A. multijuga* adaxially, in *A. nekorensis* and *A. neoebudensis* often ad- and abaxially transcurrent, in latter two species sclerified; sclerenchyma sheath present around bundles. *Leaf margin* with marginal vein and normal mesophyll. *Rhomboidal crystals* and *druses* always present in varying amounts, at least in ground tissue of midrib, usually also in pith and phloem, around major veins, in palisade, and in spongy tissue, rarely in epidermis or hypodermis cells. *Secretory idioblasts* usually present in palisade and spongy tissue, rarely completely absent, contents unknown.

2.3 – POLLEN MORPHOLOGY

Together with the leaf samples, pollen samples were taken of most species. Other samples had already been prepared by Van der Ham (see Van der Ham, 1977b). This material (see Table 2.1) was studied by Van Bergen (student's report, Rijksherbarium). Because only preliminary results were available at the time of doing the cladistic analysis, these are shortly described here (see also Table 2.3). A full account of the pollen morphology is given elsewhere (Van Bergen et al. 1995).

Only the apertural type was used in the cladistic analysis. Two types were found: (para)syntricolporate and tricolporate. Both types also occur widely in other Sapin-

TABLE 2.3. Pollen morphological characters of *Arytera*, *Mischocarpus* species, and *Cupaniopsis anacardioides*.

Species name	Pollen type[1]	Pollen ornamentation
Arytera arcuata	B	rugulate
A. bifoliolata	A(*)B(*)	rugulate / striate
A. brackenridgei	B	rugulate / reticulate
A. bullata	B(*)	rugulate / psilate
A. chartacea	B	rugulate
A. collina	B	rugulate
A. densiflora	A	rugulate / perforate
A. distylis	B	rugulate
A. divaricata	A	rugulate / perforate
A. foveolata	B(*)	rugulate / reticulate
A. gracilipes	B	rugulate
A. lautereriana	AB	rugulate / reticulate
A. lepidota	B	rugulate
A. lineosquamulata	A	rugulate
A. litoralis	A	rugulate / reticulate
A. macrobotrys	B	rugulate / perforate
A. morobeana	A(*)	rugulate / reticulate
A. multijuga	B(*)	rugulate
A. musca	A(*)	rugulate / reticulate
A. nekorensis	B	rugulate
A. neoebudensis	B	rugulate
A. novaebrittanniae	A(*)	rugulate / perforate
A. pauciflora	B(*)	rugulate / reticulate
A. pseudofoveolata	A	rugulate
Cupaniopsis anacardioides	B	
Mischocarpus anodontus	B	
M. exangulatus	B	
M. pentapetalus	B	
M. pyriformis	B(*)	
M. sundaicus	B	

[1] Asterisks indicate the presence of intermediates.

daceous genera (see Muller & Leenhouts 1976 and Van der Ham 1990 for an explanation of these terms and extensive accounts of the pollen types of Sapindaceae). Intermediate stages between these extremes also occur.

Description

Pollen small to medium sized (polar axis P = 13–20.7 µm, equatorial axis E = 19.7–28.4 µm), oblate to spheroidal (P/E = 0.57–0.96). Polar view triangular to circular, depending on apertural system; equatorial view oblate to circular. *Apertural system* tricolporate (type A) to parasyntricolporate (type B), intermediates present. Apocolpium size A = 1–12 µm (A/E = 0.07–0.32), generally larger in type B pollen. *Ornamentation* rugulate, to rugulate-psilate, rugulate-striate, or rugulate-reticulate.

Chapter 3 — PHYLOGENETIC ANALYSES

3.1 – INTRODUCTION

Despite its present subordinate position, systematics remains a discipline central to biology. In the first place, it provides biologists with *general descriptions* and *names* for the objects of their studies, and with the means to retrieve that information. This cataloguing is the domain of *taxonomy*. The other indispensable type of information systematists provide the biological scientific community with is a scheme of relationships, or phylogenetic information. The unravelling of these relationship schemes is the domain of *systematics* proper.

Traditionally, classifications were based on general similarities and dissimilarities between groups of organisms (i.e. species). The comparisons were made across a large number of traits, and the more similar, the closer the organisms were placed in the classifications. Before the conception of evolutionary theory, the reason that species could be grouped together in what were perceived as natural groupings was sought in a divine ground plan. Evolutionary theory and the genetic laws provided us with a mechanism inherent in nature itself with which to explain the existence of such natural groupings. As a consequence, a conscious effort was made to make classifications 'natural,' i.e. based on hypothesised genealogical relationship schemes of species.

Surprisingly, until the advent of phylogenetic systematics (Hennig 1950, 1966; Wiley 1981) one particular fact regarding the distribution of traits and what that distribution tells us about the genealogical relationships of taxa had been largely ignored by the systematic community. In hindsight, this is all the more curious because no more information was required to recognise it than was already available to Darwin himself. The fact I am referring to is of course that only shared *derived* traits, or synapomorphies, are informative in elucidating relationships. Obviously, some assumptions have to be made, especially regarding the probabilities that the same evolutionary novelty arises independently more than once and that a character returns to its ancestral state. However, these assumptions do not seem unrealistic.

A natural classification is indispensable if comparisons between organisms are to be made meaningfully (Brooks & McLennan 1991; Harvey & Pagel 1991). This is particularly true when comparisons are made in order to answer questions regarding the adaptive value of traits, or other problems related to the evolution of taxa. It is also an important tool in biogeography and coevolution (see e.g. Brooks and McLennan 1991 and references therein) for distinguishing random events such as chance dispersal that have affected the distribution and/or speciation of individual taxa, from causes which have affected entire biotas in a particular region or sets of commensural or parasitic species on a host species.

For these reasons I have applied phylogenetic analysis to arrive at a classification of *Arytera* which reflects as closely as possible the evolutionary relationships between the different species. The results of this analysis are described in this chapter. I have also applied these results to biogeographic questions; this is described in Chapter 4.

3.1.1 – Monophyly of *Arytera*

It is rather difficult to make the monophyly of *Arytera* plausible. Ideally, one would wish for a unique synapomorphy, i.e. a character state that is found in all members of the genus, but not in any of its relatives. One of the best characters for the genus as a whole, the distinctly lobed quality of the fruits, is not clear for the species *A. bullata*, *A. lautereriana*, and *A. macrobotrys*. Moreover, the same character also occurs outside *Arytera*, e.g. in *Guioa* and *Rhysotoechia*. Other characters which are more or less constant within *Arytera*, such as the basally connate calyx, the presence of uncrested scales on the inside of the petals, the annular, uninterrupted (albeit sometimes distinctly lobed) disc, the hairy endocarps, and the presence of an arilloid, are found even more often within other genera of the Cupanieae. Nevertheless, the combination of these six characters makes *Arytera* recognisable on a polythetic set of character states. Thus, pending the analysis, *Arytera* is accepted as monophyletic, with doubts as to the inclusion of the three species mentioned above.

3.2 – MATERIAL AND METHODS

3.2.1 – Coding

All characters were coded in binary or multistate form. Missing data were scored as unknown ('?'), as were characters that could not be scored because they depend on the presence of other characters (e.g. indument of petals in species that have no petals). The characters were chosen in such a way that they could be assumed to be mutually independent, although for some micromorphological characters (e.g. presence or absence of crystals in various parts of the leaflet) this rule could not be applied rigorously. Character states within characters were defined so as to leave as little overlap as possible. In some cases overlap could not be avoided, resulting in polymorphic species. Because there is till now no consensus in the literature on how to code polymorphic species, the effect of different ways of coding them was examined in a theoretical study.

3.2.1.1 – *Coding polymorphism*[1]

Little attention has been paid in the theoretical literature to the problem of how to code polymorphic taxa. A search through recent issues of some systematic journals resulted in a variety of methods, mostly presented in case studies. Usually, no rationale was given as to why a certain coding had been chosen. Most case studies could not be assessed on this point because no mention was made at all of polymorphism in the terminal taxa, nor were polymorphisms coded separately. This may mean that either characters displaying polymorphism were not included in the study, or that polymorphic taxa were assigned the plesiomorphic, apomorphic or unknown coding without further discussion.

1) The research reported in Sections 3.2.1.1 to 3.2.1.1.2 was conducted in collaboration with Prof. Dr. D.J. Kornet. However, any errors and idiosyncrasies in these Sections are mine. A joint paper treating the subject more fully is in preparation.

Different approaches were found:

(a) Each character state coded as present or absent in a separate column (Ranker 1990; Davis & Manos 1991; Hoot 1991);
(b) polymorphism coded as the plesiomorphic character state (Schuh 1984; Donoghue & Doyle 1989; Kluge 1989; Goldblatt et al. 1990; Lavin 1990; Hoot 1991; Platnick et al. 1991a; Rodman 1991a, b; Anderberg 1992; Wen & Stuessy 1993);
(c) polymorphism coded as the apomorphic character state (Schuh 1984; Kron & Judd 1990; Lavin 1990; Anderberg 1992);
(d) polymorphism coded as a separate character state in a multistate (ordered or unordered) transformation series (Green 1986; Kraus 1988; Thiele & Ladiges 1988; Cannatella & De Queiroz 1989; Van Welzen 1989; Cox & Urbatsch 1990; Schot 1991; Van den Bussche 1991; Ladiges et al. 1992; Van Welzen et al. 1992; Adema & Van der Ham 1993; Hill & Jordan 1993; Wen & Stuessy 1993);
(e) polymorphism coded as unknown data (Donoghue & Doyle 1989; Mishler 1990; Ryding & Bremer 1992; Wiegmann et al. 1993);
(f) polymorphism coded as such and analysed using PAUP (other phylogeny reconstruction programs based on the Wagner algorithm cannot handle polymorphism[2] (Loconte & Stevenson 1990, 1991; Sanderson 1991; Hufford & Dickison 1992; Malusa 1992; Hibbet & Vilgalys 1993);
(g) multiple polymorphisms coded as separate states in a reticulate transformation series using PAUP's step matrix option (Wiens & Titus 1991).

All options were found to have been applied to both species and higher-level phylogeny reconstructions, with the exception of option c, for which only examples from higher-level studies were found, and option g, for which only a species-level study was found. A final option, described by Nixon & Davis (1991) is

(h) to split each polymorphic taxon into monomorphic subunits which are then treated as separate terminal taxa in the analysis.

No studies were found in which this option was applied, but the survey was by no means exhaustive. Remarkably, coding methods were not always consistent even within one particular study. In such cases the authors relied on *ad hoc* arguments to choose particular codings in each case. None of the studies mentioned gave fundamental reasons for preferring one particular coding, except that higher-level studies applying coding as plesiomorphy usually argued that this coding reflects the ancestral condition in the terminal taxa.

Apart from case studies, there is very little fundamental literature on this issue. Notable exceptions are Pimentel & Riggins (1987), Nixon & Davis (1991) and Mabee & Humphries (1993). Pimentel & Riggins reject option d but mainly because they insist on ordering transformation series *a priori*; they further reject option b because

2) Zandee's program CAFCA (Zandee 1994), based on component compatibility rather than the Wagner algorithm, can also handle polymorphism through coding each character state in a separate column and indicating which columns together code for a single character. For an example of this application to polymorphism see Roos (1986).

TABLE 3.1. Character step matrix for a character with five states (combinations of alleles observed in the taxa under study) (after Mabee & Humphries 1993). Each gain or loss of an allele is given a cost of one step. Thus going from tuv to rv takes three steps: two losses (of t and u), and one gain (of r).

Allelic combination				
tu	1			
t	2	1		
rv	3	4	3	
s	4	3	2	3
	tuv	tu	t	rv

they correctly argue that the plesiomorphic state cannot be determined *a priori*, accepting as the alternative options e or h.

Nixon & Davis (1991) argue for option h, because in their opinion the other options (particularly coding polymorphism as missing values) lead to wrong measures of cladogram lengths and consistency indices. As I hope to show here, their argument is based on an incorrect assumption about the nature of a step (character state change) on a cladogram. The same assumption is made in all other coding schemes which take the presence of apomorphic character states in polymorphic taxa as phylogenetically informative and has also been made explicitly elsewhere (e.g. Platnick et al. 1991b). Further, this option is weakened by the facts that (1) a polymorphic taxon not supported by a sufficient number of autapomorphies will be spread out over the cladogram (appear as polyphyletic); (2) the monomorphic subunits need not correspond to potential natural entities, such as separated parts of a lineage (which may eventually become separate species) (cf. Kornet 1993b); and (3) each extra case of polymorphism in a taxon will increase the number of monomorphic subunits further. If the second argument can be discounted (e. g. in the case of geographically separate and morphologically distinct infraspecific taxa) I agree that the subunits could be kept separate. Probably in that case the last argument is also weakened, because the different character state distributions can then be expected to covary at least partially.

Mabee & Humphries (1993), studying allozyme data, argue that all combinatory possibilities should be assigned separate states. The cost of transformation from one state to another must then be expressed in a step matrix (Swofford 1993), where the loss or gain of each allele in going from one state to the next is given equal weight (see Table 3.1 for an example). This is similar to coding the presence or absence of each allele in a separate column, but likewise suffers from the drawback that the mere apomorphic presence of alleles is counted as phylogenetically informative.

3.2.1.1.1 – The nature of character state changes

Most solutions for coding polymorphic taxa, except options b and e, have assumed that the presence of an apomorphic state, whether or not in combination with the plesiomorphic state, is phylogenetically informative. Although intuitively appealing, I hope to show here that this is incorrect. Most solutions applied to the problem to date either disregard the presence of the plesiomorphic state in polymorphic taxa and code only the presence or absence of the apomorphic state, or code the polymorphisms as separate (and often intermediate) states in a multi-state transformation series or in an additive binary coding. To be fair, it must be said that many authors working on

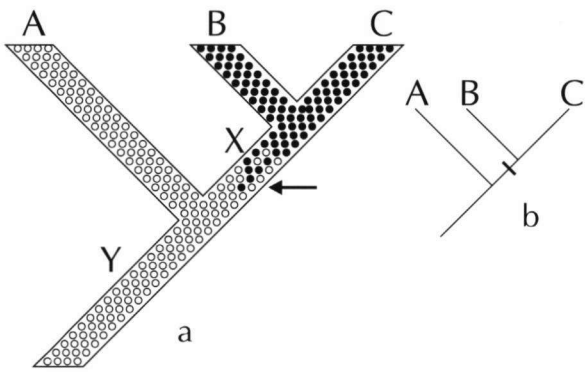


FIGURE 3.1. (a) Schematised genealogy for three extant taxa, A, B, C, and their ancestors X and Y. Each circle represents an individual; open circles are individuals with one state of a binary character, filled circles individuals with the other state. Each horizontal row of circles represents one generation. Parent–offspring relations are not shown. An evolutionary novelty arises in ancestor X (arrow) and goes to fixation, being passed on to its descendant species A and B as a synapomorphy. (b) Cladogram for the genealogy in (a). Redrawn after Kornet (unpublished manuscript).

FIGURE 3.2. If an evolutionary novelty arises in a species, two possibilities exist. (a) The novelty (arrow) does not go to fixation but disappears after some time, the species returning to monotypism for the ancestral state. (b) The evolutionary novelty (lower arrow) goes to fixation, forming an apomorphy. Now it will take a second evolutionary novelty (upper arrow) for this species to (seemingly) return to its ancestral state. Redrawn after Kornet (unpublished manuscript).

higher-level phylogenies have realised that the presence of an apomorphy for some (possibly relatively derived) part of their terminal taxa has no bearing on their analyses and they accordingly code polymorphism with the assumed plesiomorphic state for each taxon.

One of the reasons that most investigators have taken the opposite approach when working on *species*-level phylogenies is that they have considered the problem not in terms of genealogical networks but rather in terms of cladograms. However, cladograms are at best mappings of genealogical networks between individual organisms (Kornet 1993b) and as such they are generalisations (O'Hara 1993). Consequently, some of the details of the underlying structure are lost. It is just these details that matter in this case. Consider Fig. 3.1a. This shows a map of a genealogical network, and is as such an abstraction, but with sufficient detail for our purposes. On this map the different states of individual organisms are depicted for one character. Three species (A, B, C) and two ancestors (X, Y) are shown. Species A has one character state (open circle), species B and C the other character state (filled circle), which has arisen as an evolutionary novelty in ancestor X. Species B and C are said to share a synapomorphy. Figure 3.1b shows the cladogram of extant species A, B, and C.

When I speak of an evolutionary novelty I do not mean to say an apomorphy. An evolutionary novelty (e.g. a new phenotype, or a new allele of a gene) only becomes an apomorphic character state for a species when it goes to fixation (cf. Kornet 1993b),

as is the case here, because as long as the evolutionary novelty is not yet fixed, the character can always return to the fully plesiomorphic state (Fig. 3.2a). Only when it has become fixed has the historical fate of that character state become constrained. In other words, only then will all descendants retain the new character state, and it will take the fixation of a second novelty for the character to return seemingly to the old, 'plesiomorphic' state again (in cladistic parlance, a reversal) (Fig. 3.2b).

Now we have arrived at the heart of the problem. Only historical constraints can help us reconstruct phylogenies (Brooks & Wiley 1988), hence also Hennig's (1950, 1966) emphasis on the uninformative nature of plesiomorphies. On theoretical grounds alone we can reject the notion that the mere presence of a derived character state can be phylogenetically informative. The phylogenetically important moment is its fixation.

3.2.1.1.2 – Coding polymorphic species

As an example, consider Fig. 3.3a. Here, an evolutionary novelty arises in the common ancestor of species A, B, C, D, and E. This character state only reaches fixation in the common ancestor of D and E. In A, the evolutionary novelty has been lost. What if we assume that the apomorphy is the origin of the new state? Then it becomes a synapomorphy for ABCDE, and we have to postulate a reversal in A (Fig. 3.3b). Thus, we assume two (potentially phylogenetically informative) character state changes. However, if we take the fixation of the evolutionary novelty as the apomorphy, it is a synapomorphy for DE, and we only assume only one change (Fig. 3.3c).

From the point of phylogeny reconstruction, what is the difference between these assumptions? Coding the presence of the evolutionary novelty as phylogenetically informative leads to the assumption that BCDE in Fig. 3.3 form a clade, whether we code in two binary columns as in Fig. 3.4a, code the presence of the evolutionary novelty as the apomorphy (Fig. 3.4b), or code the polymorphic state separately in an ordered (Fig. 3.4c2) transformation series. Thus, none of these codings produces a result compatible with the true phylogeny of Fig. 3.3a. Coding the polymorphic state separately in an unordered transformation series also produces incorrect results, in that BC is always seen as either para- or monophyletic, rather than polyphyletic (Fig. 3.4c1). But if we code fixation of the character state as informative (cf. Kornet 1993b), or in other words disregard the occurrence of the evolutionary novelty in the polymorphic taxa, we arrive at a single cladogram fully compatible with the true phylogeny (Fig. 3.4d).

On a cladogram of the genealogy of Fig. 3.3, and including an outgroup, coding as in Fig. 3.4a–c always produces at least one extra step (i.e. a homoplasy), whereas that of Fig. 3.4d does not. This means that we need more evidence for the true phylogeny when we code as in Fig. 3.4a–c, in order to counter the effect of the extra steps, than when we apply the coding of Fig. 3.4d. Of course, this effect could be diminished by downweighting characters in which polymorphism occurs (a course suggested e.g. by Sosef 1992, 1994), but to me that seems rather circuitous if a more direct method is available. Moreover, the errors introduced by the wrong coding will never be completely countered, because the extra steps will always remain present. The other coding methods mentioned previously also have their disadvantages. Coding the polymorphic taxa from Fig. 3.3 as unknown (or as polymorphic in PAUP) results in 11 trees,

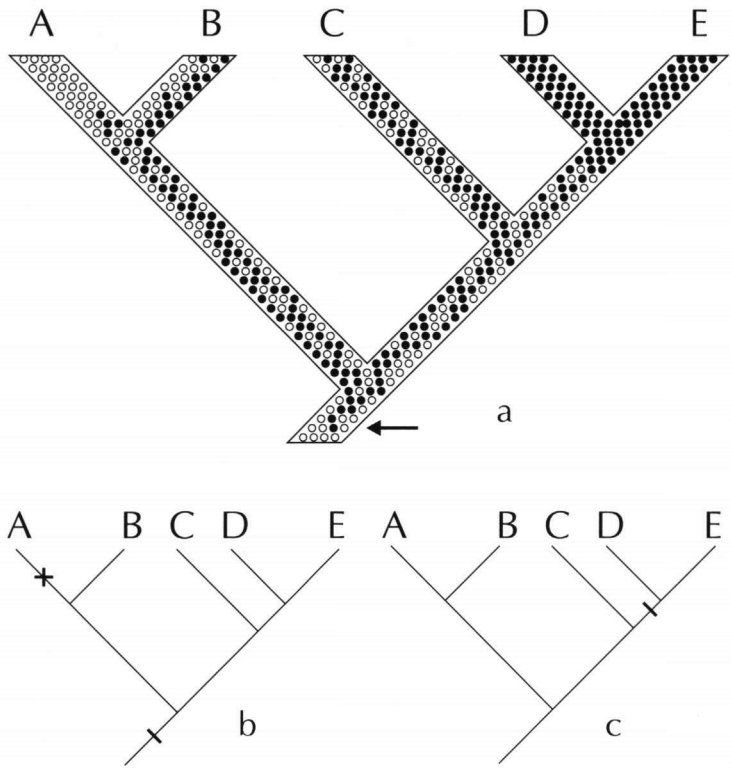


FIGURE 3.3. (a) Schematised genealogy for five extant taxa, A–E. An evolutionary novelty arises in the common ancestor of the clade (arrow), giving rise to polymorphism. The polymorphism persists in species B and C, disappears again in species A, and goes to fixation in the ancestor of species D and E. (b) If the occurrence of the evolutionary novelty is taken as the phylogenetically informative step, the new character state is a synapomorphy for the clade A–E, but a reversal has to be postulated in species A. (c) If fixation of the evolutionary novelty is taken as the phylogenetically informative step, the new character state is a synapomorphy for D and E. Redrawn after Kornet (unpublished manuscript).

of which 10 are spurious because they contain unsupported branches (Fig. 3.4e, g). The eleventh is the same as that resulting from the coding in Fig. 3.4d. Splitting up the polymorphic taxa into monomorphic units (and adding apomorphies for taxa B and C) results in 24 trees (Fig. 3.4f), of which nine are spurious. Out of the remaining 15 trees, two are fully compatible with the true phylogeny, while two more are partly compatible, in that the doubled taxa B and/or C are shown as paraphyletic.

Let us look at the problem from another viewpoint. For the five-taxon problem, there are 105 possible rooted trees. An outgroup was added to these, and for the case of coding as separate morphs, the polymorphic taxa were split into two sister taxa each. Optimising the different coding methods for the character state distribution shown in Fig. 3.3a on these trees gives the results presented in Tables 3.2 and 3.3. As can be

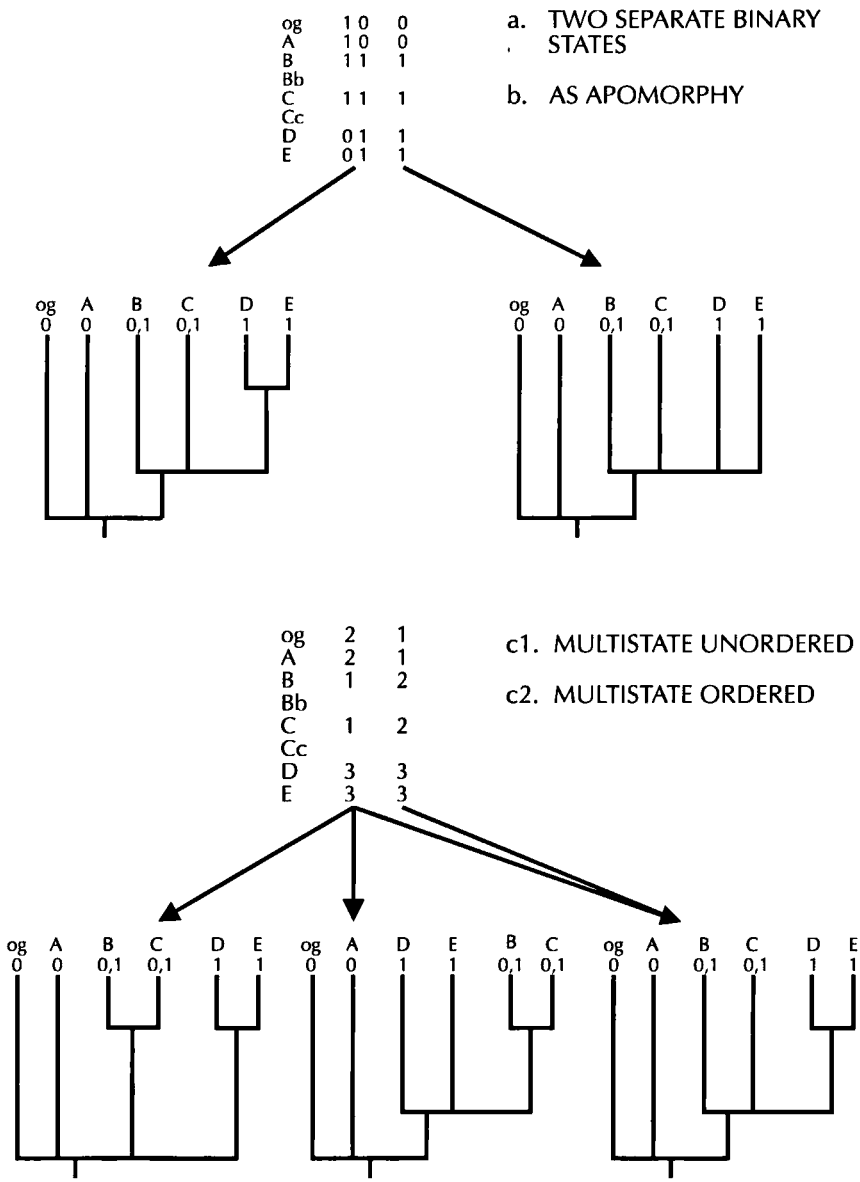
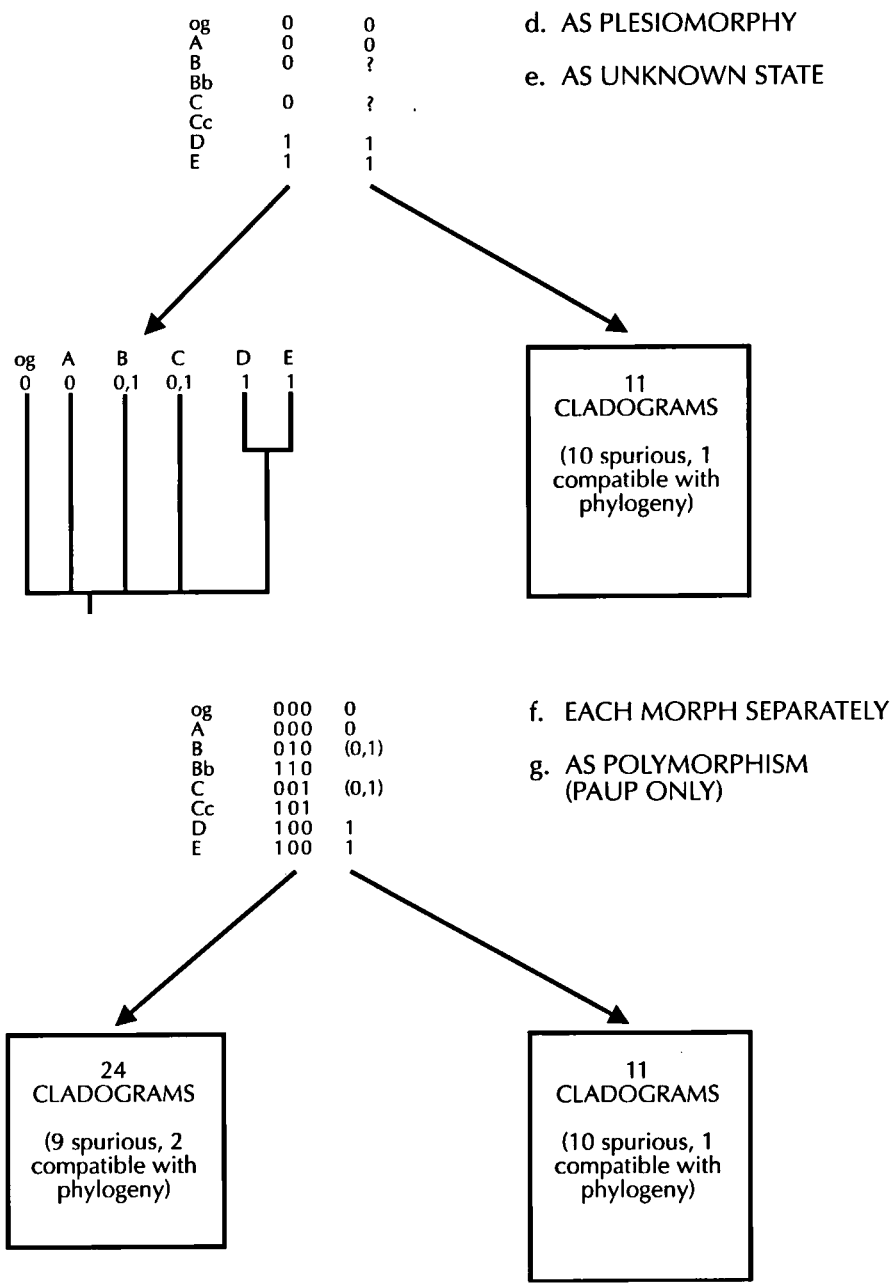


FIGURE 3.4. The effect of different ways of coding the character transformation shown in Fig. 3.3 on the shape of reconstructed cladograms. An outgroup (og) is added; for coding as separate morphs the polymorphic taxa B and C were split and an additional character was added for each polymorphic species to indicate its monophyly. (a) Coding the character in two binary columns; (b) coding the presence of the evolutionary novelty as the apomorphy; (c) coding polymorphism as a separate state in an unordered (c1) or ordered (c2) transformation series; (d) coding polymorphism as the plesiomorphic character state; (e) coding polymorphism as an unknown state; (f) coding each monotypic morph in a polymorphic species as a separate entity; (g) coding polymorphism as such.



(Figure 3.4, continued)

TABLE 3.2. Results of optimising different coding methods shown in Fig. 3.4 onto all 105 possible rooted trees for the five-taxon problem with an outgroup added. Codings: (a) two separate states; (b) as apomorphy; (c1) unordered multistate; (c2) ordered multistate; (d) as plesiomorphy; (e) as unknown, as separate morphs, or as polymorphism (in PAUP, counting as uncertainty; for counting as polymorphism two extra steps are added; steps for the apomorphies of the polymorphic taxa excluded). Tree no. 2 is the true phylogeny.

Tree nr	Number of steps						Tree nr	Number of steps						Tree nr	Number of steps					
	a	b	c1	c2	d	e		a	b	c1	c2	d	e		a	b	c1	c2	d	e
1	4	2	3	4	2	2	36	4	2	3	4	2	2	71	4	2	3	4	2	2
2	3	2	3	3	1	1	37	4	2	3	3	1	1	72	3	2	2	3	1	1
3	4	2	3	4	2	2	38	4	2	3	4	2	2	73	4	2	3	4	2	2
4	4	2	4	4	2	2	39	4	2	4	4	2	2	74	4	2	3	4	2	2
5	4	2	4	4	2	2	40	4	2	4	4	2	2	75	4	2	3	4	2	2
6	4	2	4	4	2	2	41	4	2	4	4	2	2	76	4	2	3	4	2	2
7	4	2	4	4	2	2	42	4	2	4	4	2	2	77	4	2	3	4	2	2
8	4	2	3	4	2	2	43	4	2	4	4	2	2	78	4	2	3	4	2	2
9	4	2	3	4	2	1	44	4	2	4	4	2	2	79	4	2	3	4	2	2
10	3	2	3	3	1	1	45	3	2	3	3	1	1	80	3	2	2	3	1	1
11	4	2	4	4	2	1	46	4	2	4	4	2	2	81	4	2	3	4	2	2
12	4	2	4	4	2	2	47	4	2	4	4	2	2	82	4	2	3	4	2	2
13	4	2	4	4	2	2	48	4	2	4	4	2	2	83	4	2	3	4	2	2
14	4	2	4	4	2	2	49	4	2	4	4	2	2	84	4	2	3	4	2	2
15	4	2	4	4	2	2	50	4	2	4	4	2	2	85	4	2	3	4	2	2
16	4	2	4	4	2	2	51	4	2	4	4	2	2	86	4	2	3	4	2	2
17	4	2	4	4	2	2	52	4	2	3	4	2	1	87	3	1	2	3	2	1
18	3	2	3	3	1	1	53	3	2	3	3	1	1	88	2	1	2	2	1	1
19	4	2	4	4	2	2	54	4	2	3	4	2	1	89	3	1	2	3	2	1
20	4	2	4	4	2	2	55	4	2	4	4	2	2	90	3	1	3	3	2	1
21	4	2	4	4	2	2	56	4	2	4	4	2	2	91	4	1	3	3	2	1
22	4	2	4	4	2	2	57	4	2	4	4	2	2	92	4	2	3	4	2	2
23	4	2	4	4	2	2	58	4	2	4	4	2	2	93	4	2	3	4	2	2
24	4	2	4	4	2	2	59	4	2	4	4	2	2	94	3	1	3	3	2	1
25	4	2	3	4	2	2	60	4	2	3	4	2	2	95	3	1	3	3	2	1
26	3	2	3	3	1	1	61	3	2	3	3	1	1	96	2	1	2	2	1	1
27	4	2	3	4	2	2	62	4	2	3	4	2	2	97	3	1	3	3	2	1
28	4	2	4	4	2	2	63	4	2	4	4	2	2	98	3	1	3	3	2	1
29	4	2	4	4	2	2	64	4	2	4	4	2	2	99	4	2	3	4	2	2
30	4	2	4	4	2	2	65	4	2	4	4	2	2	100	4	2	3	4	2	2
31	4	2	4	4	2	2	66	4	2	4	4	2	2	101	3	1	3	3	2	1
32	4	2	4	4	2	2	67	4	2	4	4	2	2	102	3	1	3	3	2	1
33	4	2	3	4	2	1	68	4	2	3	4	2	1	103	3	1	3	3	2	1
34	3	2	3	3	1	1	69	3	2	3	3	1	1	104	2	1	2	2	1	1
35	4	2	3	4	2	1	70	4	2	3	4	2	1	105	3	1	3	3	2	1

seen, coding in an ordered transformation series and coding as separate states (actually they are the same, the two-column coding being equivalent to the additive binary coding of the ordered transformation series) give the smallest number of most parsimonious trees (MPTs) (nos. 88, 96, 104), while coding as separate morphs, as polymorphism,

TABLE 3.3. Results of optimising the different coding methods shown in Fig. 3.4 onto all 105 possible rooted trees for the five-taxon problem with an outgroup added.

Coding	Number of most parsimonious trees	Length of MPTs
(a) Two columns	3	2
(b) As apomorphy	15	1
(c) Multistate (1) unordered	7	2
(2) ordered	3	2
(d) As plesiomorphy	15	1
(e) As unknown	35	1
(f) Separate morphs	35	1
(g) As polymorphism	35	1 (3)

or as unknown give the highest. This is just another way of expressing the results presented in Fig. 3.4, the MPTs being those trees fully compatible with any one of the trees resulting from the analysis of the single character. For these trees, the separate morphs, polymorphism, and unknown codings perform worst in that they need three extra characters to arrive unambiguously at a *single* tree (not necessarily the true phylogeny), whereas the separate states and ordered transformation series codings need only one. The other codings need two extra characters. As the homoplasy in the polymorphic character increases, the unknown and separate morphs codings perform increasingly better, but the latter has the disadvantage that it needs at least one additional character per polymorphic species. This means that if the character shows homoplasy, an ordered transformation series will need the most additional evidence to arrive at the *true* tree; the coding as plesiomorphy will need the least. The other codings will need an intermediate amount of additional evidence to arrive at the true tree. E.g. for the tree ((B E)(A(C D))), which displays maximum homoplasy for all codings, four extra characters are always needed (ACD + ACD + CD + BE), except for the coding as plesiomorphy which needs only three (ACD + CD + BE).

I have shown above that, at least theoretically, polymorphic taxa should be assigned the plesiomorphic character state. There is a snake in the grass, however, because the character should be polarised by reference to the *local* ancestral state. But the appropriate local ancestral state is only known after the phylogeny has been resolved. Also for characters that have more than two states in the group under analysis it is impossible to determine *a priori* which of two states present in a taxon is the plesiomorphic one. In this I agree with Pimentel & Riggins (1987), who state that "[i]f two or more states occur in a taxon, there is no justification for assigning the plesiomorphic state ..." (p. 207). Therefore the only other codings should be applied that do not treat the mere presence of the apomorphic state as phylogenetically informative: coding as unknown or polymorphic. For multistate characters, the latter should be preferred over the former, because then polymorphic taxa will only be placed in a clade characterised

by the presence of a character state they lack at the cost of an extra step. This can be done in PAUP. However, I do not agree with Swofford (1991, 1993) in the way he counts steps for polymorphic taxa. PAUP counts the presence of the derived state as an extra step. Rather, polymorphic taxa should be seen as ambiguous for the character, because then this presence is not counted. For analyses with other computer programs based on the Wagner algorithm, I recommend coding the polymorphic taxa as unknown data for that character. This of course does not mean that the character state in these taxa is actually not known. Rather, it should be taken to denote our ignorance as to which of the states is the plesiomorphic one, pending the analysis. Obviously, there are problems concerning missing entries and the way they are treated in phylogeny reconstruction algorithms and I can only agree with Platnick et al. (1991b) that all resulting trees should be checked carefully "... to ensure that no nodes are supported only by mutually exclusive optimisations of the same character(s)" (p. 341). Moreover, all trees resulting from the analysis should also be checked to ensure that no extra steps should be added due to incongruence between the polymorphism and the locally plesiomorphic character state. The rationale would then be that the disappearance of the previously fixed ancestral state is also a form of historical constraint. Eventually one of the remaining states is expected to go to fixation, leading to an apomorphy for the now polymorphic species, but it cannot be predicted which state that will be. Thus, strictly speaking, it might be more correct to take the complete disappearance of the once fixed ancestral state as the crucial change, rather than the fixation of the new state, but the full implications of such a change in methodology will not be worked out here. On the other hand, counting such a step when appropriate may provide an argument for discarding some trees if more than one tree results from the analysis.

3.2.2 – Analytical protocol (Hennig86, NONA, PAUP)

Several computer algorithms were applied to reconstruct cladograms. For the data set with polymorphism coded as such, PAUP 3.1.1 (Swofford 1993) had to be used, because it is the only program that can handle such codings. The data set with polymorphism coded as unknown was analysed both with PAUP and with Hennig86 (Farris 1988) in conjunction with NONA 1.0 (Goloboff 1993b).

As the number of possible trees for 33 taxa is staggering, no exhaustive search for most parsimonious trees was attempted. Instead, heuristic search strategies were employed. For PAUP, these involved building starting trees with several strategies (simple and random with up to 20 replicates), followed by branch swapping using the tree bisection–reconnection algorithm. For Hennig86, the option mh* (multiple runs of the data matrix with the taxa added in different order) was employed to obtain starting trees, followed by bb* (branch swapping). The analyses yielded similar results, but the command mh* in Hennig86 was found to be inadequate in analysing this data set: using the combination mh* + bb* gave fewer trees than PAUP. This is due to the fact that the algorithms employed in the various computer programs to construct initial trees are sensitive to the order in which taxa are added (hence the use of many random addition sequences in PAUP). Because the number of replicates in mh* is not specified in the documentation (but is certainly rather low), the program NONA version 1.0 was

used to do a more extensive search for a good set of starting trees to submit to Hennig-86's branch swapper, using the command mu*50 (50 replicates, the maximum possible). The combination mu*50 from NONA + bb* from Hennig86 again gave all trees already obtained from the PAUP runs. However, there is no guarantee that no other trees of equal or shorter length exist.

3.2.3 – **Choosing among equally parsimonious trees**

3.2.3.1 – *Successive weighting*

It is sometimes recommended (e.g. Carpenter 1988) to perform successive weighting (Farris 1969) in order to select among a set of equally parsimonious trees. The rationale behind this procedure is that characters that can be fitted perfectly on at least some most parsimonious trees for the unweighted data set (MPTs) should be given higher weight in the final analysis than characters that fit less well on any MPT. Usually the rescaled consistency index, rc (the product of the retention index, ri, and the consistency index, ci), for the best-fitting reconstruction is taken as a measure of the quality of each character, although the use of the consistency or retention index has also been suggested for this purpose. The weighting procedure is to be iterated till the rc values (and thus the weight factors) for the characters change no longer and a stable solution is attained. One of the properties of this method, however, is that often the result is not a subset of the initial set of MPTs, but rather a different set of trees which are longer than the MPTs when measured against the unweighted data set.

3.2.3.2 – *Non-successive weighting*

A second attempt at selecting among the trees from the initial analysis again employed weighting, but from a different perspective. Suppose a data set yields two equally parsimonious trees differing only in the number of steps for two binary characters, A and B. Let for tree 1 the number of steps for A and B be 1 and 8, respectively, and for tree 2, A = 2 and B = 7. Now in a sense tree 2 is 'worse' than tree 1 in that it sacrifices a perfect synapomorphy for character A in order to gain a step in the very homoplastic (and thus possibly less 'stable') character B. A simple way of choosing among trees 1 and 2 is to weight the characters according to some measure of the goodness of fit, such as ci, ri, or rc. So far the argumentation is the same as that for successive weighting. However, rather than recalculating trees using the weighted data matrix, the lengths of the original trees are recalculated. Trees which accommodate the most better-fitting characters will now be shortest (such as tree 1 in the above example). A very crude method employing this rationale is the optimal character compatibility index (OCCI; Rodrigo 1992), which simply calculates the proportion of characters with perfect fit (ci = 1) for each tree. However, an undesirable property of ci and rc in this context is that they both express amount of homoplasy as proportional to the minimum numbers of steps, rather than giving an absolute measure. Thus when the number of extra steps is the same, homoplasy in binary characters is always regarded as worse than homoplasy in multistate characters.

3.2.3.3 – *A new weighting method for characters and trees*[3]

The retention index, ri, does not have the drawback that binary characters are favoured over multistate characters because it only regards the number of *extra* steps needed to accommodate a character on a tree:

$$ri = (G_i - S_i) / (G_i - m_i),$$

where

G_i = maximum number of steps for character i on any tree,
S_i = observed number of steps for character i, and
m_i = minimum number of steps for character i on any tree.

Substituting $G_i = m_i + ES_{i,max}$ and $S_i = m_i + ES_i$:

$$ri = [(m_i + ES_{i,max}) - (m_i + ES_i)] / [(m_i + ES_{i,max}) - m_i] = (ES_{i,max} - ES_i) / ES_{i,max},$$

where

$ES_{i,max}$ = maximum number of extra steps for character i (i.e. on an unresolved bush), and
ES_i = observed number of extra steps for character i.

The rationale behind ri is that each extra step decreases the confidence placed in a character in proportion to the maximum number of extra steps possible for the character. For any character with perfect fit on the tree, ri will assume a value of 1, while for any character with the worst possible fit (each state change is an autapomorphy) ri = 0. $W = \Sigma ri$ will be highest for those trees that have their homoplasy concentrated in the fewest characters. These trees may then be thought of as fitting the data set better than others in some sense. Dividing W by the number of characters gives the average retention index for a tree on a given data set. This is different from the ensemble ri for the tree, which is calculated as $(\Sigma ES_{i,max} - \Sigma ES_i) / \Sigma ES_{i,max}$.

One effect of this measure is that *singlet* characters, i.e. characters for which $ES_{i,max} = 1$ (i.e. characters that can be synapomorphic, or symplesiomorphic, for only two taxa), are favoured over characters for which $ES_{i,max}$ can assume higher values (*multiplet* characters), independent of the number of states in those characters (Table 3.4). Whether this is a desirable property remains subject to further investigation. Just as with parsimony analysis using implied weights, described in the next Section, it is not yet a proven fact that trees with the highest W will always be in the set of MPTs. Because there is no computer implementation of this weighting method yet, this could not be investigated further. However, W (and average ri) will discriminate within sets of equally parsimonious trees.

3) The research reported in Sections 3.2.3.3 and 3.2.3.4 was conducted in collaboration with Dr. M. Zandee. However, any errors and idiosyncrasies in these Sections are mine. A joint paper treating the subject more fully has been submitted to Cladistics.

TABLE 3.4. Examples of singlet and multiplet characters, both binary and multistate. Multistate characters are assumed to be unordered.

Singlet characters ($ES_{max} = 1$)		Doublet characters ($ES_{max} = 2$)		Quadruplet characters ($ES_{max} = 4$)	
Binary	Multistate	Binary	Multistate	Binary	Multistate
0 0	0 0	0 0	0 0 0	0 1	0 0
0 0	0 1	0 0	0 1 0	0 1	0 0
1 0	0 1	0 0	0 1 0	0 1	0 1
1 0	0 2	1 0	1 1 1	0 1	0 1
1 0	0 3	1 0	1 1 1	0 1	0 2
1 0	0 4	1 0	1 1 2	1 0	1 2
1 0	0 5	1 0	1 1 2	1 0	1 3
1 0	0 6	1 0	1 2 3	1 0	1 3
1 0	1 7	1 1	1 2 4	1 0	1 4
1 1	1 8	1 1	1 3 5	1 0	1 4
1 1	2 9	1 1	2 3 6	1 0	2 5

3.2.3.4 – *Parsimony analysis using implied weights*

A similar method of weighting was proposed by Goloboff (1993a). He employed the weight factor

$$f_i = 1/(ES_i + 1),$$

which differs from ri in being a concave, rather than a linear function, and thus is more in accordance with the recommendations of Farris (1969). In order to control the concavity of the function, he added a concavity index K:

$$f_i = K/(ES_i + K) \qquad (K > 0).$$

f_i is called the fitness of character i. For higher values of K, f becomes less steep, so homoplasious characters are weighted against less strongly. Goloboff (1993b) implemented this measure in his program Pee-Wee (Parsimony analysis using Implied Weights), which constructs trees by maximising $F = \Sigma f_i$ (the fitness of the tree) rather than minimising Σo_i (where o_i = the total number of steps observed for character i) as is done in regular parsimony analysis. He thus accomplishes weighting characters according to their fit on the tree during tree construction. The tree(s) selected are those which accommodate the maximum number of best-fitting characters. Goloboff assumes these trees are self-consistent, by which he means that if characters are weighted according to the weights implied by the tree, the analysis will result in the same tree.

Unfortunately, Goloboff did not investigate the behaviour of F before publishing. He only worried about the optimal value of K for analysing various data sets. Together with Zandee (see Turner & Zandee, in press) I carried out such an investigation. For a matrix without homoplasy on the MPTs, the value of F is equal to the number of characters n, because for a perfect character $f_i = 1$, regardless of the value of K. All

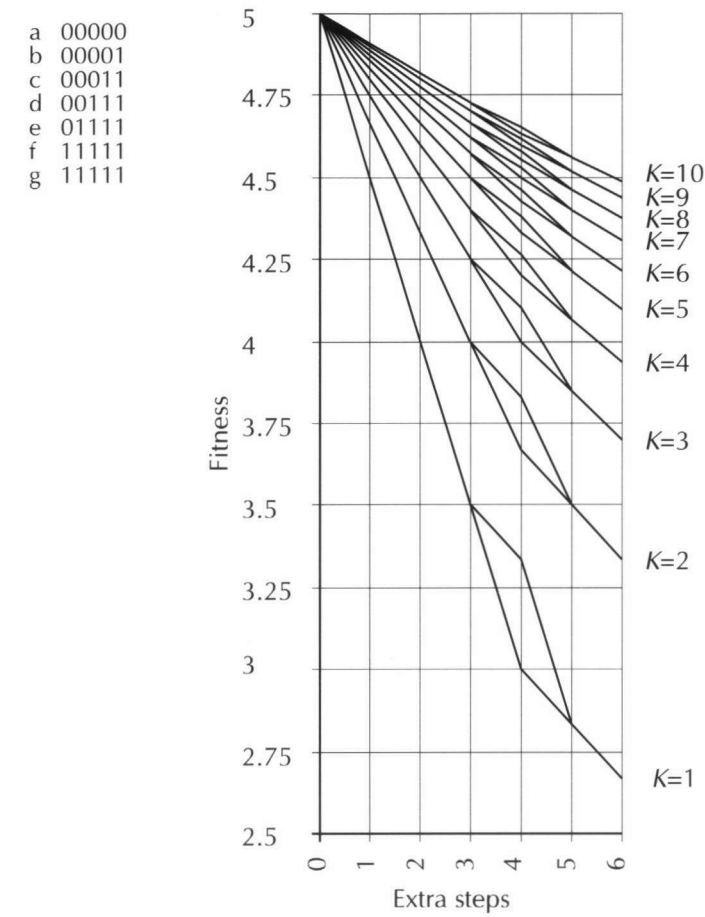


FIGURE 3.5. Plots of the different fitness values F of all possible trees for seven taxa at different values of K for a data set with no homoplasy. Note that F for the MPT (no extra steps) is equal to the number of characters (5) at all values of K. Note also the hysteresis for longer trees.

trees with one or more extra steps will have a value of F which is lower than that for the MPTs (Fig. 3.5). This figure also shows that for some sets of equally parsimonious (but suboptimal) trees, F can take on different values at the same value of K. As K is increased, the difference in fitness between trees becomes smaller, until at $K \rightarrow \infty$ F for all trees approaches n.

When homoplasy is introduced into the data set, the maximum F value decreases below n, and becomes dependent on the value of K (Fig. 3.6). For increasingly worse data sets the maximum F value may no longer be displayed by some MPTs, but can shift to longer trees (Fig. 3.7). Also, the particular subset of trees (MPTs or otherwise) with maximum F is dependent on the value of K. There seems to be no particular value of K above which the set of fittest trees is guaranteed to change no longer.

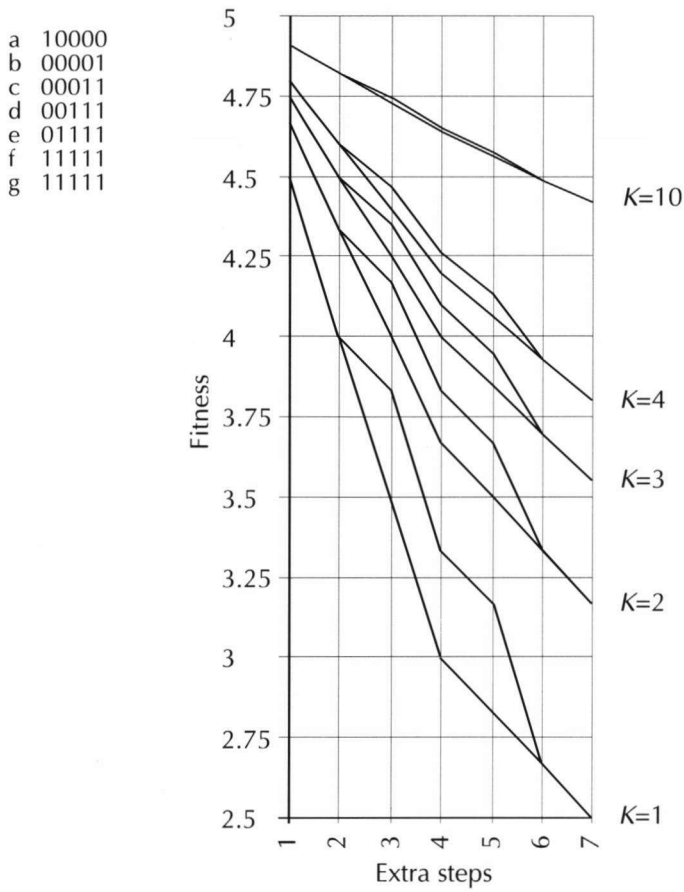


FIGURE 3.6. Plots of the different fitness values F of all possible trees for seven taxa at different values of K for a data set with a single homoplasy. The maximum F value is now smaller than the number of characters. Note that the hysteresis area is wider than in Fig. 3.5.

Because of this erratic dependence on K, the results from Pee-Wee should be interpreted with great caution. As different values of K correspond to different weighting schemes, not all values are expected to result in the same trees. Thus, F in general becomes useless as a measure of tree fitness *sensu* Goloboff (1993a) (unless a particular value of K can be assigned to each data set). In other words, only if a particular weighting scheme can be chosen on biological or theoretical grounds, can the resulting set of trees be preferred over any other trees. The results of this study also warn against applying other measures of the fitness of trees without first investigating their properties thoroughly. This goes also for the weight function W developed in the previous Section. Nevertheless, the concept of maximising the number of characters with minimum numbers of *extra* steps, as is done in Pee-Wee and with W, rather than maximising

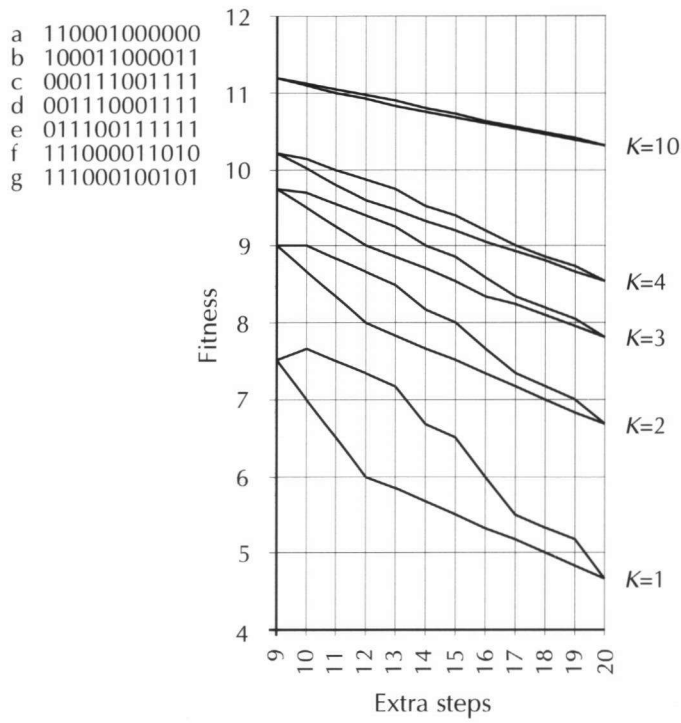


FIGURE 3.7. Plots of the different fitness values F of all possible trees for seven taxa at different values of K for a data set with much homoplasy. Note that the hysteresis area extends up to trees one step longer than the MPTs. Note also that for some non-MPTs the F value is higher than for MPTs, at least at $K = 1$.

the number of characters with minimum total number of steps as in the weighting procedures described in Sections 3.2.3.1 and 3.2.3.2, remains promising because such measures do not depend on the number of states per character. This brings us closer to a theoretically ideal fitness measure for trees resulting from a particular data set. Average ri (W/n) is independent of the number of characters also, but like most measures of tree quality decreases with increasing number of taxa and characters per taxon because as these numbers increase, so will the probability that any one character will display homoplasy. Correcting for this bias involves estimating the probability distribution of number of homoplastic (extra) steps per character (state) per taxon (or node). For a general measure of data set quality (quality in the sense of goodness of fit of the MPTs), this requires that the rate of phylogenetically informative character state change is a constant. This is an assumption which probably cannot be maintained. At best, the more relaxed assumption can be upheld that the rate of change is constant within the lifetime of a monophyletic group. This could lead to a measure for comparing different data sets for the same set of taxa. A more easily attained goal seems to be an ideal fitness measure for different trees on a single data set. Such a measure should have the following properties:

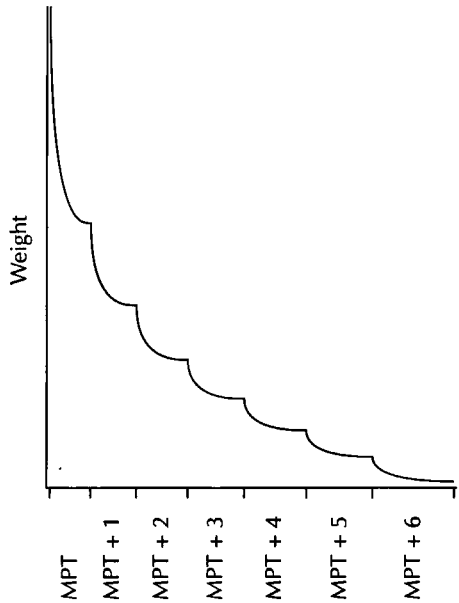


FIGURE 3.8. Plot of an ideal weight measure as a function of tree length. Trees within each length category are ordered according to decreasing values of the weight measure.

(1) It should be inversely proportional to the number of extra steps in each character and to the total number of extra steps, in order to select against trees that are not in the set of MPTs;
(2) it should be proportional to the difference in degree of homoplasy among characters on a single tree, i.e. favour those trees that have most of their homoplasies concentrated in a few very bad characters, in order to discriminate among trees of equal length.

The shape of such an ideal weight function is shown in Fig. 3.8.

3.2.3.5 – *The Redundancy Quotient*

Yet another measure for distinguishing among sets of (equally parsimonious) trees is Zandee & Geesink's (1992) Redundancy Quotient, RQ. This measure is based on the ideas of Brooks & Wiley (1988) regarding the concept of information content of phylogenetic characters.

$$RQ = 1 - H_S / H_{max},$$

where

$$H_{max} = \mathrm{ld} NS,\ H_S = -\Sigma p \mathrm{ld} p \qquad (\Sigma p = 1).$$

N is the number of nodes in a completely resolved tree and S is the maximum number of steps. p is the normalised probability that a character state change will be observed on a particular node. H_{max} is a measure of the information capacity of the tree. H_S is the entropy of the information on the tree. H_S and H_{max} are both entropies, and thus RQ is a measure of the amount of historical (evolutionary) constraint in a cladogram. The tree with the highest RQ is seen as the evolutionarily most plausible explanation of the data.

The formula with which RQ is calculated is a rather complex function dependent on the shape of the tree and on the distribution of character state changes on the tree. It is thus dependent on how the character state changes are optimised on the tree. RQ is calculated by checking for each node how many nodes (both terminal and non-terminal)

are derived from it, and how many steps support it. The value of a node increases as the number of nodes above it increases, and as the number of character state changes supporting it increases. The value of a node is decreased if the node is not supported by character state changes at all, or if it is a polytomy. Its value is also decreased by any empty nodes below it. A correction is finally carried out for the probability that a character changes states at all at any node.

The result of these calculations is that RQ differentiates between trees by selecting those trees that have more character state changes concentrated towards the root (i.e. for which the characters show maximum historical constraint), rather than in the terminal branches.

One of the properties of RQ is that it may be maximal for cladograms that are not in the set of MPTs. However, this only occurs if the MPTs are not fully resolved. The reason is that the penalty for empty branches or polytomies is higher than the penalty for an extra step supporting that branch or resolving the polytomy.

Because the computation of RQ involves a lot of juggling around with logarithms and frequencies in order to weight the support each character state change provides for each tree, the biological significance of this measure is hard to fathom. Different settings of the various parameters may result in different choices. Nevertheless, Zandee & Geesink (1992) assert that "[t]he difference between H_S and H_{max} is a measure of the difference between the character states as they appear on the cladogram and the character states [as] if they were randomly distributed on the cladogram. Or it is a measure of the difference of maximizing homology statements and maximizing homoplasy statements" (p. 3).

3.3 – DATA

3.3.1 – **Outgroups**

To find the proper outgroup for *Arytera*, initially an attempt was made to construct a phylogeny for all genera of Sapindaceae. Characters were obtained from the literature (mainly Radlkofer 1933), and from unpublished notes by Leenhouts (Rijksherbarium, Leiden). Unfortunately, the number of characters that could be collected in this way proved insufficient to arrive at a resolved cladogram. A second attempt was made with the same data, but this time only including the genera of the Cupanieae. This attempt also failed miserably. I therefore had to rely on Muller & Leenhouts' (1976) hypothesis regarding relationships among the genera of Sapindaceae for my choice of outgroups.

As the first outgroup, the genus *Mischocarpus* was selected. Van der Ham (1977a) divided the genus into five informal groups; therefore a representative from each group was selected. From the non-monotypic groups, the presumedly most 'primitive' member (according to Van der Ham) was chosen. The following five species were included: *Mischocarpus sundaicus*, *M. pentapetalus*, *M. pyriformis*, *M. anodontus*, and *M. exangulatus*. As the second outgroup, the genus *Cupaniopsis* was selected. A phylogeny for this genus has been given by Adema (1991); thus, the most basal species are known. However, because the character states in most of the basal taxa are rather poorly known (mostly from one or two specimens), it was decided to select the thoroughly investigated

species *Cupaniopsis anacardioides* as representative. Theoretically it would have been better to reconstruct the ancestral condition for each character and use these states for the second outgroup, but since the basal species are relatively poorly known anyway, in this case this option would hardly have improved the coding.

3.3.2 – Characters

In order to arrive at a phylogeny for *Arytera*, a total of 98 characters was scored as far as possible for each taxon. These characters were taken from macromorphology (61 characters; see Section 2.1), leaf anatomy (36 characters; see Section 2.2), and pollen morphology (see Section 2.3; only the data for the general pollen type were available at the time of this investigation, provided by Van Bergen [Rijksherbarium, Leiden]). Eleven of the macromorphological characters selected initially were strictly quantitative but could not be classified unambiguously into discrete states as recommended by Pimentel & Riggins (1987). Moreover, some of these could not be assumed to be independent of each other (e. g. minimum and maximum lengths / widths of organs). Therefore they were left out of the analysis. The data matrix for the analyses is shown in Table 3.5 with polymorphism coded as such. All characters were run unordered throughout. The characters and their states used are given in Table 3.6. The very incompletely known *Arytera brachyphylla* (only known from a fruiting specimen, no data available on leaf anatomy or pollen morphology) was excluded from the analysis.

Some of the character codings need justification. Also, not all the codings shown in Tables 3.5 and 3.6 are immediately clear when compared with the descriptions or the synoptical key in Chapter 5. This is because the descriptions and keys are intended for use as identification tools rather than as lists of phylogenetic characters and their states. Obviously, phylogenetic characters are often well suited for identification, and then the descriptions and key characters will match the phylogenetic characters well. In other cases, the distinctions made in the keys are too fine to be of use in the phylogenetic analyses and the different states distinguished will have to be regrouped in order to have maximum phylogenetic information. These cases are discussed below.

Character 1 (number of jugae in the leaves) does not seem to have mutually exclusive states. The number of jugae as such is quite variable even within species. This is probably due to environmental effects, whereby in some cases the maximum number of jugae, which is more constant, is not attained. I have tried various ways of coding this character in more detail, but the only almost constant gap seems to be the one between the states applied here. Character 2 shows a similar situation. Opposite leaflets occur in almost all species, sometimes combined with subopposite leaflets. Alternate leaflets are found in species which usually also display opposite and subopposite leaflets. Only rarely (in *A. bullata*, *A. macrobotrys*, and *A. multijuga*) are opposite leaflets absent. These three species are also known from relatively few collections, so their full variability for this character may not have been observed yet. Thus the different character states seem to be the extent to which the leaflets depart from being opposite. Characters 17, 20, and 22 have a situation similar to that in characters 1 and 2, and will not be discussed further here.

TABLE 3.5. Data matrix used in the phylogenetic analyses of *Arytera* with polymorphisms indicated. Inapplicable and unknown characters are indicated with a question mark.

Species	Character								
	0000000000 0123456789	1111111111 0123456789	2222222222 0123456789	3333333333 0123456789	4444444444 0123456789	5555555555 0123456789	6666666666 0123456789	7777777777 0123456789	88888888 01234567
canacard	1232121312	1211222131	1212112111 2 3	1111311111 22 2 33	1112122211	2111112211	3111112211 22	11??11?221 22 22 2	11121211 22
msundaic	4222123171	1222222222 2	11121?2?1?	1112311112	?221112211	1211222222	1111222211	12??11?122	11131211
mpentape	1232123171	1232222227	1212211117	1112322113 2	3221112211	1211112211	1111222222	12??11?221	11121211 22
mpyrifor	1232123171	1?3112211? 2	1212?11111	1112222173 3	3221112211	1211222222	1111222221	12??11?111	11131211 22
manodont	1122123311	1231122217	12121?1?1?	1112211112	?221112111	1211212121	3111222212	12??11?112	11111211 22
mexangul	5222121171	1131222127	1112111111	1212121?1 2 3	2221112112	1211122112	3111222111	11??11?112	11232211
arcuata	4121113322	1111122127 2	1?11212111 2	1111212111 3	2111122112	1111111111 22	112111??22	111?221111 2	12221111 2
bifoliol	1112112211	1211122227	2?12111111 2	1111331121	1111221211	1111221222 2 2	311111??21 2 2	111?111211 2 2	12111111 22 2
brackenr	4231113322	1?12122117 2	1?11212111 3	1111211111 3 2	1111122111	1111221122	111111??21 2222 2	1111111111 2 222	11211111
bullata	1232323171	2222222122	1312122211	1122233111	3111122111 2	2111111111	3111212?22	12??12?221	11221?21
chartace	1122123312	1?11122217 2	2212111122	1112211221 3	3111122211	1121221122	122211??11 2 22 3	1111221112	12232111
collina	1112123312	1?11122111	1212211123 2	1112211211 3	3111122211	1111112111 2 2	112211??22	1111221112 2 22	12233111
densiflo	2112?11??2	1232211217	2222111211 3	22????????1	111112?111 222	2111221122 2	211111??22	11??22?112 2	12121172
dictyone	3112112211 2	2?21222327	1212111111	1112331121 3	?111211111	2111221111	311111??11	11??12?112	1112211?
distylis	1112112311	1222122221	1212111?11	1112221121 3 2	1111221211	2111221222 2	311111??22	11??22?112	12121111 2 2

(Table 3.5, continued)

Species	character								
	0000000000 0123456789	1111111111 0123456789	2222222222 0123456789	3333333333 0123456789	4444444444 0123456789	5555555555 0123456789	6666666666 0123456789	7777777777 0123456789	88888888 01234567
divarica	1232221211	123221122?	2?22111111 2 2	1112221121 3 2 3	1111121211	2111221122	311111??21 2	11???2?112	12111112
foveolat	2232221???	123121122?	3212111112	2111122121	1111121211	1111221122 2	211111??22	11???2?112 22	12211111
gracilip	4231113312	2212122122	1?11112111	1111212111 3	1111122???	1111221122	111111??12 2	11??12?221	12222111
lauterer	1222323171 2	1222122122	3?11112211 2	1222231111	3111122111	2111221222 2	3111212?11	12??11?221	11211?11 22 2
lepidota	4231113312	2212212121	1?11112111 2	1111212111	1111122112	1111121111 2	311111??22	11??11?221 2	12222111
lineosqu	2122?11??1 2	1232211221	2222111113 2	11???????23	111112?211	2111221122	211111??22	11???2?211 2	11111?2
litorali	1222211217 2	1?32211227 2	2222111111 2	1111211121 2322 3	?111121211	2111221122	211111??11 22	11??11?112 22 22	11111112 22
macrobot	1232323171 2	1222222122	1?12122111	1112222111 2	3111122111 2	2111221121	3111211?11 2 2	11??11?221 2 22	11211?21
microphy	1112112317	1212122221	3?121???31	1111231122 2	?111221211	1111222222 2	211111??22 3	11???2?211	1??1111?
miniata	1122211217	1232221117	2?12111111	1112231127 3	2111121211	2111221122	212211??22	1122221212 2	11111117 22
morobean	2112?112??	1232211222	2212111111 3	21???????21	111112?211	2111221122	211111??22	11???2?211	12211?2
multijug	2232?21??2	1132221122	2?12211111	12???????11	2111?2?112	2111111211	1211211?22	11??12?211	21221171
musca	1122211212 2	1232211227	2212111111	2212221123 2	1111121211	2111121122	211111??21 2	11???2?221	12232112
nekorens	1112123312	2211122112	1212221123	11122???21	3111122111	2121222222	1222112221 22 2	1121222222	12233171
neoebude	1222123317 2	1?12122217	1212211121 3	1212211221 2	3111122211	1111221111 2	1222212222 3 2	1111121212 2 2	12222111
novaebri	1222211211 2	1121211127	1?12111112	1112312221	1111121211	2111221122	211111??22 3	11???2?122 2	12211112
pauciflo	1112211212	1232211227	1212111211	2211221121 3 3	?111121211	2121221122	211111??12 3	11???2?221	12211111
pseudofo	2112?1???2	1232211121	2212111113	11???????23	2111?2?211	2111221122	211111??21 2	11???2?211 22	11111?2

TABLE 3.6. Characters and their states used in the phylogenetic analyses of *Arytera*.

Character Coding	State
0: Indumentum	
1	short, straight, appressed
2	crispate-hirsute
3	short patent + long appressed
4	short patent
5	long patent
1: Leaves	
1	at most 2-jugate
2	up to 11-jugate
2: Leaflets	
1	opposite
2	up to subopposite
3	up to alternate
3: Glandular scales	
1	present
2	absent
4: Arilloid	
1	type A (1 layer)
2	type B (2 layers)
3	type C (spongy)
5: Ovary	
1	2-locular
2	3-locular
6: Stigma	
1	stigmatic lines
2	distinctly lobed
3	shortly lobed
7: Fruit inside	
1	glabrous
2	sutures hairy
3	completely hairy
8: Hairs in fruit	
1	pilose
2	strigose
9: Leaflet base	
1	symmetric
2	asymmetric
10: Leaflet margin	
1	not revolute
2	revolute
11: Midrib adaxially	
1	basally puberulous
2	glabrous
12: Domatia	
1	absent
2	opening on top
3	opening in front
13: Venation adaxially	
1	flat
2	midrib raised
14: Venation abaxially	
1	midrib raised
2	raised
15: Nerves	
1	open
2	at least apically looped
16: Veins	
1	scalariform
2	reticulate
17: Inflorescence branching	
1	along rachis
2	in axil and along rachis
3	usually not branching
18: Calyx divided	
1	< 2/3
2	> 2/3
3	sepals free
19: Punctation in leaflets	
1	absent
2	present
20: Leaf margin	
1	entire
2	(entire to) repand
3	(entire to) serrate/denticulate
21: Petiolule	
1	not grooved
2	1-grooved
3	2-grooved
22: Inflorescence	
1	never ramiflorous
2	sometimes ramiflorous
23: Calyx abaxial indument	
1	(sub)glabrous
2	hairy
24: Calyx adaxial indument	
1	(sub)glabrous
2	hairy
25: Petals	
1	not punctate
2	punctate
26: Calyx margin	
1	not membranaceous
2	membranaceous
27: Petal blade decurrent into claw	
1	gradually
2	abruptly
28: Disc	
1	complete
2	collina-type
3	microphylla-type

(Table 3.6, continued)

Character Coding	State
29: Disc	
1	glabrous
2	pilose
3	pilose on rim only
30: Anther	
1	straight
2	curved
31: Connective	
1	not protruding
2	protruding
32: Fruit opening	
1	loculicidally
2	irregularly
33: Stipe	
1	broadly cuneate
2	slender
34: Fruit lobes dorsally	
1	grooved
2	rounded
3	sharp/keeled
35: Cotyledons	
1	superposed
2	oblique
3	parallel
36: Cotyledons	
1	equal
2	upper larger
3	lower larger
37: Hypocotyl	
1	glabrous
2	hairy
38: Anther	
1	glabrous
2	hairy
39: Number of petals	
1	5
2	0
3	some reduced
40: Petal scales	
1	free
2	adnate to margin of petal
3	enation
41: Pseudofunicle	
1	absent
2	present
42: Stipe of fruit	
1	solid
2	hollow
43: Sepals	
1	connate
2	free
44: Style	
1	longer than stigma
2	absent
45: Tertiary nerves	
1	very densely reticulate
2	laxly to densely reticulate
46: Fruit axis	
1	not thickened
2	thickened
47: Hairs	
1	basal
2	subbasal
48: Hairs	
1	unicellular
2	multicellular
49: Hairs	
1	thin-walled
2	thick-walled
50: A-type (multicellular stalk, unicellular large head) glandular hairs	
1	absent
2	present
51: M-type (multicellular stalk, uni?cellular small head) glandular hairs	
1	absent
2	present
52: B-type (unicellular, very small obconical) glandular hairs	
1	absent
2	present
53: C-type (multicellular stalk, pluricellular head) glandular hairs	
1	absent
2	present
54: Adaxial cuticle thin areas	
1	absent
2	present
55: Abaxial cuticle thin areas	
1	absent
2	present
56: Adaxial cuticle	
1	smooth
2	striate
57: Abaxial cuticle	
1	smooth
2	striate

(Table 3.6, continued)

Character Coding	State
58: Anticlinal walls adaxially	
1	straight
2	undulating
59: Anticlinal walls abaxially	
1	straight
2	undulating
60: Stomata adaxially	
1	absent
2	present on lamina and along veins
3	present along (mid)veins only
61: Ridge around abaxial stomata	
1	absent
2	present
62: Adaxial hypodermis	
1	absent
2	present
63: Abaxial hypodermis	
1	absent
2	present
64: Veins adaxially	
1	not transcurrent
2	transcurrent
65: Veins abaxially	
1	not transcurrent
2	transcurrent
66: Transcurrent veins adaxially	
1	not sclerenchymatised
2	sclerenchymatised
67: Transcurrent veins abaxially	
1	not sclerenchymatised
2	sclerenchymatised
68: Crystals in phloem	
1	absent
2	present
69: Crystals in pith	
1	absent
2	present
70: Crystals in adaxial epidermis	
1	absent
2	present
71: Crystals in abaxial epidermis	
1	absent
2	present
72: Crystals in adaxial hypodermis	
1	absent
2	present
73: Crystals in abaxial hypodermis	
1	absent
2	present
74: Crystals in palisade tissue	
1	absent
2	present
75: Crystals in spongy tissue	
1	absent
2	present
76: Secretory idioblasts in hypodermis	
1	absent
2	present
77: Secretory idioblasts in palisade tissue	
1	absent
2	present
78: Secretory idioblasts in spongy tissue	
1	absent
2	present
79: Extra anticlinal divisions in adaxial epidermal cells	
1	absent
2	present
80: Midrib vascularisation	
1	simple
2	with an extra vascular bundle
81: Petals abaxially	
1	glabrous
2	hairy
82: Petals adaxially	
1	glabrous
2	hairy
83: Anticlinal walls of adaxial epidermis cells	
1	thin
2	thick
3	very thick
84: Anticlinal walls of abaxial epidermis cells	
1	thin
2	thick
3	very thick
85: Fruit	
1	globose
2	lobed
86: Seed surface	
1	smooth
2	knobby
87: Pollen type	
1	B-type (parasyntricolporate)
2	A-type (tricolporate)

In character 9, shape of leaflet base, initially several more states were distinguished: basiscopic or acroscopic side broader instead of just asymmetric. However, this resulted in much polymorphism between the latter two states. Also, in initial analyses this distinction resulted in much homoplasy, in particular for the different asymmetric states. I therefore decided to recode the character as shown in Tables 3.5 and 3.6. Character 12, shape of domatia, was also initially coded in more states than shown here. Again, this resulted in much homoplasy concentrated in some of these states. This character is a good example of the phenomenon that the phylogenetically most informative way of dividing a character into separate states can be quite different from the best descriptive terms for distinguishing species (compare the coding with the description of the domatia in the synoptical key). The coding employed here, although still resulting in substantial homoplasy, seemed the best coding attainable for this character. Similar reductions in the numbers of character states (compared to those employed initially) were carried out in characters 15, 18, 22. The shape of the style and stigma, given as a single character in the synoptical key, was split up into two characters, nos. 6 and 44. In the type of arilloid (character 4) and in the shape of the disc (character 28), three states are distinguished here rather than two.

The micromorphological characters, nos. 47–80, 83, 84, were almost all scored as binary (presence/absence) characters. In a number of cases, the independence of characters could be doubted (e.g. types of glandular hairs, characters 50–53; presence of crystals in various parts of the leaflet, characters 68–75). However, close inspection of the data matrix will reveal that the distribution of the different character states is not in full agreement with interdependence. Therefore I chose to keep these characters separate. (An alternative could have been to code these characters as multistate, but this would have resulted in many different states per character, in the case of crystals in the leaflet exceeding the maximum number of states allowed by the computer programs used.)

In view of the final analysis, further refinements might be made in the distinction of character states. The results will improve the consistency and retention indices of the resulting trees, but one always runs the risk of circular reasoning if this refinement is continued too long: because the results of an analysis show particular states in a character to be homoplasious (but not others) the homoplasious ones are united, thus reinforcing the reconstructed tree shape. However, it cannot be excluded that this tree does not correspond to the true historical relations between the taxa. The low consistency index of the tree on the original data set is in some way a measure of the confidence one can place in the resulting tree being correct in this sense. The apparent improvement obtained by recoding then gives the impression that one can have more confidence in the resulting tree, while the raw data have not changed. A second problem with reducing the number of states in a character is that although a particular character state may be (very) homoplasious, it is a good synapomorphy for some of its occurrences. If this character state is united with an other, such a synapomorphy may disappear, resulting in loss of resolution. Having tested the different coding options mentioned above, I feel that the character coding presented here is a fair compromise between these two conflicting aims.

3.4 – RESULTS

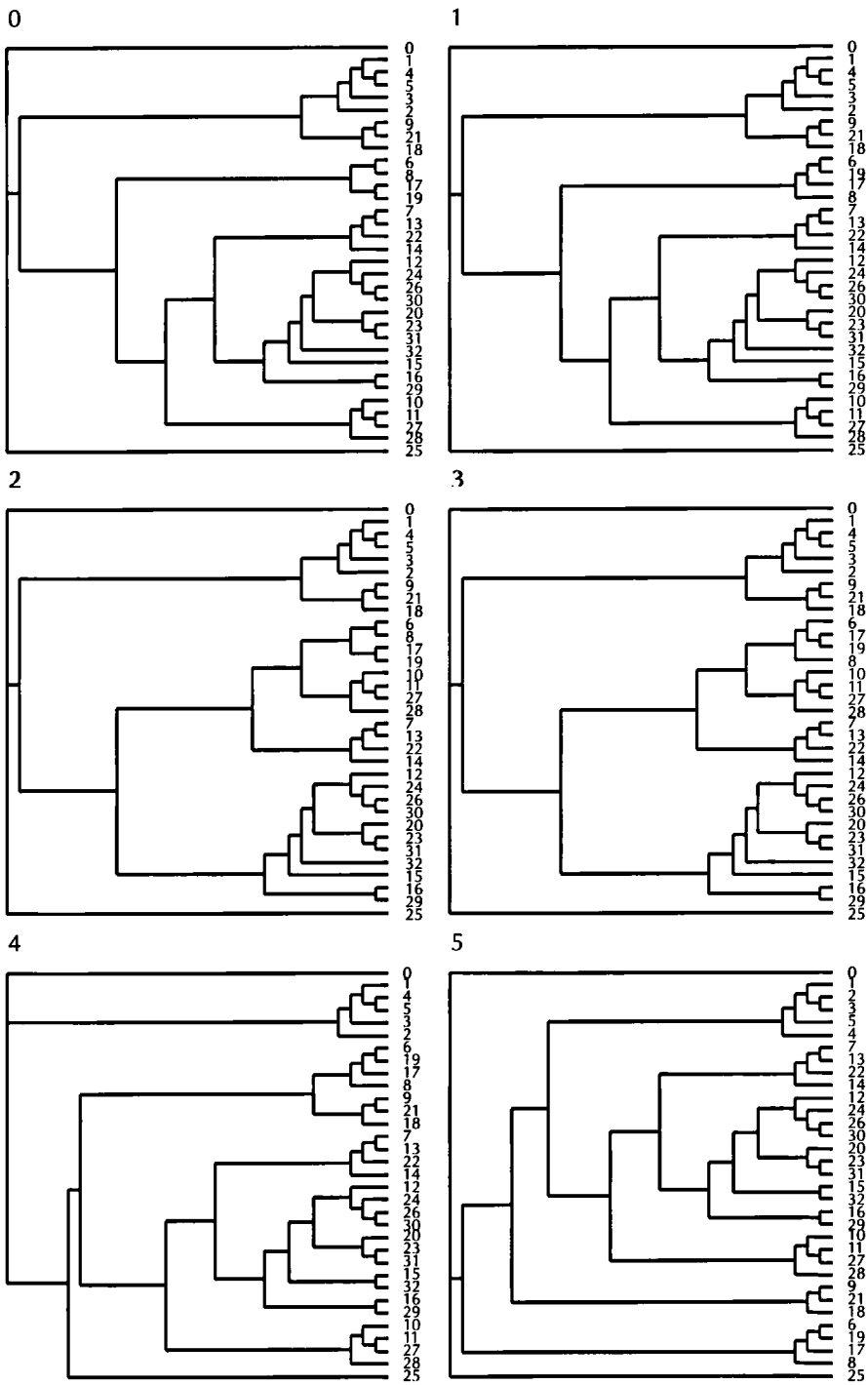
3.4.1 – **Data set with polymorphism coded as unknown**

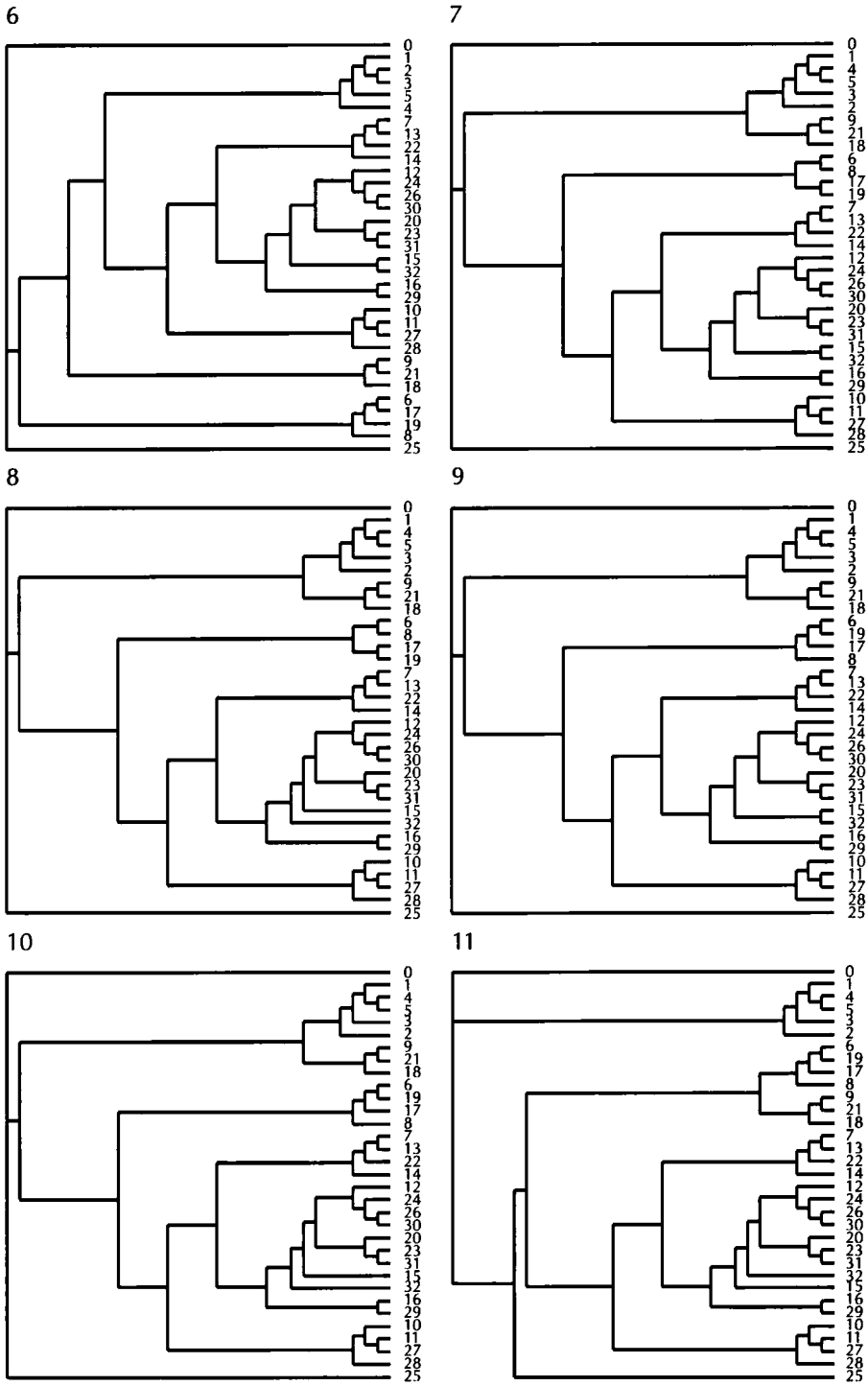
As described above, the data matrix with polymorphism coded as unknown was analysed using Hennig86 in combination with NONA, and with PAUP. Hennig86's commands mh* followed by bb* resulted in eight most parsimonious trees whereas PAUP (20 random addition sequences for the starting trees, followed by TBR branch swapping) found nine more, for a grand total of 17 MPTs. Using NONA (mu*50) to obtain initial trees enabled Hennig86 to recover all 17 MPTs. However, because the number of possible trees for 33 taxa is of the order of 10^{44}, no guarantee can be given that no more parsimonious trees exist for this data set.

The MPTs found are all shown in Fig. 3.9. Characters 43, 66, 67, 73, 76, and 80 are all autapomorphies, while characters 48, 53, and 70 are fully uninformative under this coding. These characters are therefore further left out of consideration here. The MPTs have a length of 336 steps (ci = .30, ri = .59). The values for the consistency and retention indices show that much homoplasy is present. This will be discussed in more detail in Section 3.5.2.2. These low values are not an immediate reason to distrust the results, however. Both indices depend in an unknown way on the number of taxa and the number of characters and character states in the data set, and no absolute measure has yet been devised with which the quality of a data set can be assessed. (Goloboff's [1992] Data Decisiveness [DD] assigns a value to the spread in lengths over all possible fully resolved trees for a data set; thus a high DD implies a large difference in length between the MPTs and the longest fully resolved trees. However, he notes that "[d]ecisiveness has no strict connection [...] with the strength of the preference for the most parsimonious tree(s) over *every* alternative tree" [p. 227; his italics]. As an aside, it should be noted that an absolute quality measure for data sets would have to cover all aspects of the vague notion 'quality', such as decisiveness, amount of homoplasy remaining in the MPTs, robustness of the shape of the MPTs against perturbations such as addition/deletion of taxa/characters, changes in codings or weighting schemes, etc.)

The strict consensus tree (Fig. 3.10) shows that a number of monophyletic groups are consistently present in the set of MPTs. These are: (1) the genus *Mischocarpus*; (2) the *arcuata*-group, comprising the species *Arytera arcuata*, *A. brackenridgei*, *A. gracilipes*, and *A. lepidota*; (3) the *bifoliolata*-group, consisting of *A. bifoliolata*, *A. dictyoneura*, *A. distylis*, and *A. microphylla*; (4) the *lautereriana*-group, consisting of *A. lautereriana*, *A. bullata*, and *A. macrobotrys*; (5) the *collina*-group, with the species *A. collina*, *A. chartacea*, *A. nekorensis*, and *A. neoebudensis*; (6) the *litoralis*-group, including the remaining species except *A. multijuga*, which is not grouped with other

FIGURE 3.9 (pages 55–57). All seventeen trees obtained from the analysis of the data set for *Arytera* with polymorphism coded as unknown (replace the polymorphisms in Table 3.5 with question marks). For the data set with polymorphism coded as such, trees 2, 3, 6, 15, and 16 are one step longer (see text).


0
0 1 4 5 3 2 9 21 18 6 8 17 19 7 13 22 14 12 24 26 30 20 23 31 32 15 16 29 10 11 27 28 25
1
0 1 4 5 3 2 9 21 18 6 19 17 8 7 13 22 14 12 24 26 30 20 23 31 32 15 16 29 10 11 27 28 25
2
0 1 4 5 3 2 9 21 18 6 8 17 19 10 11 27 28 7 13 22 14 12 24 26 30 20 23 31 32 15 16 29 25
3
0 1 4 5 3 2 9 21 18 6 17 19 8 10 11 27 28 7 13 22 14 12 24 26 30 20 23 31 32 15 16 29 25
4
0 1 4 5 3 2 6 19 17 8 9 21 18 7 13 22 14 12 24 26 30 20 23 31 15 32 16 29 10 11 27 28 25
5
0 1 2 3 5 4 7 13 22 14 12 24 26 30 20 23 31 15 32 16 29 10 11 27 28 9 21 18 6 19 17 8 25


6
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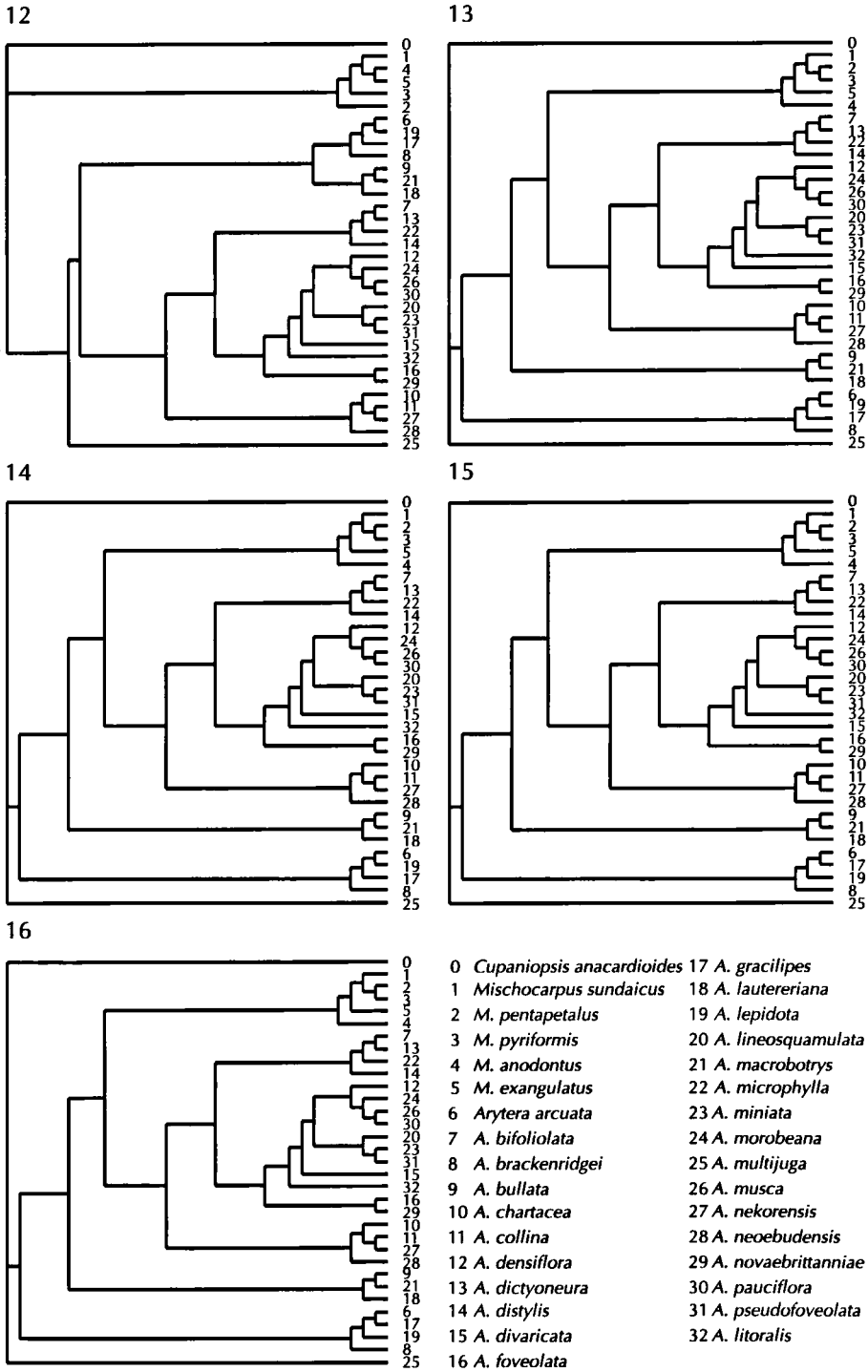
7
0 1 4 5 3 2 9 21 18 6 8 17 19 7 13 22 14 12 24 26 30 20 23 31 15 32 16 29 10 11 27 28 25
8
0 1 4 5 3 2 9 21 18 6 8 17 19 7 13 22 14 12 24 26 30 20 23 31 15 32 16 29 10 11 27 28 25
9
0 1 4 5 3 2 9 21 18 6 19 17 8 7 13 22 14 12 24 26 30 20 23 31 15 32 16 29 10 11 27 28 25
10
0 1 4 5 3 2 9 21 18 6 19 17 8 7 13 22 14 12 24 26 30 20 23 31 15 32 16 29 10 11 27 28 25
11
0 1 4 5 3 2 6 19 17 8 9 21 18 7 13 22 14 12 24 26 30 20 23 31 32 15 16 29 10 11 27 28 25



0 *Cupaniopsis anacardioides*
1 *Mischocarpus sundaicus*
2 *M. pentapetalus*
3 *M. pyriformis*
4 *M. anodontus*
5 *M. exangulatus*
6 *Arytera arcuata*
7 *A. bifoliolata*
8 *A. brackenridgei*
9 *A. bullata*
10 *A. chartacea*
11 *A. collina*
12 *A. densiflora*
13 *A. dictyoneura*
14 *A. distylis*
15 *A. divaricata*
16 *A. foveolata*
17 *A. gracilipes*
18 *A. lautereriana*
19 *A. lepidota*
20 *A. lineosquamulata*
21 *A. macrobotrys*
22 *A. microphylla*
23 *A. miniata*
24 *A. morobeana*
25 *A. multijuga*
26 *A. musca*
27 *A. nekorensis*
28 *A. neoebudensis*
29 *A. novaebrittanniae*
30 *A. pauciflora*
31 *A. pseudofoveolata*
32 *A. litoralis*

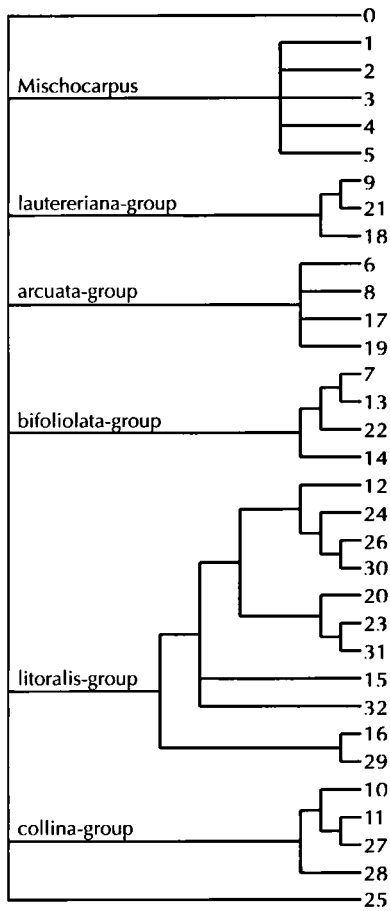


FIGURE 3.10. The strict consensus tree for all seventeen trees from Fig. 3.9. Legend as in Fig. 3.9.

species. The MPTs also agree in general on the resolution within these groups, except for the arrangement within *Mischocarpus* and in the *arcuata*-group. Within the *litoralis*-group the MPTs disagree on the relative positions of *A. divaricata* and *A. litoralis*.

Although the relationships between these different groups are fully obscured in the consensus tree, only a limited number of tree shapes are realised. Most of these come in groups of three, with all three solutions for the *A. divaricata–A. litoralis* polytomy. Most cladograms also agree that *Arytera* is para- or polyphyletic: only nos. 4, 11, and 12 allow the ingroup to be monophyletic. In all other trees *Mischocarpus* is embedded within *Arytera*. Usually the *bifoliolata*-group is sister to the *litoralis*-group, but in cladograms 2 and 3 it is sister to a clade consisting of the *collina*- and *arcuata*-groups. The latter is sister to a *Mischocarpus* + *Arytera* (excluding *A. multijuga*) clade in cladograms nos. 5, 6, 13–16. The *lautereriana*-group is sister to *Mischocarpus* in cladograms 0–3, 7–10. In the others it is sister to the *arcuata*-group (cladograms 4, 11, 12) or to a clade consisting of *Mischocarpus*, the *collina*-group, the *bifoliolata*-group, and the *litoralis*-group.

Arytera multijuga usually appeared at the root of the cladograms. Because it is relatively badly known, and has many unknown character states, I ran the data matrix with *A. multijuga* excluded. This resulted in 18 different cladograms. The strict consensus tree shows the same resolved clades as the consensus tree for the full analysis. Moreover, now the *lautererianag*roup and *Mischocarpus* are also resolved as sister groups. The *arcuata*-group is also resolved as sister to the remaining part of *Arytera*. Remarkably, the resolution in the *litoralis*-group has for the most part been lost. Apparently the deletion of a rather basal taxon with much ambiguity in its character states can cause effects much higher up in the tree.

Of these 18 cladograms, six have tree shapes that are congruent with cladograms 0, 1, 7–10 from the previous analysis. Six others resemble cladograms 1, 9, and 10, but have different arrangements within the *arcuata*-group. The remaining six cladograms have the *bifoliolata*-group and the *collina*-group as sister clades, which in turn are sister to the *litoralis*-group. Three of them have the usual arrangement of the latter, the three others have the same branching topology, but with the clade rooted at *A. pauci-*

flora. Actually this is similar to the situation for the *bifoliolata*-group: that result can be seen as the rerooting of the clade consisting of the *bifoliolata*-, *collina*-, and *litoralis*-groups between the latter two, rather than between the first two. So the only influence removing *A. multijuga* has on the shape of the cladograms is that two clades may be rooted differently, and that the constraint on the *arcuata*-group is relaxed.

3.4.2 – Data set with polymorphism coded as such

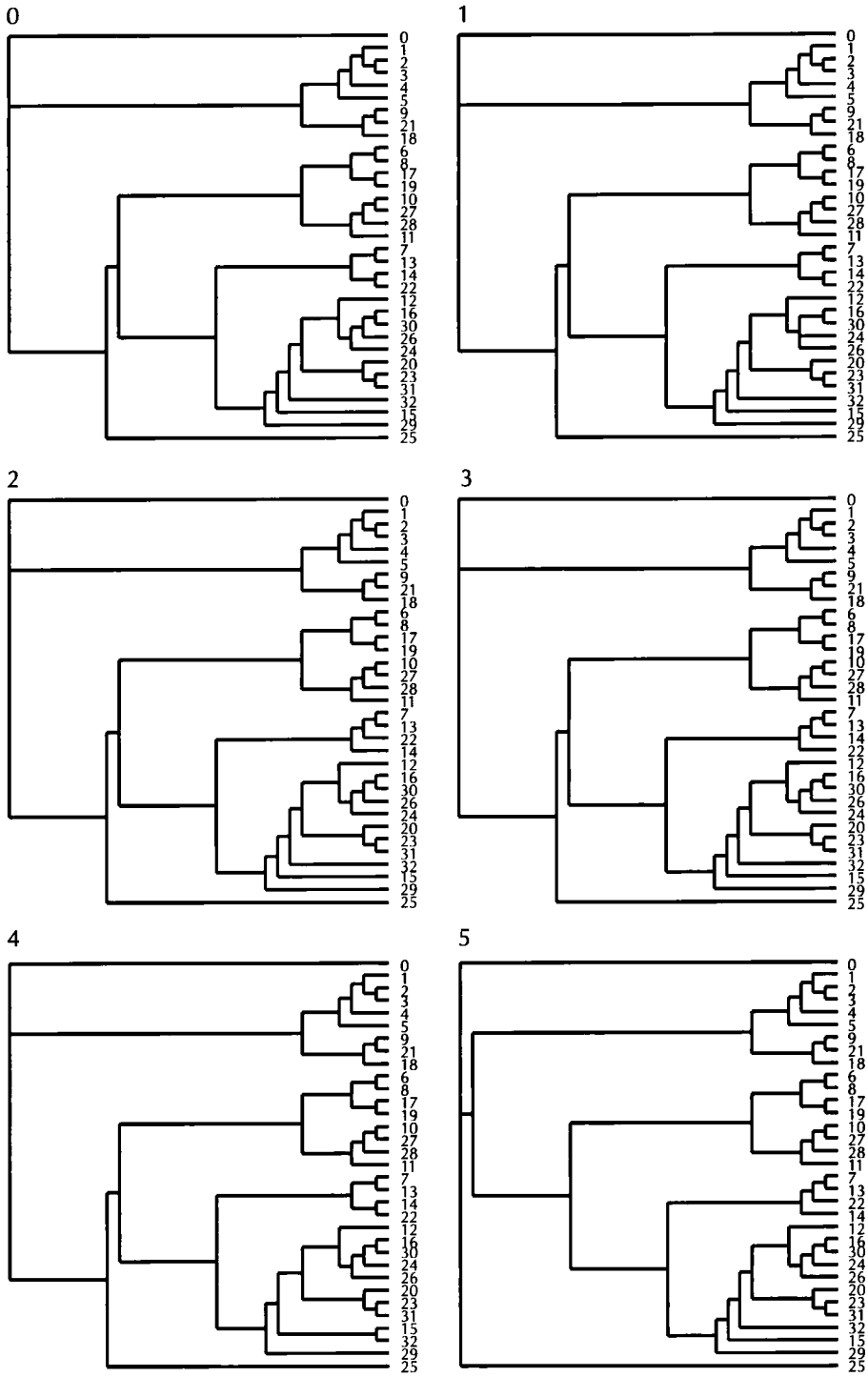
For the data matrix with polymorphism coded as such, both PAUP runs found a subset of 12 out of the 17 trees of length 338. (The length difference with the previous result is caused by characters 66 and 73, which are autapomorphic if coded as unknown, but are seen by PAUP as potentially informative due to polymorphism. However, since there is only one truly apomorphic species in the data set for each [binary] character, no placement of the polymorphic species on the tree can cause an extra step.) Trees 2, 3, 6, 15, and 16 were each one step longer. For trees 6, 15, and 16 this is due to character 60 being coded as 1+2 for *A. brackenridgei*, which results in an extra step because the reconstructed ancestral state for this species is state 3. Character 36 is coded as state 1+3 for *A. miniata* and *A. pauciflora*, while the ancestral state is a definitive state 2 in trees 2 and 3, leading to an extra step for these trees. This result slightly refines the results from the previous analysis, in that the set of MPTs is reduced by five trees. It shows that when PAUP is not available, the choice for coding polymorphism as unknown is a good one, although the polymorphic characters must be checked to exclude trees that then take on one or more extra steps.

3.4.3 – Choosing among the alternative MPTs

3.4.3.1 – *Successive weighting*

Successive weighting by the rescaled consistency index, rc (again using NONA's mu*50 + Hennig86's bb* to reconstruct the MPTs for the weighted data sets) resulted after three iterations in a stable set of nine trees of length 431 (ci = .62, ri = .86), but with lengths of 347 or 348 steps on the unweighted data set, 11 or 12 steps longer than the trees derived from the unweighted data set (Fig. 3.11).

The tree shapes were slightly different, now consistently including a clade consisting of the *arcuata*-group + the *collina*-group, and placing *A. foveolata* as sister to *A. pauciflora*. Other differences are found in the shapes of *Mischocarpus* and the *collina*-group, which both have a reversed order compared to the original results. *Arytera* is consistently shown as paraphyletic, with the *lautereriana*-group as sister to *Mischocarpus*, and *A. multijuga* as sister to all other *Arytera* species. The polytomy including *A. divaricata* is now consistently resolved with this species at the base. The only differences between the cladograms is that on the one hand the relationships between *A. distylis*, *A. microphylla*, and the other two species in the *bifoliolata*-group are ambiguous, and on the other, those between *A. morobeana*, *A. musca*, and *A. pauciflora* + *A. foveolata*. In the first case, all three resolutions are equally parsimonious. In the latter, only two full resolutions are seen, either with *A. musca* at the base, or with *A. morobeana* in that position. The third possibility is an unresolved polytomy for this clade.


0
0 1 2 3 4 5 9 21 18 6 8 17 19 10 27 28 11 7 13 14 22 12 16 30 26 24 20 23 31 32 15 29 25
1
0 1 2 3 4 5 9 21 18 6 8 17 19 10 27 28 11 7 13 14 22 12 16 30 24 26 20 23 31 32 15 29 25
2
0 1 2 3 4 5 9 21 18 6 8 17 19 10 27 28 11 7 13 22 14 12 16 30 26 24 20 23 31 32 15 29 25
3
0 1 2 3 4 5 9 21 18 6 8 17 19 10 27 28 11 7 13 14 22 12 16 30 26 24 20 23 31 32 15 29 25
4
0 1 2 3 4 5 9 21 18 6 8 17 19 10 27 28 11 7 13 14 22 12 16 30 24 26 20 23 31 15 32 29 25
5
0 1 2 3 4 5 9 21 18 6 8 17 19 10 27 28 11 7 13 22 14 12 16 30 24 26 20 23 31 32 15 29 25

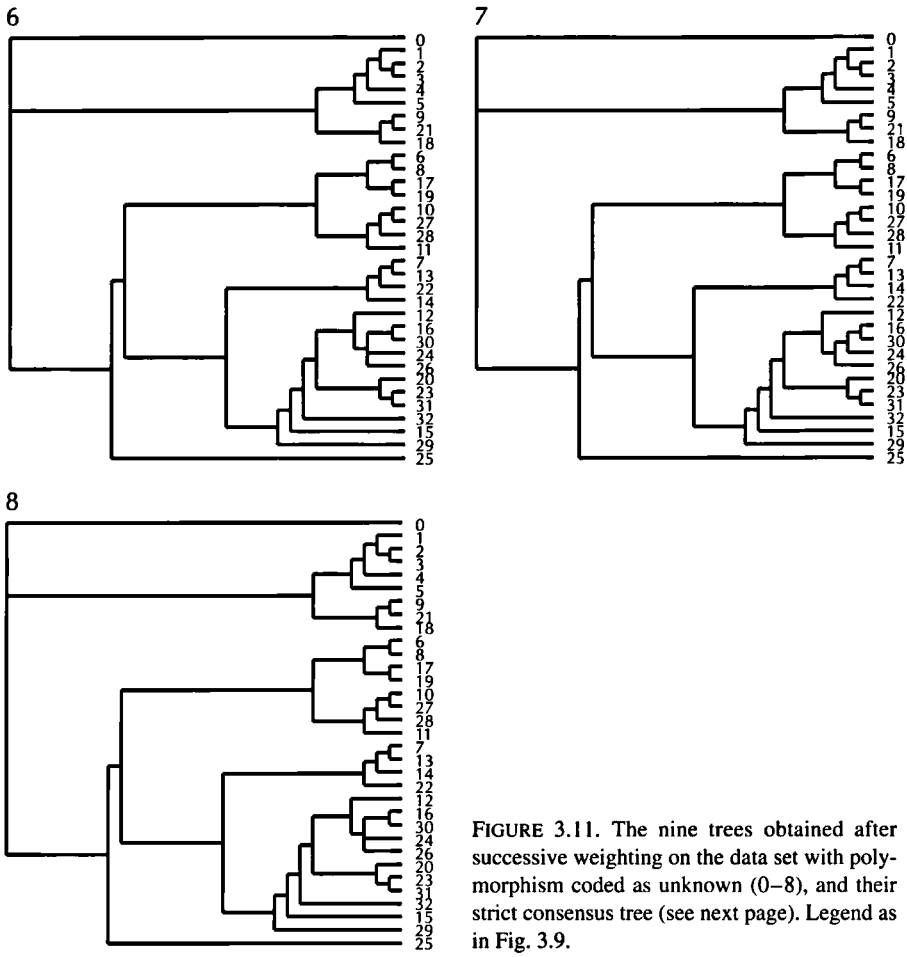
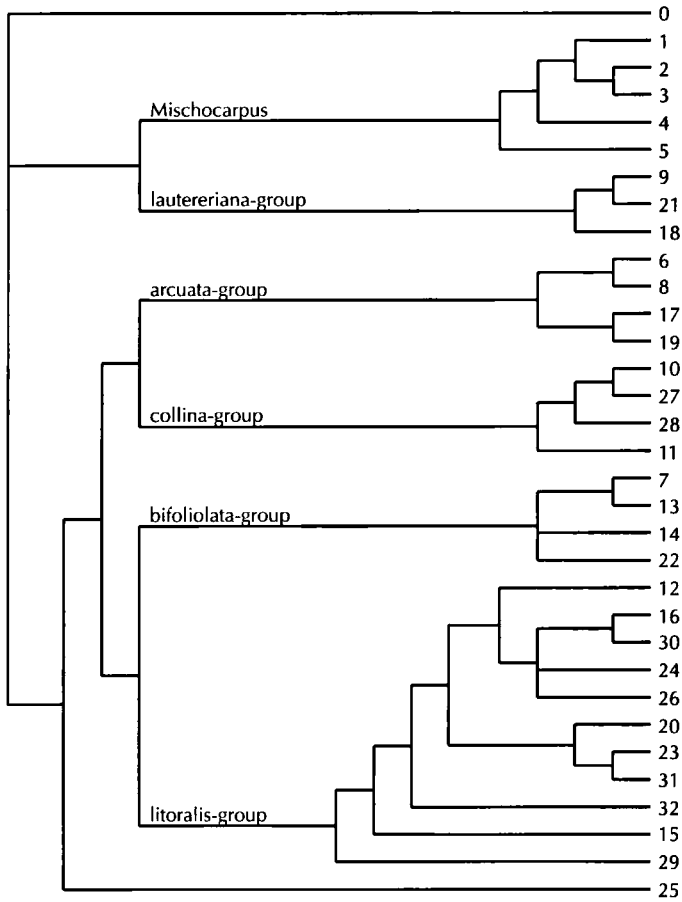


FIGURE 3.11. The nine trees obtained after successive weighting on the data set with polymorphism coded as unknown (0–8), and their strict consensus tree (see next page). Legend as in Fig. 3.9.

3.4.3.2 – *Weighted best on ci, ri, rc; weighting by W*

The OCCI (Rodrigo 1992) discriminates among the 17 trees. Tree 3 has an OCCI of 12, trees 0, 4, 7, 8, 11, and 12 an OCCI of 14, and all others an OCCI of 13. Weighting was also carried out, using the ci, (truncated) ri, and (truncated) rc values on the best-fitting trees as weight factors. Weighting according to ci (l = 10518–10678), ri (l = 1605–1618), and rc (l = 479–500) selected only trees 0, 7, and 8 as the best in all cases. A second attempt was made with the weight factor *W* developed in Section 3.2.3.3. This weight factor also selects trees 0, 7, and 8 as the 'best.' The tree lengths after weighting with the different weighting factors and the *W* values of the 17 MPTs are given in Table 3.7a; the weights of the different characters are given in Table 3.7b.



(Figure 3.11, continued)

3.4.3.3 – *Parsimony analysis using implied weights*

Rather than searching for most parsimonious trees, Pee-Wee (Goloboff 1993b) searches for trees that have the highest fitness F according to the formula given in Section 3.2.3.3. This formula downweights each character according to the number of extra steps it requires on a tree. The severeness of the downweighting is controlled by the concavity index K. In order to gain on computing time, Goloboff uses an approximation to calculate the F values in Pee-Wee, which usually gives values that are slightly too low. This also raises doubts whether the trees reported by Pee-Wee are in fact the best-fitting ones. Nevertheless, for the *Arytera* data set, no better fitting trees were found among a set of 978 randomly generated suboptimal trees with lengths up to 341 steps (Turner & Zandee, in press).

Submitting the data set for *Arytera* to Pee-Wee resulted in different trees for different values of K, none of which were in the set of MPTs. These trees are shown in Fig.

TABLE 3.7a. Tree lengths for MPTs after weighting according to (a) ci, (b) truncated ri, (c) truncated rc; tree lengths after iterative weighting on rc; *W* values and average *W* per character; and RQ.

Tree	Length after weighting			Length after iterative weighting	*W*	*W/n*	RQ
	ci	ri	rc				
0	10518	1603	479	841	45.71587207	.5786819249	.4789986351
1	10591	1611	488	851	45.00753873	.5697156802	.479101079
2	10611	1610	491	848	45.68594782	.578303137	.4781441249
3	10678	1617	500	858	45.01928116	.5698643184	.4778305701
4	10580	1618	489	847	45.42142762	.57495478	.479503417
5	10589	1610	490	832	44.99420901	.5695469495	.4793290117
6	10570	1605	488	829	44.94063758	.5688688301	.4799250127
7	10518	1603	479	841	45.71587207	.5786819249	.4795434459
8	10518	1603	479	841	45.71587207	.5786819249	.478501395
9	10591	1611	488	851	45.00753873	.5697156802	.479651534
10	10591	1611	488	851	45.00753873	.5697156802	.4786004356
11	10580	1618	489	847	45.42142762	.57495478	.4800531461
12	10580	1618	489	847	45.42142762	.57495478	.4789946498
13	10589	1610	490	832	44.99420901	.5695469495	.4798743041
14	10589	1610	490	832	44.99420901	.5695469495	.4788206331
15	10570	1605	488	829	44.94063758	.5688688301	.4804683633
16	10570	1605	488	829	44.94063758	.5688688301	.4794142129

3.12. Because of the erratic behaviour of *F* the fitness values for the 17 MPTs and the seven fittest trees at $K = 1–6$ were calculated for *K* values up to 50 (Table 3.8). The values reported here are exact values. At $K > 12$ three MPTs became the best-fitting trees in the set. These trees (nos. 0, 7, and 8) were the best-fitting MPTs regardless of the value of *K* up to at least $K = 10{,}000$. This is in itself worth noting, because for the data set published on *Fordia* by Schot (1991), a shift in the choice of MPTs occurred at $K > 15$ (Turner & Zandee, in press).

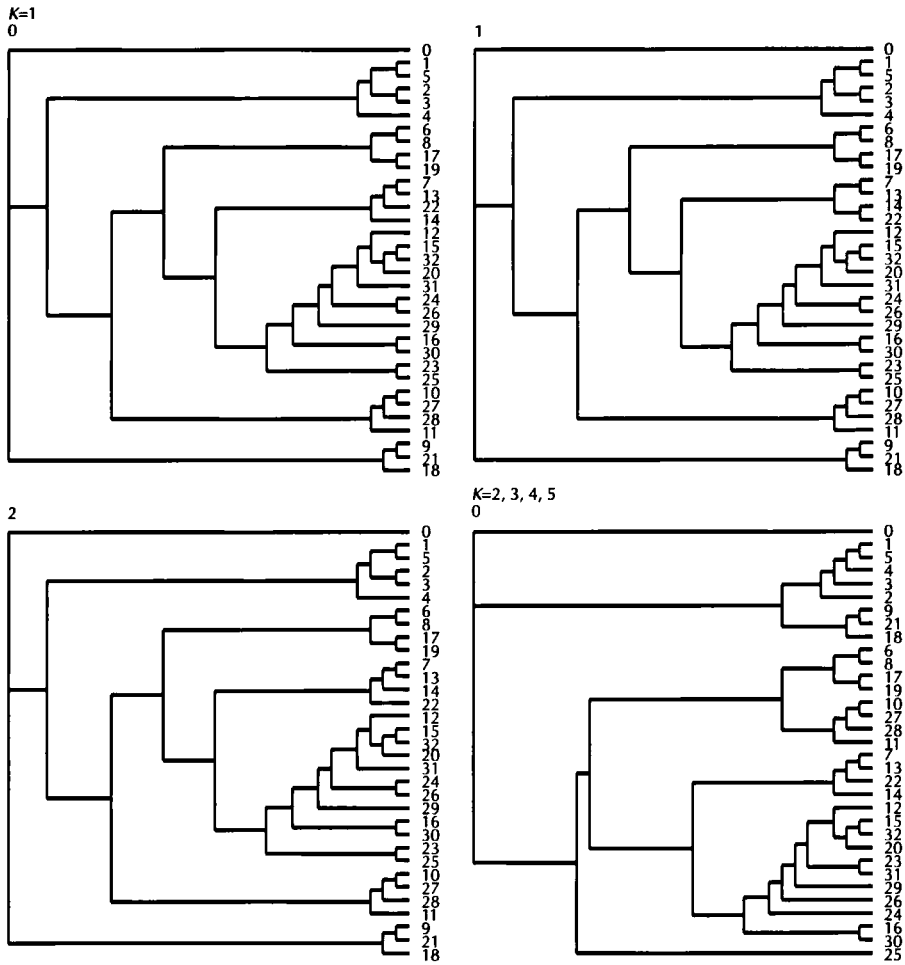
At $K = 1$ Pee-Wee resulted in three trees, each of length 357 on the unweighted data set (ci = .28, ri = .55). The shape of these trees is quite different from those of the MPTs. The *lautereriana*-group is the first clade to split off, followed by *Mischocarpus*; the shape of the latter clade is different from that in any of the MPTs, however. The next clade is the *collina*-group, followed by the *arcuata*-group, with a shape similar to that in a number of MPTs, including trees 0, 7, and 8. Next comes the *bifoliolata*-group, where the only difference is found between the three trees: either *A. distylis* or *A. microphylla* is at the base of the clade, or these taxa are the sister group of the other two. The *litoralis*-group includes *A. multijuga*, and also has a completely different shape than in the MPTs, with *A. pauciflora* and *A. foveolata* as a species pair near the base, and *A. divaricata* and *A. litoralis* as the most distal species.

TABLE 3.7b. Weight values for each character after weighting on (a) ci, (b) truncated ri, (c) truncated rc; (d) after iterative weighting on truncated rc.

Character	Weight				Character	Weight			
	ci	ri	rc	iterative weighting		ci	ri	rc	iterative weighting
0	44	4	1	1	44	100	10	10	10
1	20	7	1	0	45	50	8	4	4
2	18	5	0	0	46	100	10	10	10
3	100	10	10	10	47	20	5	1	0
4	100	10	10	10	48	100	10	10	10
5	33	8	2	1	49	33	3	1	0
6	50	8	4	4	50	33	8	2	2
7	40	8	3	3	51	100	10	10	10
8	100	10	10	10	52	50	5	2	2
9	25	7	1	1	53	100	10	10	10
10	33	5	2	0	54	14	1	0	0
11	25	0	0	0	55	20	2	0	0
12	28	6	1	1	56	33	7	2	1
13	14	4	0	0	57	16	4	0	0
14	16	5	0	0	58	14	2	0	0
15	33	8	2	2	59	12	2	0	0
16	50	9	4	4	60	33	7	2	3
17	28	6	1	1	61	33	3	1	3
18	25	3	0	0	62	33	6	2	2
19	20	3	0	0	63	50	7	3	3
20	25	5	1	1	64	50	8	4	4
21	66	0	0	0	65	100	10	10	10
22	33	3	1	1	66	100	10	10	10
23	100	10	10	10	67	100	10	10	10
24	20	3	0	0	68	20	3	0	0
25	50	5	2	2	69	16	1	0	0
26	33	7	2	1	70	100	10	10	10
27	25	0	0	0	71	50	8	4	4
28	100	10	10	10	72	50	0	0	0
29	40	4	1	0	73	100	10	10	10
30	50	7	3	10	74	33	8	2	2
31	16	1	0	0	75	33	6	2	2
32	100	10	10	10	76	100	10	10	10
33	25	5	1	1	77	16	3	0	0
34	40	4	1	1	78	12	3	0	0
35	28	5	1	1	79	20	6	1	0
36	33	3	1	1	80	100	10	10	10
37	50	6	3	3	81	25	7	1	1
38	50	9	4	4	82	25	5	1	1
39	33	3	1	2	83	22	5	1	0
40	33	6	2	2	84	33	3	1	0
41	100	10	10	10	85	100	10	10	10
42	100	10	10	10	86	100	10	10	10
43	100	10	10	10	87	33	7	2	4

TABLE 3.8. Fitness values for the 17 MPTs and the best-fitting trees at K = 1–6 for *Arytera*, calculated according to the formula given by Goloboff (1993a, b) for different values of K. Note that the values reported by Pee-Wee are multiplied by 10 and are approximations, and differ slightly from the exact values given here. Highest fitness values for each value of K are shown in **bold**.

Tree	ΣES	*K* 1	2	6	10	11	12	13	14	15	20	25	50
0	235	30,80952381	40,03737374	56,15719281	62,66630325	63,74403774	64,68653988	**65,51804802**	**66,25727666**	**66,91891912**	**69,40401746**	**71,03768699**	**74,69353308**
7	235	30,80952381	40,03737374	56,15719281	62,66630325	63,74403774	64,68653988	**65,51804802**	**66,25727666**	**66,91891912**	**69,40401746**	**71,03768699**	**74,69353308**
8	235	30,80952381	40,03737374	56,15719281	62,66630325	63,74403774	64,68653988	**65,51804802**	**66,25727666**	**66,91891912**	**69,40401746**	**71,03768699**	**74,69353308**
4	235	30,66071429	39,91753247	56,11015651	62,6412964	63,72206421	64,66707039	65,50067124	66,24166779	66,90481803	69,39493926	71,03134607	74,69161124
11	235	30,66071429	39,91753247	56,11015651	62,6412964	63,72206421	64,66707039	65,50067124	66,24166779	66,90481803	69,39493926	71,03134607	74,69161124
12	235	30,66071429	39,91753247	56,11015651	62,6412964	63,72206421	64,66707039	65,50067124	66,24166779	66,90481803	69,39493926	71,03134607	74,69161124
1	235	30,37738095	39,78419913	56,08158508	62,62864238	63,71125835	64,65772973	65,49251298	66,23447825	66,89843258	69,3910808	71,02876021	74,69089662
9	235	30,37738095	39,78419913	56,08158508	62,62864238	63,71125835	64,65772973	65,49251298	66,23447825	66,89843258	69,3910808	71,02876021	74,69089662
10	235	30,37738095	39,78419913	56,08158508	62,62864238	63,71125835	64,65772973	65,49251298	66,23447825	66,89843258	69,3910808	71,02876021	74,69089662
2	235	30,24642857	39,66911977	56,03388278	62,6043554	63,69017363	64,63926729	65,47622225	66,22000456	66,88549331	69,38311839	71,02338961	74,6894159
6	235	30,23492063	39,68975469	56,07407592	62,63419647	63,71764952	64,6645834	65,49958028	66,24159352	66,905486	69,39715765	71,03372016	74,69288851
15	235	30,23492063	39,68975469	56,07407592	62,63419647	63,71764952	64,6645834	65,49958028	66,24159352	66,905486	69,39715765	71,03372016	74,69288851
16	235	30,23492063	39,68975469	56,07407592	62,63419647	63,71764952	64,6645834	65,49958028	66,24159352	66,905486	69,39715765	71,03372016	74,69288851
5	235	30,21944444	39,66991342	56,05799201	62,62334213	63,7077639	64,65555348	65,49130714	66,23399118	66,89847985	69,39231435	71,03018614	74,69171765
13	235	30,21944444	39,66991342	56,05799201	62,62334213	63,7077639	64,65555348	65,49130714	66,23399118	66,89847985	69,39231435	71,03018614	74,69171765
14	235	30,21944444	39,66991342	56,05799201	62,62334213	63,7077639	64,65555348	65,49130714	66,23399118	66,89847985	69,39231435	71,03018614	74,69171765
3	235	29,8297619	39,43578644	55,97435897	62,57754887	63,66727986	64,61948707	65,45896035	66,20480848	66,87201292	69,37502504	71,01799686	74,68795029
K=1	256	**32,88134921**	40,99292929	55,87023503	62,16986839	63,23185731	64,16533494	64,99265918	65,73121705	66,39474919	68,90885642	70,58151136	74,38771674
K=1	256	**32,88134921**	40,99292929	55,87023503	62,16986839	63,23185731	64,16533494	64,99265918	65,73121705	66,39474919	68,90885642	70,58151136	74,38771674
K=1	256	**32,88134921**	40,99292929	55,87023503	62,16986839	63,23185731	64,16533494	64,99265918	65,73121705	66,39474919	68,90885642	70,58151136	74,38771674
K=2	246	32,78495671	**41,15634921**	56,22425075	62,51306292	63,56789594	64,49375006	65,31324985	66,04395503	66,69971813	69,17797581	70,82079756	74,53904661
K=3	246	32,78495671	**41,15634921**	56,22425075	62,51306292	63,56789594	64,49375006	65,31324985	66,04395503	66,69971813	69,17797581	70,82079756	74,53904661
K=4	246	32,78495671	**41,15634921**	56,22425075	62,51306292	63,56789594	64,49375006	65,31324985	66,04395503	66,69971813	69,17797581	70,82079756	74,53904661
K=5	246	32,78495671	**41,15634921**	56,22425075	62,51306292	63,56789594	64,49375006	65,31324985	66,04395503	66,69971813	69,17797581	70,82079756	74,53904661
K=6	237	31,41944444	40,43816739	**56,25639361**	**62,6869256**	**63,75489454**	**64,68968745**	65,51505831	66,24936785	66,90704656	69,38111749	71,01102993	74,66934517
K=6	237	31,41944444	40,43816739	**56,25639361**	**62,6869256**	**63,75489454**	**64,68968745**	65,51505831	66,24936785	66,90704656	69,38111749	71,01102993	74,66934517
K=6	237	31,41944444	40,43816739	**56,25639361**	**62,6869256**	**63,75489454**	**64,68968745**	65,51505831	66,24936785	66,90704656	69,38111749	71,01102993	74,66934517



At $K = 2-5$ one single tree is fittest (l = 347, ci = .29, ri = .57). Here, *Mischocarpus* and the *lautereriana*-group again form a sister pair at the base of the tree; *Mischocarpus* is now more similar to the result in a number of MPTs. *Arytera multijuga* appears as sister to all remaining species; the *collina*- and *arcuata*-groups are sister clades, and together sister to the *bifoliolata*- and *litoralis*-groups. The latter again has a different shape.

At $K = 6$ Pee-Wee again produces three trees (l = 338, ci = .29, ri = .58). In these trees *Arytera* is monophyletic, with *Mischocarpus* as sister group; the *lautereriana*-group is the first to split off, followed by *A. multijuga*, and the *arcuata*-, *collina*-, and *bifoliolata*-groups, in that order. All these clades have the same shape as in some MPTs (including trees 0, 7, and 8), but the latter clade can also have the other shapes

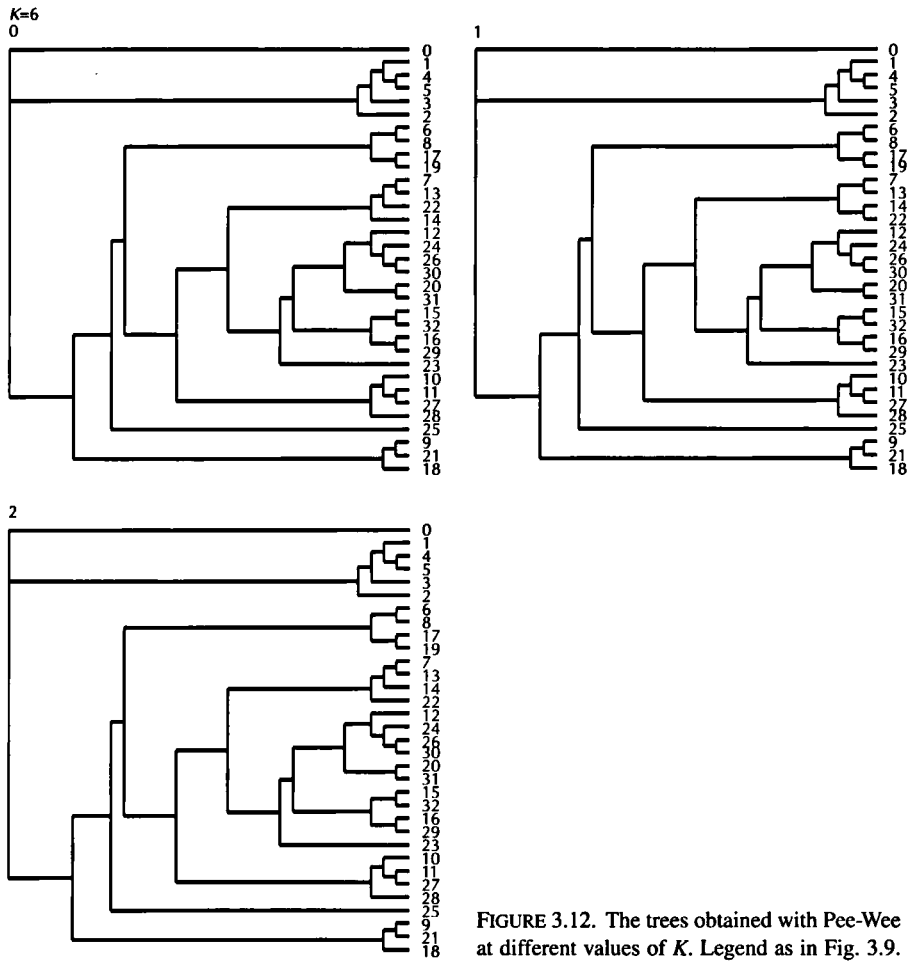


FIGURE 3.12. The trees obtained with Pee-Wee at different values of *K*. Legend as in Fig. 3.9.

described for the trees found for $K = 1$. The *litoralis*-group once more has a new shape, but now slightly resembles that found in the MPTs, albeit rooted differently.

3.4.3.4 – *RQ*

The results of the calculations of RQ are also shown in Table 3.7a. The preference of this measure is quite different from that of those discussed above: tree 15 has the highest RQ. The trees preferred by the other measures, nos. 0, 7, and 8, do no better than many others, with RQ values of .4785–.4795. Among the trees that were most parsimonious when analysed with polymorphism coded as such, tree 11 scores best with an RQ value of .4800.

3.5 – DISCUSSION

3.5.1 – **Choosing definitive cladograms**

Although the number of MPTs for the *Arytera* data set is quite low, the strict consensus cladogram is rather uninformative, especially as regards the relation between the different groups. Besides, a consensus cladogram cannot be considered as an estimate of a phylogeny, as has been repeated in the literature many times. Nevertheless many studies still present such consensus cladograms as the end result. Successive weighting and analysis using Pee-Wee resulted in still other cladograms. This situation forced me to make a choice between the different results. In this Section, I shall explicate the reasoning that led to my final choice.

First of all, MPTs are to be preferred over trees that are longer on the unweighted data set. This is because homoplasy cannot be considered solely as a measure of the reliability of a character as evidence for phylogenetic relationships. Rather, following Hennig (1966), I see homoplasy also as the result of the limited ability of the investigator to assess correctly the homology of character states. Thus, homoplasy (the lack of congruence between different characters) should lead first to reassessment of homology assumptions by "checking, correcting, and rechecking" (Hennig 1966, p. 122; see also Bryant 1989) (cf. Section 3.3.2). Theoretically, after all possibilities for re-evaluation of homology assessments have been exhausted, the residual homoplasy is due solely to the difference between phylogenetic homology (synapomorphy) and evolutionary homology (single origin of a character state). For example, if in Fig. 3.3 species B had become fixed for the derived character state independently of the fixation of that same state in the ancestor of species D and E, the phylogenetic homoplasy could not be eliminated by closer examination of the character state in the different taxa because it is truly homologous in terms of evolutionary origin. (The difference was pointed out to me by Kornet, who calls this phenomenon 'parafixation.')

Because the re-assessment of homology assumptions described above already amounts to weighting of the initial homology assumptions, I regard it as inconsistent to reweight characters in the final analysis. The choice for the final cladogram is therefore limited to the MPTs. Nevertheless, among the MPTs, some trees can be preferred over others on the basis of the residual reliability of the characters as phylogenetic markers, as is done by non-successive weighting, weighting by *W*, by the OCCI, or by using RQ. Even successive and implied weighting may lead to such a preference in certain circumstances, namely when the resulting trees are a subset of the set of MPTs.

Among the 17 MPTs for the data set with polymorphism coded as unknown, only 12 trees are most parsimonious when polymorphism is coded as such. Trees 2, 3, 6, 15, and 16 each are one step longer. This already reduces the set of trees. The remaining trees agree that the *bifoliolata*-group is the sister group of the *litoralis*-group, and that these two together are sister to the *collina*-group.

None of the remaining trees can be discarded on the grounds of containing unsupported branches or being less resolved than others. All branches of all trees are also unequivocally supported, except the branch between *A. divaricata* and *A. litoralis* or

the branch supporting these two taxa as sister species; these branches can only be supported by choosing for particular optimisations. Other criteria are needed to select among the MPTs.

The results of successive weighting and of analysis using Pee-Wee were unsatisfactory in that they produced trees that are not in the set of MPTs, and are therefore not accepted. A further reason for discarding the Pee-Wee results is that *F*'s behaviour is not constant and quite unpredictable for different values of the concavity index *K*. Pee-Wee and successive weighting do agree with the set of MPTs in recognising the different subgroups of *Arytera* as monophyletic, and in reproducing the *bifoliolata*- and *litoralis*-groups as sister clades. They also agree for the most part that the *lautereriana*-group is not included in *Arytera*.

The results of non-successive weighting by ci, ri, and rc agree that trees 0, 7, and 8 are relatively 'better' than the other MPTs. So do weighting using *W*, and in part the OCCI, which is not remarkable in that all these measures are based on the principle of preferring trees with the homoplasy concentrated in as few characters as possible. RQ showed a marked preference for different trees. However, as mentioned in Section 3.2.3.5, changing the settings of the parameters may result in a preference for other trees, like is the case with *F*. Although these various criteria select subsets of the set of MPTs on some basis for the reliability of the different characters, the 12 remaining MPTs were also checked manually to see whether some trees could be considered more plausible than others on the basis of support by particular characters, but no arguments could be derived from these considerations to prefer specific trees.

Because the rationale behind RQ (and *F*) seems susceptible to the method of modelling, the results of the other methods for distinguishing among different MPTs are preferred. As they for the most part agree that trees 0, 7, and 8 are 'best,' these trees are accepted as the final result. Their strict consensus tree is shown in Fig. 3.13. They only differ in the relative position of *A. litoralis* and *A. divaricata*. No arguments resulted from my investigation to prefer one of these three trees over another: successive weighting shows a preference for placing *A. divaricata* basal to *A. litoralis*, but the results from Pee-Wee consistently show them to be sister taxa, as does RQ in one case, in the others preferring an arrangement with *A. litoralis* as the more basal species. Any argument for choosing further among these three arrangements will have to come from other sources, e.g. biogeographic analysis.

3.5.2 – **Character development**

Now that a phylogeny is available, the characters can be identified which support each monophyletic group. Also, transformation series for each character in the data set can be reconstructed. These analyses are the subject of the following Sections. All synapomorphies and character transformations discussed are depicted in Fig. 3.13.

3.5.2.1 – *Synapomorphies for major monophyletic groups*

The characters unequivocally supporting (i.e. under any optimisation scheme) the monophyly of the *Mischocarpus* + *lautereriana*-group clade are: fruit glabrous inside

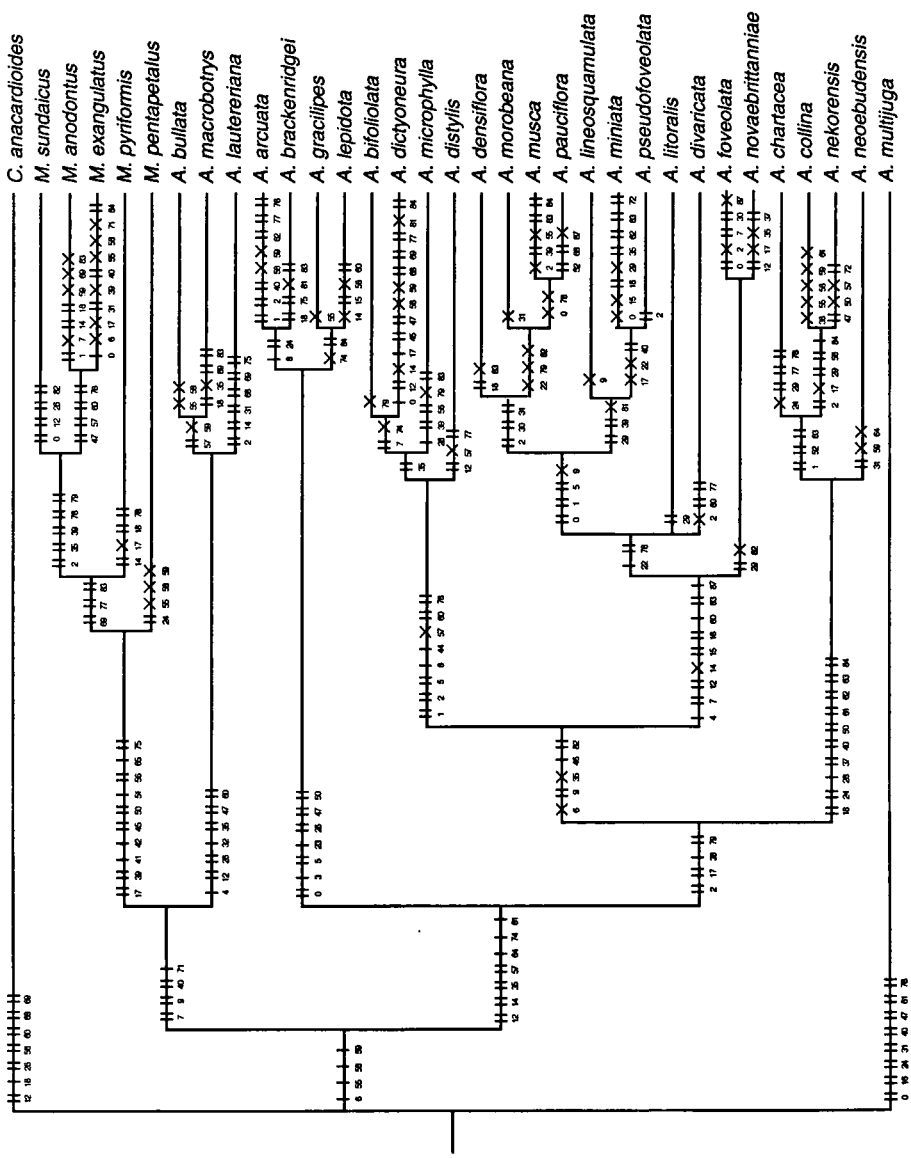


FIGURE 3.13. The strict consensus tree of the three accepted cladograms 0, 7, and 8 (Fig. 3.9). Note that they only disagree in the relative positions of *A. divaricata* and *A. litoralis*. Also depicted are the character state transformations for a number of characters discussed in Section 3.5.2. Single slashes denote unique synapomorphies, double slashes are parallel developments, crosses reversals.

[7][4] (parallel in *A. foveolata*); symmetric base of the leaflets [9] (but with a parallel in the clade *bifoliolata-* + *litoralis*-group); petal scales reduced to enations of the petal margins [40] (parallel in *collina*-group); and crystals present in the abaxial epidermis [71] (reversal in *M. exangulatus*). Its sister group is supported by flat nerves abaxially [14] (parallels in *M. pyriformis*, *M. anodontus*, and *A. lautereriana*, reversals in *A. lepidota* and the *litoralis*-group); smooth abaxial cuticle [57] (reversals in the *bifoliolata*-group, with a further reversal in *A. dictyoneura*, and *A. nekorensis*, parallels in *A. bullata* + *A. macrobotrys*, and in *M. anodontus* + *M. exangulatus*); adaxially not transcurrent veins [64] (reversal in *A. neoebudensis*); and by abaxially hairy petals [81] (reversals in *A. brackenridgei*, *A. dictyoneura*, *A. lineosquamulata* + *A. miniata* + *A. pseudofoveolata*).

Mischocarpus is supported by a reduced number of petals [39] (further shift to completely absent petals in *M. sundaicus* and *M. anodontus*, and a reversal to five petals in *M. exangulatus*; parallels in *A. musca*, *A. lineosquamulata* + *A. pseudofoveolata* + *A. miniata*); the presence of a pseudofunicle [41]; a hollow stipe [42]; very densely reticulate tertiary nerves [45] (parallel in *A. dictyoneura*); the presence of M-type glandular hairs [51]; a smooth adaxial cuticle [56] (parallels in *C. anacardioides*, *A. collina* + *A. nekorensis*, and in *A. microphylla*); and abaxially transcurrent veins [65]. Its sister group, the *lautereriana*-group, is characterised by a spongy arilloid [4]; irregularly opening fruit [32]; and stomata present adaxially along the midveins only [60] (parallels in *C. anacardioides*, *M. anodontus* + *M. exangulatus*, *A. lepidota*, the *bifoliolata*-group, and *A. divaricata*).

The *arcuata*-group is supported by the following characters: short, straight, appressed indumentum [0] (parallel in *M. sundaicus*); the presence of glandular scales [3]; a two-locular ovary [5] (parallels in the *bifoliolata*-group and the sister group of *A. litoralis* and *A. divaricata*); and an abaxially glabrous calyx [23]. Its sister group is supported by inflorescences usually branching in the axil and along the rachis [17] (probably a parallel in *Mischocarpus*; reversals in *A. collina* + *A. nekorensis*, *A. novaebrittanniae*, and *A. miniata* + *A. pseudofoveolata*); hairy anthers [38] (reversal in *A. collina*); and the presence of extra anticlinal divisions in the cells of the adaxial epidermis [79] (parallel in the upper part of *Mischocarpus*; reversals in *A. microphylla*, *A. bifoliolata*, and *A. morobeana* + *A. musca* + *A. pauciflora*).

The *collina*-group is supported by a relatively more connate calyx [18] (but seven parallel developments of this character state); a distinct type of disc [28]; a hairy hypocotyl [37] (parallel in *A. novaebrittanniae*); reduced petal scales [40] (parallel in *Mischocarpus* + *lautereriana*-group); the presence of a ridge around the abaxial stomata [61] (parallel in *A. multijuga*; reversal in *A. collina*); the presence of adaxial [62] (parallels in *A. arcuata* and *A. miniata*) and an abaxial hypodermis [63] (parallel in *A. miniata*); and thick anticlinal walls in the abaxial epidermis cells [84] (parallels in *M. exangulatus*, *A. gracilipes* + *A. lepidota*, *A. dictyoneura*, and *A. musca*). Its sister group is supported unambiguously by only two characters: symmetric leaflet base [9] (parallel in *Mischocarpus* + *lautereriana*-group; at least one reversal within the clade); and the not thickened fruit axis [46].

4) Numbers in square brackets are character numbers – See Table 3.5.

The *bifoliolata*-group is supported by five characters: leaves at most two-jugate [1] (four parallels within the *litoralis*- and *collina*-groups, and for *A. arcuata* and *M. anodontus*); opposite leaflets [2] (three parallels, for *A. collina* + *A. nekorensis*, *A. pseudofoveolata*, and the clade beginning at *A. densiflora*); strictly two-locular ovaries [5] (parallel developments in the *arcuata-group* and within the *litoralis*-group); a very short style [44]; and a reversal to a striate abaxial cuticle [57] (parallel in *A. nekorensis*, and with a further reversal in *A. dictyoneura*).

Finally, the *litoralis*-group is supported by a double-layered arilloid [41: fruit with hairy carpel margins [7] (parallel in *A. bifoliolata* + *A. dictyoneura*); domatia opening in front [12] (possibly a reversal to the plesiomorphic state, else parallels in *A. multijuga* and in *Mischocarpus*); abaxially raised nerves [14] (reversal to the plesiomorphic state, parallels in *A. lepidota* and *A. dictyoneura*); open nervation pattern [15] (parallel in *A. lepidota*, reversal in *A. miniata*); scalariform veins [16] (parallel in *A. multijuga*); and thin anticlinal walls in the adaxial epidermis [83] (parallels in *M. anodontus*, *A. bullata*, *A. brackenridgei* and *A. microphylla*, reversal in *A. densiflora*).

3.5.2.2 – *Transformation series*

The number of jugae in the leaves [1] shows a general tendency to become reduced in *Arytera*. Even though a number of species have more than two jugae, the number is still low in most of them (up to four) compared to the situation in the outgroups and in the *lautereriana*-group (usually more than six). The same reduction can be observed within *Mischocarpus*, although the trend is less pronounced there.

The number of locules in the ovary [5] also displays a trend to become reduced from three to two: the *arcuata*-group is exclusively two-locular, as are most species in the *bifoliolata*-group and the more derived species in the *litoralis*-group, the remaining species often being polymorphic for this character.

The plesiomorphic character state for the shape of the stigma [6] is shortly lobed, at least within *Arytera*. A derived state for the *litoralis*-group, stigmatic lines, is found also in *C. anacardioides*, *M. exangulatus*, and *A. multijuga*. Deeply lobed stigmata are most probably typical of the *bifoliolata*-group, but either of the latter two states may also be reconstructed as a synapomorphy for the *bifoliolata*- + *litoralis*-groups. The other stigma character [44] shows short styles to be a synapomorphy for the *bifoliolata*-group.

The endocarp of the fruits [7] is plesiomorphically completely hairy; glabrous endocarps are reconstructed as a synapomorphy for *Mischocarpus* + the *lautereriana*-group, but in view of the nature of the endocarp in the latter (with an extra sclerenchymatic layer), the validity of this synapomorphy can be doubted. The apomorphic situation is only the sutures of the carpels hairy, which has arisen twice within *Arytera*; a further development to completely glabrous endocarps is found in *A. foveolata*.

The presence of domatia [12] is reconstructed as derived within *Arytera*. Nevertheless, there seems to be a correlation with the preferred habitat: the species in the *arcuata*- and *collina*-groups, which lack domatia, occur mostly in more sclerophyllous vegetation types, as do *A. microphylla*, *A. bifoliolata*, and *C. anacardioides*. All other species in the study are predominantly rainforest plants. It can thus be doubted whether the

reconstruction of the ancestral character state for *Arytera* (domatia absent) is correct; however, the ability to form domatia may have been truly lost in the *arcuata*- and *collina*-groups, a few species of which are only known from rainforest-type vegetations.

The main nerves are plesiomorphically looped [15], the veins [16] reticulate. The apomorphic character states, nerves open, veins scalariform, are synapomorphies for the *litoralis*-group.

The calyx [18] is plesiomorphically deeply divided; the apomorphic state, calyx connate over at least 1/3 of its height, shows seven parallel developments, only one of which forms a good synapomorphy, namely for the *collina*-group.

Ramiflory [22] may have arisen once, as a synapomorphy for part of the *litoralis*-group, but displays two reversals, leaving four species with the apomorphic state and five with the secondarily acquired plesiomorphic state. It must be added, however, that these five species are all known from relatively few specimens.

Membranaceous margins of the sepals [26] have either arisen independently in the *lautereriana*-group, the *arcuata*-group, *M. sundaicus*, and *C. anacardioides*, or non-membranaceous sepal margins are derived for *Mischocarpus* and within *Arytera*. In view of the fact that the membranaceous margin in *C. anacardioides* (and other species of *Cupaniopsis*) is much more distinct than in the other species, one might conclude that this genus displays a different character state. In that case membranaceous sepal margins are derived separately in each of the groups mentioned.

An annular disc [28] is plesiomorphic within the study group. Two different apomorphic states occur: the collina-type disc as a synapomorphy for the *collina*-group, and the microphylla-type disc in *A. microphylla*.

The shape of the anther [30] develops from straight to curved inward in *A. foveolata* and the clade starting with *A. densiflora*. The latter clade may also be characterised by a protruding connective [31], but this character state has arisen independently also in four other species.

Within *Arytera* the relative position of the cotyledons in the seed [35] changes from superposed or oblique to parallel, the latter state forming a synapomorphy for *A. microphylla* + *A. bifoliolata* + *A. dictyoneura*, but with a parallel in *A. miniata*. The parallel arrangement may also be a synapomorphy for the *lautereriana*-group, although *A. macrobotrys* has oblique cotyledons. Because *C. anacardioides* displays all three states, and both superposed and oblique cotyledons occur in *Mischocarpus*, the plesiomorphic state cannot be identified with certainty.

The margin of the hypocotyl [37] is plesiomorphically glabrous. The derived state, margins hairy, is found as a synapomorphy for the mainly New Caledonian *collina*-group and in *A. novaebrittanniae*. Remarkably, the same character state is found as an apomorphy in *Cupaniopsis mackeeana* and possibly in a number of other New Caledonian species of *Cupaniopsis*.

The number of petals [39] in the study group is plesiomorphically five. Petals are completely absent in *A. microphylla*, while the number is reduced in *A. lineosquamulata* + *A. miniata* + *A. pseudofoveolata* and in *A. musca*. A reduction of the number of petals is also a synapomorphy for *Mischocarpus*, with full loss of petals in two species and a reversal to the full complement of five petals in *M. exangulatus*.

Petal scales [40] reduced to enations of the petal margin are a synapomorphy for *Mischocarpus* + *lautereriana*-group, and for the *collina*-group, while *A. multijuga*, *A. arcuata*, and *A. miniata* + *A. pseudofoveolata* show adnate scales, a state also present in *M. exangulatus*.

The plesiomorphic state for the attachment of the hairs (subbasal or basal, character 47) cannot be identified with certainty. If subbasally attached hairs are plesiomorphic, basally attached hairs have originated independently in *M. anodontus* + *M. exangulatus*, in *A. multijuga*, the *lautereriana*-group, the *arcuata*-group, *A. dictyoneura*, and *A. nekorensis*, and as a polymorphism in *A. densiflora*. If basally attached hairs are plesiomorphic, subbasally attached hairs form a synapomorphy for *Mischocarpus*, with a reversal in the two species mentioned above, and a parallel development in *C. anacardioides* and the clade consisting of the *collina*-, *bifoliolata*- and *litoralis*-groups, with reversals in at least two species.

As to the types of glandular hairs, the presence of A-type glandular hairs [50] is plesiomorphic, losses probably occurring in *Mischocarpus*, the *arcuata*-group, and the *collina*-group, with a reversal in *A. nekorensis*. Alternatively, they may have been lost in the common ancestor of *Arytera* (excluding *A. multijuga*) and *Mischocarpus*, with regains in the *lautereriana*-group, *A. nekorensis*, and the clade *bifoliolata*- + *litoralis*-groups. The presence of M-type glandular hairs [51] is a synapomorphy for *Mischocarpus*. The presence of B-type glandular hairs [52] is synapomorphic for the clade *A. chartacea* + *A. collina* + *A. nekorensis*, with a parallel in *A. pauciflora*. C-type glandular hairs [53] have only been observed in some samples of *A. distylis*.

The presence of thin areas in the adaxial and abaxial cuticle [54, 55] is synapomorphic for *Mischocarpus* + *Arytera* (excluding *A. multijuga*), but both show a number of reversals, which could not be correlated with environmental factors, however.

A striate adaxial cuticle [56] is apomorphic, with four parallel developments in *Mischocarpus*, *C. anacardioides*, *A. microphylla*, and *A. collina* + *A. nekorensis*. A striate abaxial cuticle [57], however, is plesiomorphic, smooth cuticles developing in parallel in *M. exangulatus* + *M. anodontus*, *A. bullata* + *A. macrobotrys*, and as a synapomorphy in *Arytera sensu stricto*, with reversals to striate cuticles in the *bifoliolata*-group and *A. nekorensis*, and again a reversal to smooth cuticle in *A. dictyoneura*.

The anticlinal walls of the adaxial epidermis cells [58] are plesiomorphically straight, but undulating walls form a synapomorphy for *Mischocarpus* + *Arytera* (excluding *A. multijuga*), with seven reversals to the plesiomorphic state. The anticlinal walls of the abaxial epidermis cells [59] show almost the same distribution of states, shedding severe doubt on the independence of these two characters. Deleting character 58 results in loss of resolution; deleting character 59 does not affect the results.

The absence of stomata on the adaxial side of the leaflets [60] is plesiomorphic within the study group. Presence along the midvein is apomorphic for *C. anacardioides*, *M. anodontus* + *M. exangulatus*, *A. bullata* + *A. macrobotrys*, *A. lepidota*, for *A. divaricata*, and probably for the *bifoliolata*-group. Presence over the entire lamina is probably a synapomorphy for the *litoralis*-group, but either of the apomorphic states can also be reconstructed as a synapomorphy for the *bifoliolata*- and *litoralis*-groups together. Polymorphism occurs in several species: in *A. brackenridgei* they are either absent or present over the entire lamina; in *A. neoebudensis* absent or present along the

midrib only; in *A. microphylla*, *A. novaebrittanniae*, and *A. pauciflora* present along the midvein only or over the entire lamina; and in *A. chartacea* all three states occur.

The presence of a hypodermis [62, 63] is an apomorphy for the *collina*-group, with parallel in *A. miniata* and, for an adaxial hypodermis only, in *A. arcuata*. Polymorphism occurs in *A. brackenridgei* and *A. bifoliolata* (adaxial hypodermis only). Again, this correlation casts doubt on the independence of these two characters. No change in the trees occurs if one of the two is deleted.

Adaxially transcurrent veins [64] are plesiomorphic, their absence forming a synapomorphy for *Arytera*, with a single reversal in *A. neoebudensis* and polymorphism in *A. nekorensis*. Abaxially transcurrent veins [65] are an apomorphy for *Mischocarpus*, with polymorphism in *A. neoebudensis* and *A. nekorensis*.

The presence of crystals in the phloem [68] is plesiomorphic, the character having been lost on at least five separate occasions; likewise the presence of crystals in the pith [69] is probably plesiomorphic, having been lost five times; crystals in the adaxial epidermis [70] are only found as a polymorphism in *C. anacardioides* and *A. divaricata*; crystals in the abaxial epidermis [71] are a synapomorphy for *Mischocarpus* + the *lautereriana*-group; the presence of crystals in the hypodermis, if present [72, 73] is autapomorphic for *A. miniata* and *A. nekorensis* (adaxially only). Polymorphism occurs in several other species with a hypodermis. Crystals in the palisade tissue [74] can be reconstructed as a synapomorphy for *Arytera*, with losses in *A. gracilipes* + *A. lepidota* and in *A. bifoliolata* + *A. dictyoneura*. Crystals in the spongy tissue [75] are plesiomorphic, with losses in *Mischocarpus*, *A. lautereriana*, *A. brackenridgei*, and polymorphism in several other species. Although the presence of crystals in various leaflet tissues can be assumed to be correlated, the distribution of character states shows that there is sufficient variation to assume that they are not interdependent.

The presence of secretory idioblasts in the palisade tissue [77] is plesiomorphic, showing at least six separate losses. Their presence in the spongy tissue [78] is probably also plesiomorphic, with a loss in at least seven cases.

The presence of extra anticlinal divisions in the adaxial epidermis cells [79] is apomorphic, having arisen on two occasions: in the clade *M. sundaicus* + *M. anodontus* + *M. exangulatus*, and in the clade consisting of the *collina*-, *bifoliolata*-, and *litoralis*-groups, although in view of the polymorphism for this character in *A. arcuata* and *A. brackenridgei*, it may also have arisen as an evolutionary novelty in the ancestor of *Arytera sensu stricto*, and have been lost in *A. gracilipes* + *A. lepidota*.

Abaxially hairy petals [81] also seem to be a synapomorphy for *Arytera*, with three reversals. Adaxially hairy petals [82] are plesiomorphic, the apomorphic state have arisen at least twice, in *M. sundaicus* and possibly in the clade *bifoliolata*-group + *litoralis*-group; *A. distylis* and *A. litoralis* show polymorphism and a full reversal has occurred twice.

The anticlinal walls in the adaxial epidermis [83] are plesiomorphically thick, thin walls being a synapomorphy for the *litoralis*-group, but also occurring autapomorphically in several other species. Very thick walls are a synapomorphy for *A. chartacea* + *A. collina* + *A. nekorensis*, and for part of *Mischocarpus*, but also occur in *A. musca*. The anticlinal walls of the abaxial epidermis [84] are plesiomorphically thin; thick walls have arisen independently several times, in *A. gracilipes* + *A. lepidota*,

the *collina*-group, possibly the *bifoliolata*-group, and *A. musca*. Very thick walls are a synapomorphy for *A. collina* + *A. nekorensis*. Although very thick anticlinal walls abaxially and adaxially occur in almost the same taxa, the different distribution of thin and thick walls justifies keeping these characters separate.

Finally, the pollen type [87] is plesiomorphically parasyntricolporate; the tricolporate type is probably a synapomorphy for the *litoralis*-group, with reversals in *A. foveolata* and *A. pauciflora*. Polymorphism occurs in *A. lautereriana* and *A. bifoliolata*. This transformation series is opposite to that hypothesised by Muller and Leenhouts (1976), but confirms the results obtained by Van der Ham (1990).

3.5.3 – Classification

From the accepted cladogram it is clear that *Arytera* is not monophyletic. To remedy this situation, two options are available: either *Mischocarpus* should be included in *Arytera*, or the *lautereriana*-group should be removed. The latter can then be given separate status, or included in *Mischocarpus*. Because the latter two clades are quite distinct, both from each other and from *Arytera*, I have chosen to raise the *lautereriana*-group to generic level. Thus, I separate them from the rest of *Arytera* as a new genus: *Mischarytera*. The name is taken from Radlkofer (1933), who recognised *A. lautereriana* as a separate section within *Arytera* under that name. The formal change in status and the ensuing name changes are made in Chapter 5.

Within *Arytera*, several monophyletic groups are apparent. The *arcuata*-group corresponds to sect. *Azarytera* (Radlkofer, 1879b). Its sister group includes all species placed by Radlkofer in sect. *Arytera* (*Euarytera*). Following Wiley's (1981) recommendations, I have decided to recognise the *collina*-, *bifoliolata*-, and *litoralis*-groups as formal subsections (rather than uniting the latter two at this rank) under the names subsect. *Pacifica*, subsect. *Distylis*, and subsect. *Arytera*. Within the different (sub)-sections no further formal division is made, (a) because most of them are too small to make such a division nomenclaturally meaningful, and (b) because within subsect. *Arytera* the branching order is not stable against perturbations of the data set (see e. g. the results with Pee-Wee and successive weighting).

Two problems remain with this classification, namely the position of *A. multijuga*, and of *A. brachyphylla*, which was not considered in the phylogenetic analyses. To begin with the latter, because its seeds are covered by a two-layered arilloid, and no other character clearly contradicts its position within subsect. *Arytera*, it is tentatively placed there. Unfortunately, the fruit of *A. multijuga* is unknown. Due to the unknown character states for fruit characters (which seem to be the most decisive in forming clades with this data set) the position of *A. multijuga* at the root of the tree becomes most parsimonious. Nevertheless, there is no evidence that it belongs in a different genus, nor does it seem to belong in *Mischarytera*, so it is tentatively accepted here as a true *Arytera*, albeit *incertae sedis*. In view of a number of peculiarities, such as the presence of a double vascular bundle in the midrib of the leaflets, and slightly dimorphic calyx lobes, it is not impossible that it will remain an odd species within *Arytera*. On the other hand, the macromorphological characters generally agree that it should be included in subsect. *Arytera*.

Chapter 4 — BIOGEOGRAPHIC ANALYSES [1]

4.1 – INTRODUCTION

Biogeography is the discipline concerned with the spatial distribution of organisms, and the changes in that distribution through time. Many factors determine distribution patterns, both abiotic and biotic, but the relative importance of different factors depends very much on the spatial and temporal scale at which the patterns are examined. For example, on a small spatial scale and over short periods of time (relative to the size and the duration of the life cycle of an organism), differences in microclimate, soil, and other such ecological factors will be the most important in determining whether a particular species will be found in a particular place at a particular time. On a larger spatial scale and over long periods of time, however, factors such as long-range dispersability, changes in geomorphology, and historical constraints become more important. Thus, depending on the scale of the patterns studied, a division can be made between *ecological* and *historical* biogeography. As the name suggests, the former is in the domain of ecology, and I will not be concerned with it here. The latter, however, is in the domain of systematics, and forms the subject of this Chapter.

Historical biogeography has been a point of interest to systematists and other students of evolution at least since the middle of the last century. Pioneers in the field include Sclater (1858), Darwin (1859), and Wallace (1876). The first attempts at explaining large-scale distribution patterns invoked active dispersal from a centre of origin and local extinction as the most important mechanisms leading to present-day distributions. In particular cases, land bridges were assumed to have existed along which dispersal could have taken place between large land masses which are unconnected today (e.g. Darlington 1957; Van Steenis 1962). The acceptance of Wegener's (1915) hypothesis of continental drift in the 1960s concomitant with the development of the theory of plate tectonics, provided biogeographers with alternatives to land bridges, but did not yet change their views on the mechanisms leading to the observed distribution patterns.

This situation changed with the advent of phylogenetic systematics. Biogeographers came to realise that a different mechanism played an important role in determining distribution patterns, namely vicariance, or the splitting of species into daughter species by isolation after the origin of a barrier of sorts between different parts of the ancestral species' distribution (allopatric speciation). If no dispersal occurred since the

1) Parts of the text and figures of this Chapter were taken *verbatim* from a manuscript submitted as part of the proceedings of the ASBS Symposium 'Origin and evolution of the flora of the monsoon tropics,' held in Kuranda (Qld) in July 1994. I am grateful to the publisher and editors of Austral. Syst. Bot. for their kind permission to use this material here.

ancestor of a monophyletic group first gave rise to daughter species, the phylogeny of such a group will reflect accurately the relative timing of the arisal of the different barriers separating the terminal taxa. Historical biogeography based on that principle is now known as vicariance, or cladistic, biogeography (see, e.g., Nelson & Platnick 1981; Wiley 1981, 1988a, 1988b; Brooks & McLennan 1991).

That the mechanism of vicariance is the first choice in explaining distribution patterns within vicariance biogeography does not mean to say that other mechanisms are excluded. Obviously, dispersal and (local) extinction are real phenomena, and cannot be ignored, but should be invoked only when vicariance fails to explain the observed patterns, because the latter is more general than the former two. However, the two major techniques applied in cladistic biogeography today, Brooks Parsimony Analysis/Component Compatibility Analysis (BPA/CCA) (Brooks 1981, 1990; Wiley 1981, 1988a, b; Zandee & Roos 1987) and Component Analysis (CA) *sensu* Page (1993a), differ remarkably in that BPA and CCA allow dispersal into the realm of possible explanations, while in CA any putative instance of dispersal should be removed *a priori* from the data set, because the method cannot accommodate it (although in the latest version [Page 1995] it can, provided dispersal has been accompanied by speciation).

In this Chapter, I will investigate the biogeographic history of the region in which the genera *Arytera* and *Mischarytera* occur, i.e. East Australia, New Guinea, and the Western Pacific Ocean. The biogeographic history of this region has been the subject of numerous studies in the past, beginning with Wallace (1876). Some of these studies were concerned with large-scale relationships between this and other regions, in particular other parts of Gondwana (e.g. Croizat 1958, 1962; Brundin 1966; Humphries 1981; Patterson 1981; Weston & Crisp 1987, 1994). Others considered relationships among areas within the region (e.g. Cracraft 1983b, 1986, 1991; Van Welzen 1989; Andersen 1991; Muona 1991; Crisp et al., in press). The organisms employed in these studies include plants such as southern beeches (*Nothofagus*), *Guioa*, and waratahs (Proteaceae), and animals, e.g. birds, insects, and marsupials. The methods adopted for these studies also vary. Apart from a number of older, more anecdotal investigations, they include panbiogeography (Croizat 1958; Page 1987), methods employing parsimony analysis (Brooks Parsimony Analysis: Brooks 1981, 1990; Wiley 1988a, b; Parsimony Analysis of Endemism: Rosen 1988), clique, or constrained parsimony, analysis (Component Compatibility Analysis: Zandee & Roos 1987), and Component Analysis (Nelson & Platnick 1981; Page 1993a).

In the past few years, a number of cladograms have become available for Sapindaceous genera occurring in this region (Van Welzen 1989; Adema 1991; Van Welzen et al. 1992; Adema & Van der Ham 1993; Etman 1994). These are employed here to study relationships between areas on a regional scale. The results are compared with previously published studies.

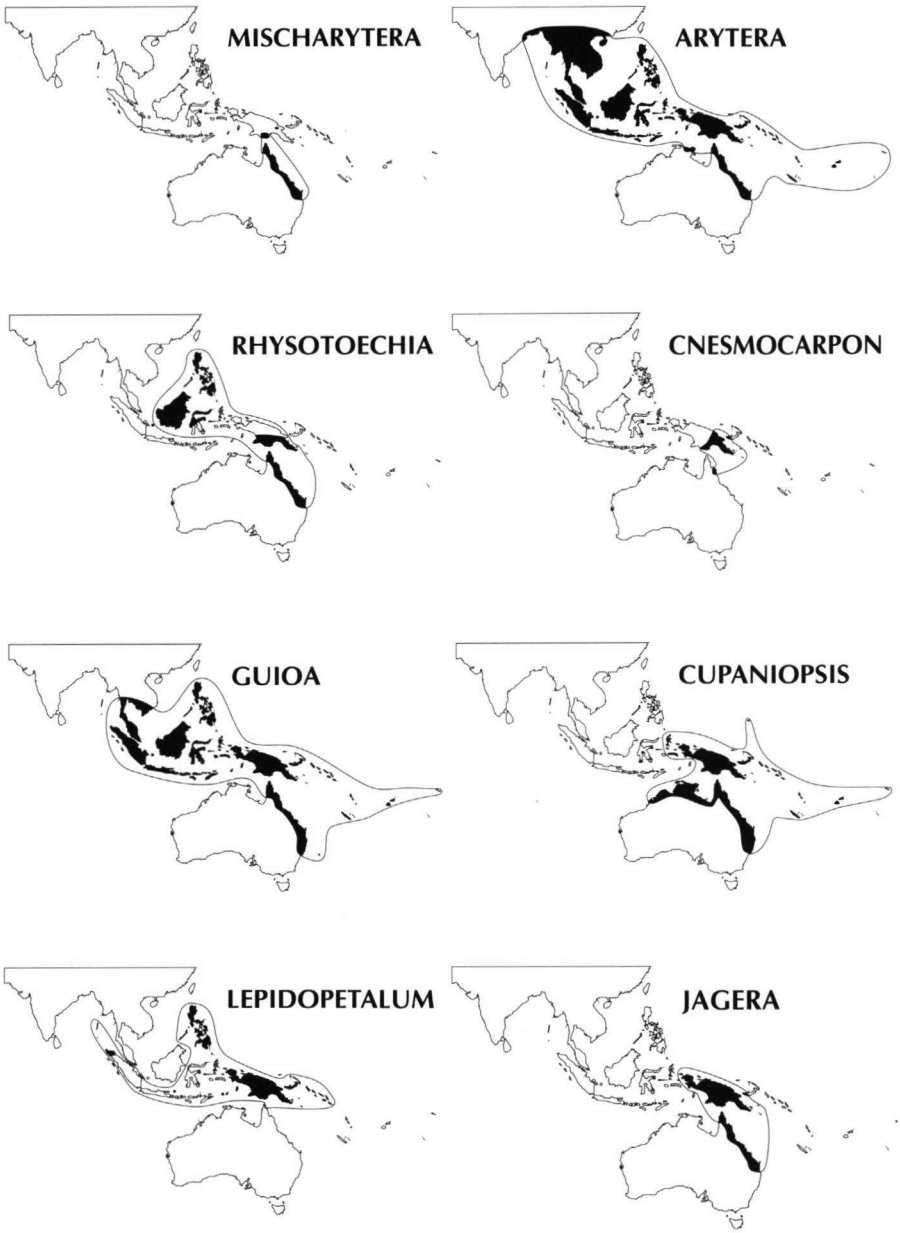


FIGURE 4.1. Distribution maps for the eight Sapindaceous genera employed in the biogeographical analysis. *Rhysotoechia* has a disjunct distribution, but may be expected in Irian Jaya and the Moluccas. *Lepidopetalum* likewise has a seemingly disjunct distribution; in fact specimens are known from the Lesser Sunda Islands, Moluccas, Sulawesi, and Java, but these could not be identified to the species level by Van Welzen et al. (1992).

4.2 – DATA

4.2.1 – **Cladograms and distribution data**

At present cladograms are available for eight genera of Sapindaceae: *Mischarytera* and *Arytera* (see Chapter 3), *Cnesmocarpon* and *Jagera* (Adema & Van der Ham 1993), *Cupaniopsis* (Adema 1991), *Guioa* (Van Welzen 1989), *Lepidopetalum* (Van Welzen et al. 1992), and *Rhysotoechia* (Etman 1994). The cladograms for these genera were all constructed using morphological characters, in some cases including leaf anatomical and pollen morphological data, and employing the phylogeny reconstruction program Hennig86 (Farris 1988). In the cases of *Cupaniopsis* and *Guioa* the cladograms are not most parsimonious reconstructions for the data, because due to the high number of homoplasies many equally parsimonious solutions resulted. Rather, the investigators of these genera decided to divide them into a number of probably mono- or paraphyletic species groups which were analysed separately. The resulting cladograms were then reunited into a single complete cladogram for each genus (see Van Welzen 1989 for details of this procedure). The *Arytera* cladogram is a strict consensus tree based on three equally parsimonious trees (see Chapter 3). *Arytera multijuga* is retained as the most basal species, although its exact position (and even its inclusion in the genus) is doubtful (see Chapter 3). All remaining cladograms are unique most parsimonious trees (MPTs), or in the case of *Lepidopetalum* a considered choice amongst several MPTs.

Distribution data for all 168 species were obtained from the literature mentioned and augmented by data provided by the respective authors and from herbarium material kept in L. The distributions of the genera are shown in Fig. 4.1. The distributions and the cladograms (see Tables 4.1 and 4.2, and Fig. 4.11 below) suggest that these genera are all Australian/New Guinean in origin and may be expected to have evolved together for a considerable period of time. They are all members of the same tribe of Sapindaceae, with similar kinds of flowers, fruits, and ecological requirements, and presumably also have similar dispersal abilities. For these reasons, their biogeographic patterns are expected to reflect the same history. This justifies combining them in a single analysis. Obviously, the results of this study are therefore not so general as when very diverse groups of organisms are used, but on the other hand the risk of comparing very different patterns is minimised.

4.2.2 – **Areas of endemism**

The 25 areas of endemism employed here are depicted in Fig. 4.2. They were adapted mainly from Van Welzen (1989), but with the following exceptions:

— *West Malesia:* In each genus the species occurring in the Malesian archipelago West of New Guinea form a monophyletic group. As this study is not concerned with relationships among areas of endemism in West Malesia, this whole area is taken as a single area of endemism here.

— *New Britain:* Van Welzen recognised three areas of endemism here: West New Britain, East New Britain, and New Ireland + Manus Island. However, only the cicada genera employed by him show evidence of vicariance in this area; also, his

analysis showed these areas to form a monophyletic set. Since in these areas none of the genera employed here have vicariated, they are united into a single area.

— *Papuan Islands:* Again, Van Welzen separated these into two parts: the East and the West Papuan Islands. The *Guioa* species occurring here form monophyletic (*G. misimaensis* and *G. plurinervis*) or paraphyletic (*G. rigidiuscula* and *G. normanbiensis*) groups. Moreover, *G. rigidiuscula* is widespread. In his analysis the East and West Papuan Islands form a paraphyletic set, with East North New Guinea + Peninsula as their monophyletic sister areas. Because no other genus in this study has endemics in the Papuan Islands, I decided to group them together into a single area too.

— *Morobe:* This area was not recognised by Van Welzen (1989), but did occur in his study of *Lepidopetalum* (Van Welzen et al. 1992). *Arytera* also has an endemic here.

— *Loyalty Islands:* This area was included by Van Welzen (1989) in New Caledonia. However, following the recommendations of Axelius (1991) it should be separated from the latter because not all species occurring there occur also on the Loyalty Islands.

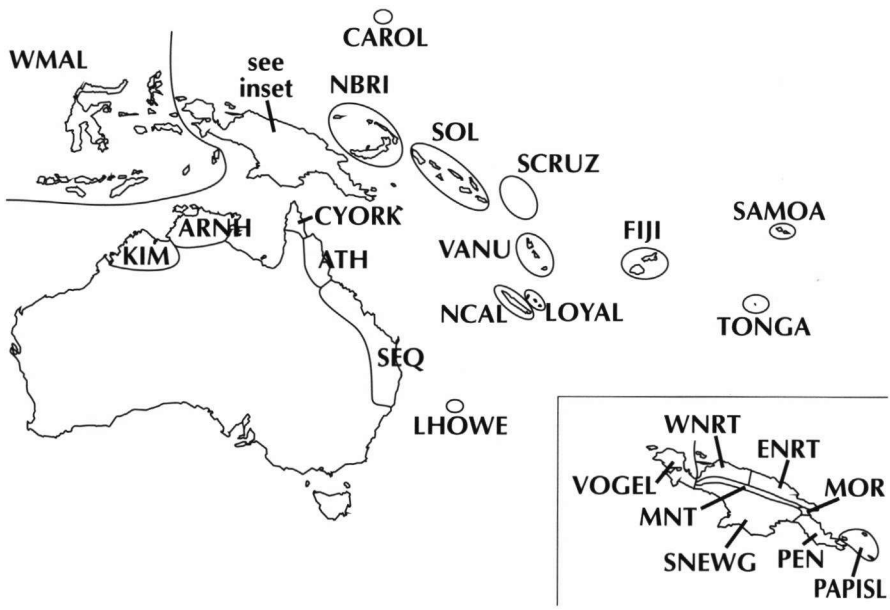


FIGURE 4.2. The 25 areas of endemism employed in the biogeographical analysis. Abbreviations: SEQ: Southeast Queensland (and northern New South Wales); ATH: Atherton Tableland; CYORK: Cape York; ARNH: Arnhem Land; KIM: Kimberley Plateau; SNEWG: South New Guinea; PEN: Peninsula; MOR: Morobe; ENRT: East North New Guinea; WNRT: West North New Guinea; MNT: Central Mountain Range; VOGEL: Vogelkop; WMAL: West Malesia; NBRI: New Britain; PAPISL: Papuan Islands; SOL: Solomon Islands; SCRUZ: Santa Cruz archipelago; VANU: Vanuatu archipelago; LOYAL: Loyalty Islands; NCAL: New Caledonia: LHOWE: Lord Howe Island; FIJI: Fiji Islands; SAMOA: Samoa; TONGA: Tonga; CAROL: Carolina Islands.

4.3 – METHODS

4.3.1 – Brooks Parsimony Analysis

Firstly, Brooks Parsimony Analysis was employed. An investigator applying BPA (or other methods of cladistic biogeography) is faced with several problems. The first problem is that of widespread taxa. In short, a taxon can be widespread for two reasons: it may not have responded to vicariance events that affected other monophyletic groups, or it may have become widespread due to dispersal. In the first case, the set of areas in which the taxon occurs is monophyletic (i.e. formed a single area of endemism in the past), while in the second case it may be para- or even polyphyletic (formed only part of a single area of endemism in the past). Several constraints have been proposed to contain this problem, which are known as Assumptions 1 and 2 (Nelson & Platnick 1981) and Assumption 0 (Zandee & Roos 1987). Under Assumptions 1 and 2, the set of areas inhabited by a widespread taxon is not taken *a priori* to be monophyletic, and is thus assumed not to be (fully) informative. Under Assumption 0, on the other hand, analogous to phylogeny reconstruction, the occurrence of the widespread taxon is assumed to be homologous in all areas until proven otherwise (by parsimony analysis). On theoretical grounds (why assume *a priori* that identical character states, i.e. the occurrences of a single taxon in several areas of endemism, are homoplasious? – note the analogy with Hennig's Auxiliary Principle) I prefer Assumption 0.

The second problem in BPA is how to code an area for those monophyletic groups that are missing from it altogether ('missing taxon' or 'missing area' problem). The problem arises because if such areas are coded as truly absent (0) for these groups, they are often artificially placed lower on the resulting generalised areagram than would be expected from inspecting the individual cladograms. The reason is that the codings in the columns for ancestral taxa are not independent of those of their descendants, leading to possible overestimation of the number of reversals in cases of extinction or primitive absence from part of an ancestral area of endemism. It is often recommended to code such areas as missing data (?) for these groups (Wiley 1988a, b; Brooks 1990). This does not mean that actual or hypothesised ancestral species have occurred in these areas in the past; rather this procedure is a technicality aimed at circumventing the interdependence of the codings for ancestral and descendant taxa. It has proven heuristically to give reasonable results.

Two different kinds of BPA analysis were performed. In one, missing areas were coded as true absence; in the other, as unknown data (also for terminal taxa, as recommended by Brooks [1990]; Wiley [1988a, b] only codes ancestral taxa as unknown). The data matrices (see Table 4.1) were analysed using the programs NONA (Goloboff 1993b) and Hennig86 (Farris 1988). The large number of areas precluded an exhaustive search for most parsimonious trees; therefore heuristic searches were carried out, building initial trees with NONA's mu*50 command followed by branch-swapping with Hennig86's bb* (see Chapter 3 for a discussion of the deficiencies of Hennig86's initial tree builder mh*).

4.3.2 – Component Compatibility Analysis

The second analytical method employed was Component Compatibility Analysis (Zandee & Roos 1987). This method is identical to BPA in the way the data are coded, and thus faces the same difficulties with widespread and missing taxa, but differs in the analytical method employed. CCA is not based on the Wagner algorithm, but uses component compatibility (the computer program CAFCA; Zandee 1994) to construct initial areagrams. As components (potential building blocks for areagrams) the distributions of terminal taxa or the combined distributions of the descendants of ancestral taxa (internal nodes in cladograms) are used. As Van Welzen (1989) has argued, this has the advantage that the components allowed in constructing areagrams are all defined by the shared *presence* of (ancestral) taxa, never by shared *absence*, as sometimes is the case with BPA. He therefore prefers CCA over BPA. Sosef (1994), though, argues that when extinction or dispersal has occurred this will result in incorrect components, which may subsequently lead to a preference for incorrect areagrams. He therefore prefers BPA, although he concedes that the resulting areagrams should be checked against components characterised by the shared absence of taxa.

Like in the BPA analyses, widespread taxa were treated under Assumption 0. Missing areas were treated as true absence or as unknown data; in addition a third protocol was employed for missing areas which takes advantage of the properties of the compatibility algorithm. This protocol is described in the next Section. All CCA runs were carried out with the following options activated:

— All columns equivalent;
— No specific outgroup area designated;
— Cladon (i.e. component) definition by partial monothetic sets;
— Selection criterion for areagrams: minimum number of steps;
— Ancestral state indicated by zeroes.

4.3.2.1 – *An alternative method for the treatment of missing areas under CCA*

As mentioned above, when missing areas are coded as true absence they are often placed lower on the generalised areagram than would be expected from inspecting the individual cladograms in which these areas are present. An example is given in

TABLE 4.1. Data matrix for BPA, coding missing taxa as unknown data (?). For CCA, the outgroup area should be removed. In order to retrieve the data matrix for the coding of missing taxa as absences replace the question marks by zeroes.

	OUTGROUP AREA
Mischarytera	00000
Arytera	0000000000000000000000000000000000000000000000
Rhysotoechia	0000000000000000000000000000000
Cnesmocarpon	0000000
Guioa	0000000000000000000000000000000000000000000000000000000000000000000
	0000000000000000000000000000000000000
Cupaniopsis	0000000000000000000000000000000000000000000000000000000000000000000
	000000000000000000000000000000000000000000000000
Lepidopetalum	00000000000
Jagera	0000

(Table 4.1, continued)

	SEQ
Mischarytera	00101
Arytera	0000111100000001010000000000001111111000100011
Rhysotoechia	1010000000000001111101000111111
Cnesmocarpon	???????
Guioa	00000000000000000000000000000011000000000000000000000000000000000000
	0000000110111000000000000001010000001
Cupaniopsis	00011100011000000010000000000110000000000000000000000000000000000000
	000000000000000001000011110111111111111110111111
Lepidopetalum	???????????
Jagera	1001

	ATH
Mischarytera	00101
Arytera	0000110000010001000000001110011011111000100011
Rhysotoechia	1011100000000001111101000111111
Cnesmocarpon	0010111
Guioa	00000000000000000000000000000011010000000000000000000000000000000000
	0000000111111000000000000001010000001
Cupaniopsis	00001000100000000001100000000010000000000000000000000000000000000000
	000000000000000000000011111111111111011110111111
Lepidopetalum	???????????
Jagera	1101

	CYORK
Mischarytera	01011
Arytera	0000100000001011000000000001111011111000100011
Rhysotoechia	0100000000000000000000000001011
Cnesmocarpon	???????
Guioa	00000000000000000000000000000001000000000000000000000000000000000000
	0000000110111000000000000001010000001
Cupaniopsis	00001000000000000001010000000010000000000000000000000000000000000000
	000000000000000000000011111111111111011110111111
Lepidopetalum	10000000001
Jagera	1001

	ARNH
Mischarytera	?????
Arytera	0000100000000000000000000000000001111000100011
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	??
	?????????????????????????????????????
Cupaniopsis	00000000000000000000000000000100000000000000000000000000000000000000
	000000000000000000000001111010000000000000000001
Lepidopetalum	???????????
Jagera	????

	KIM
Mischarytera	?????
Arytera	??
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	??
	?????????????????????????????????????
Cupaniopsis	00000000000000000000000000000100000000000000000000000000000000000000
	000000000000000000000001111010000000000000000001
Lepidopetalum	???????????
Jagera	????

(Table 4.1, continued)

	SNEWG
Mischarytera	01011
Arytera	0000100000100000000000001110011011111000100011
Rhysotoechia	0000100000001000001101000110001
Cnesmocarpon	0010111
Guioa	00000000000000000000000000100001000000000000000000000000000000000000 0000000110111000000000000001010000001
Cupaniopsis	00000010000000000000000000000100000000100000000000000000000000000000 000000000111110011000001110100000000000001111111
Lepidopetalum	10000000001
Jagera	1011

	PEN
Mischarytera	?????
Arytera	0000000000001110100000000001111010001000100011
Rhysotoechia	0000000001110110111111000110001
Cnesmocarpon	0111111
Guioa	00000000000011110000011100000001000000000000000000000000000000000000 0000000110111111100111111011010000001
Cupaniopsis	11100010000011000000000000000000000000100000000000000000000000000000 000000000111110011000001110100000111011001111111
Lepidopetalum	10000000001
Jagera	0011

	PAPISL
Mischarytera	?????
Arytera	??
Rhysotoechia	???????????????????????????????
Cnesmocarpon	0100011
Guioa	00000000000000011011010000000000000000000000000000000000000000000000 0000000000001011111110011011010000001
Cupaniopsis	00000010000000000000000000000000000000000000000000000000000000000000 000000000000000000000000000000000000000001111111
Lepidopetalum	???????????
Jagera	0011

	MNT
Mischarytera	10011
Arytera	0000000010000000000000010010011010001000100011
Rhysotoechia	0000000010000000000000001110001
Cnesmocarpon	1000001
Guioa	00000000100000000000000011010001000000000000000000000000000000000000 0000000000011000000000111011110000001
Cupaniopsis	00000011000110000000000000000000000000000000000000000000000000000000 000000000000000000000000000000000011011001111111
Lepidopetalum	???????????
Jagera	0011

	MOR
Mischarytera	?????
Arytera	0000000001000000100000000110011010001000100011
Rhysotoechia	???????????????????????????????
Cnesmocarpon	0100011
Guioa	00000000000011010000010000000000000000000000000000000000000000000000 0000000000000111100110011011010000001
Cupaniopsis	00000011000010000000000000000000000000100000000000000000000000000000 000000000111110011000001110100000011011001111111
Lepidopetalum	00100000111
Jagera	0011

(Table 4.1, continued)

	ENRT
Mischarytera	?????
Arytera	0000000000000000100000000000001010001000100011
Rhysotoechia	???????????????????????????????
Cnesmocarpon	0010111
Guioa	0000000000001001000001000000000000000000000000000000000000000000000
	0000000000000111100110011011010000001
Cupaniopsis	0000001100001000000000000000000000000011000000000000000000000000000
	000000000111110011000001110100000011011001111111
Lepidopetalum	01010001111
Jagera	0011

	WNRT
Mischarytera	?????
Arytera	0000000000000000100000000000001010001000100011
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	0000000001010000010000000000000000000000000000000000000000000000000
	0000000000000000100010011111110000001
Cupaniopsis	0000001100000000000000000000000000000001000000000000000000000000000
	000000000111110011000001110100000000000001111111
Lepidopetalum	01010001111
Jagera	0011

	VOGEL
Mischarytera	?????
Arytera	0000000000000000100000000000001010001000100011
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	0000000000000000010000000001000100000000000000000000000000000000000
	0000000110111000100010011011010000001
Cupaniopsis	0000001000000000000000000000000000000001000000000000000000000000000
	000000000111110011000001110100000000000001111111
Lepidopetalum	1000000001
Jagera	0011

	WMAL
Mischarytera	?????
Arytera	0000000000000000100000000000001010001000100011
Rhysotoechia	0000011100000000000000111110001
Cnesmocarpon	???????
Guioa	0000000000100000010000000000000100000000001111111111111111111111000
	0000001110111000100010011111110000001
Cupaniopsis	0000000000001000000000000000000000001100000000000000000000000000000
	000000000011110011000001110100000011011000011111
Lepidopetalum	0001111111
Jagera	0011

	NBRI
Mischarytera	?????
Arytera	0000000000000000101000000000001110001000100011
Rhysotoechia	???????????????????????????????
Cnesmocarpon	0110111
Guioa	0000000000000000000011000000000000000000000000000000000000000000000
	0000000000000000001110011011010000001
Cupaniopsis	0000000000001000000000000000000000000000000000000000000000000000000
	000000000000000000000000000000000011011000011111
Lepidopetalum	0100000011
Jagera	0011

(Table 4.1, continued)

	SOL
Mischarytera	?????
Arytera	0100000000000000101000000000001110001000110111
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	0000001100000000000000000000000000000000000000000000000000000000000
	0000000000000000000000000000000000011
Cupaniopsis	0000000000000010000000000000000000000000000000000000000000000000000
	000000000000000000000000000000001111011000011111
Lepidopetalum	01000000011
Jagera	????
	SCRUZ
Mischarytera	?????
Arytera	??
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	0000010000000000000000000000000000000000000000000000000000000000000
	0000000000000000000000000000000000111
Cupaniopsis	???
	??
Lepidopetalum	???????????
Jagera	????
	VANU
Mischarytera	?????
Arytera	0100000000000000000000100000000000000111110111
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	0000100000000000000000000000000000000000000000000000000000000000000
	0000000000000000000000000000000001111
Cupaniopsis	0000000000000000100000000000000000000000000000000000000000000000000
	000000000000000000000000000000111111011000011111
Lepidopetalum	???????????
Jagera	????
	LOYAL
Mischarytera	?????
Arytera	1000000000000000000010100000000000000111110111
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	0000000000000000000000000000000000110000000000000000000000000000000
	1111111110111000000000000000101000000 1
Cupaniopsis	0000000000000000000000000000000100000000000000011000000000000000000
	111000110000011111000001110100000000000000000001
Lepidopetalum	???????????
Jagera	????
	NCAL
Mischarytera	?????
Arytera	1011000000000000000111100000000000000111111111
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	0000000000000000000000000000000001111111110000000000000000000000111
	1111111110111000000000000000101000000 1
Cupaniopsis	0000000000000000000000111111100111110000111111111111111000001111111
	111111111000111111111111110100000000000000000001
Lepidopetalum	???????????
Jagera	????

(Table 4.1, continued)

———	**FIJI**
Mischarytera	?????
Arytera	0100000000000000000000000000000000000010111
Rhysotoechia	????????????????????????????????
Cnesmocarpon	???????
Guioa	0111000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000001111111
Cupaniopsis	0000000000000001110000000000000000000000000000000000000010111110010001000110000010011000001110101111111011000011111
Lepidopetalum	???????????
Jagera	????
———	**TONGA**
Mischarytera	?????
Arytera	0100000000000000000000000000000000000010111
Rhysotoechia	????????????????????????????????
Cnesmocarpon	???????
Guioa	1000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000001111111
Cupaniopsis	???
Lepidopetalum	???????????
Jagera	????
———	**SAMOA**
Mischarytera	?????
Arytera	0100000000000000000000000000000000000010111
Rhysotoechia	????????????????????????????????
Cnesmocarpon	???????
Guioa	???
Cupaniopsis	0000000000000000000000000000000000000000000000000000000100011110010001000110000010011000001110100000000000000001
Lepidopetalum	???????????
Jagera	????
———	**LHOWE**
Mischarytera	?????
Arytera	???
Rhysotoechia	????????????????????????????????
Cnesmocarpon	???????
Guioa	0000000000000000000000000000000010000000000000000000000000000000000000000000000000000000000000001111011100000000000000001010000001
Cupaniopsis	???
Lepidopetalum	???????????
Jagera	????
———	**CAROL**
Mischarytera	?????
Arytera	???
Rhysotoechia	????????????????????????????????
Cnesmocarpon	???????
Guioa	???
Cupaniopsis	0000000000000000000000000000000000000000000000000000000000001111110010001000110000010011000001110100000000000000001
Lepidopetalum	???????????
Jagera	????

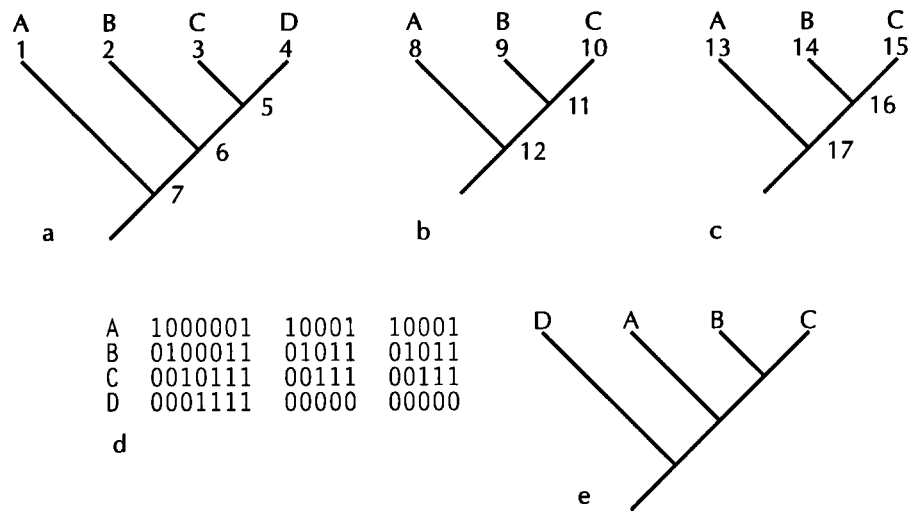


FIGURE 4.3. (a–c) Cladograms for three monophyletic groups, with the distributions of the terminal taxa indicated. (d) Data matrix for biogeographic analysis with missing area D coded as absent for the last two genera. (e) The resulting generalised areagram. Note the basal position of area D.

Fig. 4.3. Here area D is missing from the cladograms of the second and third monophyletic groups. As a result area D is placed most parsimoniously at the base of the areagram, rather than as sister area to area C. This is caused by the absence codings of D for the second and third groups, which would result in four reversals (for ancestors 11, 12, 16, 17) in area D if it were placed as sister to area C (as indicated by its position in the first monophyletic group), rather than the two extra steps (for ancestors 5 and 6) needed to place it in the basal position. The same result is obtained whether BPA is used or CCA, but in the latter analysis a second areagram is equally parsimonious: (A(D(B C))); the difference is due to the addition of an artificial all-zero outgroup area in the BPA analysis. Thus, when coding a missing area as absent, its position is the result of a trade-off between the number of extra steps caused by extinction (reversals) if the area is placed high up in the areagram, and the number of extra steps caused by dispersal (parallels) if the area is placed close to the root. In general, as in the example in Fig. 4.3, a position close to the root is more parsimonious. If the missing area in Fig. 4.3 is coded as unknown data, the resulting areagram does show a sister area relationship between areas C and D, as expected from examining the individual cladograms. However, in more complicated cases this is not necessarily the case.

Of course, area D may actually be the sister area of areas A, B, and C together, but there is nothing in the original data to support this hypothesis. Rather, the only data we have in this example regarding the position of area D come from the first cladogram, which indicates a sister area relationship with C, as is borne out by the analysis with D coded as unknown for the second and third groups. This information can be used together with the properties of CCA to decide in which component of the final area-

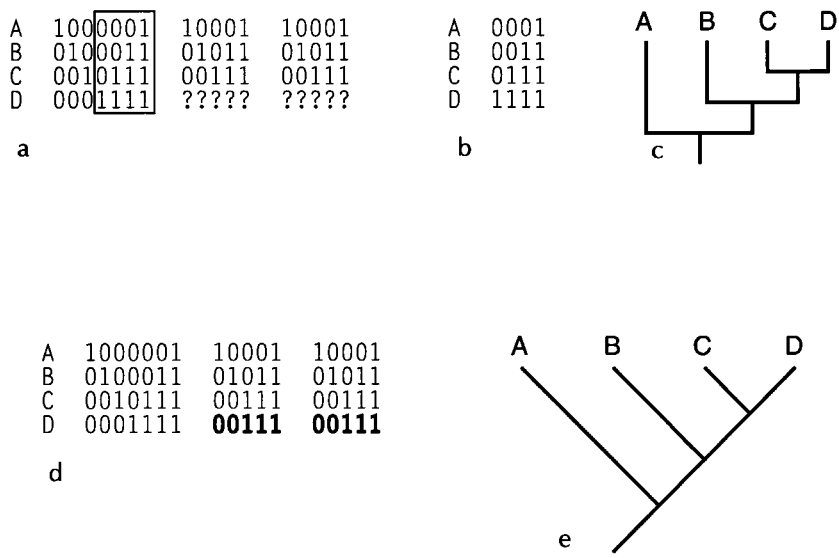
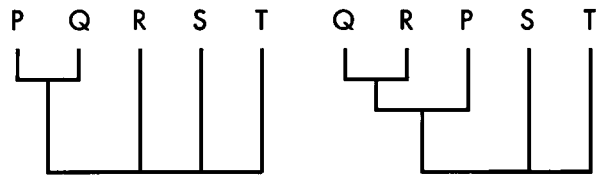


FIGURE 4.4. The procedure for coding missing areas illustrated with the example from Fig. 4.3. (a) The data matrix with missing areas coded as unknown data. (b) The matrix for analysing missing area D, consisting only of those columns from (a) which have D coded as present. (c) The resulting 'areagram' shows that D is contained in a component together with C. (d) Columns 10–12, 15–17 contain a '1' for area C and are given a '1' for area D too; columns 8, 9, 13, and 14 do not contain a '1' for area c and are coded '0' for area D (substituted codings in **bold**). (e) The result of analysing the matrix in (d).

gram(s) area D belongs (cf. Turner 1992). The procedure (illustrated in Fig. 4.4 with the example of Fig. 4.3) is as follows:

(1) Select those columns from the original data matrix which contain a '1' for the missing area under consideration (in Fig. 4.3, area D) (Fig 4.4a).
(2) Analyse the resulting partial matrix (Fig. 4.4b) with CCA. The result will be a graph (Fig. 4.4c) which cannot be interpreted as an areagram, but will show the smallest component of which the missing area is part (CD in Fig. 4.4c).
(3) Locate in the original data matrix those columns which correspond to the monophyletic groups from which the area is missing (columns 8–17 in Fig. 4.4a). Within those blocks, select the columns in which the remaining areas of the component identified in step 2 are coded as present (i.e. columns 10–12, 15–17 in Fig. 4.4a).
(4) Code the missing area as present in the columns selected in step 3, and as absent in the other columns coding for the groups from which the area is missing (bold figures in Fig. 4.4d).
(5) Reanalyse the resulting data matrix with CCA (Fig. 4.4e).

As can be seen, D is now unambiguously placed as the sister area to C. The five steps should of course be repeated for each area that is missing from one of the monophyletic groups.



a

```
P  ???????  ?????  100000111  ...
Q  1000111  ?????  010000111  ...
R  0100111  10001  001000011  ...
S  0010011  01011  000101001  ...
T  0001001  00111  000011001  ...
```

b

```
P  1000111  00000  100000111  ...
Q  1000111  10001  010000111  ...
R  0100111  10001  001000011  ...
S  0010011  01011  000101001  ...
T  0001001  00111  000011001  ...
```

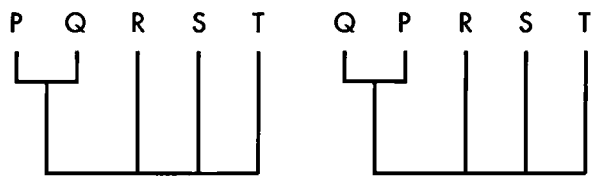
c

```
P  1000111  10001  100000111  ...
Q  1000111  10001  010000111  ...
R  0100111  10001  001000011  ...
S  0010011  01011  000101001  ...
T  0001001  00111  000011001  ...
```

d

FIGURE 4.5. (a) Area P belongs in a component with area Q, while area Q belongs in a component with area R. (b) Part of the original data matrix containing the monophyletic groups from which areas P and/or Q are missing. (c) Substituting first for P, then for Q results in absence of P from the second monophyletic group. (d) Repeating the substitution process (or substituting first for Q, then for P) results in presence codes for P in the second group.

The procedure described above is usually sufficient for analysing simple cases with few missing areas. However, in the analyses presented below, the situation is much more complicated, making additions to the protocol necessary. The first problem is that of the order in which substitutions are carried out. For example, in Fig. 4.5 we have a situation in which area P is shown to belong to a component with area Q, while area Q belongs to a component with area R. First substituting for area P and then for area Q (Fig. 4.5c) will lead to a different result than doing the exercise in the opposite order (Fig. 4.5d). This problem can be circumvented by iterating the substitution procedure till the data set changes no longer. The result is expected to be independent of the order in which the different substitutions are carried out, although I have no proof for this conjecture.



a

P	**1000111**	**00000**	100000111	...
Q	1000111	**00000**	010000111	...
R	0100111	10001	001000011	...
S	0010011	01011	000101001	...
T	0001001	00111	000011001	...

b

FIGURE 4.6. (a) Area P belongs in a component with area Q, while area Q belongs in a component with area P. The part of the original matrix shown is assumed to have the same form as in Fig. 4.5. (b) Repeated substitution leaves the second monophyletic group with absences for both areas.

A more serious problem is encountered when area P belongs to a component with area Q, while area Q belongs to a component with area P (Fig. 4.6). In this case, a monophyletic group which is absent from both areas P and Q will not receive present codings for these areas at all, with the result that their position in the final areagram will still suffer from the missing area problem. This can be avoided by analysing the columns in which both P and Q are coded as present in the original matrix, and substituting for the smallest component of which they are both part (Fig. 4.7). This procedure should be repeated for all sets of missing areas which are mutually dependent, and the different substitutions should be iterated till the data set changes no longer.

Because analysing a missing area may produce more than one most parsimonious graph, sometimes each showing a different component of which the area is part, the above procedure can result in several different final data sets, and thus in different final areagrams. This problem does not seem to be very serious, though. In the Sapindaceae data set analysed here, few missing areas gave more than one graph, and only a subset of those showed different results for the smallest component, leading to a manageable number of possible final matrices, which in some cases were even identical.

One of the properties of the procedure is that it takes into full account only the 'hard' evidence (proven presence of taxa) pertaining to the position of a missing area, not 'soft' evidence in the form of absence (which may always turn out to have been due to extinction or undercollection). In addition, instead of allowing several to many different areagrams, which is often the case when missing areas are coded as unknown data, many possibilities for the positions of the different missing areas are eliminated beforehand, resulting in a data set which gives only very few different areagrams. Thus, much ambiguity is eliminated, greatly facilitating the final choice for a particular areagram.

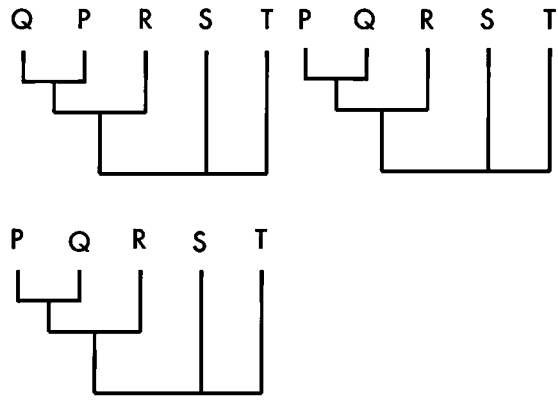


FIGURE 4.7. (a) Areas P and Q together belong in a component with area R. (b) Substituting first for P and Q separately (see Fig. 4.6), and then for P and Q together, results in presence codes for P and Q in the second monophyletic group.

The biological interpretation that can be given to this method of analysis is that monophyletic groups that are absent from an area are treated as if they were present there in accordance with the general pattern shown by other groups in the analysis. In other words, the distributions of the extant and ancestral taxa are reconstructed as they would have been if the whole clade had been primitively present in the area, and if the clade had responded to all vicariance events as they are reconstructed from the other groups.

4.3.3 – COMPONENT

The third method of analysis employed was Component Analysis, as implemented in COMPONENT, version 2.0 (Page 1993a). Due to the high number of widespread species (48, or 28.2%) only an Assumption 1 analysis was performed (widespread taxa not mapped). Missing areas were treated as missing data. Trees were searched heuristically, with the subtree pruning and regrafting option for branch swapping. The criterion minimised was 'leaves added,' which is equivalent to $^1/_2$ the number of 'items of error' of Nelson & Platnick (1981). This analysis comes closest to an Assumption 1 analysis as envisaged by them. The nexus file for analysis with COMPONENT is given in Table 4.2. Because COMPONENT can handle fully dichotomous trees only, all possible completely resolved branching orders for the phylogenies of *Arytera*, *Jagera*, and *Guioa* were investigated separately before the analysis with all genera was done in order to

TABLE 4.2. Nexus file of the data for use in COMPONENT. The RANGE commands in the distribution blocks give the distributions of the taxa over the areas of endemism. Thus, e.g. *Mischarytera lautereriana* occurs in areas 1 and 2, i.e. in Southeast Queensland and the Atherton Tablelands. The TREE commands give the different fully resolved trees in parenthetical notation. Note that numbering begins with '1' throughout.

```
#NEXUS

BEGIN TAXA;
  DIMENSIONS NTAX = 25;
  TAXLABELS
    SEQ
    ATH
    CYORK
    ARNH
    KIM
    SNEWG
    PEN
    PAPISL
    MNT
    MOR
    ENRT
    WNRT
    VOGEL
    WMAL
    NBRI
    SOL
    SCRUZ
    VANU
    LOYAL
    NCAL
    FIJI
    TONGA
    SAMOA
    LHOWE
    CAROL;
ENDBLOCK;

BEGIN DISTRIBUTION;
  TITLE = 'Mischarytera';
  NTAX = 3;
  RANGE
    Mbullata: 9,
    Mlautereriana: 1 2,
    Mmacrobotrys: 3 6;
  TREE T1 = (2,(1,3));
ENDBLOCK;

BEGIN DISTRIBUTION;
  TITLE = 'Arytera';
  NTAX = 24;
  RANGE
    Aarcuata: 19 20,
    Abifoliolata: 1 2 3 4 6,
    Abrackenridgei: 16 18 21 22 23,
    Achartacea: 20,
    Acollina: 19 20,
    Adensiflora: 9,
    Adictyoneura: 1 2,
    Adistylis: 1,
    Adivaricata: 1 2 3,
    Afoveolata: 1,
    Agracilipes: 20,
    Alepidota: 20,
    Alineosquamulata: 3 7,
    Amicrophylla: 1,
    Aminiata: 7,
    Amorobeana: 10,
    Amultijuga: 9,
    Amusca: 6,
    Anekorensis: 20,
    Aneoebudensis: 18 19 20,
    Anovaebrittanniae: 11 15,
    Apauciflora: 2,
    Apseudofoveolata: 3 7,
    Alitoralis: 7 9 10 11 12 13 14 15 16;
  TREE T1 = (17,(((1,3),(11,12)),(((8,(14,(2,7))),(((9,
    24),((6,(16,(18,22))),(13,(15,23)))),(10,21))),
    (20,(4,(5,19))))));
  TREE T2 = (17,(((1,3),(11,12)),(((8,(14,(2,7))),((9,
    (24,((6,(16,(18,22))),(13,(15,23))))),(10,21))),
    (20,(4,(5,19))))));
  TREE T3 = (17,(((1,3),(11,12)),(((8,(14,(2,7))),((24,
    (9,((6,(16,(18,22))),(13,(15,23))))),(10,21))),
    (20,(4,(5,19))))));
ENDBLOCK;

BEGIN DISTRIBUTION;
  TITLE = 'Rhysotoechia';
  NTAX = 16;
  RANGE
    Rbifoliolata: 1 2,
    Rnitida: 3,
    Rmortoniana: 1 2,
    Rflorulenta: 2,
    Rrobertsonii: 2 6,
    Rgrandifolia: 14,
    Rramiflora: 14,
    Rkoordersii: 14,
    Rcongesta: 9,
    Rmultiscapa: 7,
    Rapplanata: 7,
    Robtusa : 7,
```

(Table 4.2, continued)

```
      Rbilocularis: 6,
      Rgracilipes: 7,
      Relongata: 7,
      Rflavescens: 1 2;
   TREE T1 = (((1,2),(3,4)),(5,((9,(8,(6,7))),((10,11),
      (12,(13,(14,(15,16)))))));
ENDBLOCK;

BEGIN DISTRIBUTION;
   TITLE = 'Cnesmocarpon';
   NTAX = 4;
   RANGE
      Cdasyantha: 2 6 7 11 15,
      Cdentata: 9,
      Cdiscoloroides: 7 8 10 15,
      Cmontana: 7;
   TREE T1 = (2,(3,(1,4)));
ENDBLOCK;

BEGIN DISTRIBUTION;
   TITLE = 'Guioa';
   NTAX = 54;
   RANGE
      Glentiscifolia: 22,
      Gchrysea: 21,
      Gpunctata: 21,
      Grhoifolia: 21,
      Gnovoebudaensis: 18,
      Gmegacarpa: 17,
      Gelliptica: 11,
      Gsufusana: 11,
      Gpseudoamabilis: 9,
      Gpteropoda: 12,
      Gpatentinervis: 14,
      Gmelanopoda: 12,
      Gcontracta: 7 10 11,
      Ggrandifoliola: 7 10,
      Garyterifolia: 7,
      Grigidiuscula: 7 8 10 11,
      Gnormanbiensis: 7,
      Gmembranifolia: 12 13 14,
      Gmisimaensis: 8,
      Gplurinervis: 8,
      Gnovobritannica: 15,
      Gcomesperma: 7 8 10 11 15,
      Ghospita: 7,
      Gmolliuscula: 7,
      Gscalariformis: 9,
      Gunguiculata: 7 11,
      Goligotricha: 6,
      Gsubsericea: 9 13,
      Gmontana: 2,
      Glasioneura: 2,
      Gsemiglauca: 1,
      Gacutifolia: 1 2 3 6 7 8 9 13 14,
      Gcoriacea: 24,
      Gmicrosepala: 20,
      Gfusca: 19 20,
      Ggracilis: 19 20,
      Gpectinata: 20,
      Govalis : 19 21,
      Gcrenata: 20,
      Gcrenulata: 20,
      Gvillosa: 20,
      Gglauca : 20,
      Gasquamosa: 14,
      Ghirsuta: 14,
      Gdiplopetala: 14,
      Gbijuga : 14,
      Gpleuropteris: 14,
      Gpterorhacis: 14,
      Gpubescens: 14,
      Gdiscolor: 14,
      Gkoelreuteria: 14,
      Gacuminata: 14,
      Greticulata: 14,
      Gmyriadenia: 14;
   TREE T1 = ((8,(7,(5,(6,(4,(3,(1,2)))))),((9,10),(((11,
      12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,
      (19,20)))),(25,(23,24))))),(27,(28,((29,30),
      (31,(32,((33,(34,((38,(37,(35,36))),(42,(41,
      (39,40)))))),(43,(44,(45,((46,(47,48)),(49,(50,
      ((51,52),(53,54))))))))))))));
   TREE T2 = ((8,(7,(6,(5,(4,(3,(1,2)))))),((9,10),(((11,
      12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,(19,
      20)))),(25,(23,24))))),(27,(28,((29,30),(31,32,
      ((33,(34,((38,(37,(35,36))),(42,(41,(39,40)))))),
      (43,(44,(45,((46,(47,48)),(49,(50,((51,52),
      (53,54))))))))))))));
   TREE T3 = ((8,(7,((5,6),(4,(3,(1,2))))),((9,10),(((11,
      12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,
      (19,20)))),(25,(23,24))))),(27,(28,((29,30),(31,
      (32,((33,(34,((38,(37,(35,36))),(42,(41,(39,
      40)))))),(43,(44,(45,((46,(47,48)),(49,(50,((51,
      52),(53,54))))))))))))));
   TREE T4 = ((8,(7,(5,(6,(4,(3,(1,2)))))),((9,10),(((11,
      12),(26,(((18,(17,(16,(15,(13,14))))),(22,(21,(19,
      20)))),(25,(23,24))))),(27,(28,((29,30),(31,(32,
      ((33,(34,((38,(37,(35,36))),(42,(41,(39,40)))))),
      (43,(44,(45,((46,(47,48)),(49,(50,((51,52),(53,
      54))))))))))))));
   TREE T5 = ((8,(7,(6,(5,(4,(3,(1,2)))))),((9,10),(((11,
      12),(26,(((18,(17,(16,(15,(13,14))))),(22,(21,(19,
      20)))),(25,(23,24))))),(27,(28,((29,30),(31,(32,
      ((33,(34,((38,(37,(35,36))),(42,(41,(39,40)))))),
      (43,(44,(45,((46,(47,48)),(49,(50,((51,52),(53,
      54))))))))))))));
```

(Table 4.2, continued)

TREE T6 = ((8,(7,((5,6),(4,(3,(1,2))))))),((9,10),(((11,12),(26,(((18,(17,(16,(15,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,(50,((51,52),(53,54))))))))))));

TREE T7 = ((8,(7,(5,(6,(4,(3,(1,2))))))),((9,10),(((11,12),(26,(((18,(17,((15,16),(13,14)))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,(50,((51,52),(53,54))))))))))));

TREE T8 = ((8,(7,(6,(5,(4,(3,(1,2))))))),((9,10),(((11,12),(26,(((18,(17,((15,16),(13,14)))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,(50,((51,52),(53,54))))))))))));

TREE T9 = ((8,(7,((5,6),(4,(3,(1,2))))))),((9,10),(((11,12),(26,(((18,(17,((15,16),(13,14)))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,(50,((51,52),(53,54))))))))))));

TREE T10 = ((8,(7,(5,(6,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T11 = ((8,(7,(6,(5,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T12 = ((8,(7,((5,6),(4,(3,(1,2))))))),((9,10),(((11,12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T13 = ((8,(7,(5,(6,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,(16,(15,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T14 = ((8,(7,(6,(5,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,(16,(15,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T15 = ((8,(7,((5,6),(4,(3,(1,2)))))),((9,10),(((11,12),(26,(((18,(17,(16,(15,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T16 = ((8,(7,(5,(6,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,((15,16),(13,14)))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T17 = ((8,(7,(6,(5,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,((15,16),(13,14)))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T18 = ((8,(7,((5,6),(4,(3,(1,2)))))),((9,10),(((11,12),(26,(((18,(17,((15,16),(13,14)))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((51,52),(50,(53,54))))))))))));

TREE T19 = ((8,(7,(5,(6,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((50,(51,52)),(53,54))))))))))));

TREE T20 = ((8,(7,(6,(5,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((50,(51,52)),(53,54))))))))))));

TREE T21 = ((8,(7,((5,6),(4,(3,(1,2)))))),((9,10),(((11,12),(26,(((18,(17,(15,(16,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((50,(51,52)),(53,54))))))))))));

TREE T22 = ((8,(7,(5,(6,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,(16,(15,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((50,(51,52)),(53,54))))))))))));

TREE T23 = ((8,(7,(6,(5,(4,(3,(1,2)))))))),((9,10),(((11,12),(26,(((18,(17,(16,(15,(13,14))))),(22,(21,(19,20))))),(25,(23,24))))),(27,(28,((29,30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,40))))))),(43,(44,(45,((46,(47,48)),(49,((50,(51,52)),(53,54))))))))))));

(Table 4.2, continued)

```
  TREE T24 = ((8,(7,((5,6),(4,(3,(1,2))))))),((9,10),
    (((11,12),(26,(((18,(17,(16,(15,(13,14))))),(22,
    (21,(19,20)))),(25,(23,24))))),(27,(28,((29,
    30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,
    (39,40))))))),(43,(44,(45,((46,(47,48)),(49,((50,
    (51,52)),(53,54))))))))))))));
  TREE T25 = ((8,(7,(5,(6,(4,(3,(1,2)))))))),((9,10),
    (((11,12),(26,(((18,(17,((15,16),(13,14)))),(22,
    (21,(19,20)))),(25,(23,24))))),(27,(28,((29,30),
    (31,(32,((33,(34,((38,(37,(35,36))),(42,(41,(39,
    40))))))),(43,(44,(45,((46,(47,48)),(49,((50,(51,
    52)),(53,54))))))))))))));
  TREE T26 = ((8,(7,(6,(5,(4,(3,(1,2)))))))),((9,10),
    (((11,12),(26,((((18,(17,((15,16),(13,14)))),
    (22,(21,(19,20)))),(25,(23,24))))),(27,(28,((29,
    30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,
    (39,40))))))),(43,(44,(45,((46,(47,48)),(49,((50,
    (51,52)),(53,54))))))))))))));
  TREE T27 = ((8,(7,((5,6),(4,(3,(1,2))))))),((9,10),
    (((11,12),(26,((((18,(17,((15,16),(13,14)))),
    (22,(21,(19,20)))),(25,(23,24))))),(27,(28,((29,
    30),(31,(32,((33,(34,((38,(37,(35,36))),(42,(41,
    (39,40))))))),(43,(44,(45,((46,(47,48)),(49,((50,
    (51,52)),(53,54))))))))))))));
ENDBLOCK;

BEGIN DISTRIBUTION;
  TITLE = 'Cupaniopsis';
  NTAX = 58;
  RANGE
    Cacuticarpa: 7,
    Cnapaensis: 7,
    Cbullata: 7,
    Cnewmannii: 1,
    Cflagelliformis: 1 2 3,
    Ctomentella: 1,
    Ccurvidens: 6 7 8 9 10 11 12 13,
    Cmacropetala: 9 10 11 12,
    Cdiploglottoides: 2,
    Cshirleyana: 1,
    Cserrata: 1,
    Ceuneura: 9,
    Cstenopetala: 7 9 10 11 14,
    Crhytidocarpa: 7,
    Ckajewskii: 16,
    Cvitiensis: 21,
    Cleptobotrys: 18 21,
    Camoena : 21,
    Cbaileyana: 1,
    Cfoveolata: 2 3,
    Cdallachyi: 2,
    Cfleckeri: 3,
    Cpetiolulata: 20,
    Cphalacrocarpa: 20,
    Cmegalocarpa: 20,
    Cmacrocarpa: 20,
    Cmackeeana: 20,
    Cazantha: 20,
    Cchytradenia: 20,
    Canacardioides: 1 2 3 4 5 6,
    Cwadsworthii: 1,
    Chypodermatica: 19 20,
    Cgrisea : 20,
    Csylvatica: 20,
    Ctrigonocarpa: 20,
    Capiocarpa: 20,
    Cstrigosa: 14,
    Ccelebica: 14,
    Cbilocularis: 6 11,
    Cplatycarpa: 7 10 11 12 13,
    Csquamosa: 20,
    Crosea: 20,
    Cglobosa: 20,
    Cpennelii: 20,
    Ctontoutensis: 20,
    Coedipoda: 20,
    Cgrandiflora: 20,
    Cglomeriflora: 19 20,
    Cinoplaea: 19 20,
    Crotundifolia: 20,
    Cglabra : 20,
    Csubfalcata: 20,
    Cmouana : 20,
    Cfruticosa: 20,
    Cmyrmoctona: 20,
    Csamoensis: 23,
    Cconcolor: 21,
    Cguillauminii: 25;
  TREE T1 = ((1,(2,(3,((((6,(4,5)),(7,8)),(9,((10,11),
    (12,(13,(14,(15,(16,(17,(18,(19,20))))))))))))),
    ((21,22),(23,(24,((30,(29,(28,(27,(25,26))))),
    (31,((34,(32,33)),(((35,36),(37,(38,(39,40)))),
    (41,(((45,(44,(42,43))),(((46,47),(48,49)),((52,
    (50,51)),(53,(54,(55,(56,(57,58))))))))))))))));
ENDBLOCK;

BEGIN DISTRIBUTION;
  TITLE = 'Lepidopetalum';
  NTAX = 6;
  RANGE
    Lxylocarpum: 3 6 7 13,
    Lsubdichotomum: 11 12 15 16,
    Lfructoglabrum: 10,
    Lmicans : 11 12,
    Lmontana: 14,
    Lperrottetii: 14;
  TREE T1 = (1,(2,(3,(4,(5,6)))));
ENDBLOCK;
```

(Table 4.2, continued)

```
BEGIN DISTRIBUTION;
  TITLE = 'Jagera';
  NTAX = 3;
  RANGE
    Jpseudorhus: 1 2 3 6,
    Jjavanica australiana: 2,
    Jjavanica javanica: 6 7 8 9 10 11 12 13 14 15;
  TREE T1 = (3,(1,2));
  TREE T2 = (2,(1,3));
ENDBLOCK;
```

determine which tree shape gave the shortest areagram(s). These analyses were not run to completion; after 1000 shortest areagrams were found, the searches were interrupted. For *Arytera*, tree 3 gave the shortest areagrams; for *Jagera*, tree 2; and for *Guioa*, tree 6. These branching orders (shown in Fig. 4.11 below) were used in the analysis with all genera included.

4.4 – RESULTS

4.4.1 - **Initial analyses**

The initial impression from the gross distributional data for the genera (Fig. 4.1) is that three different types of distribution are present. The first type is the *widespread distribution*, reaching from continental SE Asia or West Malesia in the West across New Guinea and East Australia into the West Pacific as far East as the Samoa and Tonga archipelagoes. This pattern is displayed by *Arytera*, *Cupaniopsis*, and *Guioa*. The second is the *western distribution*. This distribution pattern is similar to the widespread pattern, but lacks the easterly extension into the Pacific. Examples here are *Lepidopetalum* and *Rhysotoechia*. The last pattern, shown by *Mischarytera*, *Cnesmocarpon*, and *Jagera*, is the *restricted distribution*, including only East Australia and New Guinea, with sometimes marginal extensions into West Malesia. Remarkably, *Jagera* is the sister group of the genus *Trigonachras*, which is confined to New Guinea and West Malesia (Adema & Van der Ham 1993). The sister group of these two genera together is *Cnesmocarpon*. Thus, the clade of these three genera together shows the western distribution pattern.

4.4.1.1 – *Brooks Parsimony Analysis*

First, the data matrix with missing taxa coded as true absence was analysed. This resulted in five areagrams (length 558, ci .57, ri .67), the strict consensus of which is shown in Fig. 4.8a. The East Australian areas form a component with Cape York as sister to the other two. The sister area of East Australia is South New Guinea. The West Australian areas (Kimberley Plateau and Arnhem Land) form a component which is sister to a Pacific component comprising the Carolinas, Samoa, New Caledonia and the Loyalty

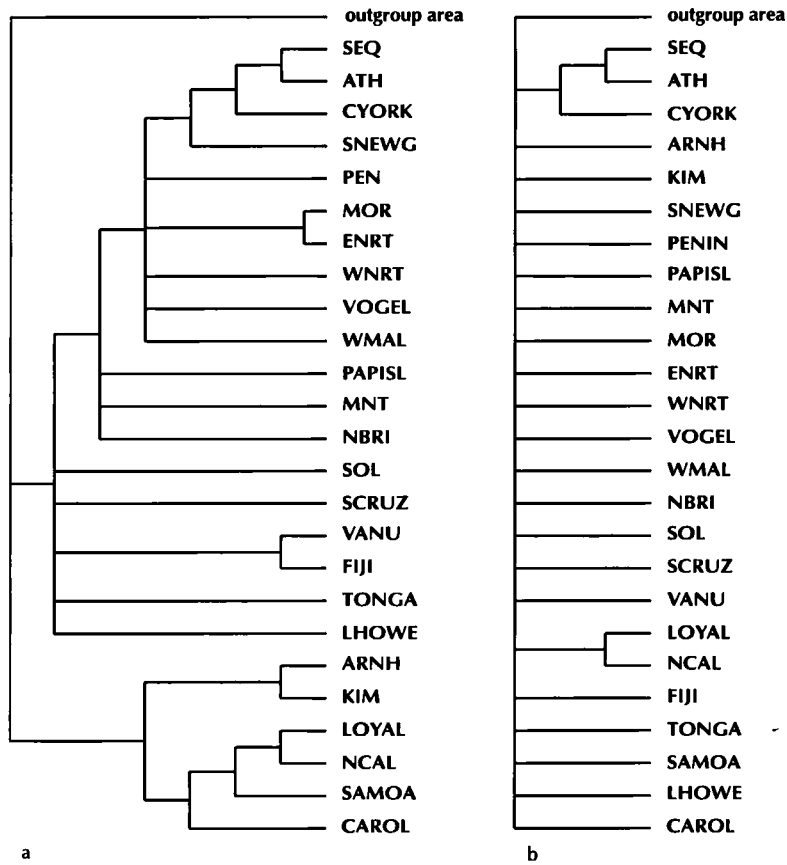


FIGURE 4.8. (a) The strict consensus tree for the five most parsimonious areagrams obtained using BPA and coding missing areas as absences. (b) The strict consensus tree for the 144 areagrams obtained with the same analysis but coding missing areas as unknown data.

Islands. This is probably due to the fact that only two genera (*Arytera* and *Cupaniopsis*) are represented in Arnhem Land with one species each, the latter also reaching the Kimberley Plateau. Also, this species (*C. anacardioides*) is sister to a clade of New Caledonian taxa. The placement of the West Australian areas is thus caused by the missing area effect and dictated by the *Cupaniopsis* cladogram. The remaining Pacific areas form an unresolved polytomy at the base of the New Guinean + Australian group. Within New Guinea, area relationships are again unresolved; only Morobe + East North New Guinea is consistently resolved as a distinct component.

Next, the data matrix was analysed with missing taxa coded as unknown data, resulting in 144 areagrams (length 499, ci .63, ri .67). The strict consensus tree is given in Fig. 4.8b. The East Australian areas again from a component, with the same branching order as in the previous analysis, but all other areas form an unresolved polytomy, with the exception of a New Caledonia + Loyalty Islands component.

TABLE 4.3. Results of the partial analyses of the data in Table 4.1 according to the protocol described in Section 4.3.2.1. Abbreviations as in Fig. 4.2.

Missing area	Minimum component including missing area
SEQ	ATH
ATH	SEQ
CYORK	ATH
ARNH	SEQ, ATH, CYORK, SNEWG, PEN, MNT, MOR, ENRT, WNRT, VOGEL, WMAL, NBRI, SOL
KIM	SEQ, ATH, CYORK, ARNH, SNEWG
SNEWG	ATH
PEN	MOR
PAPISL	NBRI
MNT	PEN *or* CYORK, SNEWG
MOR	PEN
ENRT	WNRT
WNRT	WMAL
VOGEL	PEN, MOR, ENRT, WNRT
WMAL	WNRT
NBRI	PAPISL
SOL	NBRI
SCRUZ	VANU, FIJI, TONGA
VANU	FIJI
LOYAL	NCAL
NCAL	LOYAL
FIJI	CAROL
TONGA	FIJI
SAMOA	FIJI, CAROL
LHOWE	LOYAL, NCAL
CAROL	FIJI
SEQ, ATH	CYORK
SEQ, ATH, CYORK	SNEWG
SEQ, ATH, CYORK, SNEWG	MNT
SEQ, ATH, CYORK, SNEWG, MNT	PEN, WMAL
PEN, MOR	ENRT
PAPISL, NBRI	PEN, MOR
WNRT, WMAL	ENRT
ENRT, WNRT, WMAL	MOR
PEN, MOR, ENRT, WNRT, WMAL	PAPISL, VOGEL
PEN, MOR, ENRT, WNRT, VOGEL, WMAL	PAPISL
PEN, PAPISL, MOR, NBRI	ENRT, WNRT, VOGEL, WMAL
PEN, PAPISL, MOR, ENRT, WNRT, VOGEL, WMAL, NBRI	MNT
PEN, PAPISL, MNT, MOR, ENRT, WNRT, VOGEL, WMAL, NBRI	SNEWG
SEQ, ATH, CYORK, SNEWG, MNT, MOR, ENRT, WNRT, VOGEL, WMAL, NBRI	SOL
LOYAL, NCAL	LHOWE
LOYAL, NCAL, LHOWE	WMAL
FIJI, CAROL	SAMOA
FIJI, SAMOA, CAROL	NCAL
NCAL, FIJI, SAMOA, CAROL	uninformative

4.4.1.2 – *Component Compatibility Analysis*

The same data sets as used for BPA were submitted to analysis under CCA, but without the all-zero artificial outgroup area. Unfortunately, the number of maximum cliques was very high for both data sets, either causing the program CAFCA to run out of memory before completion of the analysis (PC version), or leading to unacceptably long run times for evaluation (estimated as up to 7 days on an Apple PowerPC 7100, non-native CAFCA version). Thus, these analyses had to be abandoned.

The data were also submitted to the protocol proposed in Section 4.3.2.1. The results of the partial analyses are shown in Table 4.3. Even though for the Central Mountain Range two possible components resulted, the substitution procedure gave the same final matrix (not shown). Analysis of the data now resulted in one single areagram, which is shown in Fig. 4.9. This areagram is almost fully resolved. Three major components are evident, but unfortunately the relation between them is not resolved. The first component comprises all Australian areas together with South New Guinea. The West Australian areas area at the base of this component, followed by South New Guinea which is sister to the East Australian areas. The latter show the same relationship as in the BPA analyses.The second major component is New Guinea + West Malesia. The first area to split off here is the Central Mountain Range. The next split separates the western part of New Guinea + West Malesia from the eastern part of New Guinea. West Malesia is sister area to West North New Guinea. In the eastern New Guinean component East North New Guinea splits off first; Morobe and Peninsula are shown as sister areas, as are the Papuan Islands and New Britain. The third component is a Pacific one, with two major branches: one with Lord Howe Island, New Caledonia and the Loyalty Islands, the other with the remaining areas, which split off from West to East.

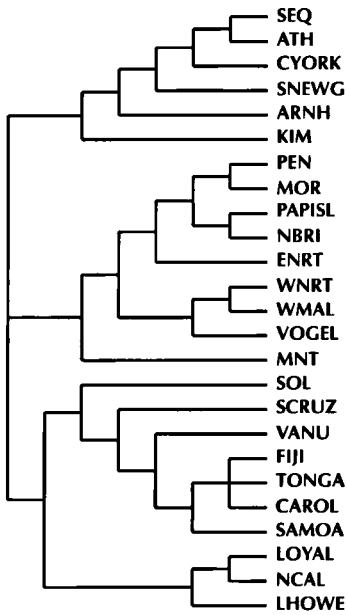


FIGURE 4.9. Areagram obtained with CCA under the protocol outlined in Section 4.3.2.1.

4.4.1.3 – *COMPONENT*

The analysis with COMPONENT was not run to completion. After running for four days on a 66 Mhz 486DX2 PC, 225 minimal areagrams of length 1015 leaves added were found; more than 100 areagrams still had to be swapped. This would have taken an estimated four days longer. By coincidence, a shorter areagram was found of only 1011 leaves added. The difference between this areagram and the areagrams found was in a part of the areagram where the strict consensus tree for the 225 areagrams

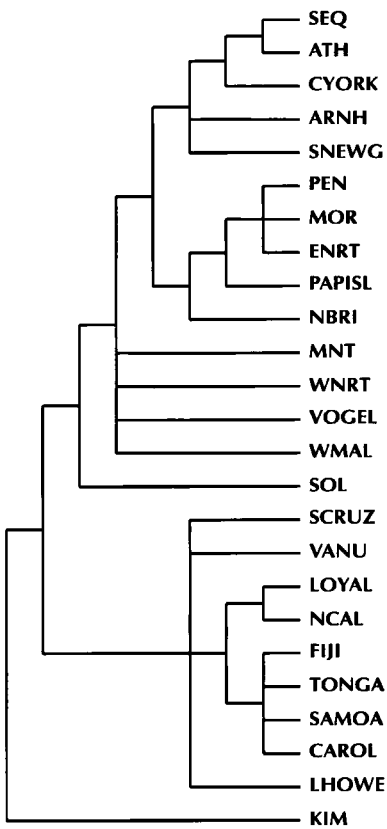


FIGURE 4.10. The strict consensus tree of 1350 trees obtained using COMPONENT.

was fully resolved. By swapping this region by hand (105 different topologies) six equally short branching orders were found for this region, which were all combinable with the resolutions found for the polytomies in the strict consensus of the 225 areagrams. The grand total of minimum-length areagrams thus became 6 × 225 = 1350 trees. The strict consensus of these trees is shown in Fig. 4.10.

As in the BPA and CCA analyses, the East Australian areas form a component, with Cape York in the basal position. The unresolved sister areas are Arnhem Land and South New Guinea. A number of other (East) New Guinean areas form the sister group to this component. Among these areas, Peninsula, Morobe and East North New Guinea form an unresolved component. The remaining New Guinean areas, together with West Malesia, are positioned basal to the East Australian + East New Guinean component as an unresolved group. Sister to this component is the Solomon Islands. The remaining islands in the West Pacific form a component which is sister to all other areas, with the exception of the Kimberley Plateau. Within the Pacific component, New Caledonia and the Loyalty Islands consistently group together, within an unresolved component consisting further of the Carolinas, Fiji, Samoa, and Tonga.

The choice of the tree shapes for *Arytera*, *Guioa*, and *Jagera* was checked by optimising the different tree shapes for these phylogenies on the 1350 areagrams. For all three genera the branching orders chosen were still the shortest; but for *Jagera* the three different shapes were of the same length.

Checking the likelihood of obtaining trees as short as these by chance is almost impossible, in view of the fact that for 25 areas there are more than 10^{30} rooted trees. Checking even a small proportion of these would take an inordinate amount of time. Because the distribution of tree lengths over all possible trees is usually highly skewed (at least for character state data matrices optimised under Fitch or Wagner optimisation; whether this is also true for areagram lengths derived using the methods of COMPONENT is not known yet but may be expected) it is not quite clear what constitutes a significant result. Still, among 2500 random areagrams generated using the equiprobable model none were shorter than 1430 leaves added. The conclusion may be that the topologies found in the analysis are at least as short as random areagrams, although no limit can be set on the probability of finding an equally short (or shorter) tree by chance.

TABLE 4.4. Comparison of the number of leaves added for the 1350 minimal trees found using COMPONENT and the number of leaves added for 2500 randomly generated trees.

Genus	Number of terminal taxa	Number of leaves added for minimal trees	Random trees		
			Number of leaves added for shortest trees	mean	sd
Mischarytera	3	7	2	5.474	2.303
Arytera	24	162–188	230	325.189	25.438
Cnesmocarpon	4	18	16	27.140	2.470
Rhysotoechia	16	33–40	27	50.768	6.357
Guioa	54	254	335	505.505	41.567
Cupaniopsis	58	473–474	565	744.641	43.301
Lepidopetalum	6	34	11	29.110	6.814
Jagera	3	23	27	34.740	1.689

The 2500 random areagrams were also used to check whether the individual cladograms were more congruent with the shortest areagrams than with the random ones. The results are shown in Table 4.4. Because no significance level for these distributions is known, the results can only be interpreted tentatively. Nevertheless, it is quite obvious that the cladograms of *Mischarytera*, *Cnesmocarpon*, *Rhysotoechia*, and *Lepidopetalum* are not significantly more congruent with the shortest areagrams than with the random areagrams. The remaining cladograms, especially of the three largest genera, are more congruent with the shortest areagrams than with any of the random areagrams. This result may well reflect the larger influence of large genera on the shape of the shortest areagrams, rather than a deviation of the smaller genera from a general pattern.

The question remains whether the results obtained with COMPONENT can be regarded as meaningful. Page (1993b) notes that the null hypothesis under which COMPONENT operates (no dispersal) should be rejected if too many leaves added (or too many losses or duplications) have to be postulated in order to reconcile the associate tree with the host tree. Unfortunately, he gives no criterion for the significance level. However, looking at the number of leaves added in comparison to the number of leaves in the cladogram for each genus (Table 4.4), the null hypothesis should probably be rejected for all genera.

4.4.2 – Discussion of initial results

Of the three analyses, the BPA results are the most unsatisfactory because (1) they resulted in numerous equally parsimonious solutions, and (2) the consensus trees are very unresolved. Judging by these two criteria the COMPONENT results are also not very satisfactory, although the consensus tree is reasonably resolved. The CCA results for the raw data could not be obtained, as explained above, but for the data submitted to the protocol suggested in Section 4.3.2.1, they are very satisfactory.

These analyses cannot be compared directly to infer which method gives the best results. The results are nevertheless not completely different from each other, so the

same signal is probably picked up by the three methods. The main difference seems to lie in the way each method accommodates data for missing areas. Unfortunately, all areas of endemism recognised in this study are missing from one or more phylogenies. Especially for the areas in which only one or two genera are present, this leads to very different results.

Treating the missing areas as true absence under BPA (Fig. 4.8a) gives, for example, a curious sister area relationship between a component consisting of Arnhem Land and the Kimberley Plateau and a component of some Pacific areas. Obviously the relationship is spurious, and entirely due to the *Cupaniopsis* phylogeny, as explained in Section 4.4.1. Another example from the same analysis is the position of Lord Howe Island, which does not group with New Caledonia + the Loyalty Islands, as might be expected from the only evidence pertaining to it, the *Guioa* phylogeny. Treating the missing areas as unknown data under BPA (Fig. 4.8b) does not help either, because now the relationships become so blurred that the strict consensus tree collapses almost completely to an uninformative polytomy, with only an East Australian component common to all trees.

The COMPONENT analysis (Fig. 4.10) also shows some anomalies. For example, notwithstanding the treatment of missing areas as unknown data in the analysis, the position of the Kimberley Plateau, and of Santa Cruz and Lord Howe Island within the Pacific component (all areas with only one species), is reminiscent of the missing area effect in BPA analyses. The reason for this phenomenon is not quite clear yet. Possibly, it can again be found in the fact that *Cupaniopsis anacardioides* is the sister species of a New Caledonian clade. The Carolinas however, with also only one species, are not placed so basally. On the other hand, *Guioa coriacea*, the only species occurring on Lord Howe Island, is the sister species of a clade of New Caledonian species. Nevertheless, Lord Howe Island is not placed immediately next to New Caledonia + the Loyalty Islands, possibly because unlike *G. coriacea* the *Arytera* and *Cupaniopsis* species there show relationships to species from Fiji, Tonga, Samoa, and the Carolinas. These contradictory results show that Component Analysis as implemented in COMPONENT suffers from similar problems as BPA.

The CCA result (Fig. 4.9) again points to a different resolution for the Pacific areas: this time they are all grouped together in a single component at the base of the areagram. In turn, this component is divided into two parts: a New Caledonia + Loyalty Islands + Lord Howe component on the one hand, and the remaining Pacific areas on the other. Arnhem Land and the Kimberley Plateau group together with South New Guinea and the East Australian areas, which at least is intuitively correct in view of the distributions of the species occurring in the first two areas.

FIGURE 4.11. Cladograms of the individual genera with a rough indication of the distributions of the terminal taxa. The exact distributions of the individual taxa can be found in Tables 4.1 and 4.2. The preferred resolutions of the polytomies used in the analyses with COMPONENT are also indicated. Note that the polytomy above *Guioa pubescens* contains species from West Malesia only; all three resolutions give equally short results. (a) *Mischarytera*; (b) *Arytera*; (c) *Rhysotoechia*; (d) *Cnesmocarpon*; (e) *Guioa*; (f) *Cupaniopsis*; (g) *Lepidopetalum*; (h) *Jagera*.

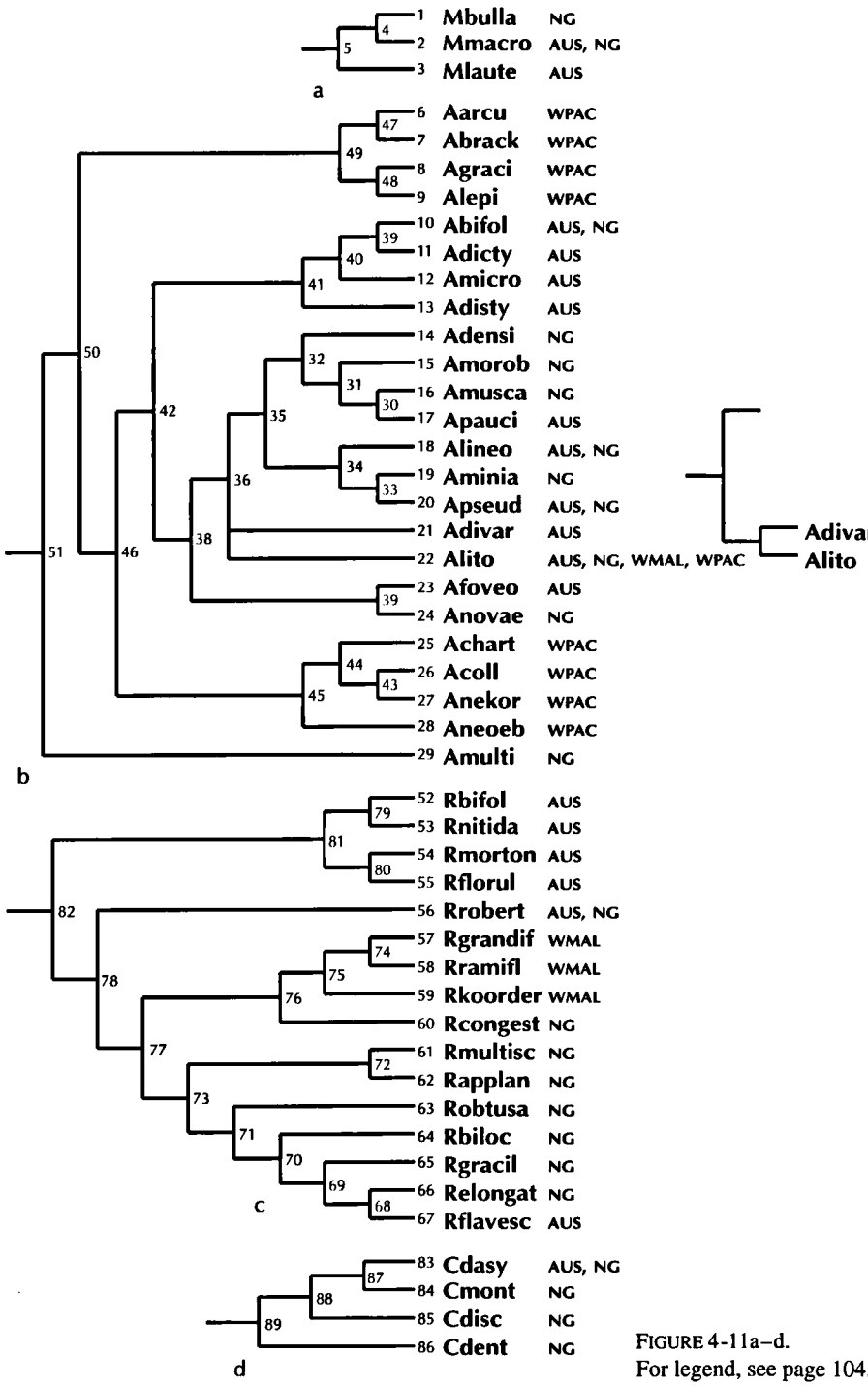
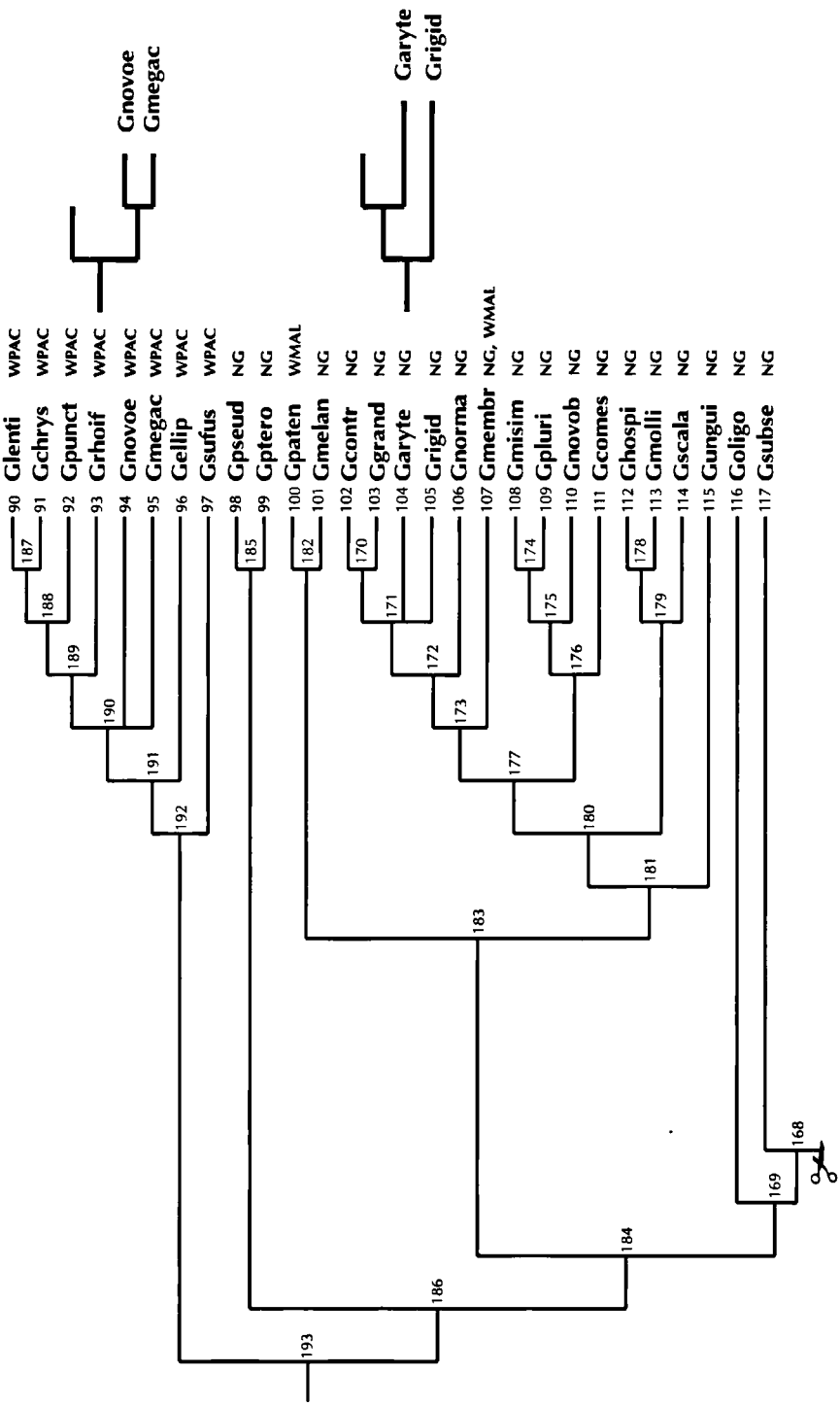


FIGURE 4-11a–d.
For legend, see page 104.


Gnovoe
Gmegac
Garyte
Grigid
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91 Gchrys WPAC
92 Gpunct WPAC
93 Grhoif WPAC
94 Gnovoe WPAC
95 Gmegac WPAC
96 Gellip WPAC
97 Gsufus WPAC
98 Gpseud NG
99 Gptero NG
100 Gpaten WMAL
101 Gmelan NG
102 Gcontr NG
103 Ggrand NG
104 Garyte NG
105 Grigid NG
106 Gnorma NG
107 Gmembr NG, WMAL
108 Gmisim NG
109 Gpluri NG
110 Gnovob NG
111 Gcomes NG
112 Ghospi NG
113 Gmolli NG
114 Gscala NG
115 Gungui NG
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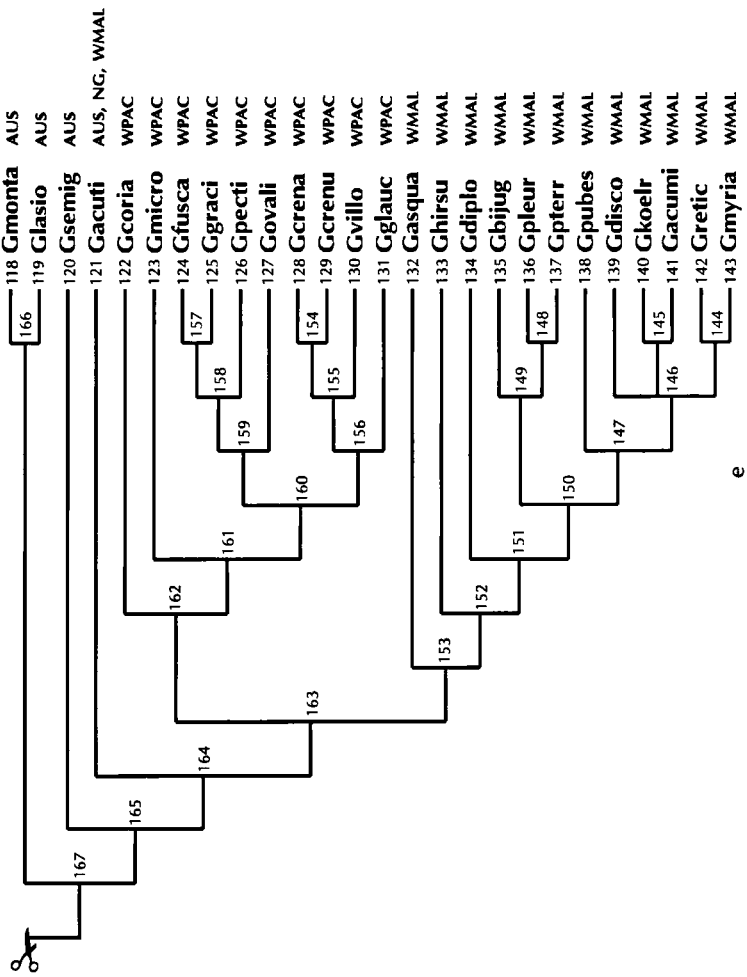
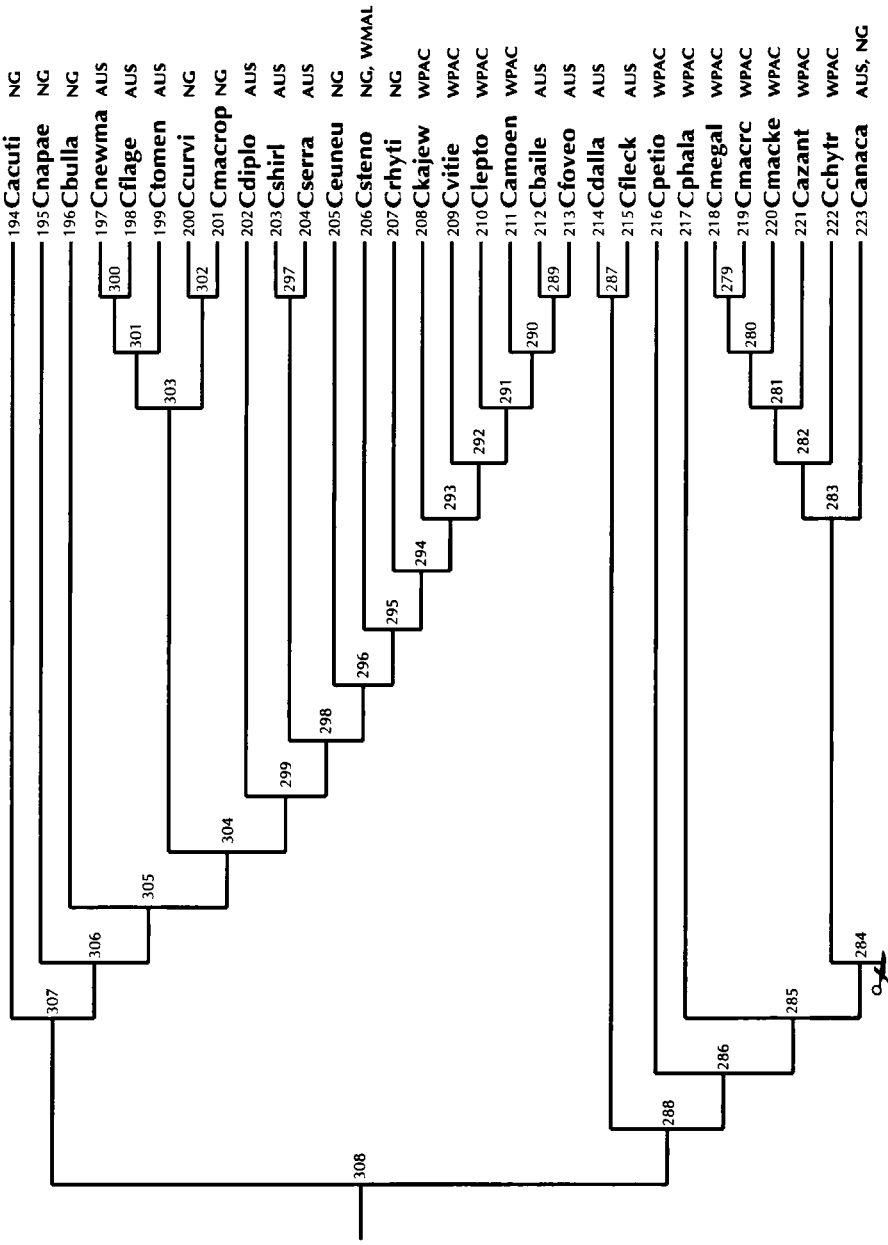


FIGURE 4-11e. For legend, see page 104.


194 Cacuti NG
195 Cnapae NG
196 Cbulla NG
197 Cnewma AUS
198 Cflage AUS
199 Ctomen AUS
200 Ccurvi NG
201 Cmacrop NG
202 Cdiplo AUS
203 Cshirl AUS
204 Cserra AUS
205 Ceuneu NG
206 Csteno NG, WMAL
207 Crhyti NG
208 Ckajew WPAC
209 Cvitie WPAC
210 Clepto WPAC
211 Camoen WPAC
212 Cbaile AUS
213 Cfoveo AUS
214 Cdalla AUS
215 Cfleck AUS
216 Cpetio WPAC
217 Cphala WPAC
218 Cmegal WPAC
219 Cmacrc WPAC
220 Cmacke WPAC
221 Cazant WPAC
222 Cchytr WPAC
223 Canaca AUS, NG
300
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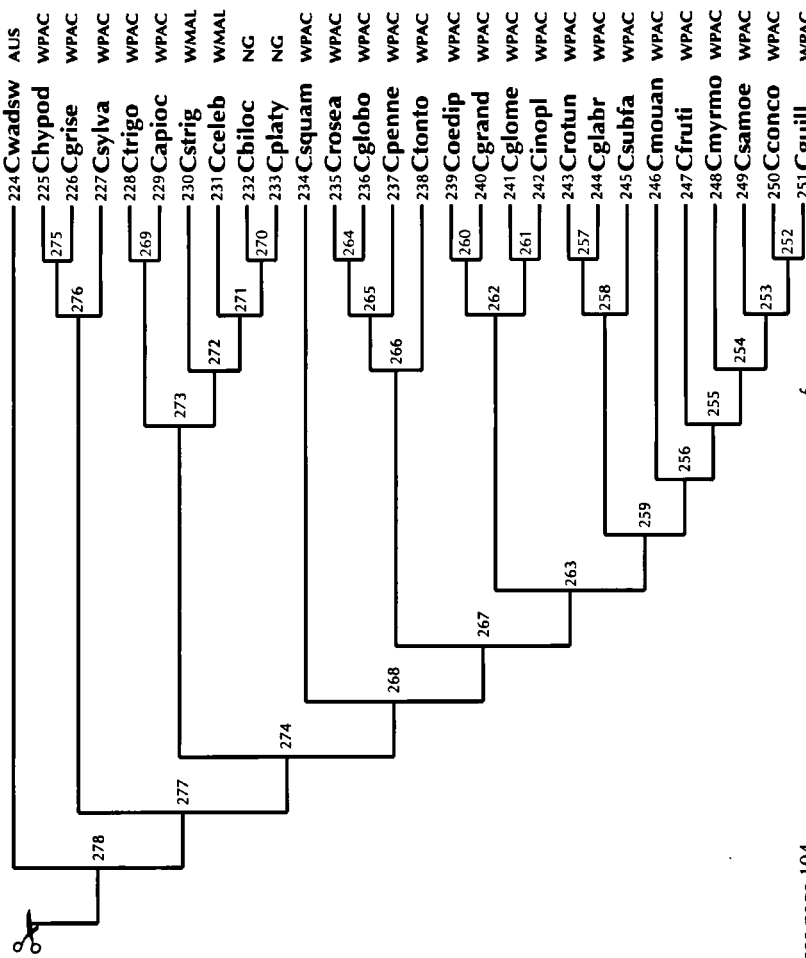

FIGURE 4-11f. For legend, see page 104.

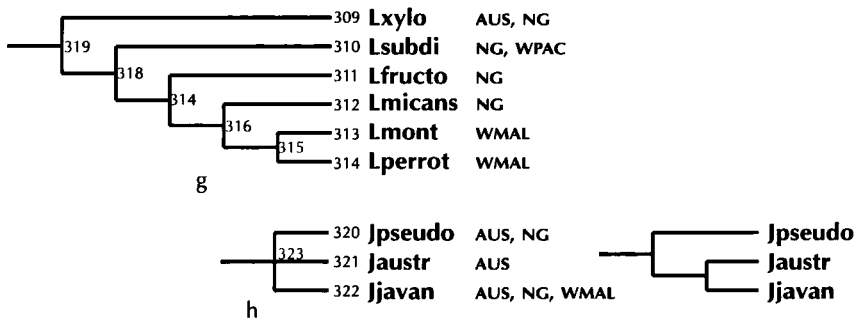

FIGURE 4.11g, h. For legend, see page 104.

4.4.3 – Additional analyses

Probably the different ways in which the Pacific areas (excluding New Caledonia and the Loyalty Islands) are treated is not exclusively due to the missing area effect. Another factor that may well be influencing the results is different patterns, which might be resolved differently by the various methods. Different patterns might occur when one phylogeny reflects a dispersal pattern for particular areas, while another phylogeny reflects a vicariance pattern. Brooks (1990) suggested that, at least in BPA, such patterns can be disentangled by splitting the affected areas into two separate occurrences. One of the problems with this is that in the reconstruction of a generalised areagram from the phylogenies of a number of clades, as in the present case, it becomes difficult to decide which occurrences of a particular area belong to which pattern. Nevertheless, an attempt was made to unravel at least a number of these patterns in the BPA and CCA modes.

First, the patterns within each clade were analysed from the phylogenies (shown in Fig. 4.11). They are quite different for the different genera. In *Arytera* the basal clades are West Pacific, including New Caledonia and the Loyalty Islands. In *Cupaniopsis* the West Pacific species are polyphyletic, with taxa from New Caledonia and the Loyalty Islands forming a clade with taxa from Samoa, Fiji, and the Carolinas, and the other Pacific species forming a clade together with East Australian and New Guinean taxa. In *Guioa* the West Pacific species again form the basal clade, but excluding New Caledonia and the Loyalty Islands, which form a clade that is sister to a species from Lord Howe Island. In turn, this clade is sister to a West Malesian clade.

The East Australian species usually group together, often forming a clade together with species from South New Guinea. This part of New Guinea is generally acknowledged to be part of the Australian craton. The other New Guinean taxa also usually group more or less together in all genera except *Cupaniopsis*, in which there are two New Guinean species groups. Remarkably, in *Arytera* and *Rhysotoechia* East Australian species reappear high up in the areagrams as sister to species from South New Guinea and Peninsula.

West Malesia also occupies different positions in the different genera. In *Arytera* it is part of the distribution of *A. litoralis*, which is widespread across New Guinea excluding South New Guinea. In *Cupaniopsis* it is sister area to New Guinea excluding the Central Mountain Range, New Britain and the Papuan Islands. In *Guioa* it is sister area to New Caledonia and the Loyalty Islands. In *Lepidopetalum* West Malesia is sister to the North New Guinean areas; in *Rhysotoechia* it is sister area to the Central Mountain Range, which together are basal to the other New Guinean areas; in *Jagera*, finally, it is again included in the New Guinean clade. These findings suggest that at least the West Malesian, West Pacific, and East Australian areas have biotas of mixed origin, and thus compound relationships with other areas.

I therefore decided to split the East Australian areas. One part reflects the basal positions of East Australia in *Arytera*, *Rhysotoechia*, *Guioa*, and *Cupaniopsis* (Australia 1). The second part (Australia 2) consists of the more apical occurrences in *Arytera* and *Rhysotoechia*, this on the assumption that these taxa have dispersed back to East Australia (possibly during one or more Pleistocene periods of low sea levels). By comparing the different combinatorial possibilities, it was found that, for BPA, the occurrences in *Cnesmocarpon* and *Lepidopetalum* are most parsimoniously explained by inclusion in the latter set. Likewise, the Pacific areas were split in two. The first set (Pacific 1) consists of areas showing a relation to New Guinea, and includes the occurrences of *Lepidopetalum*, *Guioa*, *Cupaniopsis* (excluding New Caledonia, the Loyalty Islands, and occurrences of taxa with their closest relatives in these areas), and *Arytera litoralis* on the Solomon Islands. The second part (Pacific 2) consists of the remaining occurrences of Pacific areas. The assumption here is that the biota of New Caledonia, the Loyalty Islands, and Lord Howe has arisen by vicariance (or dispersal) from East Australian ancestors (with some secondary dispersal over parts of the West Pacific island chain), while dispersal from New Guinea is probably responsible for the origin of the remaining West Pacific taxa. As to West Malesia, the relationships of the species there all point to affinities with New Guinea. The particular sister area is different in each case, however, so no attempt was made to divide West Malesia into different parts. The thus extended data matrix is given in Table 4.5.

TABLE 4.5. Data matrix for BPA after splitting the East Australian and Pacific areas. Only the split areas are shown: these should replace the corresponding areas in Table 4.1. The Loyalty Islands, New Caledonia, Lord Howe Island, the Carolinas, and Samoa are all part of Pacific 2, the Santa Cruz Islands belong to Pacific 1.

	SEQ1
Mischarytera	00101
Arytera	0000111100000001010000000000001111111000100011
Rhysotoechia	1010000000000000000000000001111
Cnesmocarpon	???????
Guioa	000000000000000000000000000000110000000000000000000000000000000000 00000000110111000000000000001010000001
Cupaniopsis	000111000110000000100000000001100000000000000000000000000000000000 0000000000000000001000011110111111111111110111111
Lepidopetalum	???????????
Jagera	????

(Table 4.5, continued)

	ATH1
Mischarytera	00101
Arytera	0000110000000001000000000000000001111000100011
Rhysotoechia	1011100000000000000000000001111
Cnesmocarpon	???????
Guioa	000000000000000000000000000011010000000000000000000000000000000000
	00000000111111000000000000001010000001
Cupaniopsis	000010001000000000011000000010000000000000000000000000000000000000
	0000000000000000000000011111111111111011110111111
Lepidopetalum	???????????
Jagera	????

	CYORK1
Mischarytera	01011
Arytera	0000100000000001000000000000001011111000100011
Rhysotoechia	0100000000000000000000000001011
Cnesmocarpon	???????
Guioa	000000000000000000000000000000010000000000000000000000000000000000
	00000000110111000000000000001010000001
Cupaniopsis	000010000000000000010100000001000000000000000000000000000000000000
	0000000000000000000000011111111111111011110111111
Lepidopetalum	???????????
Jagera	????

	SEQ2
Mischarytera	?????
Arytera	??
Rhysotoechia	0000000000000001111101000110001
Cnesmocarpon	???????
Guioa	??
	??????????????????????????????????????
Cupaniopsis	??
	???
Lepidopetalum	???????????
Jagera	1001

	ATH2
Mischarytera	?????
Arytera	0000000000010000000000001110011011111000100011
Rhysotoechia	0000000000000001111101000110001
Cnesmocarpon	0010111
Guioa	??
	??????????????????????????????????????
Cupaniopsis	??
	???
Lepidopetalum	???????????
Jagera	1101

	CYORK2
Mischarytera	?????
Arytera	0000000000001010000000000001111010001000100011
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	??
	??????????????????????????????????????
Cupaniopsis	??
	???
Lepidopetalum	10000000001
Jagera	1001

(Table 4.5, continued)

	SOL1
Mischarytera	?????
Arytera	0000000000000000100000000000001010001000100011
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	00000011000000000000000000000000000000000000000000000000000000000000
	000000000000000000000000000000000000011
Cupaniopsis	00000000000000100000000000000000000000000000000000000000000000000000
	00000000000000000000000000000000001111011000011111
Lepidopetalum	01000000011
Jagera	????

	VANU1
Mischarytera	?????
Arytera	??
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	00001000000000000000000000000000000000000000000000000000000000000000
	000000000000000000000000000000000001111
Cupaniopsis	00000000000000001000000000000000000000000000000000000000000000000000
	00000000000000000000000000000000111111011000011111
Lepidopetalum	???????????
Jagera	????

	FIJI1
Mischarytera	?????
Arytera	??
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	01110000000000000000000000000000000000000000000000000000000000000000
	000000000000000000000000000000001111111
Cupaniopsis	00000000000000011100000000000000000000000000000000000000000000000000
	00000000000000000000000000000001111111011000011111
Lepidopetalum	???????????
Jagera	????

	TONGA1
Mischarytera	?????
Arytera	??
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	10000000000000000000000000000000000000000000000000000000000000000000
	000000000000000000000000000000001111111
Cupaniopsis	??
	??
Lepidopetalum	???????????
Jagera	????

	SOL2
Mischarytera	?????
Arytera	0100000000000000000000000000000000000000010111
Rhysotoechia	???????????????????????????????
Cnesmocarpon	???????
Guioa	??
	???????????????????????????????????????
Cupaniopsis	??
	??
Lepidopetalum	???????????
Jagera	????

(Table 4.5, continued)

	VANU2
Mischarytera	?????
Arytera	0100000000000000000000100000000000000111110111
Rhysotoechia	????????????????????????????????
Cnesmocarpon	???????
Guioa	?? ??????????????????????????????????????
Cupaniopsis	?? ??
Lepidopetalum	???????????
Jagera	????

	FIJI2
Mischarytera	?????
Arytera	0100000000000000000000000000000000000000010111
Rhysotoechia	????????????????????????????????
Cnesmocarpon	???????
Guioa	?? ??????????????????????????????????????
Cupaniopsis	0000000000000000000000000000000000000000000000000000001011111001 0001000110000010011000011101000000000000000001
Lepidopetalum	???????????
Jagera	????

	TONGA2
Mischarytera	?????
Arytera	0100000000000000000000000000000000000000010111
Rhysotoechia	????????????????????????????????
Cnesmocarpon	???????
Guioa	?? ??????????????????????????????????????
Cupaniopsis	?? ??
Lepidopetalum	???????????
Jagera	????

4.4.3.1 – *Brooks Parsimony Analysis*

Under the BPA protocol, the matrix with missing taxa coded as absent gave 72 areagrams (length 560, ci .57, ri .70). The resolution of the strict consensus tree (Fig. 4.12a) is better, however, than in the previous analysis. The East Australian areas (Australia 1) still form a component, but it is now embedded in a larger component of New Guinean areas. West Malesia is also included in the New Guinean component, splitting off together with South New Guinea, Peninsula, Morobe, East North New Guinea, the Vogelkop, and West North New Guinea. The sister groups to the New Guinea + East Australia + West Malesia component are three Pacific 1 areas. The West Australian areas again group together with New Caledonia and related areas (Pacific 2). Somewhat surprisingly, East Australia 2 also forms a component, with the same branching order as Australia 1.

With the missing taxa coded as unknown the analysis resulted in 2568 areagrams of length 463 (ci .69, ri .76). Despite the large number of MPTs the resolution of the strict consensus tree is considerable (Fig. 4.12b). The East Australian areas (Australia 1)

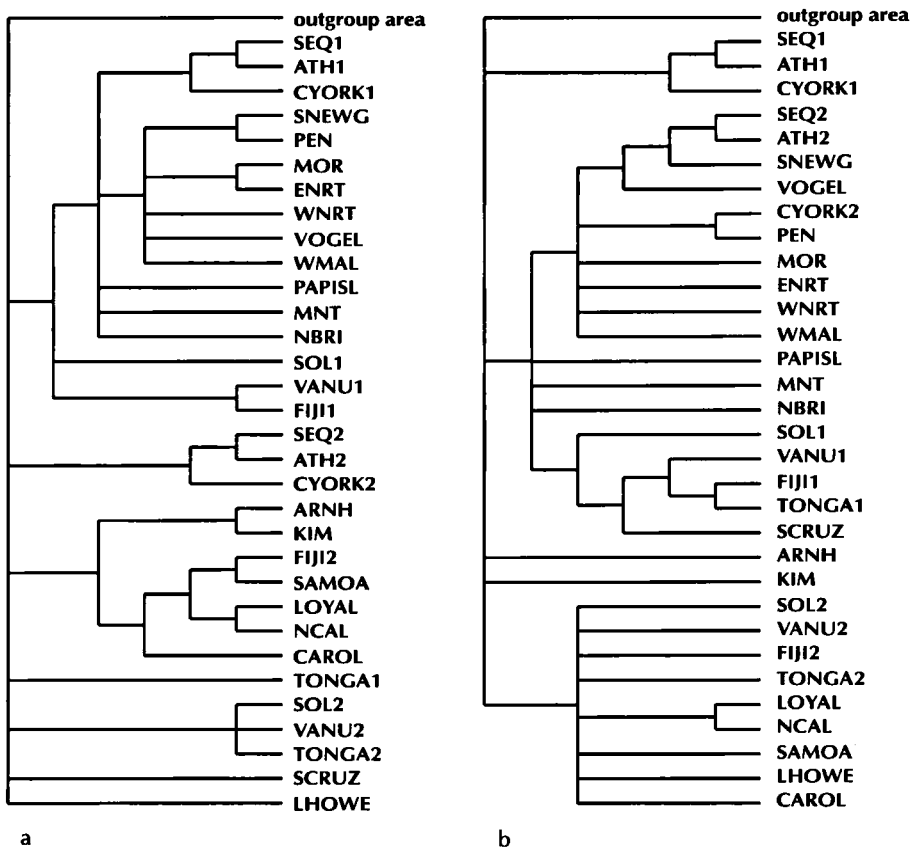

FIGURE 4.12. (a) The strict consensus tree for the 72 most parsimonious areagrams obtained after doubling the Australian and Pacific areas with BPA, coding missing areas as absences. (b) The strict consensus tree for the 2568 most parsimonious areagrams obtained after doubling the Australian and Pacific areas with BPA, coding missing areas as unknown data.

again group together, apart from Arnhem Land and the Kimberley Plateau, which are in the unresolved basal polytomy. The Pacific 2 areas also form a component, with again New Caledonia and the Loyalty Islands as sister areas. The relationships between this component and the other Pacific 2 areas remains unresolved. The areas of Pacific 1 form a pectinate component with the members splitting off from West to East. It is embedded in a New Guinea + West Malesia component, forming the unresolved base together with the Papuan Islands, New Britain, and the Central Mountain Range. The remaining New Guinean areas and West Malesia form a separate component which is also poorly resolved. South New Guinea is the sister area to two Australia 2 areas (Southeast Queensland and the Atherton Plateau), and together these areas are sister to the Vogelkop. Cape York 2 is sister to Peninsula.

TABLE 4.6. Results of the partial analyses of the data in Table 4.5 according to the protocol described in Section 4.3.2.1. Abbreviations as in Fig. 4.2.

Missing area	Minimum component including missing area
SEQ1	ATH1
ATH1	SEQ1
CYORK1	SEQ1, ATH1, SEQ2, ATH2, SNEWG, PEN, MNT, WMAL ***or*** SEQ1, ATH1, SEQ2, ATH2, CYORK2, SNEWG, PEN, PAPISL, MNT, MOR, ENRT, WNRT, VOGEL, WMAL, NBRI
SEQ2	ATH2
ATH2	SNEWG
CYORK2	PEN
ARNH	SEQ1, ATH1, CYORK1, SNEWG
KIM	SEQ1, ATH1, CYORK1, ARNH, SNEWG ***or*** SEQ1, ATH1, CYORK1, ARNH, NCAL
SNEWG	ENRT
PEN	SEQ1, ATH1, CYORK1, SNEWG, MNT, VOGEL, WMAL
PAPISL	SEQ1, ATH1, CYORK1, SNEWG, PEN, MNT, VOGEL, WMAL, LOYAL, NCAL, LHOWE
MNT	CYORK1, SNEWG
MOR	PEN
ENRT	WNRT
WNRT	WMAL
VOGEL	PEN, MOR, ENRT, WNRT
WMAL	WNRT
NBRI	PAPISL
SOL1	ENRT, WNRT, NBRI
SCRUZ	VANU1, FIJI1, TONGA1
VANU1	FIJI1
LOYAL	NCAL
NCAL	LOYAL
FIJI1	VANU1
TONGA1	FIJI1
SOL2	VANU2, FIJI2, TONGA2, SAMOA
VANU2	LOYAL, NCAL
FIJI2	CAROL
TONGA2	SOL2, VANU2, FIJI2, SAMOA
SAMOA	FIJI2, CAROL
LHOWE	LOYAL, NCAL
CAROL	FIJI2
SEQ1, ATH1	CYORK1
WNRT, WMAL	ENRT
ENRT, WNRT, WMAL	MOR
VANU1, FIJI1	SEQ1, ATH1, CYORK1
LOYAL, NCAL	LHOWE
LOYAL, NCAL, LHOWE	WMAL
FIJI2, CAROL	SAMOA
FIJI2, SAMOA, CAROL	LOYAL, NCAL

4.4.3.2 – *Component Compatibility Analysis*

The result of applying the protocol of Section 4.3.2.1 to the data set of Table 4.5 is given in Table 4.6. Substituting resulted in two distinguishable data sets (not shown), the only difference being in the coding for the Kimberley Plateau. Each matrix resulted in a single tree, one of which is shown in Fig. 4.13. The only difference with the other tree is that here the Kimberley Plateau splits off before Arnhem land, while in the other this split is not resolved. The CCA result does not corroborate the double pattern for either East Australia or the West Pacific. Pacific 1 is embedded within Pacific 2 areas, and with the exception of Cape York 2, the Australia 2 areas form the sister group of South New Guinea within an Australia 1 component.

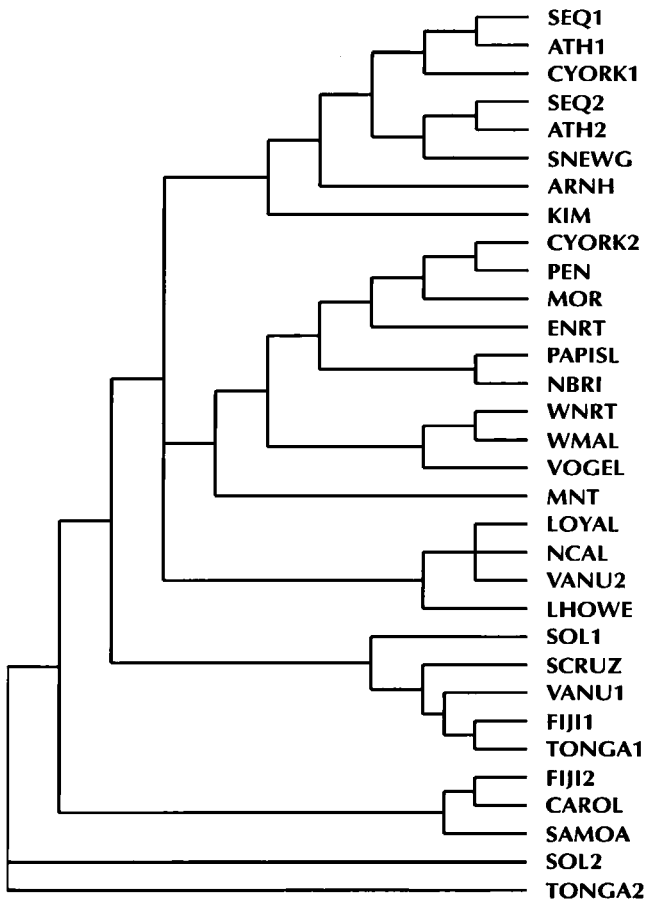

FIGURE 4.13. One of the two areagrams obtained with CCA under the protocol of Section 4.3.2.1 for the data set with doubled areas.

4.5 – DISCUSSION

Before entering into a discussion of the different results, it is worth while to discuss the geological history of the Australia–West Pacific–New Guinea–West Malesia region. Obviously, the biogeographic pattern must comply with the geological one. If the two are contradictory, either the one or the other is in error. If they agree, the geologists' results and mine are strengthened.

4.5.1 – Geological history of the western Pacific islands, New Guinea, West Malesia, and Australia

In two overview articles, Duffels & De Boer (1990) and Burrett et al. (1991) show that the West Pacific islands form part of two discrete systems. The Inner Melanesian Arc (IMA) consists of New Zealand, New Caledonia, and Lord Howe Island, and continues as the old leading edge of the Australian craton now part of the Central Mountain Range of New Guinea. The eastern end of the IMA is thought to have fragmented from the eastern margin of the Australian craton no later than the late Cretaceous (c. 80 Ma), and possibly much earlier.

The second system is the Outer Melanesian Arc (OMA) presently composed of (at least) the Solomons, Vanuatu, Fiji, and Tonga. The OMA is thought to have arisen in the Pacific as a series of microterranes and is moving westward driven by the Pacific plate. Parts of the old western end of the OMA have been accreted onto the northern edge of the Australian craton from the Miocene onward (15 Ma) and presently form the northern half of New Guinea, including most of the Central Mountain Range, the Vogelkop, and the Peninsula areas (Pigram & Davies 1987). This western end of the OMA was probably of mixed origin, including continental fragments rifted from the northern margin of the Australian craton together with the IMA (Parker & Gealey 1983, quoted in Michaux 1994), or rifted and displaced westward as the OMA collided with the craton margin. Samoa, not yet mentioned, is presently not part of the OMA, but may have been connected to it in the past (Duffels & De Boer 1990).

The West Malesian area is a composite of microterranes broken off the northern rim of the Australian craton during the early to mid-Tertiary and parts of the OMA, intermittently providing stepping stones for a westward dispersal of Gondwanan elements towards South-East Asia and conversely for South-East Asian elements towards New Guinea and Australia at least since the Miocene (15 Ma) (Audley-Charles 1987; Michaux 1991).

The Australian areas and South New Guinea are all part of the Australian craton. According to Cracraft (1986) the major vicariance events in Australia are due to the climate becoming progressively drier during Tertiary and Quaternary times. The vicariance between the Kimberley Plateau and Arnhem Land, and between Arnhem Land and the areas to the East and North, probably occurred during the Eocene (c. 40–55 Ma). The separation of South New Guinea and East Australia is sometimes ascribed to marine transgression after the Pleistocene, but similar transgressions have occurred earlier, e.g. during the Miocene (cf. Fig. 2.9 in Audley-Charles 1987). The separation

of Cape York from the more southerly areas is probably also the result of aridification, due to the uplift of the Atherton Plateau in Cenozoic times (< 65 Ma), while the barrier between the Atherton Plateau and Southeast Queensland, again a drought barrier, might be of Pleistocene age (< 2 Ma).

4.5.2 – Hypothetical areagram derived from geological evidence

Pigram and Davies' (1987) detailed account of the accretion history of New Guinea is summarised graphically in Fig. 4.14a. On the assumption that the various areas involved were at least partly subaerial from (shortly) before they docked, enabling dispersal onto them from the Australian craton, a hypothetical ancestral continental species could speciate by peripheral isolates allopatric speciation via sequential dispersal (Brooks & McLennan 1991). Its phylogeny would then reflect the graph in Fig. 4.14a rooted at the Australian craton (Fig. 4.14b). This areacladogram closely resembles the CCA result from Fig. 4.9, differing mainly in the position of East North New Guinea. New Britain might fit into this scheme on the branch leading to East North New Guinea, or alternatively to Peninsula, Morobe, or the Papuan Islands (i.e. the parts of Pigram & Davies' [1987] East Papua composite terrane) if these areas were close to it in the past. The remainder of the OMA should then be connected to New Britain, in a West to East pattern. The different position of these areas in the CCA result probably points to a stronger biogeographical connection of the OMA to New Caledonia than to New Guinea in the Sapindaceous genera included in the study.

One of the problems with the hypothetical speciation model presented in Fig. 4.14b is that the monophyletic group is supposed to have extended its range over the terranes as they came within dispersal range, and to have reacted immediately to each dispersal event with speciation. If the various terranes were not too far apart before docking, the dispersal could have extended over several terranes before any speciation occurred. In case the first speciation event took place on the terrane most distant from the centre of origin, this terrane would be shown as splitting off first on the areagram, with the closer terranes as its monophyletic sister area. Also, the supposed ancestor need not have dispersed onto all terranes; in particular, the western terranes, later forming the Vogelkop and West North New Guinea (and parts of West Malesia), may have been missed by an ancestor originally endemic to the eastern edge of the Australian craton. As will be seen from the optimisations of the different genera of Sapindaceae onto the CCA areagram, these two complications probably have occurred.

4.5.3 – Optimisation of the phylogenies onto the initial CCA areagram

If the hypothesis of two different patterns for East Australia and the Pacific islands is correct, it should also be apparent from optimisation of the phylogenies onto the generalised areagram(s) resulting from the analyses without doubled areas. Because the CCA result is the best resolved, and seems in agreement with geological evidence (see below), this areagram (Fig. 4.9) is selected for a careful analysis of the different vicariance, dispersal and extinction events. The data set with missing areas coded as

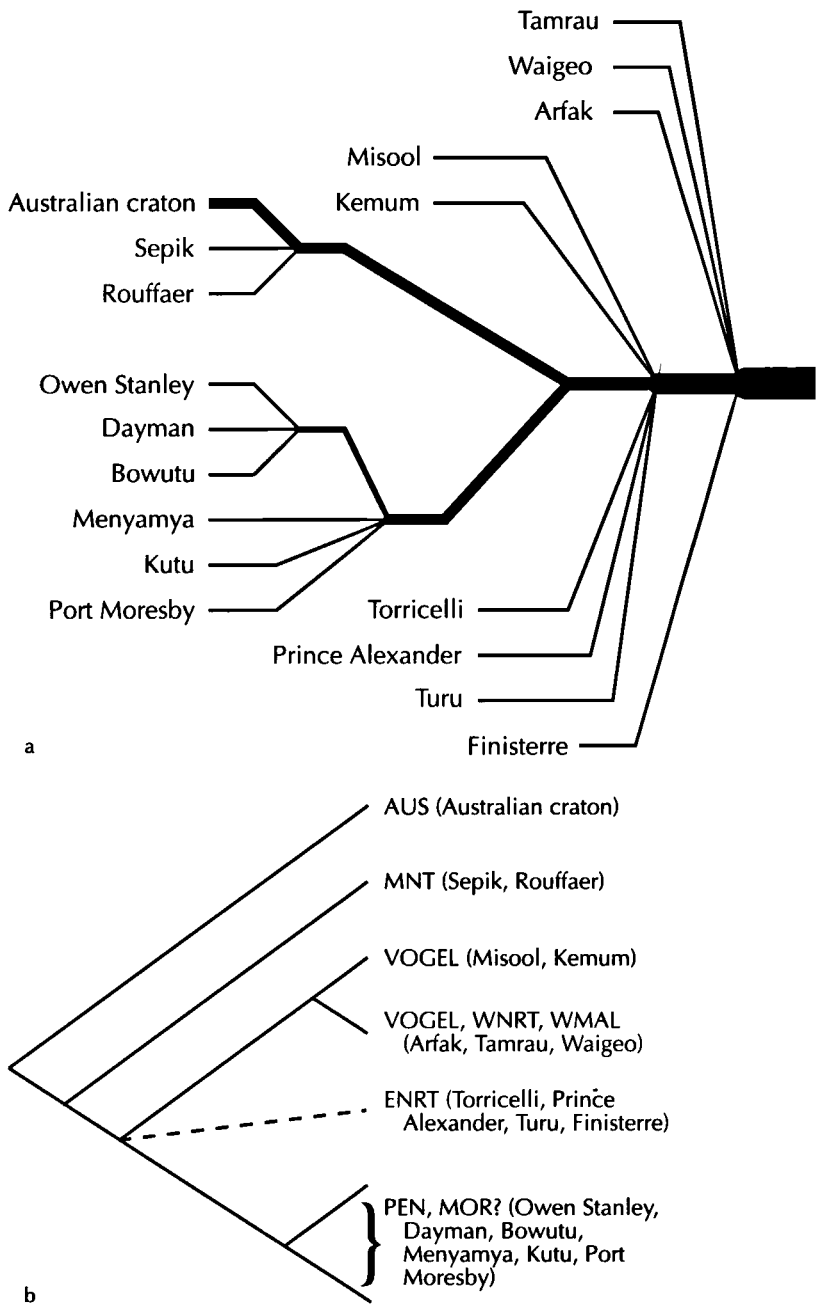

FIGURE 4.14. (a) Graph depicting schematically the accretion history of New Guinea, after Pigram & Davies (1987). (b) Hypothetical phylogeny for a monophyletic group originally present on the Australian craton and showing peripheral isolates allopatric speciation via sequential dispersal onto each terrane as it came within dispersal range.

unknown was used for the optimisations, as it does not add extra steps for those areas in which the different phylogenies are missing. Of the three possible branching orders for the basal polytomy, New Guinea + West Malesia at the base is two steps, and Australia as sister to the other two components one step longer than the one with the Pacific areas as sister to New Guinea + West Malesia + Australia. The latter is therefore preferred. The trichotomy for Fiji, Tonga, and the Carolinas is not sensitive to the different possible branching orders, and is left unresolved.

Optimising the different phylogenies onto the areagram (using either the DELTRAN or ACCTRAN modes of optimisation) is one thing, but interpreting the biogeographic history of the genera in terms of vicariant speciations, dispersal events, and (local) extinctions requires additional assumptions, as will become apparent below. These additional assumptions are best made taking into consideration the geological history of the areas.

4.5.3.1 – *Optimising steps on a generalised areagram*

As has been remarked previously in the literature (e.g. Page 1990, 1994; Van Welzen 1992), the way in which the data matrix for BPA or CCA is constructed leads to spurious extra steps on the areagram when dispersal or extinction has occurred. The reason for this is that the columns coding for the hypothesised distributions of ancestral taxa (internal nodes) are not independent of each other (Zandee & Roos 1987). As an example, consider the hypothetical situation depicted in Fig. 4.15. Optimising the phylogeny (a) onto the areagram (b) results in three reversals for ancestral species 5, 6, and 7. At least two of these reversals (extinction events) are spurious. The clade may have been primitively absent from E and F, in which case there was no extinction at

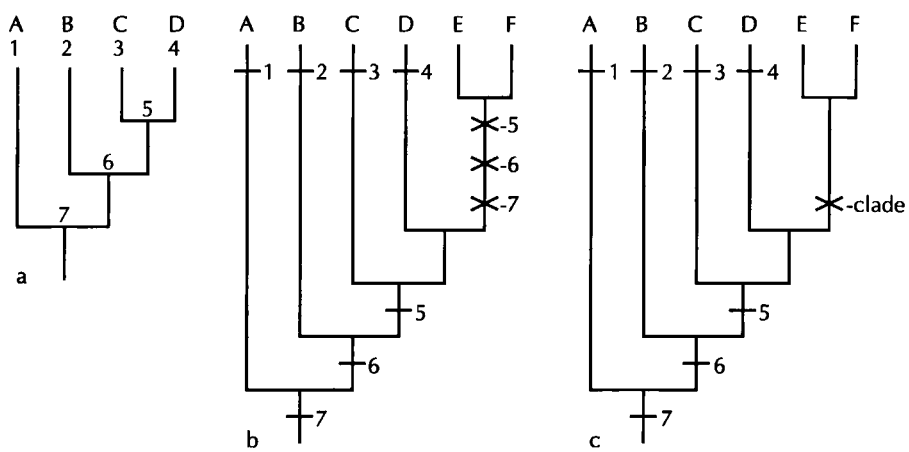

FIGURE 4.15. (a) Phylogeny and (b) areagram, both hypothetical. Optimising the phylogeny onto the areagram gives three reversals for ancestors 5, 6, and 7 on the branch leading to E and F. (c) Only one extinction event (or primitive absence) need be postulated for clade 1–4 on the branch leading to E and F. Whether the absence is primitive or due to extinction of one of the species 4, 5, 6, or 7, cannot be determined.

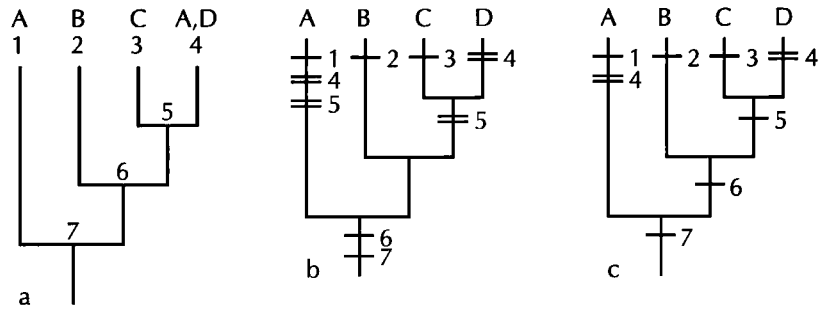

FIGURE 4.16. (a) Phylogeny and (b) areagram, both hypothetical. Optimising the phylogeny onto the areagram gives parallels for species 4 and ancestor 5, while ancestor 6 is placed one node too low. (c) Only one actual dispersal event has taken place, for species 4. Ancestors 5 and 6 were not present in area A, hence ancestor 6 can be placed on the branch leading to areas B, C, and D.

all, and all three reversals are spurious; or one of the ancestral species went extinct, in which case its ancestor(s) were present and its descendants are primitively absent, leaving two spurious reversals. A final, equally parsimonious possibility, not immediately apparent from the optimisation, is that all ancestors were present but that extant species 4 went extinct in areas E and F. Figure 4.15c shows an optimisation in which the clade went extinct in E and F at some unspecified time, indicated by a single reversal for the entire clade. Figure 4.16 shows the same phenomenon for a dispersal event. Species 4 has dispersed from area D to area A, leading to a spurious parallel in ancestor 5, and a wrong position for ancestor 6 (which was never present in area A either). As can be seen from the optimisation in (c), the only incongruence between the phylogeny and the areagram is the parallel in species 4, the result of the dispersal event.

Although the spurious events might be eliminated *a posteriori* by hand, as shown in the two examples above, this raises the question whether or not the areagrams selected by BPA or CCA are actually the most parsimonious in terms of historical events. In phylogeny reconstruction, the kind of historical events whose number is to be minimised is well-defined: each fixed character state change in a phylogeny constitutes such an event (Kornet 1993b; see also Section 3.2.1.1.1). Moreover, there is a direct correspondence between the coding of character states in the data set and the minimum number of events that can explain the found pattern of character states over the terminal taxa. In biogeographic analysis, at least when doing BPA or CCA, there is no such direct correspondence between the coded pattern of character states (occurrences of [ancestral] taxa in areas of endemism), the minimum number of character state changes that can explain the pattern, and the number of actual events that have taken place in the history of the clades.

What should be counted as historical events, then? Obviously not the character state changes derived by traditional optimisation of a BPA/CCA data set. I would suggest that the postulated events whose number is to be minimised are (1) speciation events, (2) dispersal events, and (3) extinction events. Speciation events are faithfully recorded by traditional optimisation as at least *two* state changes, namely one for each daugh-

ter species, but possibly more, if the ancestral species did not react to earlier vicariance events. Dispersal and extinction events are recorded as at least one, but often several state changes, as shown above.

The additional manipulations of the state changes exemplified in Fig. 4.15 and 4.16 reduce the number of events recorded to approximately the actual number of historical events (exactly so in the examples, but this cannot be guaranteed for more complicated cases), but I am far from certain that the areagrams selected by CCA or BPA are also most parsimonious in terms of numbers of historical events. Therefore, it would be desirable to have an optimisation algorithm to carry out the elimination of spurious events in a well-defined manner, and use this algorithm rather than Wagner parsimony to check for most parsimonious areagrams. However, as the choice for different resolutions depends in part on the mechanism of speciation invoked and on the plausibility of non-reaction to vicariance events versus true vicariance followed by dispersal (in general equally parsimonious in terms of number of character state changes), it seems unlikely that such an algorithm can be developed.

An alternative procedure might be to remove the independence of the columns coding for distributions of ancestral and extant taxa by coding the internal nodes of the cladogram of each monophyletic group as a single multistate character. This can be done in BPA by employing the step matrix option of PAUP version 3.1.1 (Swofford 1993), or in CCA by employing the column partition vector option of CAFCA. This approach was suggested by Zandee (pers. comm.), but at first sight the results seem very difficult to interpret and I did not investigate it further.

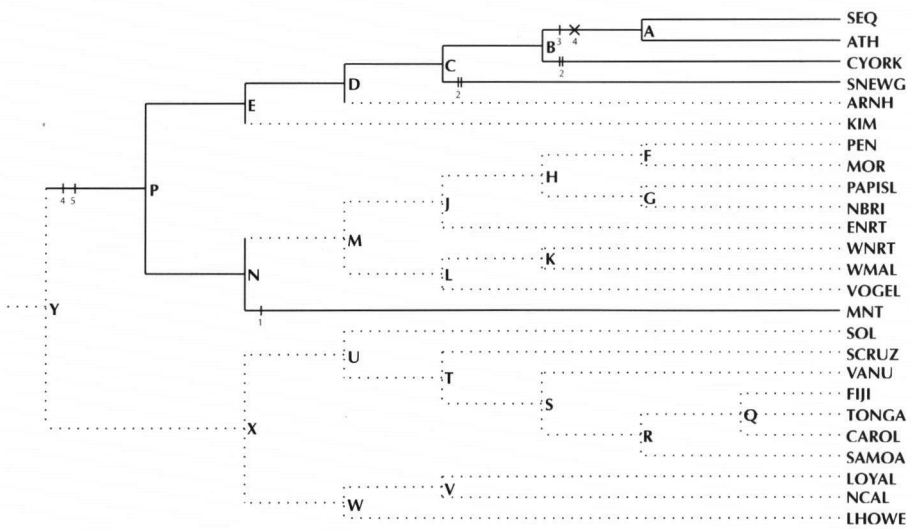

FIGURE 4.17. The CCA areagram of Fig. 4.9 with the data for *Mischarytera* optimised onto it. For the optimisation the data set of Table 4.1 was used, with missing areas coded as unknown data. Areas from which the genus is absent are indicated by dotted lines, and were not taken into consideration during optimisation. Unique apomorphies denoted by single slashes (|), parallels by double slashes (||), and reversals by crosses (×). Species and ancestors numbered as in Fig. 4.11.

4.5.3.2 – *Optimisation of the different phylogenies onto the areagram*

4.5.3.2.1 – Mischarytera

In Fig. 4.17 the CCA areagram is shown with the *Mischarytera* phylogeny optimised onto it. The genus is shown as primitively absent from nodes X and M, and from the Kimberley Plateau and Arnhem Land. Ancestor 5 did not react to all vicariance events splitting up New Guinea and Australia, only to the event separating Southeast Queensland and the Atherton Tableland from the more northerly areas (Cenozoic). Ancestor 4 then went extinct on node A. The populations in the Central Mountain Range became separate from those in South New Guinea and Cape York only later, e.g. as a result of the orogenesis (starting no earlier than the Oligocene). An alternative possibility, which is less parsimonious in terms of character state changes, is that ancestor 5 occurred primitively only on node C, did not vicariate with the separation of South New Guinea, and later dispersed northward to the Central Mountain Range, probably from South New Guinea.

The optimisation confirms the placement of *Mischarytera* on Australia 1, as suggested in Section 4.4.3.

4.5.3.2.2 – Arytera

Figure 4.18 shows the areagram with the *Arytera* data optimised onto it. Ancestor 51 is shown as primitively present in all areas, except the Kimberley Plateau, the Papuan Islands, Santa Cruz, Lord Howe, and the Carolinas. It first gave rise to *A. multijuga* (sp. 29) in the Central Mountain Range, possibly by speciation as a reaction to disper-

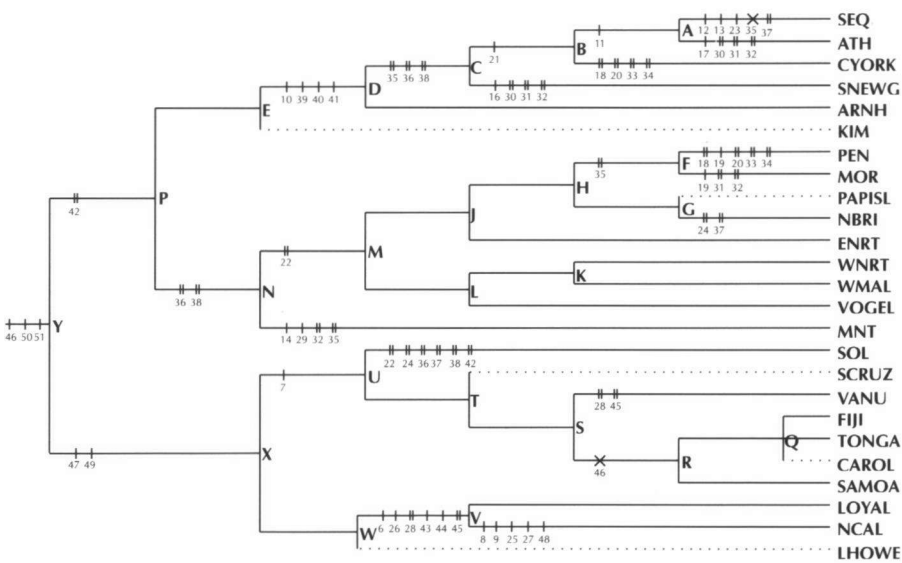

FIGURE 4.18. Optimisation of the *Arytera* phylogeny onto the CCA areagram, as in Fig. 4.17.

sal. The sister species of *A. multijuga*, ancestor 50 (or one of its descendants, ancestor species 46, 42, 38, 36, 35 or 32), reentered the Mountain area. Ancestor 50 then splits into ancestor 49 in X, and ancestor 46. Whether this was a case of vicariance with the split of the IMA from East Australia, in which case the presence of ancestor 45 in the Pacific is due to dispersal, or a case of peripheral isolates allopatric speciation (Brooks & McLennan 1991) (in which case the split of ancestor 46 may be due to the vicariance event), cannot be determined. It is even quite possible that both ancestors 49 and 45 dispersed onto the eastern end of the IMA when it was still close to East Australia, in which case ancestors 51 and 50 should be placed on node P. The presence of *A. litoralis* and *A. novaebrittanniae* (spp. 22, 24) in the Solomon Islands is probably due to dispersal from northeastern parts of New Guinea (e.g. New Britain), making the presence of ancestor 46 at the root of the areagram (and its reversal below Samoa) spurious: it should then be placed on node P. That dispersal is probable for these two terminal species is shown by the (spurious) occurrences of ancestors 36, 37, 38, and 42 in the Solomon Islands. Ancestors 47 and 49 are shown as true synapomorphies for node X. This is probably an artifact, due to migration of ancestor 47 from the IMA over the islands of the OMA up to the Solomon Islands in the West and Samoa in the East. Similarly, ancestor 45 should be removed from its occurrence in Vanuatu, because its presence there is entirely due to *A. neoebudensis* (sp. 28) having migrated there from node V.

Ancestor 42 is probably correctly placed on node P. It split into ancestor 41 on node D, and ancestor 38. This event may be due to allopatric speciation after the OMA collided with the Australian craton (beginning in the Oligocene), providing ancestor 42 with the possibility to disperse onto the former. In that case the position of ancestor 38 on node N is correct, and its occurrence on node C is due its to later dispersal (or that of one or more descendants). Ancestor 41 did not react to vicariance events separating the different areas above node D, until Southeast Queensland separated from the Atherton Plateau in the Pleistocene. Only then did species 12 and 13 (*A. microphylla* and *A. distylis*) form, possibly sympatrically with *A. bifoliolata* and *A. dictyoneura* (spp. 10 and 11). Alternatively, ancestral species 41 and 40 may have gone extinct in South New Guinea and Cape York (e.g. during a Miocene period of flooding), giving rise to *A. dictyoneura* and *A. bifoliolata* in Atherton, and the other species in Southeast Queensland, after which the two species mentioned dispersed into Southeast Queensland, and *A. bifoliolata* in addition extended its range over Arnhem Land, Cape York, and South New Guinea. Assuming that *A. bifoliolata* dispersed into Arnhem Land entails that ancestor 42 was primitively absent there, and that ancestors 39, 40 and 41 should be placed at least one node higher up.

As mentioned above, ancestor 38 either originated on node N by vicariance of ancestor 42, in which case its presence on node C is due to dispersal, or it may have been primitively present on node C, in which case it might be placed on the same node as ancestor 42 (being primitively absent in Arnhem Land and the Kimberley Plateau). The position of ancestor 37 is even harder to fathom, with a very disjunct distribution over Southeast Queensland and New Britain. Either massive extinction occurred in the lineage of ancestor 37, or the position of *A. foveolata* and/or *A. novaebrittanniae* on the phylogeny is wrong. The synapomorphies uniting these two species are indeed not

extremely convincing, and may well be due to convergent evolution (cf. Chapter 3). Ancestor 36, like ancestor 38, may have been primitively present in New Guinea only, so might be placed correctly on node N, or alternatively should also be placed on node P. If ancestor 36 was primitively present on node P, the origin of both *A. divaricata* and *A. litoralis* (spp. 21 and 22) may be due to peripheral isolates allopatric speciation in Australia and New Guinea, resp. The very wide distribution of *A. litoralis* makes it quite probable that it did not originate in all areas above node M simultaneously, but came into existence in some restricted part of that range, e.g. on node F or in East North New Guinea. That it is the only *Arytera* species occurring on node L makes it probable that it dispersed there after speciation elsewhere at or above node J (cf. Section 4.5.2).

Ancestor 35, like its ancestors, may have been primitively present in both Australia and New Guinea, in which case it should be placed together with them on node P, or it may have been primitively absent from Australia, having reached it by dispersal from parts of New Guinea. In view of the fact that no descendants of ancestor 35 occur in Southeast Queensland, and that ancestors 34 and 32 are distributed irregularly over the areas above node C, I feel that an origin in New Guinea is better justified. The optimisation shows a disjunct distribution of ancestor 35 over the Central Mountain Range and node F. In view of the fact that these areas form a continuous range, it is not unlikely that ancestor 35 was primitively absent from the intervening areas. If so, ancestor 35 did not speciate initially upon dispersing into the Central Mountain Range and node F, later reacting to the dispersal over the Peninsula and Morobe by forming ancestor 34 on the former, leaving ancestor 32 on the latter and in the Mountain area. Possibly this took place before these terranes docked with the Australian craton in the middle or late Miocene, because ancestor 32 shows vicariance between the Central Mountain Range with *A. densiflora* (sp. 14), and Morobe with ancestor 31. Alternatively, ancestors 42, 38, 36, 35, and 32 may have been absent from the Central Mountain Range, in which case the latter arrived there by dispersal from Morobe. Ancestor 31 then dispersed to South New Guinea and the Atherton Tableland, forming *A. morobeana* (sp. 15) and ancestor 30, which subsequently speciated into *A. musca* and *A. pauciflora* (spp. 16 and 17), respectively. Ancestor 34 also dispersed, to Cape York, after which it speciated (sympatrically?) into the three present species *A. lineosquamulata*, *A. miniata*, and *A. pseudofoveolata* (spp. 18–20). Alternatively, these three species may all have originated in Peninsula, after which the first and third dispersed to Cape York.

As with *Mischarytera*, the optimisation confirms the placement of the basal Australian species in the Australia 1 areas, and of the apical ones in Australia 2. The inclusion of the OMA islands in Pacific 2 also agrees with the optimisation.

4.5.3.2.3 – Rhysotoechia

The genus *Rhysotoechia* is optimised on the areagram in Fig. 4.19. The genus is primitively absent from nodes X and G, and from the Kimberley Plateau and Arnhem Land, and probably from East and West North New Guinea and the Vogelkop. The first split in the phylogeny might be due to the vicariance event separating South New Guinea from node B (due to Miocene flooding?), after which ancestor 78 dispersed to

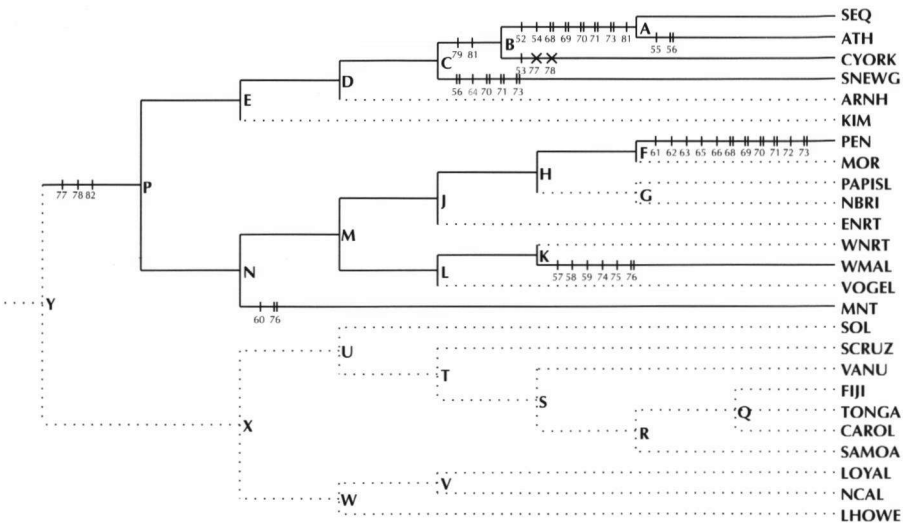

FIGURE 4.19. Optimisation of the *Rhysotoechia* phylogeny onto the CCA areagram, as in Fig. 4.17.

node N, or it may be due to sympatric speciation with descendant species 81 restricted to node B. Ancestor 81 then speciated sympatrically in part of its range into ancestor 80, while ancestor 79 remained present over the entire range, or the speciation was due to the vicariance of Cape York and node A, and ancestor 79 dispersed back to node A later. In the first scenario, ancestor 79 would have reacted to the vicariance event splitting off Cape York by forming *R. nitida* (sp. 53) in that area, with its sister taxon *R. bifoliolata* (sp. 52) on node A. Ancestor 80 may have reacted to the Pleistocene vicariance event splitting Southeast Queensland and the Atherton Tableland by forming *R. mortoniana* (sp. 54) in the former and *R. florulenta* (sp. 55) in the latter, after which *R. mortoniana* extended its range over the Atherton Plateau, or this may also have been a sympatric speciation event.

Assuming that ancestor 78 originated in South New Guinea and dispersed to node N (no earlier than the Oligocene), the split leading to *R. robertsonii* (sp. 56) and ancestor 77 is the direct result of the dispersal. *Rhysotoechia robertsonii* then also dispersed from South New Guinea to the Atherton Tableland. Ancestor 77 split into ancestors 76 and 73, possibly as a reaction to further dispersal from the Central Mountain Range. Ancestor 76 managed to disperse to West Malesia, forming ancestor 75 there and *R. congesta* in the Mountain area. Being primitively absent from New Guinea north of the Central Mountain Range, species 73 remained restricted to Peninsula, where it speciated sympatrically a number of times, ancestor 70 dispersing back to South New Guinea (forming there *R. bilocularis*, sp. 64), and ancestor 68 dispersing back to the Atherton Tableland and Southeast Queensland, forming *R. flavescens* (sp. 67).

This scenario makes the parallel occurrences of ancestors 69, 70, 71, and 73 in South New Guinea and/or node A spurious, and also the reversals for ancestors 77

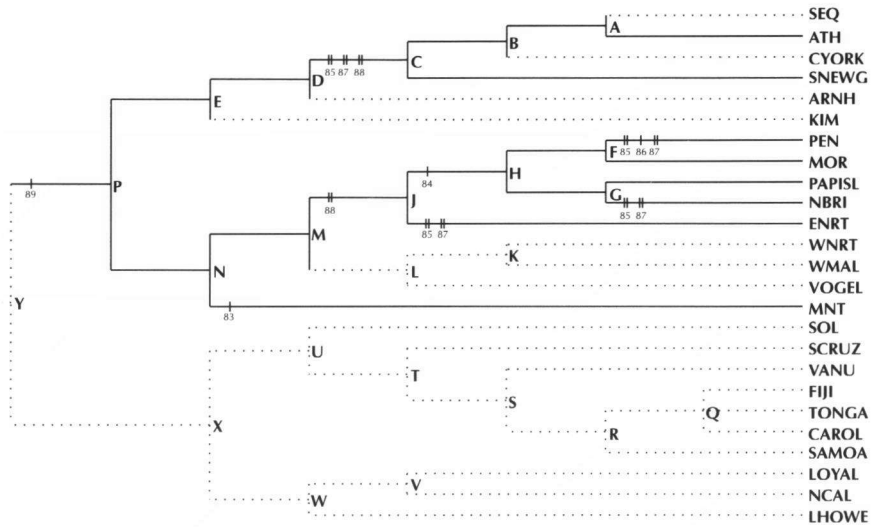

FIGURE 4.20. Optimisation of the *Cnesmocarpon* phylogeny onto the CCA areagram, as in Fig. 4.17.

and 78 in Cape York. In addition, it again confirms the split between Australia 1 and 2, but the occurrence of *R. robertsonii* on the Atherton Tableland should be included in Australia 2.

4.5.3.2.4 – Cnesmocarpon

The patchy distribution of the genus *Cnesmocarpon* on the Australian craton (absent from Southeast Queensland and Cape York) makes an origin in accreted New Guinea probable (Fig. 4.20). In that case ancestor 89 should be placed on node N, showing vicariant speciation into *Cn. dentata* (sp. 83) after dispersing from the Central Mountain Range to node J, where ancestor 88 was formed (the genus is also primitively absent from node L). Possibly ancestor 88 also shows vicariant speciation between East North New Guinea, producing ancestor 87 there, and node H, with *Cn. discoloroides* (sp. 84). A second dispersal (or sympatric speciation) of ancestor 87 from East North New Guinea to Peninsula gave rise to *Cn. montana* and *Cn. dasyantha* (spp. 86 and 85). The latter (or ancestor 87) also dispersed to New Britain, South New Guinea, and the Atherton Tableland.

Once more the optimisation corroborates the placement of *Cnesmocarpon* in Australia 2.

4.5.3.2.5 – Guioa

The optimisation of the genus *Guioa* is shown in Fig. 4.21. Ancestor 193 is shown as primitively present over all areas, except Arnhem Land, the Kimberley Plateau, the Carolinas, and Samoa. The first split, into ancestors 192 and 186, is shown as due to

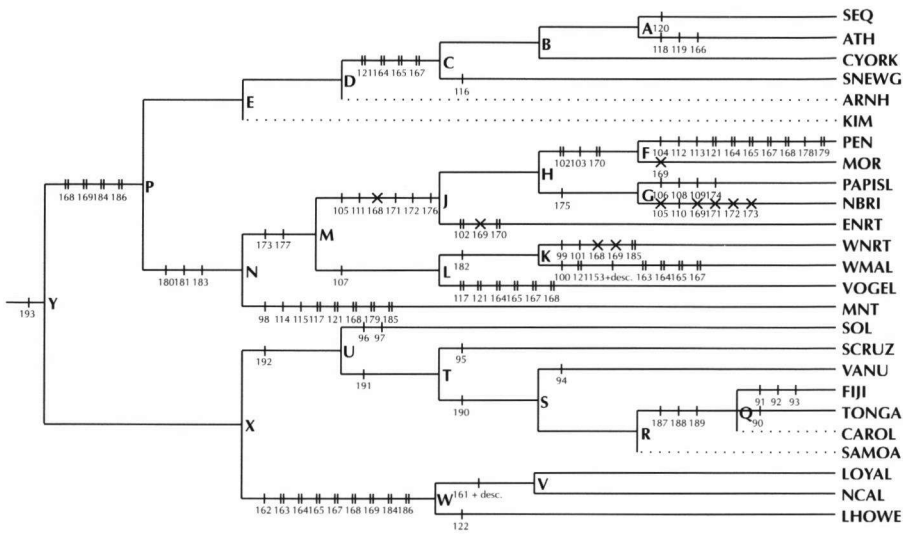

FIGURE 4.21. Optimisation of the *Guioa* phylogeny onto the CCA areagram, as in Fig. 4.17.

vicariance separating the OMA islands from node P, at least if we assume that *Guioa* was primitively absent from node W. This may very well be correct, in view of the massive parallels between ancestors 186–164 on node W and nodes N and C. Ancestor 192 and its descendants show a seemingly vicariant speciation pattern which is probably best explained by peripheral isolates allopatric speciation via sequential dispersal (cf. Brooks & McLennan 1991) from the western to the eastern end of the OMA. The split between ancestors 192 and 186 may alternatively be due to a dispersal event by ancestor 193 from node P to the Solomon Islands. This would entail that the first split in the *Guioa* phylogeny took place after extensive dispersal from the Australian craton over large parts of the OMA, probably before or simultaneously with the first docking in the Oligocene.

Ancestor 186 split into ancestors 185 and 184, possibly by sympatric, or peripheral isolates allopatric, speciation in the Central Mountain Range of the former, which might have dispersed to West North New Guinea, forming *G. pteropoda* (sp. 99) there.

Ancestor 184 vicariated with the major separation of nodes N and C into ancestors 183 and 169, respectively. In New Guinea the next speciation event is possibly due to another case of sympatric or peripheral isolates allopatric speciation, on node K. The species originating there, ancestor 182, vicariated with the split between West North New Guinea and West Malesia. It should be mentioned that the species in the latter area, *G. patentinervis* (sp. 100), is restricted to the Moluccas. Possibly, ancestor 181 is the species in the lineage of ancestor 184 reentering the Central Mountain Range (from node M or J?), resulting in *G. unguiculata* (sp. 115) and ancestor 180, or this may be again a case of peripheral isolates or sympatric speciation, with the vicariance event splitting off the Central Mountain Range leading to ancestor 179. The latter may then

be assumed to have dispersed to Peninsula, where it formed *G. hospita* and *G. molliuscula* (spp. 112, 113).

Ancestor 177 split sympatrically or allopatrically on nodes L and J, in the latter case followed by dispersal of ancestor 173 onto node J. Ancestor 176, on node J, again split via either mechanism, producing ancestor 175 on node G and *G. comesperma* (sp. 111) in East North New Guinea or on node F, after which it dispersed into the remainder of its range. Ancestor 175 in its turn speciated allopatrically, forming *G. novobritannica* in New Britain and ancestor 174 on the Papuan Islands. The close phylogenetic relation between these species may indicate that in the past these two areas were less far apart than at present, e.g. with New Britain passing slightly to the North of the docking East Papua composite terrane of Pigram & Davies (1987) (cf. Section 4.5.2).

Ancestor 173, either primitively present on node M or dispersing back from node L to node J, speciated into ancestor 172 on the latter and *G. membranifolia* (sp. 107) on the former. In West Malesia, this species is also restricted to the Moluccas. Ancestor 173 seems to be primitively absent from New Britain, which lends support to the hypothesis that it dispersed onto node J from node L. It underwent speciation, possibly allopatrically, forming *G. normanbiensis* (sp. 106) on the Papuan Islands and ancestor 171 probably on node F. *Guioa rigidiuscula* (sp. 105) would then have dispersed from node F to the adjacent Papuan Islands and East North New Guinea, while its sister groups, ancestor 170 and *G. aryterifolia* (sp. 104) remained restricted to node F.

Ancestor 169 first speciated sympatrically or as a peripheral isolate in South New Guinea, forming *G. oligotricha* (sp. 116) and ancestor 168, which probably dispersed to South New Guinea, the Central Mountain Range and the Vogelkop, forming *G. subsericea* (sp. 117) in the latter two areas and ancestor 167 in the remainder. This ancestral species did not react to the various vicariance events on the Australian craton till the Atherton Tableland split off in the Pleistocene, when it formed (sympatrically?) ancestor 166 which in turn gave rise to *G. montana* and *G. lasioneura* (spp. 118, 119). Ancestor 165 remained present in the other areas above node C and also reacted to the same vicariance event by forming *G. semiglauca* (sp. 120) in Southeast Queensland. Ancestor 164 would then initially have been restricted to South New Guinea and the Cape York area, from which it extended its range southward to include the Atherton Tableland and Southeast Queensland, and northward into the Central Mountain Range, the Vogelkop, entire West Malesia and the Peninsula. It also managed to extend its range over the eastern end of the IMA (node W).

Curiously, the next speciation event separates *G. acutifolia* (sp. 121) on the Australian craton (node C), the Central Mountain Range, the Vogelkop, the Peninsula, and the Moluccas (West Malesia) from ancestor 163, which is reconstructed with a very disjunct distribution in West Malesia and on node W. This odd result may be due to convergence, resulting in a spurious sister group relationship between the West Malesian species (descending from ancestor 153) and the species on the IMA islands (descendants of ancestor 162). The synapomorphy for ancestor 163 is a distinct stipe, which may have developed in parallel. Alternatively, *G. acutifolia* may have speciated sympatrically with ancestor 163, which must then have been primitively present on node P but suffered extinction in Australia and New Guinea.

Ancestor 162 may initially have been present on node W, or have been restricted to Lord Howe Island. In the first case, the event separating *G. coriacea* (sp. 122) from ancestor 161 is a true vicariance event, in the second it is due to speciation after further dispersal of the latter to New Caledonia and the Loyalty Islands.

The position of the *Guioa* species on the OMA islands and the numerous inconsistencies of the phylogeny with the areagram may indicate that its ancestor was already widespread over the OMA before it began accreting onto the Australian craton in the Oligocene, leading to alternative vicariance patterns as postulated in Section 4.5.2. This would be in agreement with the odd pattern found for the Pacific 1 and 2 areas in the CCA analyses, because then *Guioa* would show a third pattern for the West Pacific OMA islands.

4.5.3.2.6 – Cupaniopsis

The optimisation of *Cupaniopsis* onto the areagram (Fig. 4.22) is characterised by a large number of parallels in direct ancestor–descendant lineages, which indicate either a number of old dispersal events, or great incongruence between the biogeographical pattern reconstructed here and the true biogeographical history of the genus. The reconstruction shows *Cupaniopsis* as primitively present in all areas except the Santa Cruz group, Tonga, and Lord Howe Island. However, it may be assumed that it was also primitively absent from the Kimberley Plateau and Arnhem Land, which were reached only by *C. anacardioides* (sp. 223). The parallels mentioned above occur in the lineages leading from ancestor 307 to *C. curvidens* (sp. 200) on nodes N versus node C and South New Guinea; from ancestor 307 to ancestor 293 on node N and the Central Mountain Range versus nodes C and B versus the Solomon Islands, Vanuatu, and Fiji; and from ancestor 288 to ancestor 283 on node E versus node V; from ancestor 288 to ancestor 274 on node V versus node M versus node R versus node E and South New Guinea; and of ancestor 288 to ancestor 254 on node V versus node R. Further, primitive absence from node G and West Malesia is indicated by numerous reversals in direct ancestor-descendant lineages, from ancestor 288 to ancestor 270 on node G; from ancestor 303 to *C. curvidens* (sp. 200) in New Britain and West Malesia; and from ancestor 299 to *C. stenopetala* (sp. 206) on the Papuan Islands.

Starting from the terminal taxa, *C. baileyana* and *C. foveolata* (spp. 212, 123) are derived from ancestor 289, which is shown as primitively present on node B. If this position is correct, it did not react to the event separating Cape York, later vicariating with the split between Southeast Queensland and the Atherton Tableland. Alternatively, it may have been primitively absent from Cape York, *C. foveolata* having dispersed there after its speciation. The origin of ancestor 289 is unclear: its ancestors occur also on some islands in the OMA. Thus the most probable reconstruction is dispersal from e. g. Fiji back to Australia. However, this seems highly improbable in view of the wide disjunction. An alternative is that the phylogeny of *Cupaniopsis* is incorrect on this point. The most closely related species on New Guinea is *C. rhytidocarpa* (sp. 207), which occurs on the Peninsula. Thus ancestor 289 might be placed together with the other species descending from ancestor 294 due to convergent evolution of their syn-

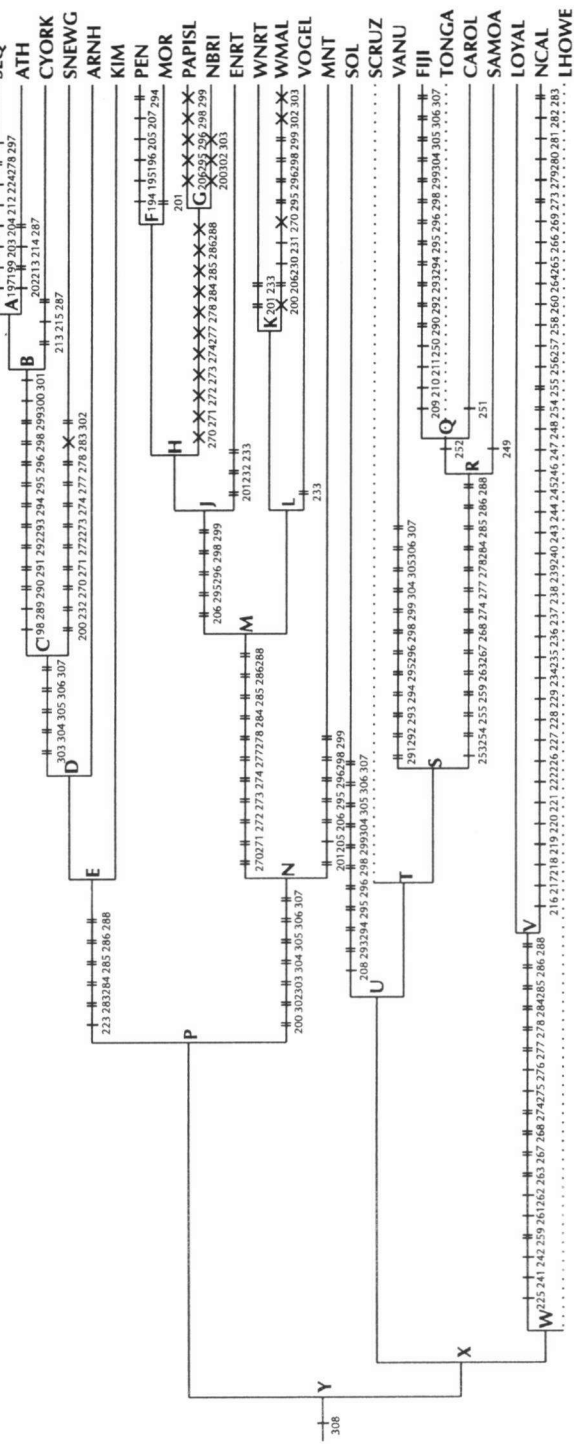

FIGURE 4.22. Optimisation of the *Cupaniopsis* phylogeny onto the CCA areagram, as in Fig. 4.17.

apomorphy, colporate pollen. The development of colporate pollen from (para)syncolporate pollen has probably occurred a number of times in the phylogeny of the Sapindaceae, e.g. in *Arytera* (Chapter 3; see also Van der Ham 1990). Dispersal from Peninsula to the Atherton Tableland was also hypothesised for other species in this study, while a movement from Peninsula to the islands in the OMA seems more likely than the reconstructed dispersal.

A similar very disjunct ancestral distribution is shown by ancestor 273, with descendants on New Caledonia, New Guinea and in West Malesia. Because ancestor 273 is placed within a clade that occurs almost exclusively on New Caledonia and the Loyalty Islands, the position of ancestor 272 (which developed into the species in New Guinea and West Malesia) may also be erroneous. Disregarding the distributions of ancestors 272 and 289 and their respective descendants greatly simplifies the optimisations. Thus, ancestor 277 and its descendants become endemic to node V, with dispersal of ancestor 254 from there to node R with subsequent speciation into *C. samoensis* (sp. 249) and ancestor 253, which in turn speciated in Fiji to *C. concolor* (sp. 250) and in the Carolinas to *C. guillauminii* (sp. 251).

Apparently ancestor 288 was primitively present on nodes C and V, possibly having vicariated into ancestors 287 and 286 with the separation of the IMA from continental Australia. If so, then *C. anacardioides* and *C. wadsworthii* (spp. 223, 224) dispersed back to the mainland from node V. Alternatively, ancestor 288 was present only on either node V or node C, having dispersed a number of times to the other node. Thus, the two species mentioned may also have been primitively absent from node C, although this seems less likely in view of the sister relationship between ancestors 288 and 307, which is found on nodes N and C. The occurrence of *C. anacardioides* in Arnhem Land and the Kimberley Plateau (and possibly in South New Guinea) is probably due to it having dispersed there from node C (or B), like *Arytera bifoliolata*.

Ancestor 307 was primitively present on nodes N and C, or only on the former. As explained above, it was probably primitively absent from at least node G and West Malesia. In view of the ancestral position of its sister group, ancestor 288, it probably originated due to dispersal from the Australian craton to node N, either sympatrically, or allopatrically, after which it dispersed once or several times back to node C or B. The first species to split off from ancestor 307 (*C. acuticarpa*, *C. napaensis*, and *C. bullata*, spp. 195, 196, 197) are all endemic to Peninsula. This may be due to several cases of sympatric or peripheral isolates allopatric speciation followed by redispersal into Peninsula, or indicate that ancestor 307 was originally confined to that area. Because ancestor 304 is widespread over nodes N and C, the latter possibility is considered less likely. Ancestor 304 split (sympatrically?) into ancestor 303, possibly originally confined to node C, and ancestor 299, which was probably widespread. In turn, ancestor 303 most likely vicariated with the separation of South New Guinea from node B (due to Miocene flooding?), producing ancestor 302 on the former, and ancestor 301 on the latter. Ancestor 301 did not react to the first vicariance event separating Cape York from node A, but did react to the event separating Southeast Queensland, forming two endemic species there, *C. newmannii* and *C. tomentella* (spp. 197, 199), and the widespread *C. flagelliformis* (sp. 198). Ancestor 302 probably dispersed from South New Guinea onto node N, either allopatrically forming *C. curvidens* (sp. 200) in the

southern part of its range and *C. macropetala* (sp. 201) in its northern part, after which the former also dispersed over the remainder of node N, or sympatrically.

Ancestor 299 probably formed several species by sympatric or peripheral isolates speciation in the Atherton Tableland and Southeast Queensland (spp. 202–204), ancestor 296 becoming confined to node N. *Cupaniopsis euneura* (sp. 205) then formed in the Central Mountain Range, possibly by allopatric speciation, leaving ancestor 295 on node M. This species then split into *C. stenopetala* (sp. 206), which may have re-entered the Central Mountain Range, and ancestor 294, which was confined to the Peninsula. The latter probably dispersed from there onto the OMA islands eastward (node U), resulting in *C. rhytidocarpa* (sp. 207) on Peninsula and ancestor 293 on node U (or only on the Solomon Islands). The remainder of the phylogeny shows another case of peripheral isolates allopatric speciation via sequential dispersal eastward to Vanuatu and Fiji, producing several endemic species on those island groups.

The optimisation of the *Cupaniopsis* phylogeny does not confirm unequivocally the presence of exclusively Australia 1 taxa. Several descendants of ancestor 307 may have dispersed back to Australia from (South) New Guinea; if so, they should be placed in Australia 2. A third Australian pattern (Australia 3) may also be present, namely dispersal back from the IMA to the Australian mainland.

4.5.3.2.7 – Lepidopetalum

The genus *Lepidopetalum* shows a more straightforward pattern than the two previous large genera. Its optimisation on the areagram, shown in Fig. 4.23, shows it is primitively present on node Y. The genus is shown as primitively absent from nodes W, T,

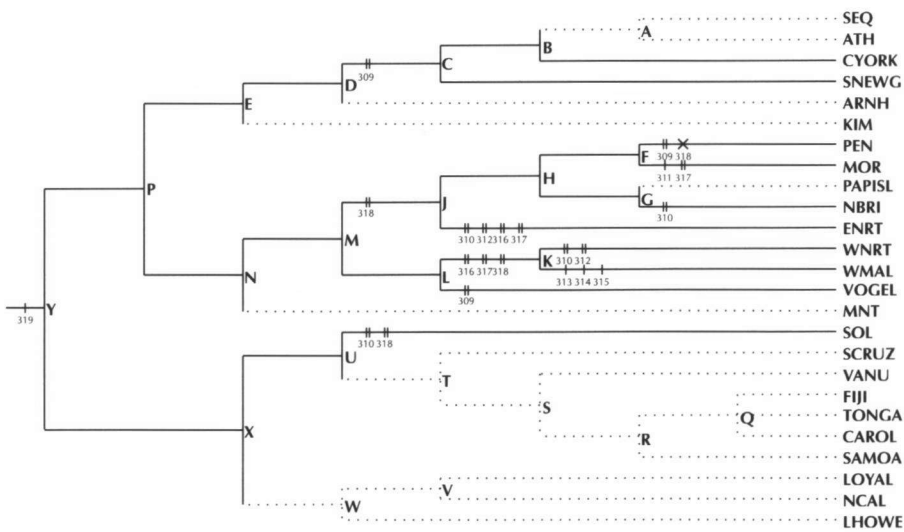

FIGURE 4.23. Optimisation of the *Lepidopetalum* phylogeny onto the CCA areagram, as in Fig. 4.17.

and A, and from Arnhem Land, the Kimberley Plateau, the Central Mountain Range, and the Papuan Islands. However, we may safely assume that its presence on the Solomon Islands is due to dispersal of *L. subdichotomum* (sp. 310) or its ancestor 318 from e.g. New Britain. Thus ancestor 319 was confined to node P. The first split is probably due to the vicariance separating the Australian craton from the accreted terranes (approx. Oligocene), resulting in *L. xylocarpum* (sp. 309) on node C and its sister, ancestor 318, on nodes J and K (and the Solomon Islands?). The former species probably later dispersed into the Vogelkop and Peninsula areas, rather than being primitively present there. Ancestor 318 may have been primitively absent from the Vogelkop and West Malesia (cf. Section 4.5.2), in which case its correct ancestral position is on node J. Its absence from the Peninsula may also be primitive, if the original dispersal northward was onto the Sepik terrane, followed by displacement further North as this terrane became uplifted into the present Central Mountain Range (after the Oligocene docking event). In that case *Lepidopetalum* would be the only genus in this analysis which was not capable of adapting to the environmental change due to the uplift, which would then also have created the barrier separating the southern and northern populations of ancestor 319.

The next event is the speciation of ancestor 318 into *L. subdichotomum* (sp. 310) and ancestor 317. This may be a case of allopatric speciation after dispersal of ancestor 318 onto the Solomon Islands (and New Britain?), or may have been sympatric in East and West North New Guinea with later dispersal of *L. subdichotomum* eastward. The next event, giving rise to *L. fructoglabrum* (sp. 312) and ancestor 316, is probably due to allopatric speciation, although the nature of the barrier is not clear. Possibly it is related to the docking of the Finisterre terrane north of the Morobe area of endemism about 2 million years ago. The next event is again an allopatric speciation event, probably

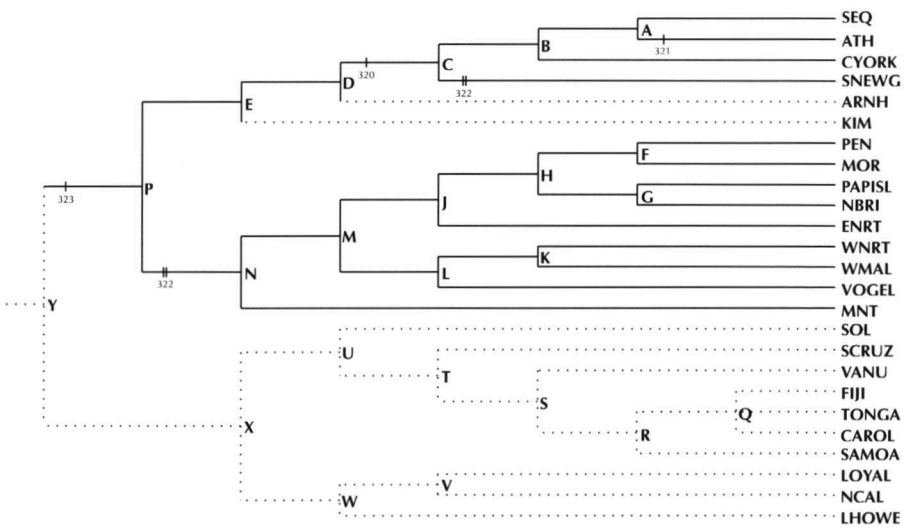

FIGURE 4.24. Optimisation of the *Jagera* phylogeny onto the CCA areagram, as in Fig. 4.17.

due to the dispersal of ancestor 316 into West Malesia, where it gave rise to ancestor 315, leaving *L. micans* (sp. 312) in East and West North New Guinea.

The optimisation leaves unresolved the question whether *L. xylocarpum* should be placed in Australia 1 or 2.

4.5.3.2.8 – Jagera

Because the phylogeny for *Jagera* is not resolved, its biogeographic history cannot be inferred satisfactorily. The optimisation on the areagram (Fig. 4.24) shows primitive presence (ancestor 323) on node P. If the areagram is correct, the phylogeny might be resolved with *J. javanica javanica* (sp. 322) splitting off first, leaving *J. javanica australiana* and *J. pseudorhus* (spp. 321, 320) as sister species on node C. This is the resolution resulting from the cladistic analysis with macromorphological characters only (see Adema & Van der Ham 1993). Whether the genus originated on node C or node N cannot be made up from the optimisation, both possibilities being equally likely. If the hypothesis that *Cnesmocarpon* originated on node N is correct (see above), however, the position of that genus basal to the sister taxa *Jagera* and *Trigonachras*, which occurs in West Malesia and New Guinea, makes the origin of *Jagera* on node C unlikely. In that case the basal split may be due to a dispersal event from node N to node C. The ancestor of *J. j. australiana* and *J. pseudorhus* would then not have reacted to the vicariance events of nodes C and B, only speciating (sympatrically?) in the Atherton Tablelands when this area separated from Southeast Queensland in the Pleistocene. This scenario would agree with the assumption made when doubling that *Jagera* belongs to the Australia 2 biota.

4.5.3.3 – *Comparison of optimisations with assumptions made when doubling the Australian and Pacific areas*

The above optimisations show that the assumptions made when doubling the various East Australian and Pacific areas for the BPA analysis are generally corroborated. In particular the splitting of East Australia is well supported. However, not all dispersal events reconstructed coincide with the initial dispersal assumptions. For example, all Australian *Cupaniopsis* species were placed in Australia 1 in the analyses with doubled areas, but the optimisation reconstructs several species as having dispersed from New Guinea to Australia. Some species may even have dispersed from the IMA, in a third Australian pattern. As to the OMA areas, the assumption that the *Guioa* species on the OMA arrived there from New Guinea is not borne out by the optimisations. The double pathway is very apparent in *Cupaniopsis*, however, with two distinct clades on the OMA, one related to New Caledonia, the other to New Guinea. The occurrences of *Lepidopetalum* and *Arytera novaebrittanniae* and *A. litoralis* on the Solomon Islands are also clearly due to dispersal from New Guinea.

4.5.4 – **Comparison of the different results**

Comparison of the five different results obtained thus far (Fig. 4.8, 4.9, 4.10, 4.12, 4.13, 4.25) brings to light a number of similarities, but also some differences. The first

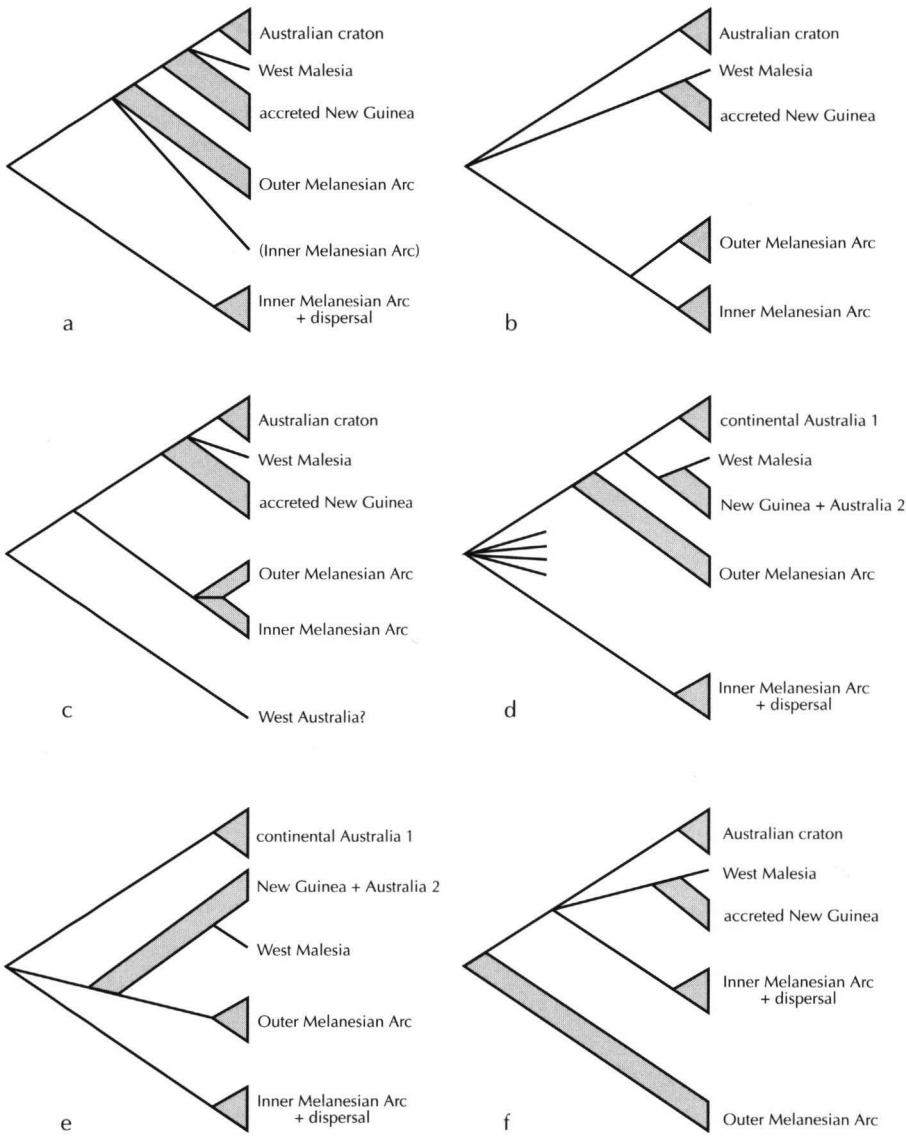

FIGURE 4.25. Schematic representation of the large-scale patterns observable in the different analytical results of (a) Fig. 4.8a; (b) Fig. 4.9; (c) Fig. 4.10; (d) Fig. 4.12a; (e) Fig. 4.12b; and (f) Fig. 4.13.

similarity is found in the relative positions of the East Australia (1) areas, with Cape York as the sister of a component consisting of the other two areas. Secondly, New Guinea + West Malesia form a mono- or paraphyletic group in all analyses; in those cases in which a New Guinea + West Malesia + East Australia component is present,

East Australia's sister area is South New Guinea. Remarkably, in the CCA analysis with doubled areas (Fig. 4.13, 4.25f) South New Guinea is still the sister area of East Australia 2, which together are sister to East Australia 1. Both BPA analyses with doubled areas (Fig. 4.12, 4.25d, e) show South New Guinea as one of the last areas to split off within a New Guinea component, and not as closely related to East Australia 1. Quite possibly this points to South New Guinea also being an area with two different patterns, like East Australia.

The dual position of the West Pacific areas is also apparent from the comparison. In the BPA analysis without doubled areas, and coding missing areas as absence (Fig. 4.8a, 4.25a), Samoa and the Carolinas group with New Caledonia and the Loyalty Islands as a Pacific 2 component, while the remaining Pacific areas are the sister group(s) of New Guinea + West Malesia + East Australia. In the CCA analysis without doubled areas (Fig. 4.9, 4.25b) the West Pacific areas form a component, with New Caledonia + Loyalty Islands + Lord Howe as sister to the remaining areas, which split off from West to East. In the BPA analysis with doubled areas, coding missing areas as absences (Fig. 4.12a, 4.25d), the same grouping of Pacific 2 areas is seen as in the analysis without doubled areas, while part of Pacific 1 groups as sister of New Guinea + West Malesia + East Australia. The other Pacific areas group in the unresolved polytomy at the base of the areagram. In the second BPA analysis, with missing areas coded as unknown data (Fig. 4.12b, 4.25e), Pacific 2 forms a component, as does Pacific 1 which, with the typical West-to-East pattern, is embedded within the New Guinea + West Malesia component. The CCA pattern with doubled areas (Fig. 4.13, 4.25f) is not so clear about the different patterns, with Pacific 1, showing the West-to-East pattern, within a paraphyletic Pacific 2 group near the base of the areagram. This result still seems to reflect some missing area effect for Pacific 1. The CCA analysis without doubled areas (Fig. 4.9, 4.25b) also shows the West-to-East pattern for the Pacific areas, but now they occupy the position dictated by Pacific 2, as sister to New Caledonia + Loyalty Islands + Lord Howe Island.

The COMPONENT result (Fig. 4.10, 4.25c), although rejected because dispersal seemed to be invalidating the results, nevertheless shows similar large-scale patterns to those from the different BPA and CCA analyses. The Australian clade is essentially present, including South New Guinea, as is the larger Australia + New Guinea + West Malesia component. Its sister region is the Pacific component also displayed in the CCA analysis without doubled areas, but excluding the Solomon Islands, which are shown as part of New Guinea.

In conclusion, the different analyses, although differing in their assumptions and methodology, and also resulting in areagrams differing in their details, seem to agree on the large-scale patterns in the data.

4.5.5 – **Final choice for an areagram**

The choice among the different results is complicated by the different methods used to derive them. The COMPONENT results were already rejected in Section 4.4.3.1, for reasons given there. Within the set of BPA analyses, the results without doubling of the areas lack much resolution, which is only slightly improved by doubling the Aus-

tralian and Pacific areas. Furthermore, the consistency and retention indices for the analyses with doubled areas are only slightly better than for the analyses without doubling (missing areas coded as absent ci = .57 in both cases, ri = .67→.70; missing areas coded as unknown data ci = .63→.69, ri = .67→.76). The CCA results are much better resolved, but the analysis with doubled areas does not confirm the assumption that two patterns are involved for East Australia and the West Pacific. Because the optimisation of the different phylogenies onto the CCA result without doubled areas recovers most of the different patterns assumed when doubling areas, this areagram is preferred. Further support for this CCA areagram comes from its close similarity to the postulated history of the accretion of terranes onto the northern edge of the Australian craton (see Fig. 4.14). Although none of the phylogenies closely follows the reconstructed pattern, this similarity may be explained as resulting from an averaging out of the various dispersal and vicariance events in the eight phylogenies to coincide with the sequence of accretion events.

The areagram resulting from the CCA analysis without doubled areas, but employing the protocol outlined in Section 4.3.2.1, is therefore accepted as the final result of the biogeographical analyses, with the basal trichotomy resolved in favour of an Australia + New Guinea + West Malesia component.

4.6 – SUMMARY OF PATTERNS FOUND

In summary, the broad pattern (Fig. 4.26) suggested by the Sapindaceous genera investigated in this study is that of an old Gondwanan biota vicariating first to form a separate New Caledonian biota, either due to the vicariance event separating the eastern end of the IMA from East Australia (beginning no later than c. 80 Ma), or by dispersal when the gap between the two areas was still bridgable. This may have occurred

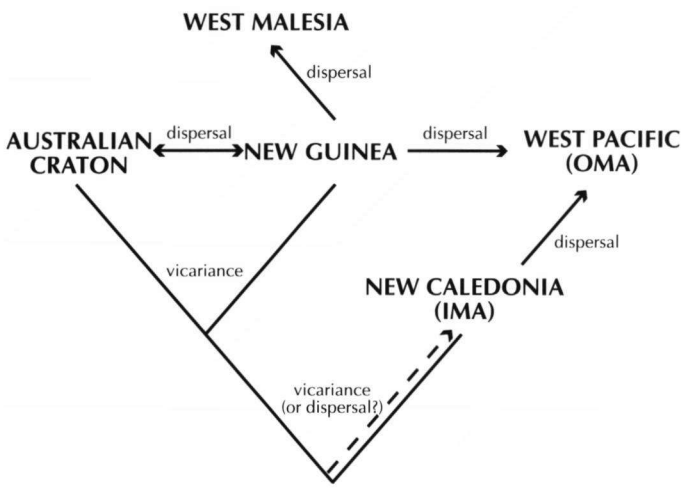

FIGURE 4.26. Summary of the major events affecting the Sapindaceous taxa in the Gondwanan biota.

several times, at least within *Arytera*, which has two separate New Caledonian clades, and possibly also in *Cupaniopsis*. From the New Caledonian areas, dispersal took place eventually reaching the Solomon Islands in the West and Samoa in the East. A second dispersal into the West Pacific originated in New Guinea and followed the chain of islands forming the OMA. This dispersal may have taken place before or after the East Australian biota split from the New Guinean one, but speciation on the not accreted parts of the OMA only occurred after this vicariance event. The basal split between East Australia and New Guinea suggests that the vicariance between these two regions may be older than the often suggested period of post-Pleistocene rise in sea level (cf. Cracraft 1986, Van Welzen 1989). Possibly, it can be ascribed to an earlier period of marine transgression, e.g. during the Miocene (cf. Audley-Charles 1987). At some time after the New Caledonian speciation events the Australian biota also spread to West Malesia. That this was indeed a dispersal and not a vicariance event is indicated by the various positions taken by West Malesia in the different phylogenies. The final events affecting the Australian biota seems to have been dispersal of several taxa westward into Arnhem Land and the Kimberley Plateau, and a reinvasion of New Guinean taxa, both possibly during a period of low sea levels in the Pleistocene.

4.6.1 – Comparison with the results of other studies

A comparison with areagrams obtained by other investigators shows that their results are largely corroborated by mine. Cracraft (1983b, 1986), analysing the distributions of a number of bird genera in Australia, arrived at almost the same sequence of vicariance events for that region. His areagrams differ from mine only in uniting Arnhem Land and the Kimberley Plateau in a single component, and in the position of South New Guinea as sister to Cape York, rather than to an East Australian component. Cracraft (1991) again examined the biogeography of Australia using data from Australian birds, mammals, snakes, lizards, and frogs. Almost all separate analyses of these groups and all combined analyses showed a component identical to the Australia craton component in my analysis, if only the areas in common to both studies are considered. (Unfortunately Cracraft's [1991] study did not include South New Guinea.) The major difference between his and my results is the consistent Arnhem Land + Kimberley Plateau component already apparent in his earlier study. Van Welzen (1989), however, produced the same sequence of vicariance events for the Australian craton as found by me, from a combined analysis of Cracraft's (1986) data and the *Guioa* phylogeny.

Van Welzen (1989) also produced areagrams for the biogeographic history of New Guinea, based on his *Guioa* data in combination with data for the cicada genera *Cosmopsaltria* and *Diceropyga*, and using the original form of CCA. His result differs considerably from mine in some respects, although other parts of the areagrams are quite similar. For example, in both areagrams the Central Mountain Range is one of the first areas to split off, but in Van Welzen's result it forms a component with the Vogelkop, which here is in a component with West North New Guinea (and West Malesia). The component consisting of Peninsula, the Papuan Islands, New Britain and East North New Guinea (and Morobe) found here, is partly also observable in Van

Welzen's results, although their positions differ from mine, and in Van Welzen's analysis the component also includes West North New Guinea and South New Guinea.

Van Welzen et al.'s (1992) result for *Lepidopetalum* resembles the result obtained here in that South New Guinea (+ Australia) is shown to be the sister area for the accreted terranes of northern New Guinea + West Malesia. It should be remembered, however, that in that study South New Guinea included the Vogelkop and Peninsula areas. North New Guinea was not differentiated in a western and eastern part in the *Lepidopetalum* analysis, but the whole northern part of New Guinea is shown as sister area to West Malesia, which compares well to the West North New Guinea + West Malesia component in the areagram obtained here.

For the Pacific islands of the OMA, Van Welzen (1989) obtained an areagram based on the *Guioa* data and the cicada genus *Aceropyga*. The West to East pattern obtained here is repeated exactly in that study. Van Welzen also came to the conclusion that the seemingly vicariant pattern was caused by sequential dispersal in an easterly direction. The relationship among the IMA islands is dictated entirely by the *Guioa* phylogeny in this study, it being the only genus occurring on Lord Howe Island. Thus it is not surprising that the result found here exactly copies that found by Van Welzen (1989).

Andersen (1991), studying marine water striders, also obtained results that are quite well comparable to mine. The genera studied by him all have Australia (including the IMA islands and South New Guinea) in a basal position, either alone (*Halobates*, *Xenobates*, and '*Halovelia papuensis*'-group areagrams) or in a component together with the West Pacific islands, which include Fiji, Tonga, Samoa, and the Carolinas but exclude Vanuatu and the Solomon Islands (*Halovelia* and generalised areagrams). The next component in all his analyses is Papua, which contains the accreted terranes of New Guinea together with the most westerly islands of the OMA, either as a solitary component (*Halovelia*, *Xenobates*, and generalised areagrams) or together with the West Pacific (*Halobates* areagram). In all areagrams West Malesia is a single component which is sister to Papua (+ West Pacific). Remarkably, in the *Halovelia* and generalised areagrams the most basal area is East Asia (including eastern China, Taiwan, and South Japan). A similar ancient sister group relationship between East Asia and an Australia + New Guinea + West Pacific + West Malesia component has been suggested for cicadas by Duffels (pers. comm.).

Muona (1991) made an extensive study of the biogeography of Eucnemid beetle genera occurring in Southeast Asia and the western Pacific. Although his first aim was to obtain large-scale relationships on a regional scale, and establish relations with other surrounding regions, his results can be compared on a number of counts with those obtained here. The islands in the Pacific Ocean show a number of different relations: his 'new genus 4' and *Dromaeoloides* display a sister area relationship between the OMA islands and a New Guinea + East Australia component, where in the latter genus the outgroup area is New Caledonia. This resembles the situation found here in the CCA analysis. Other patterns found for the OMA islands do not include East Australia, and therefore show only a close relation between the OMA islands and New Guinea (*Porraulacus*, *Maelodrus*, *Serrifornax*), with West Malesia either as sister area to New Guinea or to an OMA + New Guinea component. Most taxa occurring in East Australia and New Guinea show a close relationship between the two; three

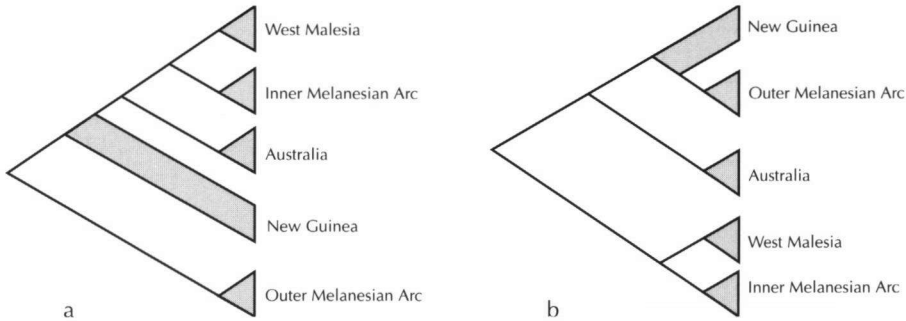

FIGURE 4.27. (a) Van Welzen's (1989) generalised areagram corrected for compilation errors (see text). (b) The same areagram, but rooted between the IMA and the Australian craton.

different basic patterns are observable. The majority of the genera (*Arrhipis*, *Calyptocerus*, *Cladidus*, *Dendrocharis*, *Epipleuris*, and *Rhagomicrus*) show West Malesia as sister to a New Guinea + (East) Australia component, usually with South America as outgroup area. The genera *Dyscharachthis* and *Farsus* show a similar pattern, but lack representatives in West Malesia. The third pattern, and the one which resembles most the result obtained here, is East Australia as sister to a New Guinea + West Malesia component, displayed by *Feaia* and *Hemiopsida*.

Van Welzen (1989) also provided a generalised areagram assembled from his analyses for several smaller regions, namely Australia + New Caledonia, the OMA islands, New Guinea, and West Malesia. However, the relation between these different regions is reconstructed incorrectly, because not all relevant outgroup areas were included in the partial analyses. Thus, e.g. in the analysis of New Guinea, the outgroup for *Guioa*, *Cupaniopsis anacardioides*, was included but without taking into consideration its occurrence in Australia. This led to a wrong rooting for the reassembled areagram, which is most obvious from the incorrect position of the Pacific islands compared to the *Guioa* phylogeny which was used to connect the different areagrams (cf. his Fig. 55 with Fig. 4.11e). A corrected areagram is shown in Fig. 4.27. The result is comparable to that obtained here, but rooted differently. If Van Welzen's areagram is rerooted between the IMA and Australia (Fig. 4.27) the relation between these two areas and a paraphyletic accreted New Guinea is the same as that obtained here. Differences are found in the position of South New Guinea, and of the OMA islands and West Malesia, which have switched places.

Chapter 5 – REVISION

Note: The descriptions were made from herbarium specimens; thus all colours are for material *in sicco* (additional observations on colours in fresh material are given in the field notes); all measurements on flower parts were taken from rehydrated material.

5.1 – KEY TO THE GENERA TREATED IN THIS REVISION

1 a. Fruit glabrous inside, with a sclerenchymatic layer on the inside of the pericarp radiating from the placenta and separating from the endocarp when ripe. Calyx punctate, teeth with a membranaceous margin. Leaves 3–11-jugate; leaflets (densely) punctate [Australia, New Guinea] ..... ***Mischarytera*** (p. 210)

b. Fruit glabrous or variably hairy inside, without such a sclerenchymatic layer. Calyx not punctate, margin not membranaceous. Leaves usually 1–4-jugate, rarely 5- or 6-jugate; leaflets usually not or only sparsely punctate ..... ***Arytera*** (p. 149)

5.2 – SYNOPTIC KEY TO THE SPECIES TREATED IN THIS REVISION

The numbers in the key refer to the numbers of the species as given in the descriptions. Numbers printed in **bold**: the species shows more than one character state; numbers in parentheses: character state rare; numbers with a question mark: character state unknown.

1. Indument
   a. Short, straight, appressed: A2, A3, A5, A6, A9, A10, A15, **A16**, A17, A20, A21, A22, A23, A24, M1, M2, M3
   b. Short, straight, patent: A1, A4, A12, A13, **A16**
   c. Short, straight, patent *and* long, straight, appressed: A8
   d. Long, crispate, patent: A7, A11, A14, A18, A19, A25

2. Glandular scales
   a. Present: A1, A4, A12, A13
   b. Absent: A2, A3, A5, A6, A7, A8, A9, A10, A11, A14, A15, A16, A17, A18, A19, A20, A21, A22, A23, A24, A25, M1, M2, M3

3. Leaves
   a. One-jugate: **A1**, A2, **A4**, **A5**, **A6**, **A8**, A9, (**A10**), (**A11**), (**A12**), (**A13**), **A14**, **A15**, A16, **A17**, **A18**, A21, A24,
   b. Two-jugate: **A1**, A3, **A4**, **A5**, **A6**, A7, **A8**, **A10**, **A11**, **A12**, **A13**, **A14**, **A15**, **A17**, **A18**, A20, **A22**, **A23**, **A24**, A25, (**M2**)
   c. Three-jugate: (**A1**), **A4**, (**A6**), **A10**, **A11**, **A12**, **A13**, **A15**, **A22**, **A23**, **M1**, **M2**, **M3**
   d. Four-jugate: (**A1**), **A4**, **A10**, **A12**, **A13**, (**A15**), A19, **A22**, **A23**, **M1**, **M2**, **M3**
   e. More than four-jugate: **A4**, **A13**, **M1**, **M2**, **M3**

4. Leaflet shape
   a. (Sub)orbicular: (**A1**)
   b. Ovate: **A1**, **A2**, **A4**, **A6**, **A8**, **A9**, **A11**, **A12**, **A13**, **A14**, **A15**, **A17**, **A18**, **A22**, A23, **A24**, **A25**, **M2**
   c. Elliptic: **A1**, **A2**, **A3**, **A4**, **A5**, **A6**, A7, **A8**, **A9**, **A10**, **A11**, **A12**, **A13**, **A14**, **A15**, **A16**, **A17**, **A18**, **A19**, **A20**, A21, **A22**, **A24**, **A25**, M1, **M2**, **M3**
   d. Obovate: **A1**, (**A2**), **A3**, **A5**, (**A9**), **A10**, **A12**, (**A15**), **A16**, **A18**, **A19**, **A20**, **M3**

5. Leaflet punctation
   a. Absent: **A1**, **A2**, A3, **A4**, **A5**, A6, **A7**, **A8**, A9, **A10**, **A11**, A13, A14, **A15**, A16, **A17**, **A20**, (**A22**), **A23**, (**A24**), A25
   b. Present: (**A1**), **A2**, **A4**, (**A5**), **A7**, (**A8**), **A10**, **A11**, A12, **A15**, **A17**, A18, A19, (**A20**), **A22**, **A23**, **A24**, M1, M2, M3

6. Leaflet base, shape
   a. Rounded to obtuse: **A3**, **A6**, **A8**, (**A15**), **A24**
   b. Acute: **A2**, **A3**, **A5**, (**A6**), **A7**, **A8**, **A9**, **A10**, **A11**, **A12**, **A14**, **A15**, **A17**, **A18**, A19, **A20**, **A21**, **A22**, A23, **A24**, **A25**, **M1**, **M2**, **M3**
   c. Attenuate: A1, **A2**, A4, **A5**, **A7**, **A8**, **A9**, **A10**, **A11**, **A12**, A13, **A14**, **A15**, A16, **A17**, **A18**, **A20**, **A21**, **A22**, **A24**, **A25**, **M1**, **M2**, **M3**

7. Leaflet base, symmetry
   a. Symmetric: (**A1**), A2, A3, **A5**, **A6**, (**A7**), A8, A9, A10, **A11**, **A12**, **A13**, A14, **A15**, **A16**, **A17**, **A18**, **A20**, **A21**, **A22**, A23, **A24**, **A25**, M1, M2, M3
   b. Basiscopic side broader: **A1**, A4, **A5**, **A6**, **A7**, **A12**, **A13**, (**A15**), **A16**, (**A17**), A19, **A20**, **A21**, (**A22**), **A24**, **A25**
   c. Acroscopic side broader: **A11**, (**A12**), (**A13**), **A15**, **A16**, **A18**, (**A25**)

8. Leaflet apex
   a. Retuse: **A1**, A5, A6, **A10**, (**A12**), (**A13**), (**A15**), **A16**, **A17**, (**A18**), **A21**
   b. Obtuse: **A1**, **A2**, **A4**, **A8**, **A9**, **A10**, **A11**, **A12**, (**A13**), (**A15**), **A16**, **A17**, (**A18**), **A20**, **A21**, **A24**, **M1**, **M2**
   c. Rounded: **A1**, **A2**, **A3**, **A4**, **A8**, **A9**, **A10**, **A11**, **A12**, **A13**, (**A15**), **A16**, **A17**, (**A18**), **A20**, **A22**, **A24**, **A25**, **M1**, **M2**
   d. Acute: (**A1**), **A2**, **A3**, **A4**, **A7**, **A8**, **A9**, **A10**, **A11**, **A12**, **A13**, (**A15**), **A16**, **A17**, **A18**, **A20**, **A22**, **A24**, **A25**, **M1**, **M2**
   e. Acuminate: **A2**, **A3**, **A4**, **A7**, **A8**, **A9**, **A10**, **A11**, **A12**, **A13**, A14, **A15**, **A17**, **A18**, **A20**, **A22**, **A23**, **A24**, **A25**, **M1**, **M2**, M3
   f. Cuspidate: (**A4**), **A11**, **A15**, A19, **A23**
   g. Caudate: **A23**

9. Leaflet domatia
   a. Absent: A1, A2, A4, A5, A6, A12, A13, (**A15**), A16, A21, A22
   b. Pockets: **A7**, A10, **A11**, **A14**, **A15**, (**A17**), **A18**, A19, **A20**, A24, **A25**
   c. Sacs: A3, **A7**, **A9**, **A11**, **A14**, **A15**, **A17**, **A18**, (**A20**), A23, **A25**, **M1**, **M2**, M3
   d. Pits: A8, (**A9**), (**A15**), **M1**, **M2**

10. Nerves abaxially
    a. Flat: **A1**, A2, A3, A4, A5, A6, A9, **A12**, A16, A21, A22, M2
    b. Raised: **A1**, A7, A8, A10, A11, **A12**, A13, A14, A15, A17, A18, A19, A20, A23, A24, A25, M1, M3

11. Nerves marginally
    a. Looped: A1, A2, **A4**, A5, A6, A8, A9, **A12**, **A13**, A16, **A17**, A19, A21, A22, M1, M2, M3
    b. Open: A3, **A4**, A7, A10, A11, **A12**, **A13**, A14, A15, **A17**, A18, A20, A23, A24, A25

12. Veins
    a. Scalariform: A3, A7, A10, A11, A14, **A15**, A17, A18, A19, A20, A23, A24, A25
    b. Reticulate: A1, A2, A4, A5, A6, A8, A9, A12, A13, **A15**, A16, A21, A22, M1, M2, M3

13. Inflorescences
    a. Ramiflorous: **A7**, (**A10**), **A14**, (**A15**)
    b. Axillary to pseusoterminal: A1, A2, A3, A4, A5, A6, **A7**, A8, A9, **A10**, A11, A12, A13, **A14**, **A15**, A16, A17, A18, A19, A20, A21, A22, A23, A24, A25, M1, M2, M3

14. Inflorescence branching
    a. In axil: **A2**, **A3** (**A5**), **A7**, **A9**, **A10**, (**A11**), **A14**, (**A15**), **A16**, **A18**, (**A20**), (**A22**), **A24**
    b. Along rachis: A1, **A2**, **A3**, A4, **A5**, A6, **A7**, (**A8**), **A9**, **A10**, **A11**, A12, A13, **A14**, **A15**, (**A16**), A17, **A18**, A19, **A20**, A21, **A22**, A23, **A24**, **A25**, M1, M2, M3
    c. Not branching: **A8**, **A25**

15. Cymules
    a. Dichasial: A1, A3?, **A4**, A5, A6, **A7**, A8?, **A10**, **A11**, A12, A13, **A14**, **A15**, A17?, A19, A20, A21, A22, A23, A24, A25, M1, **M2**, M3
    b. Monochasial: A3?, (**A4**), A8?, **A10**, **A11**, **A14**, (**A15**), **A16**, A17?, A18
    c. Pleiochasial: A2, A3?, A8?, A17?
    d. Cincinnate: A3?, **A7**, A8?, A9, A17?, **M2**
    f. Single-flowered: A3?, A8?, **A16**, A17?

16. Bracts
    a. Triangular: A1, A2, A3, A4, A5, A6, A8, A9, A10, **A11**, A12, A13, A14, **A15**, A16, A17, A18, A19, A20, A21, A22, A23, A24, A25, M1, **M2**, M3
    b. Narrowly triangular: A7
    c. Ovate: **A11**, **A15**, **M2**

17. Calyx shape
    a. Slightly dimorphic: A3?, A19
    b. Symmetric: A1, A2, A3?, A4, A5, A6, A7, A8, A9, A10, A11, A12, A13, A14, A15, A16, A17, A18, A20, A21, A22, A23, A24, A25, M1, M2, M3

18. Sepals
    a. Basally connate: A1, A2, A3?, A8, **A9**, **A10**, A11, A12, **A13**, **A14**, A15, A16, **A17**, A18, A19, A20, A23, **A25**, M1, M2, **M3**
    b. Connate up to 1/3: A3?, **A4**, A5, A6, A7, **A9**, **A10**, **A13**, **A14**, **A17**, **A21**, A22, A24, **A25**, **M3**
    c. Connate up to 2/3: A3?, **A4**, **A21**

19. Calyx
    a. Punctate: A3?, (**A6**), **A13**, (**A15**), M1, M2, M3
    b. Not punctate: A1, A2, A4, A5, **A6**, A7, A8, A9, A10, A11, A12, **A13**, A14, **A15**, A16, A17, A18, A19, A20, A21, A22, A23, A24, A25

20. Calyx abaxially
    a. Hairy: A2, A3?, A5, A6, A7, A8, A9, A10, A11, **A12**, (**A13**) A14, A15, A16, A17, A18, A19, A20, A21, A22, A23, A24, A25, M1, **M2**, M3
    b. Glabrous: A1, A3?, A4, **A12**, **A13**, **M2**

21. Calyx adaxially
    a. Hairy: A1, **A2**, A3?, A4, (**A5**), A6, (**A9**), **A10**, (**A13**), (**A14**), (**A16**), (**A18**), A19, A21, A22
    b. Glabrous: **A2**, A3?, **A5**, A7, A8, **A9**, **A10**, A11, A12, **A13**, **A14**, A15, **A16**, A17, **A18**, A20, A23, A24, A25, M1, M2, M3

22. Petals
    a. Absent: A3?, A16
    b. Some reduced: A3?, A8?, **A14**, (**A15**), A17?, **A20**, **A25**
    c. Five: A1, A2, A3?, A4, A5, A6, A7, A8?, A9, A10, A11, A12, A13, **A14**, **A15**, A17?, A18, A19, **A20**, A21, A22, A23, A24, **A25**, M1, M2, M3

23. Petal blade
    a. Punctate: A3?, (**A6**), A21, M1, M3
    b. Not punctate: A1, A2, A3?, A4, A5, **A6**, A7, A8, A9, A10, A11, A12, A13, A14, A15, A16, A17, A18, A19, A20, A22, A23, A24, A25, M2

24. Petal blade
    a. Abruptly decurrent into claw: A3?, A7, **A9**, **A10**, **A14**, (**A15**), A24, M1, M2
    b. Gradually decurrent into claw: A1, A2, A3?, A4, A5, A6, A8, **A9**, **A10**, A11, A12, A13, **A14**, **A15**, A16, A17, A18, A19, A20, A21, A22, A23, A25, M3

25. Petal margin
    a. Denticulate near apex: A3?, **A7**, A13, (**A19**), A22, M2, **M3**
    b. Entire: A1, A2, A3?, A4, A5, A6, **A7**, A8, A9, A10, A11, A12, A14, A15, A16, A17, A18, **A19**, A20, A21, A23, A24, A25, M1, **M3**

26. Petal apex
    a. Truncate: **A1**, A3?
    b. Obtuse: **A1**, A3?, **A5**, **A6**, **A9**, **A10**, **A12**, **A13**, **A14**, **A15**, A17, **A18**, **A19**, **A20**, **A21**, **A22**, A23, A25, **M2**
    c. Rounded: **A1**, A3?, **A4**, **A5**, **A6**, **A7**, **A9**, **A10**, **A12**, **A13**, **A14**, **A15**, **A18**, **A19**, **A20**, **A21**, **A22**, M1, **M2**, **M3**
    d. Acute: **A1**, **A2**, A3?, **A4**, **A5**, **A6**, **A7**, A8, **A9**, **A10**, A11, **A14**, **A15**, **A18**, **A19**, **A20**, **A21**, **A24**, **M2**, **M3**
    e. Acuminate: **A2**, A3?, **A9**, **A15**, (**A20**), **A24**

27. Petals abaxially
    a. Glabrous: A3?, **A4**, A8, **A12**, **A14**, **A15**, A17, **A19**, **A22**, A25, M1, **M2**, M3
    b. Hairy: A1., A2, A3?, (**A4**), A5, A6, A7, A9, A10, A11, **A12**, A13, (**A14**), **A15**, A16, A18, (**A19**), A20, A21, **A22**, A23, A24, (**M2**)

28. Petals adaxially
    a. Glabrous: **A2**, A3?, **A7**, **A8**, **A9**, **A10**, **A11**, **A12**, A14, **A15**, **A17**, **A18**, **A19**, **A23**, **A24**, A25
    b. Hairy: A1, **A2**, A3?, A4, A5, A6, (**A7**), **A9**, (**A10**), **A11**, **A12**, A13, (**A15**), A16, **A18**, **A19**, A20, A21, A22, **A23**, **A24**, M1, M2, M3

29. Petal scales
    a. Enation of margin: A3?, **A5**, A6, A21, A22, M1, M2, **M3**
    b. Adnate to petal margin: A1, A3?, **A5**, **A8**, **A15**, A17, A19, **A24**, A25, **M3**
    c. Free: A2, A3?, A4, A7, **A8**, A9, A10, A11, A12, A13, A14, **A15**, A18, A20, A23, **A24**

30. Disc shape
    a. Lobed: A3?, A5, A6, A16, A21, A22
    b. Not lobed: A1, A2, A3?, A4, A7, A8, A9, A10, A11, A12, A13, A14, A15, A17, A18, A19, A20, A23, A24, A25, M1, M2, M3

31. Disc
    a. Glabrous: **A1**, A2, A3?, **A4**, **A7**, A8, A9, **A10**, A12, A13, **A15**, A16, A17, **A18**, A19, A20, **A22**, A24, M1, M2, M3
    b. Hairy on rim: A3?, **A4**, A6, **A7**, A14, **A15**, **A18**, A21, **A22**, A25
    c. Completely hairy: **A1**, A3?, A5, (**A10**), A11, **A15**, A23

32. Filaments
    a. Basally hairy: A1, A2, A3?, A4, A8, A13, A17, A21, M1, M2
    b. Completely hairy: A3?, A5, A6, A7, A9, A10, A11, A12, A14, A15, A16, A18, A19, A20, A22, A23, A24, A25, M3

33. Anthers
    a. More than 1 mm long: (**A2**), A3?, A7, A8, A9, A10, A11, A14?, (**A15**), A17?, A18, A19, A20, A24
    b. Less than 1 mm long: A1, **A2**, A3?, A4, A5, A6, A12, A13, A14?, **A15**, A16, A17?, A21, A22, A23, A25, M1, M2, M3

34. Anthers
    a. Curved inward: A3?, A7, A11, A18, A20, A24
    b. Straight: A1, A2, A3?, A4, A5, A6, A8, A9, A10, A12, A13, A14, A15, A16, A17, A19, A21, A22, A23, A25, M1, M2, M3

35. Anthers
    a. Glabrous: A1, A3?, A4, **A5**, **A6**, A12, A13, A19, **A25**, M1, **M2**, M3
    b. Hairy: A2, A3?, **A5**, (**A6**), A7, A8, A9, A10, A11, A14, A15, A16, A17, A18, A20, A21, A22, A23, A24, **A25**, (**M2**)

36. Anthers
    a. Connective protruding apically: A3?, A7, A19, A20, A22, A24
    b. Connective not protruding: A1, A2, A3?, A4, A5, A6, A8, A9, A10, A11, A12, A13, A14, A15, A16, A17, A18, A21, A23, A25, M1, M2, M3

37. Ovary
    a. Three-locular: **A3**, A5, A6, (**A8**), A10, A11, (**A14**), (**A15**), A19, (**A20**), A21, **A22**, (**A24**), M1, M2, M3
    b. Two-locular: A1, A2, **A3**, A4, A7, **A8**, A9, A12, A13, **A14**, **A15**, A16, A17, A18, **A20**, (**A22**), A23, **A24**, A25

38. Stigma
    a. Stigmatic lines: A3, A7?, A10, A11, **A12**, A14, A15, **A15**, **A17**, **A18**, A19?, **A20**, A23, A24, A25?

(38. Stigma)

b. Apically lobed: A1, A4, A5, A6, A7?, **A12**, A13, (**A15**), (**A17**), (**A18**), A19?, (**A20**), A21, A22, A25?, M1, M2, M3

c. Completely lobed: A2, A7?, A8, A9, A16, A19?, A25?

39. Central axis of fruit

a. Thickened: A1, A4, A5, A6, A7?, A12, A13, A14?, A18?, A19?, A21, A22, A25?, M1, M2, M3

b. Not thickened: A2, A3, A7?, A8, A9, A10, A11, A14?, A15, A16, A17, A18?, A19?, A20, A23, A24, A25?

40. Fruit inside

a. Glabrous: A7?, A11, A14?, A18?, A19?, A25?, M1, M2, M3

b. Hairy on sutures: A2, A7?, A8, **A9**, A10, AA14?, A15, A17, A18?, A19?, A20, A23, A24, A25?

c. Completely hairy: A1, A3, A4, A5, A6, A7?, **A9**, A12, A13, A14?, A16, A18?, A19?, A21, A22, A25?

41. Stipe length

a. More than 3 mm: **A5**, **A6**, A7?, **A8**, **A9**, A14?, A18?, A19?, A21, **A22**, A25?, M1, M2

b. Less than 3 mm: A1, A2, A3, A4, **A5**, **A6**, A7?, **A8**, **A9**, A10, A11, A12, A13, A14?, A15, A16, A17, A18?, A19?, A20, **A22**, A23, A24, A25?, M3

42. Endocarp

a. With sclerenchymatic layer radiating from attachment of seed: A7?, A14?, A18?, A19?, A25?, M1, M2, M3

b. Without such a layer: A1, A2, A3, A4, A5, A6, A7?, A8, A9, A10, A11, A12, A13, A14?, A15, A16, A17, A18?, A19?, A20, A21, A22, A23, A24, A25?

43. Arilloid

a. Alate: A7?, A14?, A18?, A19?, A21?, A25?, M2

b. Not alate: A1, A2, A3, A4, A5, A6, A7?, A8, A9, A10, A11, A12, A13, A14?, A15, A16, A17, A18?, A19?, A20, A21?, A22, A23, A24, A25?, M1, M3

44. Arilloid

a. Two-layered: A3, A7?, A10, A11, A14?, A15, A17, A19?, A20, A23, A24?, A25?

b. One-layered: A1, A2, A4, A5, A6, A7?, A8, A9, A12, A13, A14?, A16, A18, A19?, A21, A22, A24?, A25?, M1, M2, M3

45. Cotyledons

a. Dorsoventrally above each other: A1, **A3**, A4, A5, A6, A7?, A12, A13, A14?, **A15**, A18?, A19?, A21?, A22, A23, A25?

b. Obliquely dorsoventrally above each other: **A3**, A7?, A9, A10, A11, A14?, **A15**, (**A17**), A18?, A19?, **A20**, A21?, A24, A25?, M3

c. Laterally beside each other: A2, A7?, A8, A14?, **A15**, A16, **A17**, A18?, A19?, **A20**, A21?, A25?, M1, M2

46. Radicle length

a. Less than 1 mm: A2, **A3**, A7?, A8, A9, **A10**, A11, A14?, **A15**, A16, A17, A18?, A19?, A20, A21?, **A23**, A24, A25?

b. From 1 to 3 mm: A1, **A3**, **A4**, **A5**, A7?, **A10**, **A12**, A13, A14?, **A15**, A18?, A19?, A21?, **A23**, A25?, M2, M3

(46. Radicle length)

c. More than 3 mm: **A4**, **A5**, A6, A7?, **A12**, A14?, A18?, A19?, A21?, A22, A25?, M1

47. Radicle margin

a. Hairy: A5, A6, A7?, A14?, A18?, A19?, A21?, A22, A23, A25?

b. Glabrous: A1, A2, A3, A4, A5, A6, A7?, A8, A9, A10, A11, A12, A13, A14?, A15, A16, A17, A18?, A19?, A20, A21?, A24, A25?, M1, M2, M3

48. Geography

a. SE Asia, Malesia excluding New Guinea: **A15**

b. New Guinea: **A2**, A3, A7, **A14**, **A15**, A17, A18, A19, A20, **A23**, **A25**, M1, **M3**

c. Australia: **A2**, A8, A9, A10, A11, **A14**, A16, A24, **A25**, M2, **M3**

d. Solomon Islands: **A4**, **A15**, **A23**

e. Vanuatu: **A4**, A22

f. Loyalty Islands: **A1**, **A6**, A22

g. New Caledonia: **A1**, A5, **A6**, A12, A13, A21, A22

h. Fiji, Tonga, Samoa: **A4**

5.3 – *ARYTERA*

5.3.1 – Generic description

ARYTERA Blume

Arytera Blume, Rumphia 3 (1849) 169; Benth., Fl. Austr. 1 (1863) 451; Radlk., Sapind. Holl.-Ind. (1879) 44; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 551; in Durand, Ind. Gen. (1888) 80; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20 (1890) 267, 293; in Engl. & Prantl, Nat. Pflanzenfam. III, 5 (1895) 350; King, J. As. Soc. Beng. 65 (1896) 446; Koord. & Valeton, Meded. Plantent. 61 (1903) 215; Radlk. in Engl., Bot. Jahrb. 56 (1920) 254, 258f; Domin, Bibl. Bot. 89, 4 (1927) 908; Francis, Austr. Rain For. Trees (1929) 234; Radlk. in Engl., Pflanzenr. 98 (1933) 1268; Guillaumin & Virot, Mém. Mus. Natl. Hist. Nat. B 4 (1953) 19; Guillaumin, Mém. Mus. Natl. Hist. Nat. B 8 (1959) 136; Balgooy, Blumea Suppl. 5 (1966) 196, map 108; R.W. Ham, Blumea 23 (1977) 289; A.C. Sm., Fl. Vit. Nov. 3 (1983) 600; S.T. Reynolds, Austrobaileya 2 (1985) 158; Fl. Austral. 25 (1985) 87, 198; H. Turner, Blumea 38 (1993) 137; Fl. Males. I, 11 (3) (1994) 467. — Lectotype species (Reynolds 1985: 158): *Arytera litoralis* Blume.

Zygolepis Turcz., Bull. Soc. Nat. Mosc. 21 (1848) 573; Flora 31 (1848) 708. — Type species: *Zygolepis rufescens* Turcz.

Trees or rarely *shrubs*. *Indument* consisting of rather short, appressed or patent, straight hairs or of longer, patent, crispate hairs; glandular scales present on vegetative parts, inflorescence, pedicels, abaxial side of calyx, pistil, and fruit in sect. *Azarytera*. *Branchlets* terete, smooth (to slightly rough), hairy at least when young, rarely (sub)glabrous (sect. *Azarytera*), then buds 'varnished' with a resin-like, shiny exudate. *Leaves* paripinnate, 1–6-jugate; petiole pulvinate, lenticels present or absent; rachis (hemi)terete, not, rarely slightly winged. *Leaflets* opposite to alternate, petioluled; petiolules usually consisting of a pulvinus only, not, 1-, or 2-grooved, lenticels present

or absent; blade ovate to elliptic to obovate to suborbicular, usually not falcate, coriaceous to chartaceous, punctate or not; base obtuse to attenuate, symmetric or oblique; margin entire to slightly repand, not to slightly, rarely (*A. nekorensis*) strongly revolute; apex variable, retuse to caudate, very apex retuse to rounded (to slightly acute), usually not mucronulate; upper surface smooth, glabrous, midrib sometimes hairy, rarely (*A. multijuga*) slightly to densely hairy all over; lower surface smooth, without papillae, glabrous to hairy, usually more so on venation, domatia often present in axils of nerves; venation on upper surface flat, midrib usually slightly raised, on lower surface usually raised (to only midrib raised); nerves marginally looped or open; veins reticulate or scalariform, lax, rarely dense. *Inflorescences* thyrsoid, axillary to pseudoterminal, rarely ramiflorous, branching along rachis or in axil, rarely not branched; rachis terete to flattened, usually hairy; cymules usually dichasial or monochasial, rarely pleiochasial (*A. bifoliolata*), cincinnate (*A densiflora, A. distylis*), or reduced to a single flower (*A. microphylla*). *Bracts* and *bracteoles* triangular (to ovate), margin entire, abaxially usually hairy, adaxially (sub)glabrous (to pilose). *Flowers* actinomorphic, seemingly hermaphrodite, but presumably functionally unisexual, male flowers with an underdeveloped pistil and relatively long stamens, female flowers with a well-developed pistil and short stamens; male and female flowers presumably usually in same inflorescence. *Calyx* 5-dentate to -partite, persistent in fruit; teeth equal, rarely (*A. multijuga*) slightly dimorphic, teeth triangular to ovate, margin entire, usually not membranaceous; outside hairy, inside glabrous to hairy. *Petals* 5, rarely several reduced or completely absent, equal, usually with a more or less distinct claw; scales present, free, adnate to, or enation of petal margin, not crested. *Disc* annular, complete, glabrous or hairy. *Stamens* (5–)7 or 8(–10); filament at least basally pilose; anther basifix, straight or curved inward, usually pilose; thecae latrorsely opening with a longitudinal slit; connective sometimes slightly protruding beyond thecae. *Pistil:* ovary 2- or 3-locular, smooth, rarely (*A. neoebudensis*) lower half grooved, hairy; ovules one per locule, ascending, apotropous, campylotropous; style and stigma elongating in fruit, usually (sub)persistent; stigma not to minutely lobed, with 2 or 3 stigmatic lines, or distinctly 2- or 3-lobed with lobes recurved in fruit. *Fruit* a capsule, with 1–3 well-developed lobes, opening loculicidally, more or less obcordate to obovoid in lateral view, axil thickened transversely or not, outside glabrescent when ripe, smooth to rugose to verrucose, inside glabrous or hairy on sutures to completely pilose; stipe short to long, broadly cuneate to slender; dissepiments complete; lobes laterally not or slightly flattened, edge of margin rounded to keeled; exocarp thick, coriaceous; mesocarp thick, coraceous to woody; endocarp thin, chartaceous. *Seed* orbicular to (ob)ovoid to ellipsoid; arilloid apically open, covering seed half to completely, sometimes inside folded towards base, consisting of 1 or 2 layers; hilum (sub)basal; micropylar wart usually indistinct, to somewhat protruding in some species; exotesta thin to slightly thickened in part not covered by arilloid, coriaceous to almost woody; endotesta thin, approx. membranaceous. *Embryo:* cotyledons (obliquely) dorsoventrally above or laterally beside each other, apices not elongated, surface smooth; radicle dorsoventrally flattened, inserted in a pocket formed by endotesta, margin glabrous or (at least basally) hairy; plumule inconspicuous.

5.3.2 – Infrageneric classification

Arytera sect. *Azarytera* Radlk.

Arytera sect. *Azarytera* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 554. — Lectotype species (here designated): *Arytera arcuata* Radlk.

Glandular scales present, young shoots 'varnished'; *calyx* abaxially glabrous; *ovary* always two-lobed.

Species: *A. arcuata, A. brackenridgei, A. gracilipes, A. lepidota.*

Arytera sect. *Arytera*

Arytera Blume, Rumphia 3 (1849) 169. – [*Arytera* sect. *Euarytera* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 551, nom. illeg. (I.C.B.N. [1994] Artt. 21.3, 32.1.b).] — Lectotype species (Reynolds 1985: 158): *Arytera litoralis* Blume.

Inflorescence usually branching in axil and along rachis; *anther* hairy; *ovary* two- or three-lobed.

Species: See under the subsections.

Arytera subsect. *Pacifica* H. Turner, *subsectio nov.*

Petalae squamulae enationes minutae e petalae margine, discus plus minusve distincte 5-lobatus, fructus axis distincte incrassatus, radicula saltem basi pubescens. — Typus: *Arytera collina* (Panch. et Séb.) Radlk.

Petal scales minute enations of the petal margin; *disc* more or less distinctly five-lobed; *fruit* axis distinctly thickened; *radicle* of embryo at least basally hairy.

Species: *A. chartacea, A. collina, A. nekorensis, A. neoebudensis.*

Arytera subsect. *Distylis* H. Turner, *subsectio nov.*

Ab *Aryterae* subsectionibus ceteris in stylo brevissimo, stigmate lobis duobus recurvatis differt. — Typus: *Arytera distylis* (F. Muell. ex Benth.) Radlk.

Style very short; *stigma* with two recurved lobes.

Species: *A. bifoliolata, A. dictyoneura, A. distylis, A. microphylla.*

Arytera subsect. *Arytera*

Arytera Blume, Rumphia 3 (1849) 169. — [*Arytera* sect. *Euarytera* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 551, nom. illeg. (I.C.B.N. [1994] Artt. 21.3, 32.1.b).] — Lectotype species (Reynolds 1985: 158): *Arytera litoralis* Blume.

Leaves: secondary venation not looped, tertiary venation scalariform; *arilloid* two-layered.

Species: *A. densiflora, A. divaricata, A. foveolata, A. lineosquamulata, A. litoralis, A. miniata, A. morobeana, A. musca, A. novaebrittanniae, A. pauciflora, A. pseudo-foveolata.*

Species incertae sedis:

Arytera brachyphylla: In view of the two-layered arilloid and scalariform tertiary venation this species most probably belongs in subsect. *Arytera*.

Arytera multijuga: Because the fruits of this species are not known, it is very difficult to make an educated guess as to its proper taxonomic position. It shares with subsect. *Arytera* the tertiary scalariform venation, and the stigmatic lines on the unlobed style. On the other hand, this placement is contradicted by a number of anatomical character states: basally attached hairs, undulating anticlinal walls in the epidermis, thin areas in the cuticle, the presence of a ridge around abaxial stomata. The definitive assignment of *A. multijuga* to one of the above (sub)sections will have to wait till more data become available.

5.3.3 – **Keys**

5.3.3.1 – *Key to the infrageneric taxa*

1 a. Glandular scales present on leaf and/or inflorescence. Ovary always 2-celled. Young branches (sub)glabrous; buds 'varnished' ..... **Section Azarytera**
b. Glandular scales absent on leaf and/or inflorescence. Ovary 2- or 3-celled. Young branches hairy, buds not 'varnished' – **Section Arytera** **2**
2 a. Central axis of fruit distinctly thickened. Petal scales minute enations. Disc usually distinctly 5-lobed. Ovary and fruit 3-, rarely 2-locular ..... **Subsection Pacifica**
b. Central axis of fruit not thickened. Petal scales adnate to margin of petal or free. Disc usually not lobed. Ovary and fruit 2- or 3-locular **3**
3 a. Tertiary venation reticulate. Style very short; stigma 2-lobed, lobes recurved in fruit. Arilloid one-layered ..... **Subsection Distylis**
b. Tertiary venation (more or less) scalariform. Style distinct; stigma of 2 or 3 stigmatic lines. Arilloid two-layered ..... **Subsection Arytera**

5.3.3.2 – *General key to the species*

1 a. Glandular scales absent on leaf and/or inflorescence. Ovary 2- or 3-celled. Young branches hairy, buds not 'varnished' **2**
b. Glandular scales present on leaf and/or inflorescence. Ovary always 2-celled. Young branches (sub)glabrous; buds 'varnished' [West Pacific up to Solomon Islands] **23**
2 a. Indument on young shoots and inflorescences consisting of rather long, crispate hairs **3**
b. Indument on young shoots and inflorescences consisting of short, rarely long, straight hairs **8**
3 a. Leaves 4-jugate; leaflets adaxially slightly to densely hairy on venation; nerves looped marginally. Bracts and bracteoles subglabrous to puberulous adaxially. Sepals: two outer slightly shorter than three inner ones, puberulous adaxially [Papua New Guinea] ..... **A19: A. multijuga**

b. Leaves 1–3-jugate; leaflets adaxially at most subglabrous; nerves open marginally. Bracts and bracteoles (sub)glabrous adaxially. Sepals equal, (sub)glabrous adaxially **4**

4 a. Anthers ≥ 1 mm long, curved inward **5**

b. Anthers < 1 mm long, straight **7**

5 a. Inflorescences short (up to 5 cm long). Petal scales 0.8–1.2 mm long. Pedicels > 1.5 mm [Papua New Guinea] ..... **A18: A. morobeana**

b. Inflorescences long (up to 16 cm long); petal scales 0.2–0.6 mm long; pedicels < 1.5 mm **6**

6 a. Ovary 3-locular. Bracts and bracteoles triangular to ovate. Connective of stamens not protruding apically. Petal blade gradually decurrent into claw. — Fruit glabrous inside [Australia] ..... **A11: A. foveolata**

b. Ovary 2-locular. Bracts and bracteoles narrowly triangular. Connective of stamens slightly protruding apically. Petal blade abruptly decurrent into claw [Papua New Guinea] ..... **A7: A. densiflora**

7 a. Scales on petals free, almost linear, often forked at the apex. Disc hairy on rim only [Australia, Papua New Guinea] ..... **A14: A. lineosquamulata**

b. Scales on petals adnate to petal margin, about half as broad as the petals, not forked at the apex. Disc hairy on rim and between stamens [Australia, Papua New Guinea] ..... **A25: A. pseudofoveolata**

8 a. Ovary and fruit 3-, rarely 2-locular; central axis of fruit distinctly thickened. Radicle long (2–6.5 mm), margin always at least basally hairy. Calyx always connate up to at least 1/3 of its height. Petal scales an enation of the margin, at most 0.5 mm long. Disc more or less distinctly five-lobed. Apex of leaflets retuse to slightly acuminate, very apex always retuse to obtuse [New Caledonia, Vanuatu] **9**

b. Ovary and fruit 2- or 3-locular. Central axis of fruit not thickened. Radicle usually short (up to 1 mm, in *A. litoralis* and *A. divaricata* up to 3 mm), margin glabrous (hairy in *A. novaebrittanniae*: apex of leaflets acuminate to caudate). Calyx at most connate up to 1/3 of its height. Petal scales free to adnate to margin, 0.1–1.2 mm long. Disc not lobed (5- or 6-lobed in *A. microphylla*: petals usually absent). Apex of leaflets variable [SE Asia, Malesia, Australia, Solomon Islands] **12**

9 a. Leaflets always 1-jugate, margin strongly revolute. Petiole short (up to c. 1 cm). Apical process of rachis distinct [New Caledonia] ..... **A21: A. nekorensis**

b. Leaflets 1–4-jugate, margin at most slightly revolute. Petiole longer (> c. 1 cm). Apical process of rachis indistinct **10**

10 a. Leaves 2–4-jugate. Apex of leaflets rounded to shortly acuminate. Petals outside subglabrous, margin apically denticulate. Fruit inside less densely hairy on middle of valves [New Caledonia, Vanuatu] ..... **A22: A. neoebudensis**

b. Leaves 1- or 2-, rarely 3-jugate. Apex of leaflets retuse. Petals outside hairy, margin entire. Fruit inside equally densely hairy all over valves [New Caledonia] **11**

11 a. Base of leaflets attenuate to acute. Petiolules short (1.5–6 mm). Indument on inside of fruit pale yellowish ..... **A5: A. chartacea**

b. Base of leaflets obtuse (to acute). Petiolules long (4–25 mm). Indument on inside of fruit darker yellow to rust-red ..... **A6: A. collina**

12 a. Stigma distinctly lobed, recurved in fruit. Ovary and fruit 2-locular (in *A. dictyoneura* rarely 3-locular: veins distinct, densely reticulate). Arilloid always consisting of one layer. Lateral veins marginally looped **13**

b. Stigma consisting of stigmatic lines on style, at most apically minutely lobed. Ovary and fruit 2- or 3-locular. Arilloid presumably always consisting of two layers. Lateral veins marginally usually open **16**

13 a. Leaves 1- or 2-jugate; veins densely reticulate, distinct. Petals with a long claw (0.6–0.8 mm) [Australia] ..... **A8: A. dictyoneura**

b. Leaves 1-jugate; veins laxly reticulate, not distinct. Petals, if present, with a short claw (up to 0.5 mm) **14**

14 a. Domatia few present. Anthers large (> 1 mm) [Australia] ..... **A9: A. distylis**

b. Domatia absent. Anthers smaller (0.3–1.1 mm) **15**

15 a. Leaflets large (over 5 cm long), petiolule long (2–10 mm). Cymules 1–7-flowered. Petals present. Disc not lobed. Fruit inside hairy on sutures only [Australia, Papua New Guinea] ..... **A2: A. bifoliolata**

b. Leaflets small (up to 6 cm long), petiolule short (< 2 mm). Cymules 1- or 2-flowered. Petals usually absent, rarely one or two sepaloid petals present. Disc 5- or 6-lobed. Fruit inside completely hairy [Australia] ..... **A16: A. microphylla**

16 a. Leaves up to 4-jugate **17**

b. Leaves at most 2-jugate **19**

17 a. Hilum large (c. 7 by 5 mm). Margin of radicle hairy. Petals inside usually hairy, never longer than calyx. Leaflet apex acuminate to caudate, index up to 5. Domatia large sacs opening on top [Papua New Guinea] ..... **A23: A. novaebrittanniae**

b. Hilum usually (much) smaller. Margin of radicle glabrous. Petals inside usually (sub)glabrous, often slightly longer than calyx. Leaflet apex retuse to at most cuspidate, index up to 4.5. Domatia pockets to sacs, often pustular, usually opening in front, rarely pits opening on top or completely absent. — Usually leaves 1- or 2-jugate in New Guinea and Solomon Islands **18**

18 a. Leaflet index up to 2.7 (3.4), apex retuse to shortly acuminate. Anther large (> 1 mm long). Ovary and fruit 3-locular [Australia] ..... **A10: A. divaricata**

b. Leaflet index up to 4.5, apex acuminate to cuspidate, rarely retuse or rounded. Anther small (≤ 1.1 mm). Ovary and fruit usually 2-locular [SE Asia to New Guinea, Solomon Islands] ..... **A15: A. litoralis**

19 a. Leaflets oblong-elliptic to -obovate, venation abaxially almost flat. Fruit inside completely hairy [Papua New Guinea] ..... **A3: A. brachyphylla**

b. Leaflets not oblong in shape, venation raised abaxially. Fruit inside hairy only on sutures **20**

20 a. Cymules 1–3-flowered. Petal blade abruptly decurrent into a minute claw. Veins distinctly scalariform, rather dense [Australia] ..... **A24: A. pauciflora**

b. Cymules presumably always up to 7-flowered. Petal blade gradually decurrent into a usually distinct claw. Veins weakly scalariform, lax [SE Asia to New Guinea, Solomon Islands] **21**

21 a. Leaflet index up to 4.5, apex usually acuminate to cuspidate (rarely retuse or rounded). Inflorescences up to 20 cm long. Cotyledons usually (obliquely) dorsoventrally above each other [SE Asia up to New Guinea, Solomon Islands] ... . **A15: A. litoralis**

b. Leaflet index up to 3, apex retuse to slightly acuminate. Inflorescences up to 13 cm long. Cotyledons laterally beside to obliquely dorsoventrally above each other [Papua New Guinea] **22**

22 a. Petiole up to 5 cm long. Leaflets ovate to elliptic. Petals obovate. Anther straight, c. 0.6 mm ..... **A17: A. miniata**

b. Petiole up to 11 cm long. Leaflets elliptic to slightly obovate. Petals elliptic to orbicular. Anther curved inward, > 1 mm ..... **A20: A. musca**

23 a. Fruit obcordate, inside with straight hairs. Nerves usually marginally looped **24**

b. Fruit ellipsoid to obovoid, inside with crispate hairs. Nerves marginally open basally, looped apically [New Caledonia] **25**

24 a. Leaves 1- or 2(–4)-jugate. Apex of leaflets retuse to obtuse, rarely acute, but then very apex retuse to obtuse. Petals abaxially pilose [New Caledonia, Tonga?] ..... **A1: A. arcuata**

b. Leaves 2–5-jugate. Apex of leaflets obtuse to acuminate, very apex obtuse to rounded. Petals abaxially (sub)glabrous [Solomon Islands, Vanuatu, Fiji, Tonga, Samoa] ..... **A4: A. brackenridgei**

25 a. Leaflets punctate. Petals abaxially and adaxially at most hairy at base, margin entire ..... **A12: A. gracilipes**

b. Leaflets not punctate. Petals abaxially and adaxially hairy, margin denticulate near apex ..... **A13: A. lepidota**

5.3.3.3 – *Regional keys to the species*

5.3.3.3.1 – SE Asia and Malesia West of New Guinea

Only one species occurs in this region: ..... **A15: A. litoralis**

5.3.3.3.2 – New Guinea

1 a. Indument on young shoots and inflorescences consisting of rather long, crispate hairs **2**

b. Indument on young shoots and inflorescences consisting of short, rarely long, straight hairs **6**

2 a. Leaves 4-jugate. Leaflets adaxially and abaxially slightly to densely hairy on venation. Nerves looped marginally. Bracts and bracteoles subglabrous to puberulous adaxially. Sepals outer two slightly shorter than three inner ones, puberulous adaxially ..... **A19: A. multijuga**

b. Leaves 1- or 2-jugate. Leaflets adaxially at most subglabrous. Nerves open marginally. Bracts and bracteoles glabrous adaxially. Sepals equal, (sub)glabrous adaxially **3**

3 a. Anthers ≥ 1 mm long, curved inward, densely pilose **4**
b. Anthers < 1 mm long, straight **5**
4 a. Inflorescences short (< 5 cm). Bracts and bracteoles triangular. Petal scales large (0.8–1.2 mm long); blade gradually decurrent into claw. Connective of stamens not protruding apically. Pedicels long (> 1.5 mm) ..... **A18: A. morobeana**
b. Inflorescences long (> 4.5 cm). Bracts and bracteoles narrowly triangular. Petal scales small (0.2–0.6 mm long); blade abruptly decurrent into claw. Connective of stamens protruding apically. Pedicels short (< 1.5 mm) .. **A7: A. densiflora**
5 a. Scales on petals free, almost linear, often forked at the apex. Disc hairy on rim only ..... **A14: A. lineosquamulata**
b. Scales on petals adnate to petal margin, about half as broad as the petals, not forked at the apex. Disc hairy on rim and between stamens ..... **A25: A. pseudofoveolata**
6 a. Stigma distinctly lobed, recurved in fruit. Ovary and fruit 2-locular. Arilloid always consisting of one layer. Lateral veins marginally looped. Domatia absent ..... **A2: A. bifoliolata**
b. Stigma consisting of stigmatic lines on the style, at most apically minutely lobed. Ovary and fruit 2- or 3-locular. Arilloid presumably always consisting of two layers. Lateral veins marginally at least basally open. Domatia usually present **7**
7 a. Leaves up to 4-jugate **8**
b. Leaves at most 2-jugate **9**
8 a. Hilum large (c. 7 by 5 mm). Margin of radicle hairy. Petals inside usually hairy, never longer than calyx. Leaflet index up to 5, apex acuminate to caudate. Domatia large sacs opening on top ..... **A23: A. novaebrittanniae**
b. Hilum usually (much) smaller. Margin of radicle glabrous. Petals inside usually (sub)glabrous, often slightly longer than calyx. Leaflet index up to 4.5, apex retuse to at most cuspidate. Domatia pockets to sacs, often pustular, usually opening in front, rarely pits opening on top or completely absent ..... **A15: A. litoralis**
9 a. Leaflets oblong-elliptic to -obovate. Lateral veins abaxially almost flat. Fruit inside completely hairy ..... **A3: A. brachyphylla**
b. Leaflets not oblong in shape. Lateral veins raised abaxially. Fruit inside hairy only on sutures **10**
10 a. Leaflet index up to 4.5, apex usually acuminate to cuspidate (rarely retuse or rounded). Inflorescences up to 20 cm long. Cotyledons usually (obliquely) dorsoventrally above each other ..... **A15: A. litoralis**
b. Leaflet index up to 3, apex retuse to slightly acuminate. Inflorescences up to 13 cm long. Cotyledons laterally beside to obliquely dorsoventrally above each other **11**
11 a. Petiole up to 5 cm long. Leaflets ovate to elliptic. Petals obovate. Anther straight, small (c. 0.6 mm) ..... **A17: A. miniata**
b. Petiole up to 11 cm long. Leaflets elliptic to obovate. Petals elliptic to orbicular. Anther curved inward, large (> 1 mm) ..... **A20: A. musca**

5.3.3.3.3 – Australia

1 a. Indument on young shoots and inflorescences consisting of rather long, crispate hairs 2
b. Indument on young shoots and inflorescences consisting of short, rarely long, straight hairs 4
2 a. Leaves usually 2- or 3-jugate. Anthers more than 1 mm long, curved inward; connective of stamens slightly protruding apically. Ovary 3-locular. — Fruit inside glabrous ..... **A10: A. foveolata**
b. Leaves 1- or 2-jugate. Anthers less than 1 mm long, straight, connective of stamens not protruding apically. Ovary usually 2-locular 3
3 a. Scales on petals free, almost linear, often forked at the apex. Disc hairy on rim only ..... **A14: A. lineosquamulata**
b. Scales on petals adnate to petal margin, about half as broad as the petals, not forked at the apex. Disc hairy on rim and between stamens ..... **A25: A. pseudofoveolata**
4 a. Stigma distinctly lobed, recurved in fruit. Ovary and fruit 2-locular (in *A. dictyoneura* rarely 3-locular: veins distinct, densely reticulate). Arilloid always consisting of one layer. Lateral veins marginally looped, veins reticulate 5
b. Stigma consisting of stigmatic lines on style, at most apically minutely lobed. Ovary and fruit 2- or 3-locular. Arilloid consisting of two layers. Lateral veins marginally open, veins scalariform 8
5 a. Leaves 1- or 2-jugate. Veins densely reticulate, distinct. Petals with a long claw (0.6–0.8 mm) ..... **A8: A. dictyoneura**
b. Leaves 1-jugate. Veins laxly reticulate, not distinct. Petals, if present, with a short claw (up to 0.5 mm) 6
6 a. Domatia few present. Anthers large (> 1 mm) ..... **A9: A. distylis**
b. Domatia absent. Anthers smaller (0.3–1.1 mm) 7
7 a. Leaflets large (over 5 cm long), petiolule long (2–10 mm). Cymules 1–7-flowered. Petals present. Disc not lobed. Fruit inside hairy on sutures only ..... **A2: A. bifoliolata**
b. Leaflets small (up to 6 cm long), petiolule short (< 2 mm). Cymules 1- or 2-flowered. Petals absent, rarely one or two sepaloid petals present. Disc 5- or 6-lobed. Fruit inside completely hairy ..... **A16: A. microphylla**
8 a. Leaves 2–4-jugate, veins lax. Ovary and fruit 3-locular ..... **A10: A. divaricata**
b. Leaves 1- or 2-jugate, veins rather dense. Ovary and fruit 2-locular ..... **A24: A. pauciflora**

5.3.3.3.4 – Pacific Islands

1 a. Glandular scales absent on leaf and/or inflorescence. Buds not 'varnished.' Ovary 3-, rarely 2-celled. Young branches hairy 2
b. Glandular scales present on leaf and/or inflorescence. Buds 'varnished.' Ovary 2-celled. Young branches (sub)glabrous 6

2 a. Calyx only basally connate. Central axis of fruit not thickened. Radicle short (up to 3 mm), margin glabrous. Petal scales free to basally adnate to margin, 0.2–1.2 mm long. Disc not lobed. Apex of leaflets usually acuminate to cuspidate (rarely retuse or rounded) ..... **A15: A. litoralis**
b. Calyx always connate up to at least 1/3 of its height. Central axis of fruit distinctly thickened. Radicle long (2–6.5 mm), margin always at least basally hairy. Petal scales an enation of the margin, at most 0.5 mm long. Disc 5-lobed. Apex of leaflets retuse to slightly acuminate **3**

3 a. Leaflets always 1-jugate, margin strongly revolute. Petiole short (up to c. 1 cm); apical process of rachis distinct ..... **A21: A. nekorensis**
b. Leaflets 1–4-jugate, margin at most slightly revolute. Petiole longer (> c. 1 cm); apical process of rachis indistinct **4**

4 a. Leaves 2–4-jugate. Apex of leaflets rounded to shortly acuminate. Petals outside (sub)glabrous, margin apically denticulate. Fruit inside less densely hairy on middle of valves ..... **A22: A. neoebudensis**
b. Leaves 1- or 2-, rarely 3-jugate. Apex of leaflets retuse. Petals outside hairy, margin entire. Fruit inside equally densely hairy all over valves **5**

5 a. Base of leaflets attenuate to acute; petiolules short (1.5–6 mm). Indument of inside of fruit pale yellowish ..... **A5: A. chartacea**
b. Base of leaflets obtuse (to acute); petiolules long (4–25 mm). Indument of inside of fruit darker yellow to rust-red ..... **A6: A. collina**

6 a. Fruit obcordate, inside with straight hairs. Nerves usually marginally looped **7**
b. Fruit obovoid, inside with crispate hairs. Nerves marginally open basally, looped apically **8**

7 a. Leaves 1- or 2(–4)-jugate. Apex of leaflets retuse to obtuse, rarely to acute, but then very apex retuse to obtuse. Petals abaxially pilose ..... **A1: A. arcuata**
b. Leaves 2–5-jugate. Apex of leaflets obtuse to acuminate, very apex obtuse to rounded. Petals abaxially (sub)glabrous ..... **A4: A. brackenridgei**

8 a. Leaflets punctate. Petals abaxially and adaxially at most hairy at base, margin entire ..... **A12: A. gracilipes**
b. Leaflets not punctate. Petals abaxially and adaxially hairy, margin denticulate near apex ..... **A13: A. lepidota**

5.3.4 – Species descriptions

A1 - *Arytera arcuata* Radlk. — Fig. 5.1, 5.2

Arytera arcuata Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 554; in Engl., Pflanzenr. 98 (1933) 1284; Guillaumin, Fl. Nouv.-Caléd. (1948) 201. — *Cupaniopsis arcuata* Guillaumin, Bull. Mus. Nat. Hist. Nat. 18 (1917) 171. — Lectotype (here designated): *Balansa 150* (holo M; iso BM, FI, K, NY, P), Nouméa, New Caledonia.

Cupania tenax auct. non Cunn. ex Benth.: F. Muell., Fragm. 9 (1875) 94.

[*Cupania micrantha* Panch. ex Guillaumin in Lecomte, Not. Syst. 1, 11 (1911) 331, in syn., nom. nud., nom. inval. (I.C.B.N. [1994] Art. 34.1.c).]

Tree or *shrub*. *Indument* of short, straight, patent hairs; glandular scales present on vegetative parts, inflorescence, pedicels, abaxial side of calyx, pistil, and fruit; buds

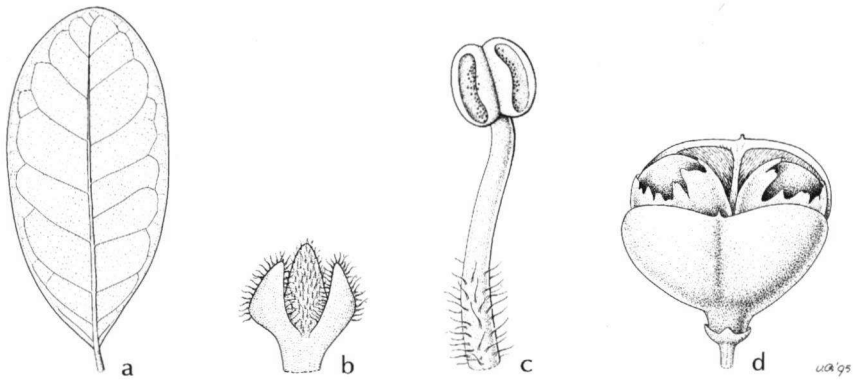

FIGURE 5.1. *Arytera arcuata* Radlk. (a) Leaflet, × 0.5; (b) petal, × 25; (c) stamen, × 12.5; (d) fruit, × 3 (a–c: *MacKee 37881*; d: *Veillon 6563*.)

'varnished.' *Branchlets* smooth, glabrous to subpuberulous when young; flowering twigs 1–3 mm thick. *Leaves* 1- or 2(–4)-jugate; petiole 0.7–3.8 cm long, lenticels absent abaxially; rachis 0.4–2.7 cm long, hemiterete, glabrous to (sub)tomentose. *Leaflets* opposite to subopposite; petiolules 3–19 mm long, not (2-)grooved, lenticels rarely few present abaxially; blade elliptic to (ob)ovate to suborbicular, 2.2–13.5 by 0.9–6 cm, index 1.4–3.9, not to slightly falcate, coriaceous to slightly chartaceous, rarely punctate; base attenuate, usually somewhat oblique, basiscopic side broader; margin entire, flat to slightly undulating, not revolute to revolute; apex retuse to obtuse (to acute, then very apex obtuse to retuse), not mucronulate; upper surface glabrous, mid-rib puberulous to tomentose towards base; lower surface glabrous (to mid-rib puberulous to tomentose towards base), colour usually different from that of upper surface, domatia absent; venation on upper surface flat, midrib rarely (slightly) raised, colour same as lamina to distinctly reddish brown, on lower surface flat to (slightly) raised, midrib always raised; nerves 3–21 mm apart, marginally looped; veins usually laxly reticulate, not distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis; rachis (terete to slightly) flattened, 2.8–15 cm long, glabrous to puberulous when young; first-order branches up to 6.7 cm long; cymules dichasial, 1–4-flowered. *Bracts* and *bracteoles* triangular, margin entire, adaxially (sub)glabrous, abaxially glabrous; bracts 0.3–0.5 mm long; bracteoles 0.1–0.2 mm long. *Pedicels* 0.4–1.8 mm long, elongating up to 5 mm in fruit, glabrous to puberulous. *Flowers* 1.5–2.5 mm diam. *Calyx* 5(–6)-dentate, 0.4–1.4 mm high, teeth 0.3–1.1 mm high, triangular, not punctate, margin entire, not membranaceous, apex acute (to slightly obtuse); outside glabrous, inside subpuberulous. *Petals* 5, rhomboid to deltoid, 0.3–1.1 by 0.2–0.9 mm, index 0.5–3.5, not punctate, claw 0.1–0.5 mm long, margin entire, apex acute to truncate; blade gradually decurrent into claw, outside pilose, inside pilose, margin pilose; scales 0.2–0.9 mm long, adnate to margin, basally not auricled, apex usually broadened. *Disc* not lobed, glabrous to slightly pilose. *Stamens* (male) 5–8; filament 1.3–2.6 mm long, basally pilose; anther 0.3–0.5 mm long, straight, glabrous; connective not protruding. *Pistil* (female): ovary 2-locular, 0.6–2 mm long, sericeous; style and stigma 0.5–1.4 mm

long, elongating up to 0.8–2.3 mm in fruit, 2-lobed, in fruit upper 0.1–0.4 mm stigmatic. *Fruit* distinctly obcordate, with 1 or 2 well-developed lobes, 0.9–1.5 cm high by 0.6–1.4 cm broad, axil thickened transversely, outside glabrous to subpuberulous, smooth to slightly rugose, inside strigose, hairs rust-red to pale yellow; stipe up to 3 mm long, broadly cuneate; edge of margin rounded to sharp; angle between lobes c. 180°; blackish to dull brown; lobes laterally not to slightly flattened, valves 8–12 mm high by 5–7 mm long; endocarp pale brown. *Seed* ellipsoid to obovoid, laterally not to slightly flattened, 5–11 by 3.5–6 mm, reddish brown to blackish; arilloid covering seed completely, lobed, inside not folded towards base, thin, membranaceous, consisting of 1 layer, soft, pale yellow; hilum elliptic to circular to triangular, 1–3.5 by 1–4 mm; endotesta pale brown. *Embryo:* cotyledons dorsoventrally above each other, unequal, upper larger, apices not elongated; radicle 1.2–3 mm long, glabrous.

Field notes — Tree or shrub 1–12 m high, 10–35 cm dbh. Crown dense, rounded. Bark bright brown, often tinged grey, almost smooth to rough. Leaves (very) dark green above, light to dark green below. Flower buds green; flowers greenish yellow to cream to white, very fragrant; filaments white. Fruits few, green turning brown. Arilloid orange.

Distribution — New Caledonia and Loyalty Islands; possibly also on Tonga (see note 2).

Habitat & Ecology — Coastal areas up to 200 m, predominantly on calcareous soils, but also reported from sand, clay and schists. In meso- and sclerophyll forests and scrubs, together with *Acacia spiralis*, *A. farnesiana*, *Araucaria cookii*, *Lantana camara*, and *Melaleuca*. Flowers reported to be frequented by bees. Flowering Feb.–May; fruiting Apr.–Nov.

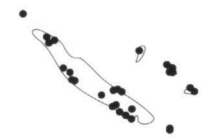

FIGURE 5.2. *Arytera arcuata* Radlk. Distribution map.

Vernacular name — Pö hao (Lifou).

Notes — (1) Exceptionally, the leaves can be 3- or 4-jugate (e.g. *M. Schmid 1326, 2157*; *Webster 18341*). On the Loyalty Islands the shape of the leaflets is occasionally suborbicular; however, in several cases the same branch carried leaves with suborbicular and elliptic leaflets, so this character could not be used to distinguish a separate form or variety.

(2) A specimen from Tonga with suborbicular leaflets (*Parks 16317*) closely resembles the present species. However, the material carries only very young fruits and deteriorated remains of flowers, so its identity could not be ascertained with certainty. *Arytera arcuata* is otherwise not known from outside New Caledonia.

(3) Occasionally three-lobed fruits are found.

(4) In one case (*Le Rat 570*) a flower with 6-dentate calyx and 6 petals was found.

Specimens studied — NEW CALEDONIA. New Caledonia: 67 specimens; Loyalty Islands: 11 specimens.

A2 - **Arytera bifoliolata** S.T. Reynolds — Fig. 5.3, 5.4

Arytera bifoliolata S.T. Reynolds, Fl. Austr. 25 (1985) 198; Austrobaileya 2 (1985) 161; H. Turner, Fl. Males. I, 11 (3) (1994) 470. — Type: *Hyland 2533* (holo BRI, n.v.; iso K, L), Lockerbie, Cape York Peninsula, Queensland, Australia, 5 Dec. 1962.

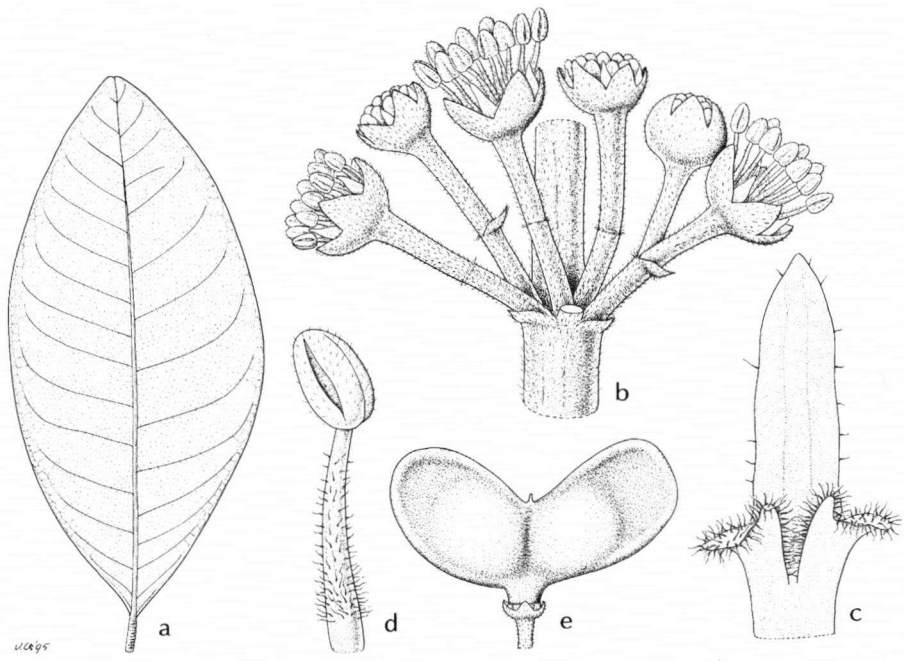

FIGURE 5.3. *Arytera bifoliolata* S.T. Reynolds. (a) Leaflet, × 0.5; (b) cymule, × 6; (c) petal, × 25; (d) stamen, × 12.5; (e) fruit, × 3. (a–d: *Sharpe 4184*; e: *Godwin C2322*.)

Tree or *shrub*. *Indument* of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth to slightly rough, puberulous to sericeous when young; flowering twigs 1–4 mm thick. *Leaves* 1-jugate; petiole 0.6–5.5 cm long, hemiterete, puberulous to sericeous when young, lenticels present abaxially. *Leaflets* opposite; petiolules pulvini only, 2–10 mm long, not to slightly 1-grooved, lenticels present abaxially; blade ovate to elliptic (to obovate), 5.3–18.6 by 1.8–7 cm, index 1.9–3.6, not to slightly falcate, coriaceous to chartaceous, sometimes punctate; base acute to attenuate, symmetric; margin entire to slightly repand, flat to slightly undulating, not revolute; apex rounded to slightly acuminate, very apex retuse to rounded (to acute), not mucronulate; upper surface glabrous; lower surface glabrous, colour same as that of upper surface, domatia absent; venation on upper surface flat, colour same as lamina to midrib reddish brown, on lower surface flat, midrib raised; nerves 3–20 mm apart, marginally indistinctly looped; veins laxly reticulate, not distinct. *Inflorescences* axillary to pseudoterminal, branching in axil and along rachis; rachis flattened, 2–9.5 cm long, puberulous to subsericeous when young; first-order branches up to 3.5 cm long; cymules pleiochasial, 1–7-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous to sericeous, adaxially glabrous; bracts 0.5–0.6 mm long; bracteoles 0.2–0.4 mm long. *Pedicels* 1–5 mm long, elongating up to 7 mm in fruit, puberulous to sericeous. *Flowers* 2–3 mm diam. *Calyx* 0.9–2 mm high, teeth 0.7–1.9 mm high, triangular to ovate, not punctate, margin entire, not membranaceous, apex

acute; outside puberulous to sericeous, inside glabrous to subpuberulous. *Petals* 5, ovate to rhomboid, 1.6–2.5 by 0.5–1.3 mm, index 1.4–3.2, not punctate; claw 0.2–0.5 mm long, margin entire, apex acute to acuminate; blade gradually decurrent into claw, outside puberulous to pilose, inside (sub)glabrous, margin pilose; scales 0.5–1.1 mm long, free, basally not auricled, apex sometimes broadened, rather densely pilose. *Disc* not lobed, glabrous. *Stamens* (male) 7–9; filament 2.5–4 mm long, basally pilose; anther 0.5–1.1 mm long, straight, pilose; connective not protruding. *Pistil* (female): ovary 2-locular, 1.3 mm long, puberulous; style and stigma 0.7 mm long, elongating up to 0.8–1.5 mm in fruit, in fruit 2-lobed, upper 0.8–1.5 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 0.6–1.3 cm high by 0.5–1.7 cm broad, axil not thickened transversely, outside subglabrous, slightly to distinctly rugose to verrucose, inside pilose on sutures; stipe 0.5–2 mm long, broadly cuneate; edge of margin sharp to keeled; angle between lobes c. 180°; blackish; lobes laterally flattened, valves 4–7.5 mm high by 6–11 mm long; endocarp light brown. *Seed* ellipsoid to ovoid, laterally flattened, c. 10 by 5 mm, light brown; arilloid covering seed completely, lobed, inside not folded towards base, thin, chartaceous, consisting of 1 layer, drab yellow; hilum elliptic, c. 2 by 1.3 mm; endotesta reddish brown. *Embryo*: cotyledons secondarily laterally beside each other, equal, apices not elongated; radicle c. 0.3 mm long, glabrous.

Field notes — Tree or shrub 5–10 m high, 15 cm dbh; trunk spirally fluted. Bark dark claret-brown, smooth, occasionally flaky. Flowers (greenish) yellow. Young fruit green.

Distribution — New Guinea: Southeast Irian Jaya; Australia: Northern Territories and N Queensland.

Habitat & Ecology — Vine forests on lateritic soils together with *Albizia toona*, also on dunes, or along creeks among rainforest trees to 25 m high (*Melia*, *Cryptocarya*, *Nauclea*, *Mallotus*, *Macaranga*, *Pipterus*, *Ficus*). Altitude sea level to 80 m. Flowering Apr., Aug.–Dec.; fruiting Nov., Dec.

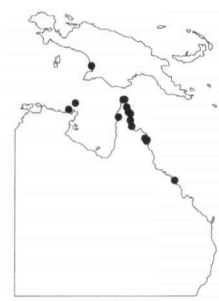

FIGURE 5.4. *Arytera bifoliolata* S.T. Reynolds. Distribution map.

Specimens studied — NEW GUINEA. Irian Jaya: *Reksodihardjo 224*. — AUSTRALIA. Northern Territories: *Latz 3506*, *Russel-Smith & Lucas 4515*; Queensland: 16 specimens.

A3 - Arytera brachyphylla Radlk. — Fig. 5.5, 5.6

Arytera brachyphylla Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 552; in D'Albertis, Nuov. Guin. 2 (1880) 396; Bot. Jahrb. 56 (1921) 301; in Engl., Pflanzenr. 98 (1933) 1277; H. Turner, Fl. Males. I, 11 (3) (1994) 471. — *Cupania brachyphylla* F. Muell., Notes Pap. Pl. 6 (1885) 6. — Type: *D'Albertis s.n.* (holo FI; iso M), Fly River, New Guinea, 1877.

Tree. *Indument* of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, puberulous when young; fruiting twigs 4–4.5 mm thick. *Leaves* 2-jugate; petiole 4–5.8 cm long, lenticels present abaxially; rachis 2.5–4.1 cm long, terete, glabrous to puberulous. *Leaflets* opposite, petioluled; petiolules pulvini only, 4–9.5 mm long, 1-grooved, lenticels present abaxially; oblong-elliptic to -obovate, 8.3–15 by 4.5–8.5 cm, index 1.5–2.1, not falcate, thickly chartaceous, not

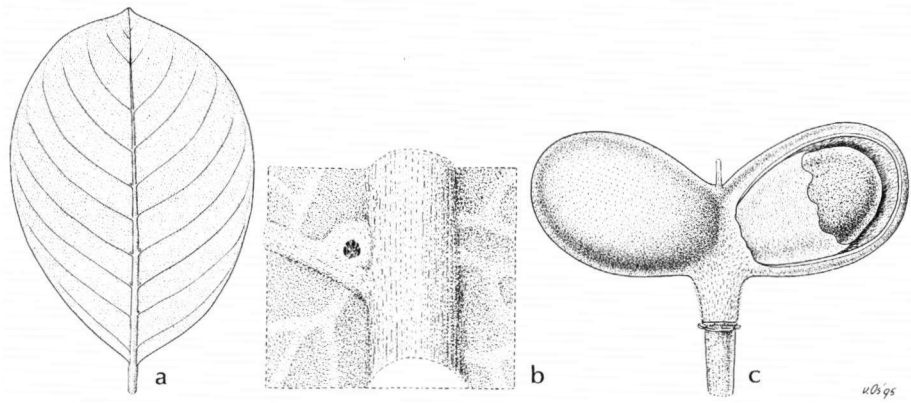

FIGURE 5.5. *Arytera brachyphylla* Radlk. (a) Leaflet, × 0.5; (b) domatium, × 12.5; (c) fruit, × 3. (a–c: *D'Albertis s. n.*, 1877.)

punctate; base acute to almost rounded, symmetric; margin entire, flat, not revolute; apex rounded to shortly acuminate, very apex obtuse to rounded, not mucronulate; upper surface glabrous; lower surface (sub)puberulous on venation, colour slightly different from that of upper surface, domatia sacs opening on top, sometimes sunken; venation on upper surface flat, midrib slightly raised, colour same as lamina, on lower surface almost flat, midrib distinctly raised; nerves 4–14 mm apart, marginally open; veins scalariform, laxly reticulate, not very distinct. *Infructescence* axillary to pseudoterminal, branching in axil and along rachis; rachis terete, 6.5–14 cm long, puberulous when young; first-order branches up to 7 cm long. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous, adaxially glabrous. *Pedicels* 4–6 mm long in fruit, puberulous. *Flowers* not observed. *Pistil*: ovary 2- or 3-locular; style and stigma elongating up to 2–2.5 mm in fruit, not lobed, in fruit upper 0.7–1.5 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 0.8–1.3 cm high by 0.9–2.1 cm broad, axil not thickened transversely, outside (sub)puberulous, smooth to slightly verrucose, inside completely pilose; stipe c. 2 mm long, slender; edge of margin rounded; angle between lobes c. 180°; blackish brown; lobes laterally not flattened, valves 5.5–9.5 mm high by 7.5–11 mm long; endocarp pale brown. *Seed* approx. orbicular to slightly obovoid, laterally not flattened, 6–9 by 6–10 mm, blackish; arilloid covering seed 1/2–2/3, not to slightly lobed, inside not to slightly folded towards base, thick towards base, coriaceous, consisting of 2 layers, outer layer thin, soft, yellow, inner layer thick, firm, chocolate; hilum elliptic, 2.5–3.5 by 1.5–2 mm; endotesta brown. *Embryo*: cotyledons (obliquely) dorsoventrally above each other, equal, apices not elongated; radicle 0.6–1.5 mm long, glabrous.

Distribution — Papua New Guinea: Western Province.

Note — Only known from the type specimen.

FIGURE 5.6. *Arytera brachyphylla* Radlk. Distribution map.

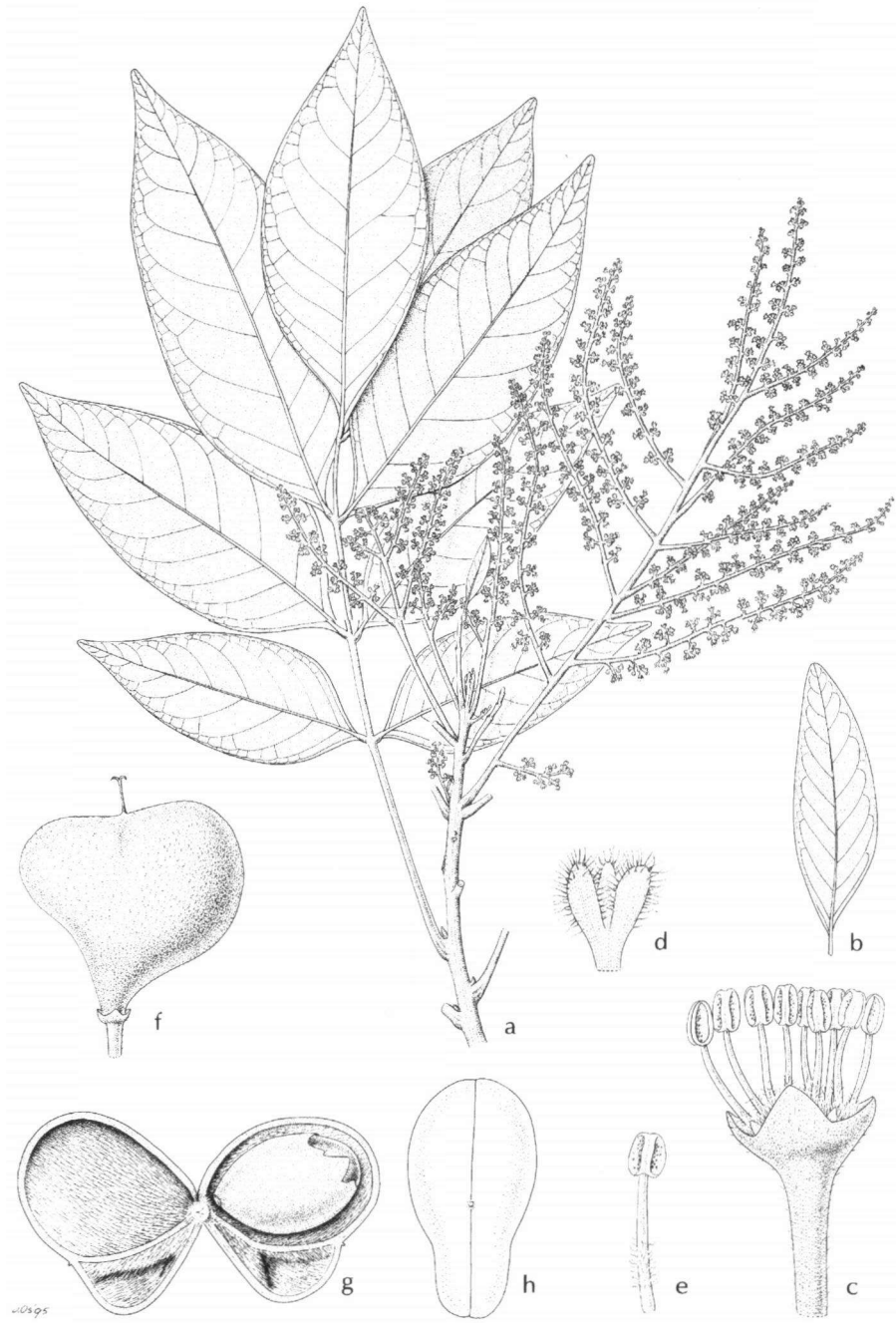

FIGURE 5.7. *Arytera brackenridgei* (A. Gray) Radlk. (a) Habit, × 0.5; (b) leaflet, × 0.5; (c) flower, × 12.5; (d) petal, × 25; (e) stamen, × 12.5; (f) fruit, × 3; (g) dehisced fruit showing hairy inside, and seed with arilloid, × 3; (h) schematic top view of fruit, × 3. (a, b: *BSIP 5645*; c–e: *A. C. Smith 4562*; f–h: *A. C. Smith 6399*.)

A4 - Arytera brackenridgei (A. Gray) Radlk. — Fig. 5.7, 5.8

Arytera brackenridgei (A. Gray) Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 555; in Engl., Pflanzenr. 98 (1933) 1286; A.C. Sm., Fl. Vit. Nov. 3 (1985) 602, figs. 145A, 146A, B. — *Cupania brackenridgei* A. Gray in Wilkes, U.S. Expl. Exped. Bot. 1 (1854) 255; (*Cupania (?) brackenridgei* Seem., Fl. Vit. 2 (1865) 46). — Type: *Wilkes (U.S. Expl. Exped.) s.n.* (holo US sheet no. 17733, n.v.; iso P), Fiji, 1838–1842.

Arytera oligolepis Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 555; in Engl., Pflanzenr. 98 (1933) 1288. — *Cupania?* sp. A. Gray in Wilkes, U.S. Expl. Exped. Bot. 1 (1854) 257 (in note under *Cupania lentiscifolia*). — Type: *Wilkes (U.S. Expl. Exped.) s.n.* (holo probably US, n.v.; iso M), Upolo, Samoa, 1838–1842.

Arytera samoensis Radlk. in K. Rech., Denkschr. Math.-Nat. Cl. Königl. Akad. Wiss. Wien 85 (1910) 305; in Engl., Pflanzenr. 98 (1933) 1286; A.C. Sm., Fl. Vit. Nov. 3 (1985) 602 (in. syn.). — Type: *K. & L. Rechinger 675* (holo W, n.v.; iso M), Savaii Isl., Samoa, July 1905.

Arytera xanthoneura Radlk., Bot. Jahrb. 56 (1920) 302; in Engl., Pflanzenr. 98 (1933) 1284. — *Ratonia sp.* Oliver in Guppy, Solomon Isl. (1887) 296. — Type: *Guppy 273* (holo K?; iso M), Oima Isl., Solomon Isl., Aug. 1884.

Arytera setosa Radlk., Fedde Rep. 20 (1924) 38; in Engl., Pflanzenr. 98 (1933) 1287. — Type: *Powell 348* (holo K; iso M), Samoa.

Arytera livida Radlk., Fedde Rep. 20 (1924) 38; in Engl., Pflanzenr., 98 (1933) 1287. — Type: *Powell 23* (holo K; iso M), Samoa.

Cupaniopsis aneityensis Guillaumin, J. Arnold Arbor. 14 (1933) 56. — Type: *Kajewski 827*, p.p. (holo A; iso BISH, K, P), Anelgauhat Bay, Aneityum Isl., Vanuatu, 28 Feb. 1929.

Tree or *shrub*. *Indument* of short, straight, patent hairs; glandular scales present on vegetative parts, inflorescence, pedicels, abaxial side of calyx, pistil, and fruit; buds 'varnished.' *Branchlets* smooth, glabrous to subpuberulous when young; flowering twigs 1–5 mm thick. *Leaves* 2–5-jugate; petiole 2–11.2 cm long, lenticels usually absent abaxially; rachis 1.5–13.8 cm long, hemiterete to flattened, glabrous to (sub)puberulous. *Leaflets* opposite to alternate, subsessile to petioluled; petiolules 2–10 mm long, not to slightly 2-grooved, lenticels rarely present abaxially; blade ovate to elliptic, 2.9–16.5 by 0.8–6.4 cm, index 1.9–5.5, not (to slightly) falcate, chartaceous to coriaceous, sometimes punctate; base attenuate, slightly oblique, basiscopic side broader; margin entire, flat to slightly undulating, not revolute to slightly revolute; apex obtuse to acute to acuminate (to slightly cuspidate), very apex obtuse to rounded, not mucronulate; upper surface glabrous to subpuberulous on basal part of midrib; lower surface glabrous to subpuberulous, colour (slightly) different (more olive to brown) from that of upper surface, domatia absent; venation on upper surface flat, midrib slightly raised, colour (yellowish to) reddish brown, sometimes only midrib so, on lower surface flat, midrib raised; nerves 2–21 mm apart, marginally looped, sometimes only apically so; veins laxly reticulate, (in)distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis; rachis (slightly) flattened, (3.5–)6.7–25 cm long, puberulous when young; first-order branches up to 14 cm long; cymules dichasial (to monochasial), 1–7-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially glabrous (to subpuberulous), adaxially glabrous (to sericeous); bracts 0.3–1 mm long; bracteoles 0.1–0.4 mm long. *Pedicels* 0.8–2.4 mm long, elongating up to 4 mm in fruit, glabrous to puberulous. *Flowers* 1.2–3.2 mm diam. *Calyx* 0.6–1.6 mm high, teeth 0.2–1 mm high, triangular, not punctate, margin entire, not membranaceous, apex acute; outside glabrous, inside

puberulous to sericeous on teeth. *Petals* 5, ovate to rhomboid to elliptic, 0.2–1.4 by 0.1–0.8 mm, index 0.8–4.6, not punctate; claw up to 0.4 mm long, margin entire, apex rounded to acute; blade gradually decurrent into claw, outside (sub)glabrous, inside pilose, margin pilose; scales 0.2–0.8 mm long, free, basally rarely slightly auricled, apex broadened, pilose. *Disc* not lobed, glabrous to pilose on rim. *Stamens* (male) 6–9; filament 1–3.5 mm long, basally pilose; anther 0.4–0.7 mm long, straight, glabrous; connective not protruding. *Pistil* (female): ovary 2-locular, 0.6–2.2 mm long, sericeous to pilose; style and stigma 0.3–1.6 mm long, elongating up to 2.7 mm in fruit, 2-lobed, in fruit upper 0.3–0.8 mm stigmatic. *Fruit* distinctly obcordate, with 1 or 2 well-developed lobes, 0.9–1.7 cm high by 0.9–1.7 cm broad, axil thickened transversely, outside glabrous to subpuberulous, smooth to rugose to verrucose, inside yellow to rust-red strigose; stipe up to 2 mm long, broadly cuneate; edge of margin rounded to slightly keeled; angle between lobes c. 180°; dull to blackish brown; lobes laterally not to slightly flattened, valves 4–9 mm high by 6–18 mm long; endocarp straw to pale light brown. *Seed* ellipsoid to obovoid, laterally not to slightly flattened, 5.5–11 by 4–8 mm, light brown to orange brown (to blackish); arilloid covering seed 2/3 to completely, lobed, inside not folded towards base, thin, fleshy membranaceous, consisting of 1 layer, soft, pale yellow; hilum elliptic to triangular to transversely elliptic, 1–5 by 1–5 mm; endotesta pale brown. *Embryo*: cotyledons dorsoventrally above each other, equal to unequal, then upper larger, apices not elongated; radicle 1.2–3.5 mm long, glabrous.

Field notes — Tree 6–30 m high, 10–90 cm dbh. Buttresses rarely present, then up to 90 cm high, thick, equal. Crown open to compact, roundish, dark and dense or fairly thin, foliage essentially in one layer; branches short appressed reddish tomentose, black. Bark light to dark grey brown and black, smooth to slightly fissured, sloughing in thin flakes, lenticels inconspicuous, thin, regularly spaced in approx. vertical faint fissure lines; outer bark light salmon-pink to cream mottled with pink vessels; inner bark thin discrete layer, semi-transparent light pink or reddish brown, irregular surface on wood, staining rusty brown on contact with air after cutting, crumbly break. Sapwood white to light chocolate, moderately thick; heartwood white to yellow brown, hard, wavy

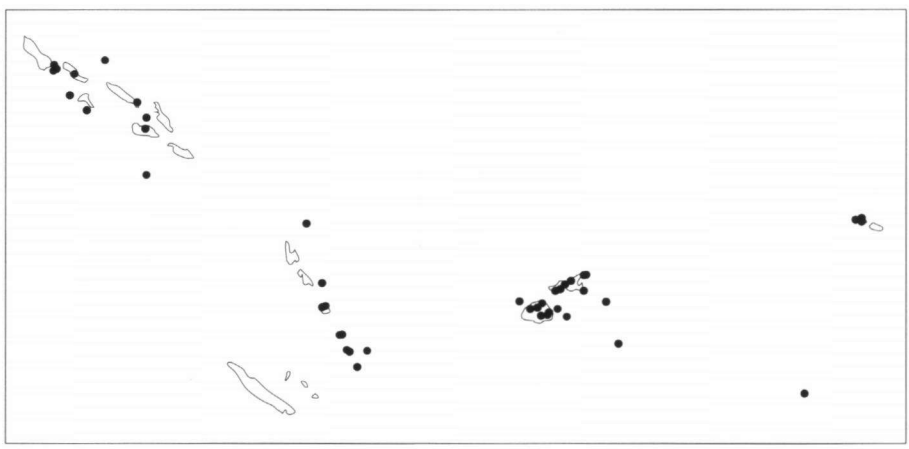

FIGURE 5.8. *Arytera brackenridgei* (A. Gray) Radlk. Distribution map.

grain. Leaves mid to dark green, shiny above, lighter and duller below, both sides with yellow-green midrib. Flower buds light green with russet hairs; flowers small, white to yellow green, fragrant; petals yellow; filaments white; anthers yellow. Fruit green turning brown; seeds [arilloid?] orange-red.

Distribution — Solomon Islands; Vanuatu; Fiji Islands; Tonga; Samoa.

Habitat & Ecology — In primary and secondary rainforest, also on savannahs, on limestone and lava fields. Often described as common. Altitude sea level to 1050 m. Flowering Feb.–Aug., Nov.; fruiting Jan., March–Nov.

Uses — Wood used in ground and air (house) constructions and for tool handles.

Vernacular names — *Solomon Islands:* Felfelo gwane, Nekale, Sufusane. *Vanuatu:* Katawbikin, Langar, Nung-arl. *Fiji:* Drausasa, Kauloa, Marasa, Masa, Ndrausasa, Ndrengandrenga, Ravulevu. *Samoa:* Aopo'asau, Laulili'i, Oga, Tapumatau, Taputo'i.

Notes — (1) Occasionally (e.g. *A.C. Smith 5067*) a three-lobed fruit is observed.

(2) This species was described from different localities under many different names by Radlkofer, mostly from young or incomplete material. Now that much more material has become available, these different 'forms,' which were distinguished mainly on leaflet shape, are seen to intergrade. The leaflets are more ovate, more chartaceous, and less often punctate with a usually less revolute margin in the western part of the range (Solomon Islands, Vanuatu).

Specimens studied — FIJI: 35 specimens. — SAMOA: 15 specimens. — SOLOMON ISLANDS: 11 specimens. — TONGA: *Crosby 32*. — VANUATU: 20 specimens.

A5 - Arytera chartacea Radlk. — Fig. 5.9, 5.10

Arytera chartacea Radlk., Sapind. Holl.-Ind. (1879) 44 45; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 553; in Engl., Pflanzenr. 98 (1933) 1281; Guillaumin, Fl. Nouv.-Caléd. (1948) 201. — Lectotype (here designated): *Balansa 147* (holo P; iso K, M, NY), Port des Français près de Nouméa, Sep. 1868.

Tree. Indument of short straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* terete, (slightly) rough to approx. smooth, puberulous when young; flowering twigs 1–2.5 mm thick. *Leaves* 1- or 2-jugate; petiole 0.9–2.8 cm long, lenticels usually present abaxially; rachis 0.7–2.4 cm long, hemiterete, puberulous. *Leaflets* opposite to subopposite, subsessile to petioluled; petiolules 1.5–6 mm long, 1-grooved, lenticels usually present abaxially; blade elliptic to obovate, 2.7–8.9 by 1.1–3.7 cm, index 1.8–3.3, not falcate, coriaceous to somewhat chartaceous, rarely minutely punctate; base somewhat attenuate to acute, symmetric to slightly oblique, then basiscopic side broader; margin entire (to slightly repand), flat to slightly undulating, not to slightly revolute; apex retuse, not mucronulate; upper surface glabrous (to midrib subpuberulous at base); lower surface subglabrous to subpuberulous, especially on midrib, colour same as that of upper surface, domatia absent; venation on upper surface flat, colour same as lamina, midrib yellow to reddish brown, on lower surface flat, midrib raised; nerves 3–11 mm apart, marginally looped; veins densely reticulate, not distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis (and in axil); rachis approx. terete to flattened, 2.5–13.7 cm long, puberulous when young; first-order branches up to 9.4 cm long; cymules dichasial, 1–7-flowered. *Bracts* and *brac-*

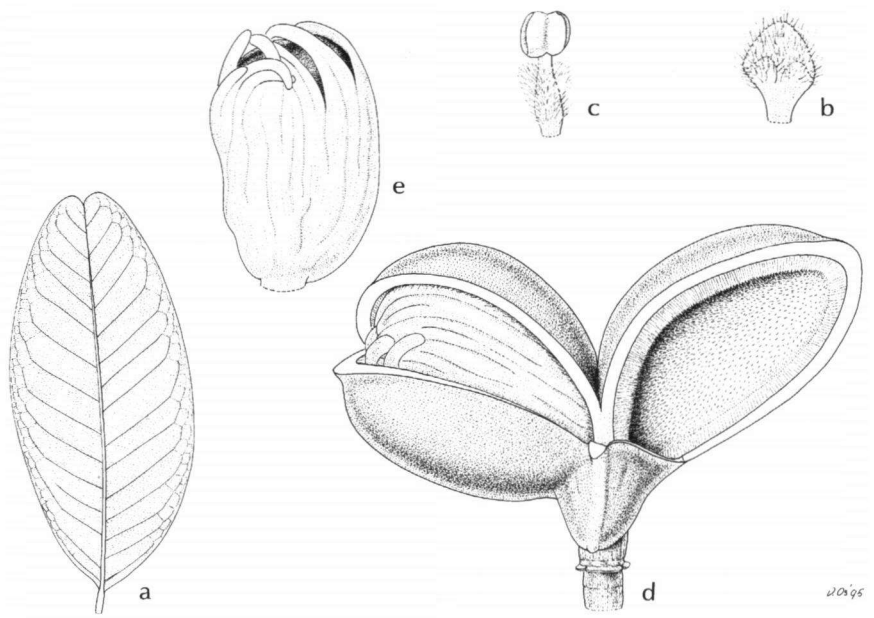

FIGURE 5.9. *Arytera chartacea* Radlk. (a) Leaflet, × 0.5; (b) petal, × 25; (c) stamen, × 12.5; (d) fruit, × 3; (e) seed with arilloid, × 2. (a, d, e: *Veillon 6886*; b, c: *MacKee 24968*.)

teoles triangular, margin entire, abaxially puberulous, adaxially glabrous; bracts 0.3–1 mm long; bracteoles minute. *Pedicels* 1–3 mm long, elongating up to 6 mm in fruit, puberulous. *Flowers* 1.7–3.5 mm diam. *Calyx* 0.6–1.4 mm high, teeth 0.4–0.9 mm high, triangular to somewhat semicircular, not punctate, margin entire, not membranaceous, apex acute to obtuse; outside puberulous, inside subglabrous. *Petals* 5, elliptic to rhomboid, 0.6–1.6 by 0.2–1 mm, index 1.1–2.6(–4), not punctate; claw 0.2–0.9 mm long, margin entire, apex obtuse to acute; blade gradually decurrent into claw, outside pilose, inside pilose, margin pilose, apex usually glabrous; scales up to 0.4 mm long, adnate to, or enation of, margin, basally not auricled, apex broadened. *Disc* slightly 5-lobed, sparsely pilose. *Stamens* (male) (7–)8(–10); filament 1.8–3.2 mm long, pilose; anther 0.4–0.6 mm long, straight, pilose when young; connective not protruding. *Pistil* (female): ovary 3-locular, 1.5–3 mm long, pilose; style and stigma 0.8–1.5 mm long, elongating up to 1.8 mm in fruit, 3-lobed in fruit, in fruit upper c. 0.3 mm stigmatic. *Fruit* slightly obcordate, with 1–3 well-developed lobes, 1.3–2.3 cm high by 1–3.3 cm broad, axil thickened transversely, outside puberulous, rugose, inside densely pale yellowish pilose; stipe 2–6 mm long, slender; edge of margin rounded to slightly keeled; angle between lobes 120–180°; dull greyish brown; lobes laterally not flattened, valves 7–14 mm high by 11–21 mm long; endocarp pale brown to orange brown. *Seed* ellipsoid to slightly obovoid, laterally not flattened, 8.5–20 by 5–10 mm, brown; arilloid covering seed completely, lobed, inside not folded towards base, thick towards base, fleshy membranaceous, consisting of 1 layer, soft, orange-yellow; hilum elliptic to circular, 2–5.5

by 1–5 mm; endotesta pale brown. *Embryo*: cotyledons dorsoventrally above each other, approx. equal, apices not elongated; radicle 2–5 mm long, margin slightly pilose, tip glabrous.

Field notes — Tree 5–15 m tall, bole 15–50 cm dbh. Crown dense, rounded or spreading. Bark bright brown to grey, somewhat to rather rough to somewhat longitudinally striated. Leaves bright to dark green, shiny below or on both sides. Flower buds green; flowers white to greenish, slightly smelling. Fruits brown, arilloid red.

Distribution — SW New Caledonia, along the coast.

Habitat & Ecology — (Degraded) coastal, gallery, and sclerophyll forests and scrubs. On calcareous or nummulitic schists, phthanite [granite?] with rubble, alluvial soil, and serpentine. Altitude from sea level to 180 m. Flowering Dec.–March; fruiting Feb.–Sep., Nov., Dec.

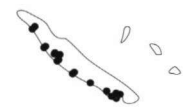

FIGURE 5.10. *Arytera chartacea* Radlk. Distribution map.

Note — In one specimen (*MacKee 37882*) a single flower with six calyx lobes, six petals and ten stamens was observed. Another specimen (*MacKee 26330*) had one flower with only seven stamens.

Specimens studied — NEW CALEDONIA: 37 specimens.

A6 - Arytera collina (Panch. & Séb.) Radlk. — Fig. 5.11, 5.12

Arytera collina (Panch. & Séb.) Radlk. in Lecomte, Not. Syst. 2, 1 (1911) 10; in Engl., Pflanzenr. 98 (1933) 1282; Guillaumin, Fl. Nouv.-Caléd. (1948) 201. — *Cupania collina* Panch. & Séb. in Séb., Not. Bois Nouv.-Caléd. (1874) 230. — Lectotype (here designated): *Pancher 'Bois' 79* (holo P).

Arytera pachyphylla Radlk., Sapind. Holl.-Ind. (1877) 44, 45; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 554. — [*Cupania paniculata* Panch. ex Guillaumin, Not. Syst. 1 (1909) 330, in syn., nom. nud., nom. inval. (I.C.B.N. [1994] Art. 34.1.c).] — Syntypes: *Baudouin 690* (holo P), Port de France; *Deplanche 280* (holo P; iso K), 1867.

Guioa collina auct. non Schltr.: Schltr., Bot. Jahrb. 39 (1907) 175 p.p., *Guioa villosa* Radlk. excl.; Guillaumin, Not. Syst. 1 (1909) 329 p.p., *Guioa villosa* Radlk. excl.

Tree. *Indument* of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, puberulous when young; flowering twigs 1–5 mm thick. *Leaves* 1- or 2- (or 3-)jugate; petiole 0.9–4.2(–7.4) cm long, lenticels sometimes present abaxially; rachis 0.9–3.5 cm long, (hemi)terete, puberulous. *Leaflets* opposite, petioluled; petiolules 4–25 mm long, puberulous, 1-grooved, lenticels sometimes present abaxially; blade ovate to elliptic, 3.2–13.3 by 1.8–6.6 cm, index 1.2–2.8, not falcate, very coriaceous, not punctate; base (acute to) obtuse, symmetric to slightly oblique, then basiscopic side broader; margin entire, flat to slightly undulating, not revolute; apex retuse, not mucronulate; upper surface glabrous, midrib sometimes (sub)puberulous; lower surface (sub)puberulous, scale-like dots present, colour same as to different from that of upper surface, domatia absent; venation on upper surface flat, colour same as lamina, midrib same to straw to reddish brown, on lower surface flat, midrib raised; nerves 3–14 mm apart, marginally looped; veins laxly reticulate, not distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis; rachis terete to flattened, 4.5–23 cm long, puberulous when young; first-order branches up to 13.6 cm

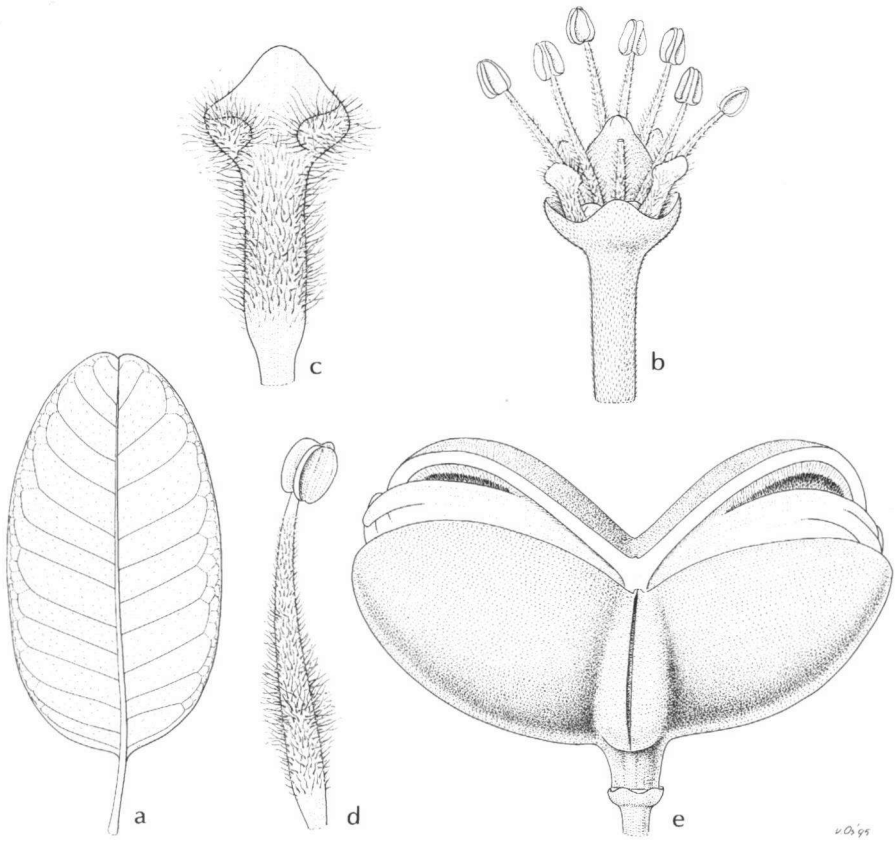

FIGURE 5.11. *Arytera collina* (Panch. & Séb.) Radlk. (a) Leaflet, × 0.5; (b) flower, × 6; (c) petal, × 25; (d) stamen, × 12.5; (e) fruit, × 3. (a, e: *MacKee 43887*; b–d: *MacKee 33563*.)

long; cymules dichasial, 1–7-flowered. *Bracts* and *bracteoles* triangular, margin entire, adaxially glabrous to puberulous, abaxially puberulous; bracts 0.4–1 mm long; bracteoles 0.1–0.3 mm long. *Pedicels* 1–4 mm long, elongating up to 5 mm in fruit, puberulous. *Flowers* 2.5–4 mm diam. *Calyx* 0.8–1.4 mm high, teeth 0.5–1 mm high, triangular (to slightly ovate), usually not punctate, margin entire, not membranaceous, apex acute to obtuse; outside puberulous, inside connate part glabrous, free part (sub)puberulous. *Petals* 5, obovate, 1–1.8(–2.6) by 0.5–1 mm, index (1.2–)1.6–2.6, usually not punctate; claw (male) 0.3–1.5 mm long, (female) up to 0.5 mm long, margin entire, apex obtuse to acute; blade gradually decurrent into claw, outside pilose, inside pilose, margin pilose, tip completely glabrous; scales up to 0.2 (0.4) mm long, enation of margin, basally not auricled, apex not broadened, membranaceous margin indistinct. *Disc* distinctly 5-lobed (to with 5 slits), pilose at apex of lobes. *Stamens* (male) 8–10; filament 1.5–4 mm long, pilose; anther 0.4–0.7 mm long, straight, (sub)glabrous; connective not protruding. *Pistil* (female): ovary 3-locular, 1.3–2.4 mm long, puberulous; style and stigma 0.3–1.2 mm long, elongating up to 2.3 mm in fruit,

3-lobed in fruit, in fruit upper 0.5 mm stigmatic. *Fruit* slightly obcordate, with 1–3 well-developed lobes, 1.3–2.5 cm high by 1.1–3.5 cm broad, axil thickened transversely, outside subpuberulous, rugose, inside densely yellowish to rusty pilose; stipe 1–4 mm long, slender; edge of margin rounded to slightly keeled; angle between lobes 100–160°; dull brown to blackish brown; lobes laterally slightly flattened, valves 9–17 mm high by 8–20 mm long; endocarp pale brown. *Seed* ellipsoid to obovoid, laterally not flattened, 11–19 by 7–15 mm, dark brown to blackish; arilloid covering seed completely, lobed, inside not folded towards base, thick towards base, fleshy to membranaceous, consisting of 1 layer, soft, yellow to orange; hilum elliptic (to circular), 3.5–5 by 3–3.5 mm; endotesta pale to dark brown. *Embryo*: cotyledons dorsoventrally above each other, approx. equal, apices not elongated; radicle 3–5 mm long, margin pilose basally.

Field notes — Small to large tree 1.5–12 m; trunk 10–30 cm dbh. Bark light brown to pale grey to whitish, smooth to somewhat rough. Leaves bright to dark green above, lighter green below, shiny above. Flowers white to cream. Fruit green, turning yellow to brown; arilloid lively red.

Distribution — New Caledonia, Maré.

Habitat & Ecology — In thickets, low forest or (degraded) sclerophyll forest on calcareous substrate, rocky serpentinic terrain, phthanitic [granitic?] rubble, basalt or black clayey soil, mostly along the coast. Found together with *Terminalia cherrieri*. Altitude sea level to 200 m. Flowering May–Aug.; fruiting (June, July) Aug.–Jan.

Note—Rarely (e.g. *Pancher 'Bois' 79* and *MacKee 12489*) 4-merous flowers are en-countered.

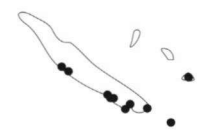

FIGURE 5.12. *Arytera collina* (Panch & Séb.) Radlk. Distribution map.

Specimens studied — NEW CALEDONIA: 51 specimens.

A7 - **Arytera densiflora** Radlk. — Fig. 5.13, 5.14

Arytera densiflora Radlk., Bot. Jahrb. 56 (1920) 301; in Engl., Pflanzenr. 98 (1933) 1278; H. Turner, Fl. Males. I, 11 (3) (1994) 472. — Type: *Ledermann 9555* (holo B†; iso K, L, M), Kaiserin-Augusta-Fluss Exp., Etappenberg, Papua New Guinea, Oct. 1912.

Tree. *Indument* of long, crispate, patent hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, crispate-hirsute when young; flowering twigs 3–5 mm thick. *Leaves* 2-jugate; petiole 3–9(–18) cm long, lenticels rarely present abaxially; rachis 2.5–4.5 cm long, (hemi)terete, densely crispate-hirsute. *Leaflets* opposite, subsessile to petioluled; petiolules pulvini only, 5–7 mm long, 1-grooved, lenticels rarely present abaxially; blade elliptic, 6.6–20.7 by 4–8.8 cm, index 1.5–3.1, not falcate, chartaceous to slightly coriaceous, rarely punctate; base slightly attenuate to acute, slightly oblique, basiscopic side broader (to symmetric); margin entire to slightly repand, flat to slightly undulating, not revolute; apex acuminate to cuspidate, very apex retuse to obtuse, not mucronulate; upper surface (sub)glabrous; lower surface crispate-hirsute especially on venation, colour slightly different from that of upper surface (olive to brownish), domatia pockets to sacs opening in front; venation on upper surface flat, midrib slightly raised, colour same as lamina to slightly reddish brown, on lower sur-

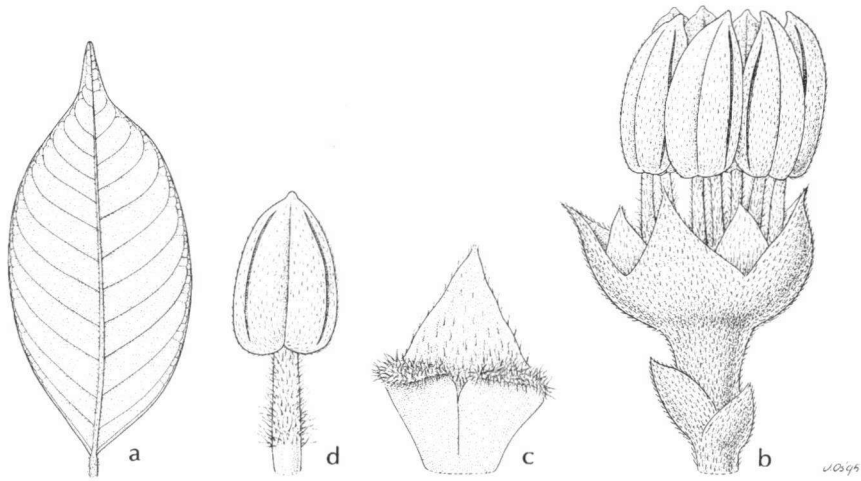

FIGURE 5.13. *Arytera densiflora* Radlk. (a) Leaflet, × 0.5; (b) flower, × 12.5; (c) petal, × 25; (d) stamen, × 12.5. (a–d: *Schodde 2438*.)

face raised; nerves 6–22 mm apart, marginally open; veins scalariform, laxly reticulate, distinct. *Inflorescences* axillary to pseudoterminal to ramiflorous, branching in axil and along rachis; rachis terete to slightly flattened, 4.5–16 cm long, densely crispate-hirsute when young; first-order branches up to 7.5 cm long; cymules dichasial to cincinnate, 1–6-flowered. *Bracts* and *bracteoles* narrowly triangular, margin entire, abaxially crispate-hirsute, adaxially glabrous; bracts 0.8–1.5 mm long; bracteoles 0.5–0.7 mm long. *Pedicels* 0.8–1.5 mm long, crispate-hirsute. *Flowers* 1.5–3 mm diam. *Calyx* 0.9–1.3 mm high, teeth 0.6–1 mm high, triangular to ovate, not punctate, margin entire, not membranaceous, apex acute to obtuse; outside crispate-hirsute, inside glabrous. *Petals* 5, triangular to rhomboid to almost orbicular, 0.7–1.4 by 0.5–0.9 mm, index 1–2, not punctate; claw 0.1–0.2 mm long, margin entire to sometimes slightly denticulate, apex rounded to acute; blade abruptly decurrent into claw, outside subpilose, inside (sub)glabrous, margin pilose; scales 0.2–0.5 mm long, free, basally not to slightly auricled, apex broadened, densely pilose. *Disc* not lobed, glabrous to subpilose on rim. *Stamens* (male?) 8; filament 1–1.6 mm long, densely pilose; anther 1.1–1.6 mm long, incurved, densely pilose; connective protruding. *Pistil* (female): ovary 2-locular, c. 1 mm long, pilose; style and stigma c. 1 mm long. *Fruit* not observed.

Field notes — Tree or treelet 2–5 m high. Flower buds yellow; petals white; filaments white; anthers yellow.

Distribution — Papua New Guinea: central mountain range.

Habitat & Ecology — Primary (riverine) forest; old well-drained volcanic soil. Altitude 600–850 m. Flowering Oct.

Vernacular names — Tsabiania (Kutubu language).

Note — *Schodde 2438* from Lake Kutubu is different from the other specimens in the much larger sac-like domatia on

FIGURE 5.14. *Arytera densiflora* Radlk. Distribution map.

the underside of the leaflets and in having some leaflets sparsely minutely punctate. The type specimen has more rhomboid to orbicular petals than the other specimens.

Specimens studied — NEW GUINEA. East Sepik Province: *Ledermann 9555*; Southern Highlands Province: *Jacobs 9509*; *Schodde 2438*.

A8 - Arytera dictyoneura S.T. Reynolds — Fig. 5.15, 5.16

Arytera dictyoneura S.T. Reynolds, Fl. Austr. 25 (1985) 198; Austrobaileya 2 (1985) 164. — Type: *W.J.F. McDonald 3439* (holo BRI; iso L), c. 6 km from Forest Station on Scott Road, NE of Boyne River crossing, Bulburin State Forest 391, Queensland, Dec. 1981.

Tree or *shrub*. *Indument* of both long, straight, appressed and short, straight, patent hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, puberulous to sericeous when young; flowering twigs 2–2.5 mm thick. *Leaves* 1- or 2-jugate; petiole 0.7–5.2 cm long, lenticels absent abaxially; rachis 0.7–3.4 cm long, hemiterete, puberulous to sericeous. *Leaflets* opposite, subsessile to petioluled; petiolules pulvini only, 2–7(–11) mm long, 1-grooved, lenticels present abaxially; blade ovate to elliptic, 2.5–11.2 by 1–5.9 cm, index 1.8–3.8, not falcate, coriaceous, not punctate to slightly punctate along venation; base slightly attenuate to rounded, symmetric; margin entire, flat, slightly revolute; apex obtuse to slightly acuminate, very apex retuse to obtuse, not mucronulate; upper and lower surfaces glabrous to subpuberulous on midrib, lower subglabrous to subpuberulous, especially on midrib, colour same as to slightly different from that of upper surface, domatia few large pits opening on top; venation on upper surface flat, colour same as lamina to slightly yellowish, on lower surface slightly, midrib distinctly raised; nerves 2–22 mm apart, marginally looped; veins densely reticulate, distinct. *Infructescence* axillary, not branching (or branching along rachis); rachis terete to slightly flattened, 3–6.7 cm long, puberulous to sericeous when young; first-order branches up to 2.2 cm long. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous, adaxially glabrous; bracts 0.5–1 mm long; bracteoles 0.2–0.5 mm

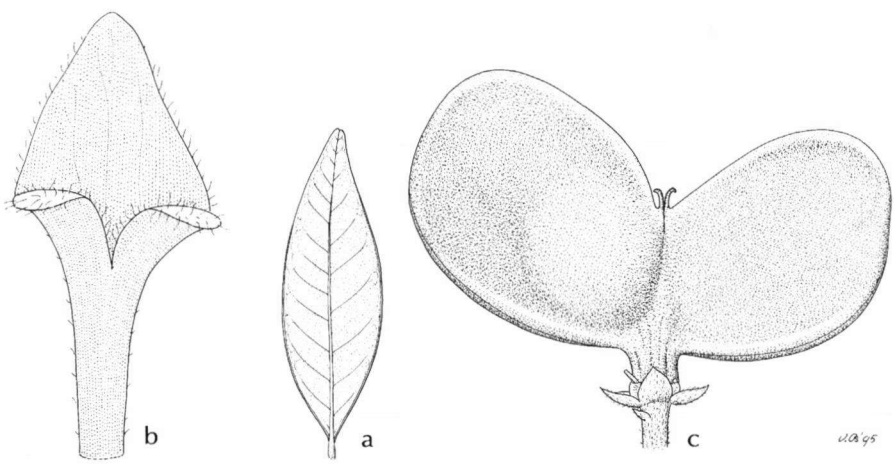

FIGURE 5.15. *Arytera dictyoneura* S.T. Reynolds. (a) Leaflet, × 0.5; (b) petal, × 25; (c) fruit, × 3. (a–c: *W.J.F. McDonald 3439*.)

long. *Pedicels* 1–3.5 mm long in fruit, puberulous. *Flowers* not observed. *Calyx* 1.7–2.1 mm high, teeth 1.5–2 mm high, not punctate, triangular to ovate, margin entire, not membranaceous, apex acute; outside puberulous, inside glabrous. *Petals* (only remains under fruit seen) elliptic to ovate, 2.6–3.3 by 1.2–1.6 mm, index 1.9–2.3, not punctate; claw 0.6–0.8 mm long, margin entire, apex acute; blade gradually decurrent into claw, outside glabrous, inside subglabrous, margin subpilose in lower half; scales 0.8–1 mm long, free to adnate to margin, basally not auricled, apex not to slightly broadened. *Disc* not lobed, glabrous. *Stamens* (female): filament c. 1.3 mm long, basally pilose; anther 1.1–1.2 mm long, straight, pilose; connective not protruding. *Pistil* (female): ovary 2- (or 3-)locular, style and stigma elongating up to 2 mm in fruit, 2- (or 3-)lobed, in fruit upper 1.5–2 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 0.9–1.6 cm high by 1.2–2 cm broad, axil not thickened transversely, outside subglabrous, smooth to rugose, inside pilose along sutures; stipe 2–4.5 mm long, slender; edge of margin sharp to keeled; angle between lobes 120–180°; reddish brown; lobes laterally not flattened, valves 0.5–0.9 mm high by 0.8–1.2 mm long; endocarp pale brown. *Seed* orbicular, laterally flattened, c. 6 by 6 mm, brown; arilloid covering seed 3/4 to completely, lobed, inside not folded towards base, thin, chartaceous, consisting of 1 layer, firm, pale yellow; hilum elliptic, c. 1.5 by 0.5 mm; endotesta light brown. *Embryo:* cotyledons secondarily laterally beside each other, equal to unequal, then lower larger, apices not elongated; radicle 0.3–0.5 mm long, glabrous.

Field notes — Tree or shrub 4–7 m high. Fruit orange-yellow.

Distribution — Australia: Southern Queensland.

Habitat & Ecology — Notophyll vine forest and low microphyll vine forest, also in heavily logged areas. On andesite and light brown soils. Fruiting Dec., Feb.

Specimens studied — AUSTRALIA. Queensland: *Forster & Bean 5800, MacDonald 3439, Thorsborne 8.*

FIGURE 5.16. *Arytera dictyoneura* S.T. Reynolds. Distribution map.

A9 - Arytera distylis (F. Muell. ex Benth.) Radlk. — Fig. 5.17, 5.18

Arytera distylis (F. Muell. ex Benth.) Radlk., Sapind. Holl.-Ind. (1879) 44; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 553; in Engl., Pflanzenr. 98 (1933) 1280; S.T. Reynolds, Fl. Austr. 25 (1985) 90; Austrobaileya 2 (1985) 160. — *Ratonia distylis* F. Muell. ex Benth., Fl. Austr. 1 (1863) 462. — *Nephelium distyle* F. Muell., Fragm. 9 (1875) 99. — Lectotype (here designated): *Leichhardt s. n.* (holo MEL sheet no. 1586016), Bunija Creek Brush, 13 Sep. 1845.

Tree or *shrub. Indument* of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, puberulous to sericeous when young; flowering twigs 0.5–2.5 mm thick. *Leaves* 1-jugate; petiole 0.3–2.3 cm long, puberulous to sericeous when young, terete to flattened, lenticels present abaxially. *Leaflets* opposite, subsessile to petioluled; petiolules pulvini only, 1–9 mm long, 1-grooved, lenticels present abaxially; blade ovate to elliptic (to obovate), 2.7–11.9 by 0.5–4.1 cm, index 2.1–4.4(–6.2), not to slightly falcate, coriaceous to chartaceous, not punctate; base attenuate to acute, symmetric; margin entire, flat to slightly undulating, not revolute;

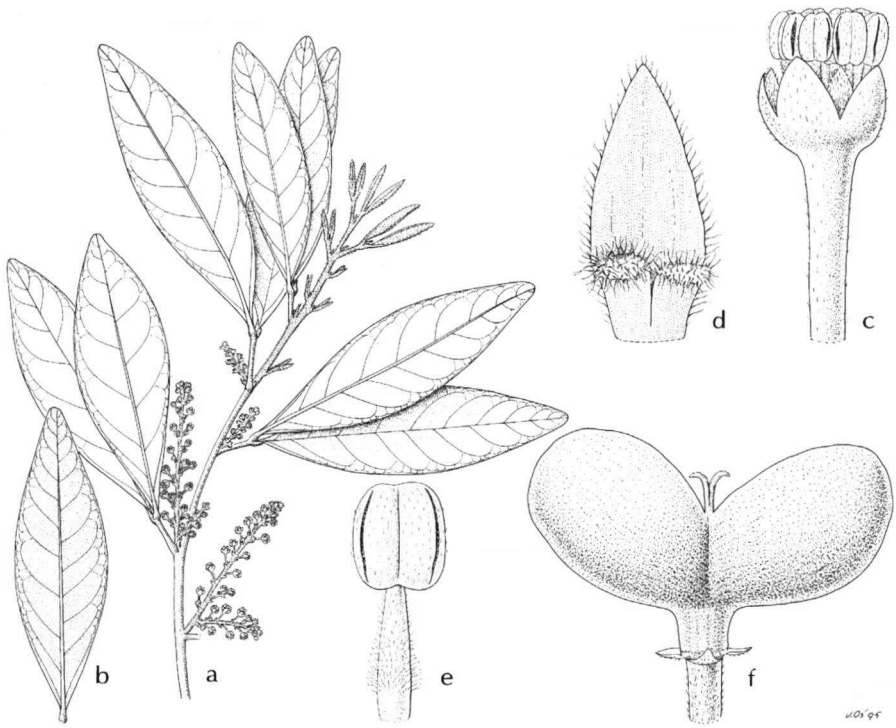

FIGURE 5.17. *Arytera distylis* (F. Muell. ex Benth.) Radlk. (a) Habit, × 0.5; (b) leaflet, × 0.5; (c) flower, × 6; (d) petal, × 25; (e) stamen, × 12.5; (f) fruit, × 3. (a–e: *Schodde 5579*; f: *C.T. White s.n.*)

apex rounded to acuminate, very apex retuse to rounded, sometimes mucronulate; upper surface glabrous; lower surface subglabrous to sericeous on midrib, colour same as to slightly lighter than that of upper surface, domatia few, sacs (to pits), opening on top (or in front), situated in middle part (and in lower half) of leaf blade; venation on both surfaces flat, midrib (slightly) raised, colour same as or slightly lighter than lamina on upper surface; nerves 2–18 mm apart, marginally looped; veins laxly reticulate, usually not distinct. *Inflorescences* axillary to pseudoterminal, branching in axil and along rachis; rachis terete to flattened, 1.1–9.5 cm long, puberulous to sericeous when young; first-order branches up to 7.5 cm long; cymules cincinnate, 1–3-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous to sericeous, adaxially glabrous; bracts 0.5–1.2 mm long; bracteoles 0.1–0.5 mm long. *Pedicels* 1–5 mm long, puberulous to sericeous. *Flowers* 2–3.5 mm diam. *Calyx* 0.8–1.4 mm high, teeth 0.6–1.1 mm high, triangular to ovate, not punctate, margin entire, not membranaceous, apex obtuse to acuminate; outside puberulous, inside (sub)glabrous. *Petals* 5, ovate to rhomboid to triangular, 0.4–2 by 0.3–1.1 mm, index 1–2, not punctate; claw up to 0.4 mm long, margin entire, apex obtuse to slightly acuminate; blade abruptly to gradually decurrent into claw, outside puberulous to pilose, inside subglabrous to puberulous, margin puberulous to pilose; scales 0.1–0.7 mm long, free, basally not auricled, apex

usually broadened, membranaceous margin absent. *Disc* not lobed, glabrous. *Stamens* (male) 6–8; filament 0.6–1.7 mm long, pilose; anther 1–1.2 mm long, straight, pilose; connective not protruding. *Pistil* (female): ovary 2-locular, 0.5–1.5 mm long, puberulous to pilose; style and stigma 0.5–1.5 mm long, elongating up to 0.8–2 mm in fruit, 2-lobed, in fruit upper 0.5–0.7 mm stigmatic. *Fruit* slightly obcordate, with (1 or) 2 well-developed lobes, 0.7–1.3 cm high by 0.8–1.8 cm broad, axil not thickened transversely, outside glabrous to subpuberulous, rugose to verrucose (to smooth), inside pilose throughout or on sutures only; stipe 1–4 mm long, slender; edge of margin rounded to keeled; angle between lobes 150–180°; dull reddish brown to blackish; lobes laterally flattened, valves 3.5–7 mm high by 4–10 mm long; endocarp light to dark brown. *Seed* ellipsoid, laterally not flattened, 8–8.5 by 4–5 mm, dark brown to yellowish; arilloid covering seed 3/4 to completely , margin dentate, inside not folded towards base, thin, membranaceous, consisting of 1 layer, yellow-brown; hilum elliptic, 1–1.8 by 0.5–1.2 mm; endotesta dark brown. *Embryo:* cotyledons obliquely dorsoventrally above each other, equal to unequal, then upper larger, apices not elongated; radicle 0.2–1 mm long, glabrous.

Field notes — Tree or shrub 2–20 m high, trunk c. 3.4 cm dbh, channelled at the butt. Outer bark brownish with obscure longitudinal lenticellate lines; inner bark greenish and pale red brown streaked on the outside, reddish brown and obscurely concentrically layered within, 1 cm thick. Sapwood ill-defined, wood darkening inwards from pale straw to light brown with darker bands. Leaflets dull rather dark green above, mid-green below. Flowers cream to yellowish green. Fruits orange.

Distribution — Australia: Queensland, New South Wales.

Habitat & Ecology — In rainforest, notophyll and microphyll vine forest, often in brush along the margins. Altitude 150–550 m. Flowering Sep., Oct.; fruiting observed throughout the year.

Vernacular name — Mabbee.

Specimens studied — AUSTRALIA. Queensland: 25 specimens; New South Wales: 18 specimens.

FIGURE 5.18. *Arytera distylis* (F. Muell ex Benth.) Radlk. Distribution map.

A10 - Arytera divaricata F. Muell. — Fig. 5.19, 5.20

Arytera divaricata F. Muell., Trans. Phil. Inst. Vict. 3 (1859) 25; Radlk., Sapind. Holl.-Ind. (1877) 44; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 552; in Engl., Pflanzenr. 98 (1933) 1278; S.T. Reynolds, Fl. Austr. 25 (1985) 92, 198; Austrobaileya 2 (1985) 164. — *Nephelium divaricatum* F. Muell. ex Benth., Fl. Austr. 1 (1863) 467; F. Muell., Fragm. 9 (1875) 98. — Lectotype (Reynolds 1985: 198): *Hill s.n.* (holo MEL sheet no. 75411), Moreton Bay, Australia.

Nephelium beckleri Benth., Fl. Austr. 1 (1863) 467. — Type: *Beckler s.n.* (holo MEL sheet no. 75413; iso K; MEL sheet nos. 75414, 75415; NSW sheet no. 166321), Clarence River, Australia.

Cupania oshanesiana F. Muell., Fragm. 9 (1875) 96 (excl. fr.). — *Ratonia oshanesiana* F. Muell., Fragm. 9 (1875) 96 (in syn.) (excl. fr.). — *Arytera oshanesiana* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (187) 554; in Engl., Pflanzenr. 98 (1933) 1283 (excl. fr.). — Lectotype (Reynolds 1985: 164): *O'Shanesy s.n.* (holo MEL sheet no. 75429; iso MEL sheet no. 75430), Gracemere, Australia, July 1866.

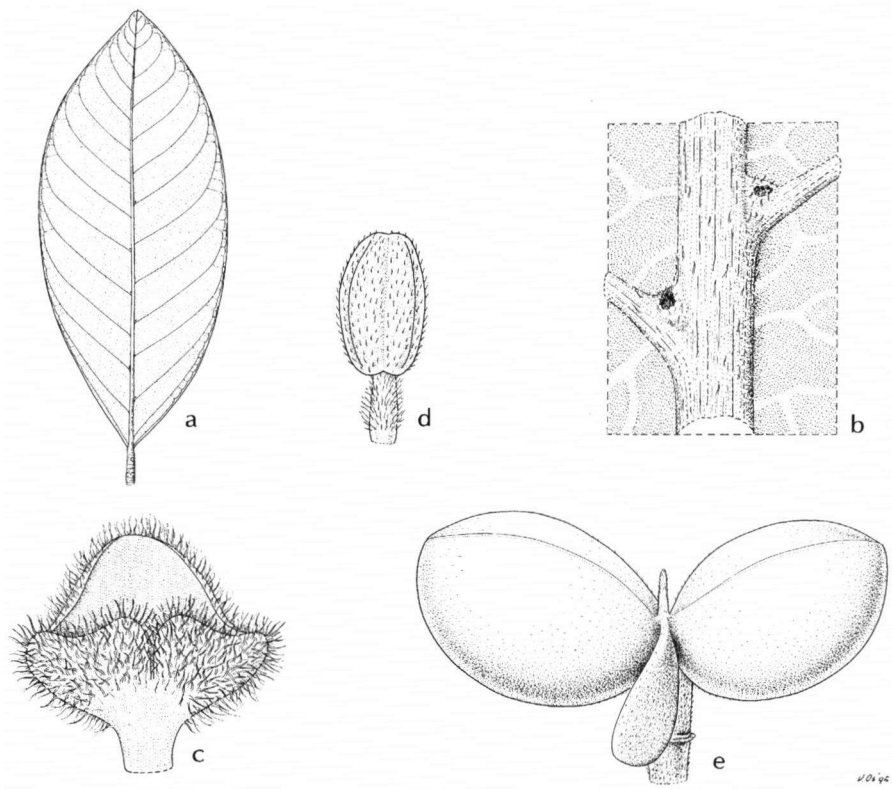

FIGURE 5.19. *Arytera divaricata* F. Muell. (a) Leaflet, × 0.5; (b) domatia, × 12.5; (c) petal, × 25; (d) stamen, × 12.5; (e) fruit, × 3. (a–d: *K.J. White 743*; e: *Anon. s.n.*, MEL 1586039.)

Tree. Indument of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, puberulous when young; flowering twigs 2–6 mm thick. *Leaves* (1–)2–4-jugate; petiole 2–7.5 cm long, lenticels usually present; rachis 1.8–7.7 cm long, terete to slightly flattened, glabrous. *Leaflets* opposite to subopposite to alternate, subsessile to petioluled; petiolules pulvini only, 3–14 mm long, not to slightly 1-grooved, lenticels usually present; blade elliptic to obovate, 2.6–15 by 1.4–6.1 cm, index (1.2–)1.6–2.7(–3.4), not falcate, coriaceous, sometimes sparsely punctate; base slightly attenuate to acute (to obtuse), symmetric; margin entire to slightly repand, flat to slightly undulating, not revolute; apex retuse to shortly acuminate, very apex retuse to rounded, not mucronulate; upper surface glabrous; lower surface subglabrous to subpuberulous, especially on venation, colour same as to slightly different from that of upper surface (lighter or darker, brownish, greener), domatia pockets opening in front; venation on upper surface flat, midrib flat to slightly angular, colour same as to slightly more yellowish than lamina, on lower surface raised; nerves 3–21 mm apart, marginally open; veins scalariform, laxly reticulate, distinct. *Inflorescences* axillary to pseudoterminal (to ramiflorous), branching in axil and along rachis; rachis (slightly)

flattened, 2.5–22 cm long, puberulous when young; first-order branches up to 10 cm long; cymules dichasial to monochasial, 2–11-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous, adaxially (sub)glabrous; bracts 0.5–2 mm long; bracteoles 0.5–0.8 mm long. *Pedicels* 0.5–4 mm long, puberulous. *Flowers* 2–3 mm diam. *Calyx* 0.9–1.6 mm high, teeth 0.5–1.4 mm high, triangular to ovate, slightly imbricate, not punctate, margin entire, not membranaceous, apex acute to obtuse; outside puberulous, inside glabrous to subpuberulous. *Petals* 5, broadly triangular to ovate to rhomboid, 0.4–1.9 by 0.5–1.6 mm, index 0.7–1.7, not punctate; claw up to 0.3 mm long, margin entire, apex obtuse to slightly acute; blade abruptly to gradually decurrent into claw, outside pilose, inside (sub)glabrous, margin pilose; scales 0.1–1 mm long, free, basally not auricled, apex broadened, densely villous. *Disc* not lobed, (sub)-glabrous. *Stamens* (male) 8 or 9; filament 1–3.1 mm long, densely pilose; anther 1–1.5 mm long, straight, pilose; connective not protruding. *Pistil* (female): ovary 3-locular, 1–1.5 mm long, puberulous; style and stigma 0.5–0.7 mm long, elongating up to 3 mm in fruit, not lobed, in fruit upper 1.5 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 (or 3) well-developed lobes, 0.8–1.4 cm high by 0.7–2.7 cm broad, axil not thickened transversely, outside puberulous, glabrescent, smooth (to slightly verrucose), inside pilose along sutures; stipe 1–3 mm long, slender; edge of margin rounded to somewhat keeled; angle between lobes 45–180°; blackish; lobes laterally not flattened, valves 5–11 mm high by 5–17 mm long; endocarp pale brown. *Seed* orbicular to ellipsoid to ovoid, laterally not to slightly flattened, 7.5–11 by 4–7.5 mm, dark brown; arilloid covering seed 3/4 to completely, lobed, inside not folded towards base, thick towards base, coriaceous, consisting of 2 layers, outer layer thin, soft, pale yellow, inner layer thick, firm, chocolate; hilum elliptic, 1.4–2.5 by 1–2 mm; endotesta blackish. *Embryo:* cotyledons obliquely dorsoventrally above each other, equal to unequal, then upper or lower larger, apices not elongated; radicle 0.5–2 mm long, glabrous.

Field notes — Canopy tree 7–30 m, dbh 20–60 cm. Leaflets occasionally opposite. Flowers white. Fruits green.

Distribution — Australia: Queensland, New South Wales.

Habitat & Ecology — In rainforests of floodplains and over ridges. Flowering March, July; fruiting June–Nov.

Specimens studied — AUSTRALIA. Queensland: 73 specimens; New South Wales: 28 specimens.

FIGURE 5.20. *Arytera divaricata* F. Muell. Distribution map.

A11 - Arytera foveolata F. Muell. — Fig. 5.21, 5.22

Arytera foveolata F. Muell., Trans. Phil. Inst. Vict. 3 (1859) 24; Radlk. Sapind. Holl.-Ind. (1879) 44; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 553; in Engl., Pflanzenr. 98 (1933) 1279; S.T. Reynolds, Fl. Austr. 25 (1985) 92; Austrobaileya 2 (1985) 163. — *Nephelium foveolatum* F. Muell. ex Benth., Fl. Austr. 1 (1863) 466. — Type: *Hill & Mueller s.n.* (holo K), Moreton Bay, Australia.

Euphoria leichhardtii var. *hebepetala* Benth., Fl. Austr. 1 (1863) 468. — *Arytera leichhardtii* var. *hebepetala* Radlk., Sapind. Holl.-Ind. (1879) 44; in Engl., Pflanzenr. 98 (1933) 1280. — Type: *Leichhardt s.n.* (holo K; iso M, MEL sheet nos. 74655, 74656), Nurrum Nurrum, Australia.

Arytera leichhardtii auct. non (Benth.) Radlk.: Radlk., Sapind. Holl.-Ind. (1879) 44; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 553; in Engl., Pflanzenr. 98 (1933) 1280 (see note 1).

Tree or *shrub*. *Indument* of long, crispate, patent hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, crispate-hirsute when young; flowering twigs 1.5–5 mm thick. *Leaves* (1-) 2- or 3-jugate; petiole 1.3–6.2 cm long, lenticels present abaxially; rachis 0.9–5.5 cm long, hemiterete, not to slightly winged, crispate-hirsute, glabrescent. *Leaflets* opposite to alternate, petioluled; petiolules pulvini only, 2–6 mm long, slightly to distinctly 1-grooved, lenticels present abaxially; blade ovate to elliptic, 3.2–10.7 by 1.7–4 cm, index 1.6–3.2, not falcate, coriaceous to very coriaceous, not to sparsely punctate; base attenuate to acute, symmetric to oblique, then acroscopic side broader; margin slightly repand to dentate, flat to slightly undulating, not revolute; apex rounded to cuspidate, very apex retuse to acute, sometimes mucronulate; upper surface glabrous; lower surface crispate-hirsute especially along midrib, colour same to slightly lighter than that of upper surface, domatia pockets to sacs opening in front;

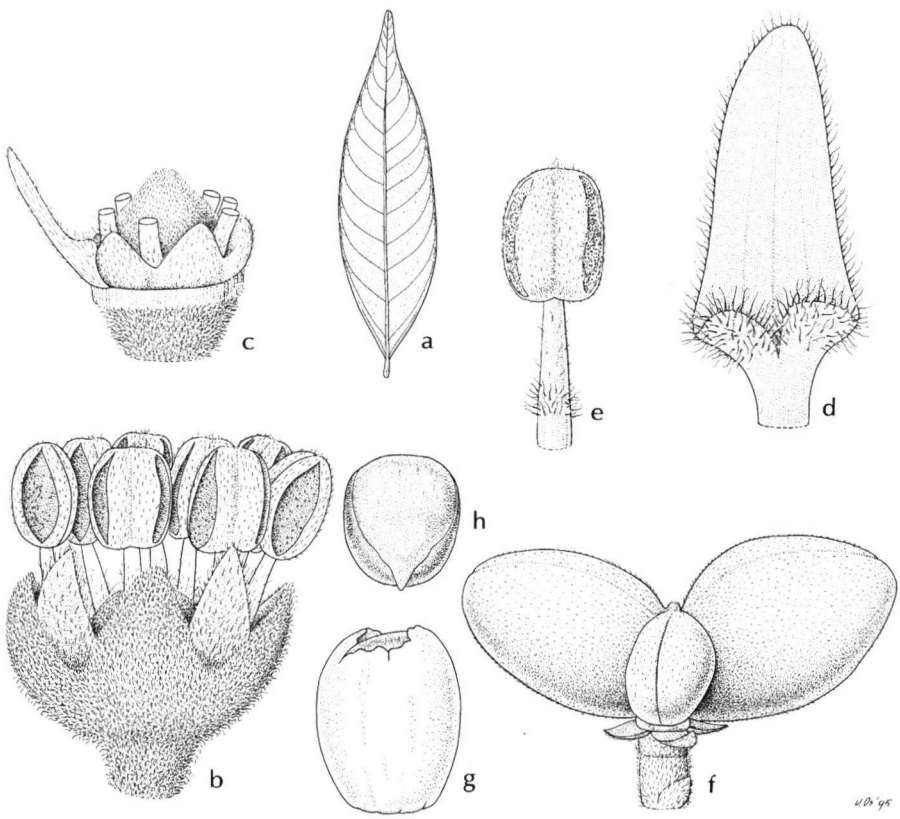

FIGURE 5.21. *Arytera foveolata* F. Muell. (a) Leaflet, × 0.5; (b) flower, × 12.5; (c) dissected flower showing disc, × 12.5; (d) petal, × 25; (e) stamen, × 12.5; (f) fruit, × 3; (g) seed with arilloid, × 3; (h) embryo, × 3. (a–e: *Lam 7673*; f–h: *Bird s. n.*, 24 Jan. 1982.)

venation on upper surface flat, colour same as to slightly lighter than lamina, on lower surface raised; nerves 2.5–12 mm apart, marginally open; veins somewhat densely reticulate, scalariform, distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis (and in axil); rachis terete, 1.5–14 cm long, crispate-sericeous to -hirsute when young; first-order branches up to 7 cm long; cymules dichasial to monochasial, 1–3-flowered. *Bracts* and *bracteoles* triangular to ovate, margin entire, abaxially crispate-hirsute, adaxially (sub)glabrous; bracts 1–2 mm long; bracteoles 0.5–1 mm long. *Pedicels* 0.5–1 mm long, elongating up to 2.5 mm in fruit, crispate-hirsute. *Flowers* 2–3 mm diam. *Calyx* 1.6–2.2 mm high, teeth 1.5–2 mm high, not punctate, triangular to ovate, margin entire, not membranaceous, apex acute; outside crispate-hirsute, inside glabrous. *Petals* 5, rhomboid to ovate, 0.5–2 by 0.3–1 mm, index 1.3–3, not punctate; claw 0.2–0.4 mm long, margin entire, apex acute; blade gradually decurrent into claw, outside pilose, inside subglabrous to subpilose, margin pilose; scales 0.3–0.6 mm long, free, basally sometimes auricled, apex broadened, membranaceous margin absent. *Disc* not lobed, pilose. *Stamens* (male) 8 (9); filament 1.2–2.5 mm long, pilose; anther 1.1–1.7 mm long, slightly curved inward, pilose; connective not protruding. *Pistil* (female): ovary 3-locular, 1–2.2 mm long, puberulous; style and stigma 1 mm long, elongating up to 3.5 mm in fruit, not lobed, in fruit upper c. 3.5 mm stigmatic. *Fruit* slightly obcordate, with 1–3 well-developed lobes, 0.7–1 cm high by 1.2–1.6 cm broad, axil not thickened transversely, outside rather densely crispate-puberulous, smooth, inside glabrous; stipe up to 1 mm long, broadly cuneate; edge of margin grooved; angle between lobes c. 120°; light to dark brown; lobes laterally not flattened, valves 4–8 mm high by 7–10 mm long; endocarp pale brown. *Seed* ellipsoid to obovoid, laterally not flattened, 5–9 by 3.5–5 mm, dull brown; arilloid covering seed 2/3 to completely, lobed, inside not folded towards base, thick towards base, coriaceous, consisting of 2 layers, outer layer thin, soft, pale yellow, inner layer thick, firm, chocolate-brown; hilum orbicular to elliptic, c. 2 by 1.5–2 mm; endotesta brown. *Embryo:* cotyledons obliquely dorsoventrally above each other, unequal, upper larger, apices not elongated; radicle 0.5–1 mm long, glabrous.

Field notes — Tree or large shrub 6–10 m high, openly branched, not with dense canopy. Flowers pale yellow. Fruit orange.

Distribution — Australia: Queensland, New South Wales.

Habitat & Ecology — In depauperate rainforest, dry forest, and Araucarian vine scrub with *Croton insularis*, *Cupaniopsis serrata* var. *tomentella*, *Acacia maideni* and *Cassia tomentella*. On basalt hills and steep hillside slopes, on shallow loams over stony clays, or on colluvial scree. Altitude 100–600 m. Flowering Aug.–Oct.; fruiting Oct.–Dec.

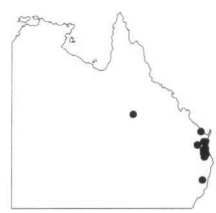

FIGURE 5.22. *Arytera foveolata* F. Muell. Distribution map.

Notes — (1) When Radlkofer transferred *Euphoria leichhardtii* Benth. tentatively to *Arytera*, the material he had available was in his own words insufficient to be certain of its place within the latter genus. As Reynolds has argued (Austrobaileya 1 [1983] 496), he probably only saw material of var. *hebepetala*, as is borne out by his description in 1933: "germen 3-lobum" (*Dimocarpus leichhardtii* [Benth.] S.T. Reynolds always has two-lobed ovaries). Therefore

A. leichhardtii Radlk. is to be regarded as a misapplied name. (See also under Excluded species: *Arytera leichhardtii*.)

Specimens studied — AUSTRALIA. Queensland: 18 specimens; New South Wales: *W.T. Jones C243*.

A12 - Arytera gracilipes Radlk. — Fig. 5.23, 5.24

Arytera gracilipes Radlk., Fedde Rep. 20 (1924) 38; in Engl., Pflanzenr. 98 (1933) 1286; Guillaumin, Fl. Nouv.-Caléd. (1948) 201. — Lectotype (here designated): *Vieillard 2403* (holo K; iso M, P), Montagnes de Pouenloitch près Gatope, 1861–67.

Tree or *shrub*. *Indument* of short, straight, patent hairs; few caducous glandular scales present on vegetative parts, inflorescence, pedicels, abaxial side of calyx, pistil, and fruit; buds 'varnished.' *Branchlets* smooth, glabrous when young; flowering twigs 2–5 mm thick. *Leaves* (1–)2–4-jugate; petiole 1.7–7.2 cm long, lenticels absent abaxially; rachis 1.5–12 cm long, hemiterete, (sub)glabrous. *Leaflets* (sub)opposite to alternate, petioluled; petiolules 3–16 mm long, not to slightly 2-grooved, lenticels usually absent; blade slightly ovate to elliptic to slightly obovate, 3.3–11.7 by 1.1–3.9 cm, index 2–4.2, not to slightly falcate, coriaceous, punctate; base acute to slightly attenuate, symmetric to (slightly) oblique, then basiscopic (or acroscopic) side broader; margin entire, flat to slightly undulating, revolute; apex (retuse to) obtuse to acuminate, very apex (retuse to) obtuse, not mucronulate; upper surface glabrous; lower surface glabrous, colour same as to distinctly different from that of upper surface, domatia absent; venation on upper surface flat, midrib flat to slightly raised, colour same as lamina, midrib same to straw to reddish brown, on lower surface flat to slightly raised, midrib raised; nerves 3–18 mm apart, marginally open basally, looped apically; veins densely to laxly reticulate, usually not distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis; rachis flattened, (1–)3.2–18 cm long, tomentose when young;

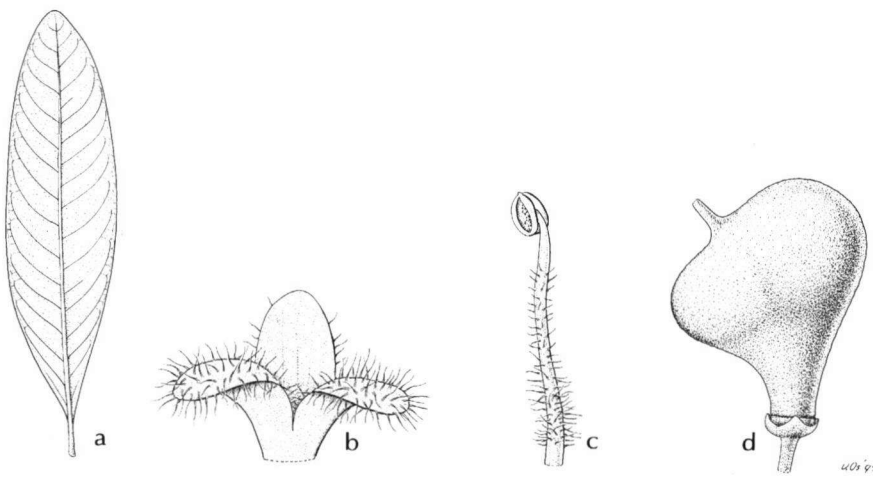

FIGURE 5.23. *Arytera gracilipes* Radlk. (a) Leaflet, × 0.5; (b) petal, × 25; (c) stamen, × 12.5; (d) fruit, × 3. (a–c: *MacKee 38028*; d: *MacKee 33345*.)

first-order branches up to 7.5 cm long; cymules dichasial, 1–6-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially (sub)glabrous to subtomentose, adaxially glabrous; bracts 0.3–1 mm long; bracteoles minute. *Pedicels* 0.5–1.5 mm long, elongating up to 3 mm in fruit, (sub)tomentose to (sub)puberulous. *Flowers* 1.5–2.5 mm diam. *Calyx* 0.7–1.1 mm high, teeth 0.5–1 mm high, sometimes punctate, triangular to approx. elliptic, margin entire, subpuberulous basally, not membranaceous, apex obtuse; outside (sub)glabrous, inside glabrous. *Petals* 5, elliptic to (ob)ovate, 0.5–1.2 by 0.3–0.7 mm, index 1.2–2.3, not punctate; claw up to 0.3 mm long, margin entire, apex rounded to obtuse; blade gradually decurrent into claw, outside and inside subglabrous to subpilose basally, margin pilose; scales 0.6–1.1 mm long, free, basally not auricled, apex broadened, membranaceous margin indistinct. *Disc* not lobed, glabrous. *Stamens* (male) (7) 8 (9); filament 1.5–2.5 mm long, pilose; anther 0.3–0.5 mm long, straight, glabrous; connective not protruding. *Pistil* (female): ovary 2-locular, 1.3–1.4 mm long, sericeous; style and stigma c. 1.3 mm long, elongating up to 3 mm in fruit, not lobed but with two stigmatic lines, in fruit sometimes 2-lobed, in fruit upper 0.3–0.7 mm stigmatic. *Fruit* obovoid, with 1 or 2 well-developed lobes, 0.9–1.4 cm high by 0.8–1.2 cm broad, axil thickened transversely, outside subglabrous, smooth to slightly rugose, inside densely crispately pilose; stipe up to 3 mm long, broadly cuneate; edge of margin rounded to sharp; angle between lobes c. 180°; blackish brown; lobes laterally not to slightly flattened, valves 7–13 mm high by 4–6 mm long; endocarp (pale) brown. *Seed* ellipsoid to obovoid, laterally not flattened, 7–10 by 3.5–6 mm, blackish; arilloid covering seed 3/4 to completely, lobed, inside not folded towards base, thin, membranaceous, consisting of 1 layer, soft, yellow; hilum triangular, 2–3 by 2–2.5 mm; endotesta pale brown. *Embryo:* cotyledons dorsoventrally above each other, unequal, upper larger, apices not elongated; radicle 2.5–3.5 mm long, glabrous.

Field notes — Tree or shrub 1.5–10 m high, c. 30 cm dbh. Bark brown, almost smooth. Leaves shiny dark green, sometimes darker above. Flower buds light brown, flowers white, slightly fragrant. Fruit brown; arilloid yellow.

Distribution — New Caledonia.

Habitat & Ecology — Gallery forest and thickets on (rocky) serpentinic terrain, sometimes along streams. Paraforestière formation on alluvium. Altitude sea level to 600 m. Flowering Feb.–Apr.; fruiting Apr.–Nov.

Note — *Jaffré 1131* contains several 3-locular fruits.

Specimens studied — NEW CALEDONIA: 29 specimens.

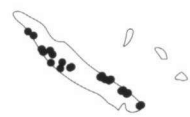

FIGURE 5.24. *Arytera gracilipes* Radlk. Distribution map.

A13 - Arytera lepidota Radlk. — Fig. 5.25, 5.26

Arytera lepidota Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 555; in Engl., Pflanzenr. 98 (1933) 1285; Guillaumin, Fl. Nouv.-Caléd. (1948) 201. — Lectotype (here designated): *Pancher "Mus. Neocal." 222* (holo P; iso K, M, NY), Mont Dore, New Caledonia.

Tree. Indument of short, straight, patent hairs; glandular scales present on vegetative parts, inflorescence, pedicels, abaxial side of calyx, pistil, and fruit; buds 'varnished.' *Branchlets* smooth, glabrous when young; flowering twigs 2–5 mm thick. *Leaves* (1–)

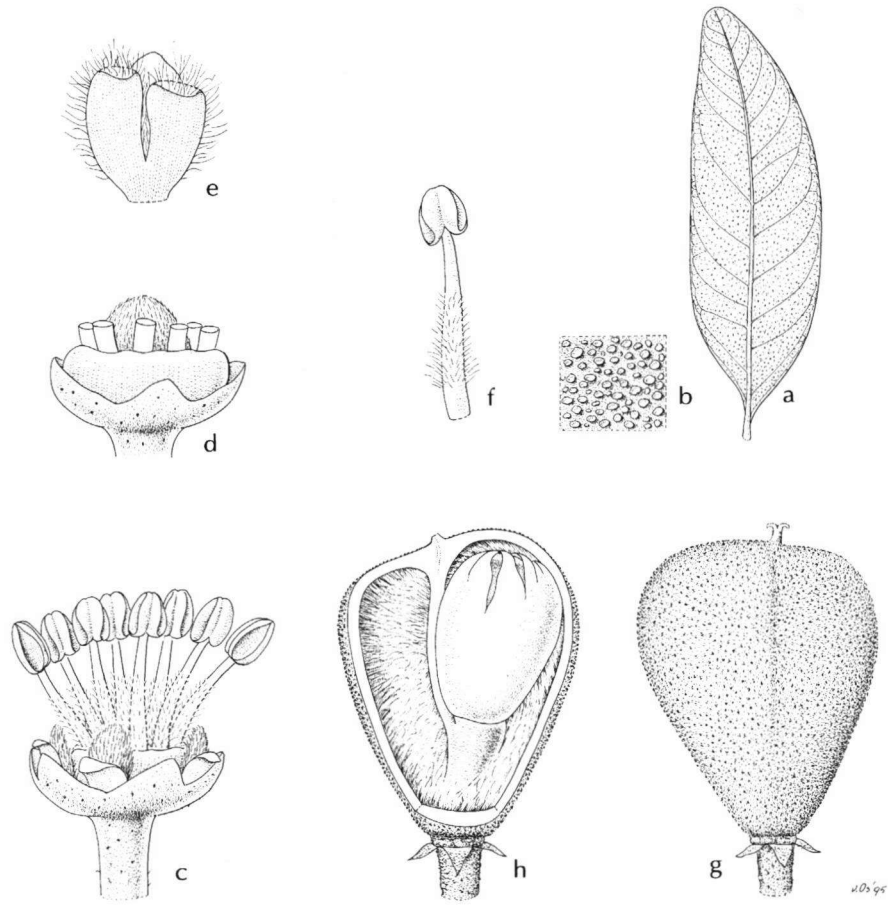

FIGURE 5.25. *Arytera lepidota* Radlk. (a) Leaflet, × 0.5; (b) detail of glandular scales on leaflet, × 25; (c) flower, × 12.5; (d) dissected flower showing disc; (e) petal, × 25; (f) stamen, × 12.5; (g) fruit, × 3; (h) partly dissected fruit showing hairy inside, and seed with arilloid, × 3. (a, b, g, h: *McPherson 2338*; c–f: *McPherson 5667*.)

2–6-jugate; petiole 2–7.8 cm long, few lenticels absent abaxially; rachis 1-19.5 cm long, hemiterete, (sub)glabrous to (sub)tomentose when young. *Leaflets* (sub)opposite to alternate, petioluled; petiolules 4–20 mm long, not to slightly 2-grooved, lenticels absent abaxially; blade ovate to elliptic, 4.1–14 by 1.7–5.3 cm, index 1.8–3.3(–4.8), usually not falcate, (very) coriaceous, not punctate; base (slightly) attenuate, symmetric to slightly oblique, then usually basiscopic side broader; margin entire, flat to slightly undulating, revolute; apex (retuse to) rounded to slightly acuminate, very apex rounded to obtuse, not mucronulate; both surfaces glabrous, lower colour different from that of upper surface, domatia absent; venation on upper surface flat to slightly sunken, midrib

flat to slightly raised, colour same as to somewhat darker than lamina, especially midrib, on lower surface raised; nerves 3–20 mm apart, marginally open basally, looped towards tip; veins laxly reticulate, not distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis; rachis (slightly) flattened (to terete), 7.5–21.2 cm long, tomentose to puberulous when young; first-order branches up to 10.7 cm long; cymules dichasial, 1–7-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially subglabrous, adaxially glabrous; bracts 0.3–1.2 mm long; bracteoles minute. *Pedicels* 1–2 mm long, in fruit elongating up to 2–4 mm, tomentose to puberulous. *Flowers* 1.8–2.2 mm diam. *Calyx* 0.7–1.2 mm high, teeth 0.5–0.9 mm high, triangular, not punctate, margin entire, not membranaceous, apex acute to obtuse; outside glabrous to puberulous, inside (sub)glabrous. *Petals* 5, shape elliptic to obovate, 0.7–1.1 by 0.3–0.7 mm, index 1.3–2.7, not punctate; claw 0.1–0.2 mm long, margin denticulate near tip, apex rounded to obtuse; blade gradually decurrent into claw, outside subpilose, inside subpilose, margin pilose; scales 0.4–1 mm long, almost free, basally not auricled, apex broadened. *Disc* not lobed, glabrous. *Stamens* (male) 7 or 8; filament 1.5–2.8 mm long, basally pilose; anther 0.3–0.6 mm long, straight, glabrous; connective not protruding. *Pistil* (female): ovary 2-locular, 1.3 mm long, sericeous; style and stigma elongating up to 0.8–1.2 mm in fruit, 2-lobed, in fruit upper 0.2–0.3 mm stigmatic. *Fruit* approx. obovoid, with 1 or 2 well-developed lobes, 1.1–1.6 cm high by 0.9–1.2 cm broad, axil thickened transversely, outside (sub)glabrous, smooth, inside crispately pilose, hairs rust-red to pale yellow; stipe 1–3 mm long, broadly cuneate; edge of margin rounded; angle between lobes c. 180°; dull brown to blackish brown; lobes laterally not flattened, valves 7–15 mm high by 5–6.5 mm long; endocarp pale brown. *Seed* ellipsoid to obovoid, laterally not flattened, 8–10.5 by 5–7 mm, dark brown to black; arilloid covering seed completely, lobed, inside not folded towards base, thin, membranaceous, consisting of 1 layer, soft, pale yellow; hilum elliptic to circular, 2–3 by 1.7–3 mm; endotesta pale brown. *Embryo:* cotyledons dorsoventrally above each other, unequal, upper larger, apices not elongated; radicle 2.5–3 mm long, glabrous.

Field notes — Tree, rarely shrub, 3–16 m high, 30 cm dbh. Bark bright brown, sometimes with grey blotches, smooth. Leaves bright shiny (dark) green above, bright to pale greyish green to brown beneath; young leaves brown beneath. Flowers white; filaments white. Fruit brown.

Distribution — New Caledonia: SE end of main island.

Habitat & Ecology — In moist forest and gallery forest on serpentine and serpentine-derived alluvium, on slopes and valley floors. Altitude 10–850 m. Flowering Jan.–Apr., Sep.; fruiting Apr.–Sep.

Notes — In one specimen (*Suprin 659*, NOU) a three-lobed fruit was observed.

Specimens studied — NEW CALEDONIA: 19 specimens.

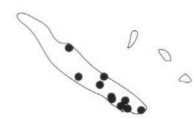

FIGURE 5.26. *Arytera lepidota* Radlk. Distribution map.

A14 - Arytera lineosquamulata H. Turner — Fig. 5.27, 5.28

Arytera lineosquamulata H. Turner, Blumea 38 (1993) 138; Fl. Males. I, 11 (3) (1994) 473. — Type: *Carr 14969* (holo L; iso NY, A), Boridi, Papua New Guinea, 15 Nov. 1935.

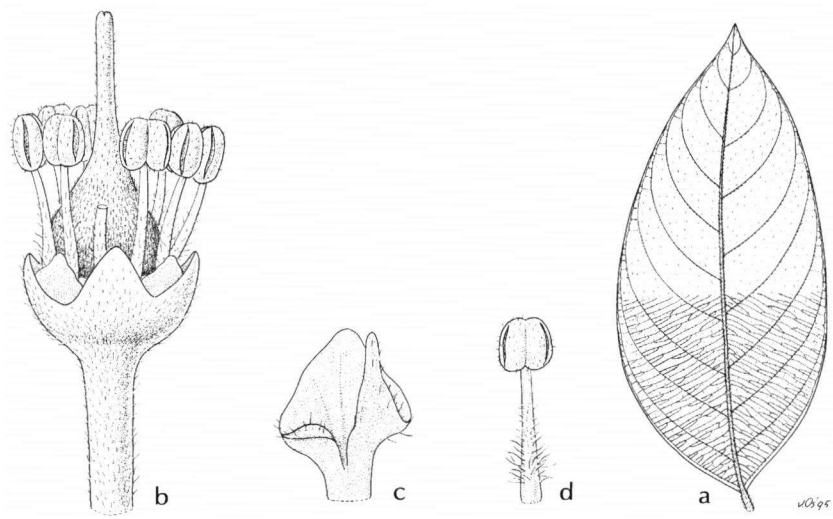

FIGURE 5.27. *Arytera lineosquamulata* H. Turner. (a) Leaflet, lower part with detail of tertiary venation pattern, × 0.5; (b) flower, × 25; (c) petal, × 25; (d) stamen, × 12.5. (a–d: *Carr 14969*.)

Tree. *Indument* of long, crispate, patent hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, densely crispate-hirsute when young; flowering twigs 2–3 mm thick. *Leaves* 1- or 2-jugate; petiole 2–6 cm long, lenticels present abaxially; rachis 1.5–3.5 cm long, terete, densely crispate-hirsute. *Leaflets* opposite to subopposite, petioluled; petiolules pulvini only, 5–8 mm long, 1-grooved, lenticels present abaxially; blade ovate to elliptic, 6.7–16.2 by 2.8–6 cm, index 2.2–2.8, not falcate, chartaceous to coriaceous, not punctate; base slightly attenuate to acute, symmetric; margin entire to slightly repand, flat, not revolute; apex acuminate, very apex obtuse to rounded, not mucronulate; upper surface glabrous; lower surface glabrous to sparsely crispate-hirsute, more so on venation, colour slightly different from that of upper surface (brown), domatia small pockets to sacs opening in front; venation on upper surface flat, midrib slightly raised, colour reddish, on lower surface raised; nerves 7–15 mm apart, marginally open; veins scalariform, laxly reticulate, distinct. *Inflorescences* axillary to pseudoterminal to ramiflorous on young branches, branching in axil and along rachis; rachis terete, 5.5–15 cm long, densely crispate-hirsute when young; first-order branches up to 8 cm long; cymules dichasial to monochasial, 1–4-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially densely crispate-hirsute, adaxially subglabrous; bracts 0.3–1 mm long; bracteoles 0.1–0.3 mm long. *Pedicels* 1–2 mm long, densely crispate-hirsute. *Flowers* 1.5–3 mm diam. *Calyx* 5- (or 6-)dentate, 0.9–1.2 mm high, teeth 0.5–0.9 mm high, triangular to ovate, not punctate, margin entire, apex acute to somewhat obtuse; outside densely crispate-hirsute, inside (sub)glabrous. *Petals* 2–5, often more or less reduced, obovate to ovate to suborbicular, 0.3–1 by 0.2–0.7 mm, index 1–2.5, not punctate; claw 0.2–0.3 mm long, margin entire, apex obtuse to acute; blade abruptly to gradually decurrent into claw, outside (sub)glabrous, inside glabrous, margin (sub)pilose; scales almost linear, often one or both reduced, 0.3–0.8 mm long,

approx. free, basally sometimes auricled, apex often forked, not broadened, sparsely pilose. *Disc* not lobed, pilose on rim. *Stamens* (female) 7 or 8; filament 0.7–1.5 mm long, pilose; anther 0.5–0.7 mm long, straight, pilose; connective not protruding. *Pistil* (female): ovary 2-(or 3-)locular, 1 mm long, puberulous; style and stigma 1.7–2 mm long, twisted, upper 0.7–1 mm stigmatic. *Fruit* not observed.

Field notes — Tree c. 12 m high. Flowers greenish.

Distribution — Papua New Guinea: Central Province; Australia: N Queensland.

Habitat & Ecology — Secondary forest and semi-deciduous mesophyll vine forest, on alluvial soils derived from a mixture of acid and basic rocks. Altitude c. 1000 m. Flowering Nov.

Specimens studied — PAPUA NEW GUINEA. Central Province: *Carr 14969*. — AUSTRALIA. Queensland: *Webb & Tracey 13258*.

FIGURE 5.28. *Arytera lineosquamulata* H. Turner. Distribution map.

A15 - Arytera litoralis Blume — Fig. 5.29, 5.30

Arytera litoralis Blume, Rumphia 3 (1849) 170; Miq., Fl. Ind. Bat. 1, 2 (1859) 568; Radlk., Sapind. Holl.-Ind. (1879) 12, 45, 91; Koord., Exk. Fl. Java 2 (1912) 545; Merr., Fl. Manila (1912) 304; Ridl., Fl. Mal. Pen. 1 (1922) 507; Radlk. in Engl., Pflanzenr. 98 (1933) 1272; Gagnep., Fl. Gén. Indo-Chine, Suppl. 1 (1950) 982, fig. 125: 1–10; Backer & Bakh. f., Fl. Java 2 (1965) 140; H. Turner, Blumea 38 (1993) 142; Fl. Males. I, 11 (3) (1994) 473. — *Euphoria xerocarpa* Blume, Bijdr. (1825) 234, p.p. (excl. fruits, see note 1). — *Nephelium xerocarpum* Cambess., Mém. Mus. Hist. Nat. Paris 18 (1829) 30. — *Ratonia litoralis* Teijsm. & Binnend., Cat. Hort. Bogor. (1866) 216; Fern.-Villar, Nov. App. (1880) 52 (p.p.). — *Arytera ochracea* Blume ex Koord., Exk. Fl. Java 2 (1912) 542 (in syn.). — [*Arytera litoralis* f. *genuina* Radlk. in Gibbs, J. Linn. Soc. Bot. 42 (1914) 65, nom. inval. (I.C.B.N. [1994] Art. 24.3).] — *Arytera xerocarpa* (Blume) Adelb., Blumea 6 (1948) 324. — Lectotype (H. Turner, 1993: 143): *Blume 1314* (holo L), Nusa Kambangan, Java, Indonesia.

?*Euphoria annularis* Blanco, Fl. Filip. (1837) 285; ed. 2 (1845) 199; ed. 3, 2 (1878) 7; Fern.-Villar, Nov. App. (1880) 52 (in syn.). — ?*Atalaya annularis* Blume, Rumphia 3 (1849) 186; Fern.-Villar, Nov. App. (1880) 52 (in syn.). — Type: not designated.

?*Schmidelia conferta* Blanco, Fl. Filip. ed. 2 (1845) 217; ed. 3, 2 (1878) 41; Merr., Sp. Blanc. (1918) 241 (in syn.). — Neotype: *Merrill Sp. Blanc. 861* (holo PNH†; iso A, BO, L, P, US), Bosabon, Rizal, Luzon, Philippines, 9 March 1915.

[*Sapindus adenophyllus* Wall., Cat. (1847) nr. 8044, nom. nud., nom. inval. (I.C.B.N. [1994] Art. 32.1.c).] — *Cupania adenophylla* Planch. ex Hiern in Hook. f., Fl. Br. Ind. 1 (1865) 677. — *Cupania (Arytera) adenophylla* Kurz, J. As. Soc. Beng. 44 (1875) 188. — *Ratonia adenophylla* Kurz, Pegu Rep. (1875) App. A 38, B 40. —Type: *Wallich 8044* (holo K; iso P), Moulmein, Burma, 1836.

Zygolepis rufescens Turcz., Bull. Soc. Imp. Nat. Mosc. 21 (1848) 709; Miq., Fl. Ind. Bat. 1, 2 (1859) 563. — [*Ratonia zygolepis* Turcz., Bull. Soc. Imp. Nat. Mosc. 36 (1863) 586, nom. illeg. (I.C.B.N. [1994] Art. 52.1).] — *Arytera rufescens* Radlk., Sapind. Holl.-Ind. (1879) 44. — *Ratonia rufescens* Fern.-Villar, Nov. App. (1880) 52. — *Arytera litoralis* f. *rufescens* Radlk. in Gibbs, J. Linn. Soc. Bot. 42 (1914) 65. — Type: *Cuming 1761* (holo MW, n.v.; iso A, BM, K, MO, P), Cebu, Philippines.

Arytera gigantosperma Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 674; in Engl., Pflanzenr. 98 (1933) 1272. — Type: *Beccari s. n.* (holo FI sheet no. 2842; iso M), Abita, ad Ayer Mancior, Padang, Sumatra, Indonesia, Aug. 1878.

Arytera angustifolia Radlk., Sapind. Holl.-Ind. (1879) 44. — *Arytera litoralis* f. *angustifolia* Radlk. in Gibbs, J. Linn. Soc. Bot. 42 (1914) 65. — Type: *Teijsmann s. n.* (holo U), Karimon, Java, Indonesia.

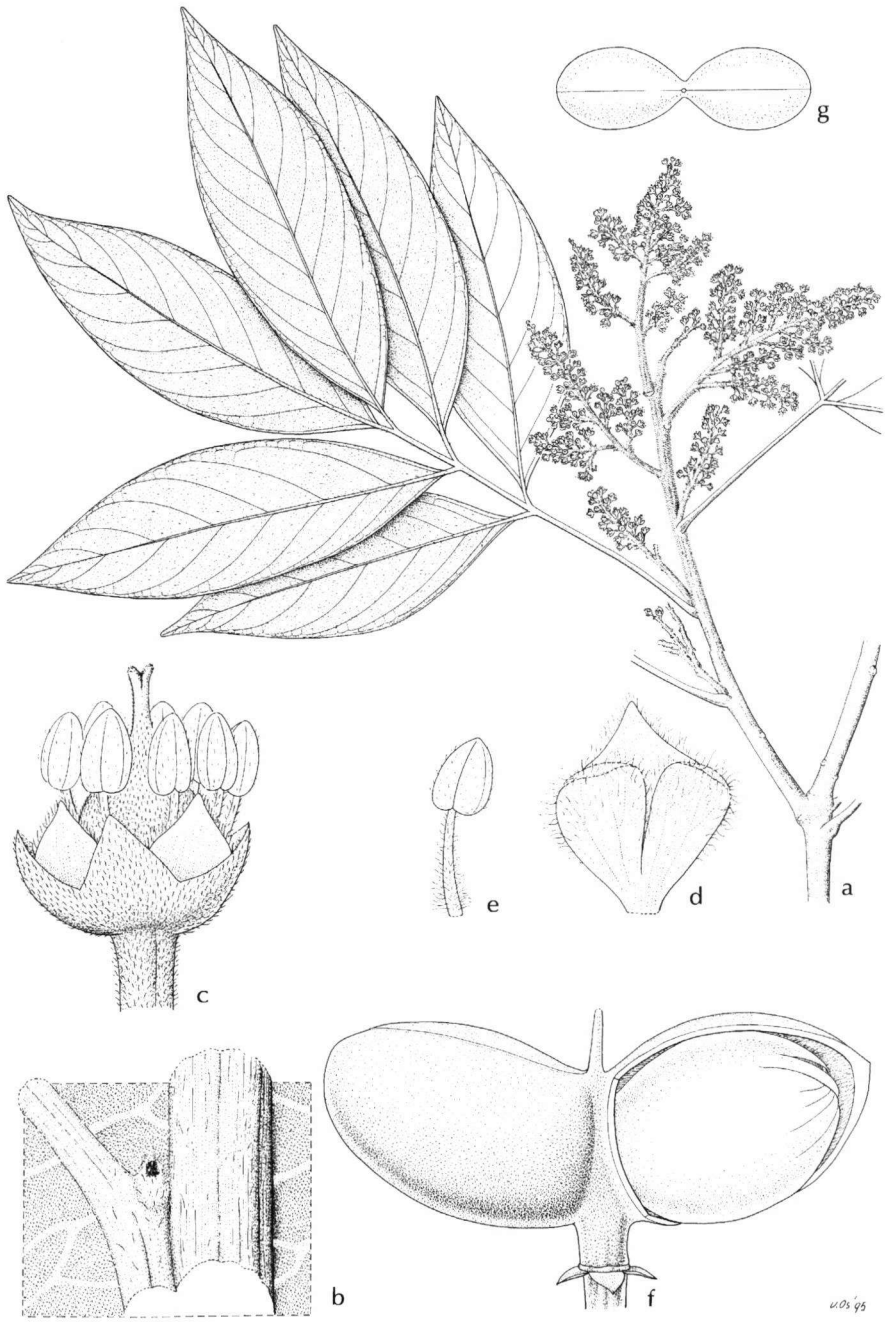

FIGURE 5.29. *Arytera litoralis* Blume. (a) Habit, × 0.5; (b) domatium, × 25; (c) flower, × 25; (d) petal, × 25; (e) stamen, × 12.5; (f) fruit, × 3; (g) schematic top view of fruit, × 1.5. (a–e: *Lambach 1241*; f, g: *SAN 26289*.)

Guioa geminata Lauterb. & K. Schum. in K.Schum. & Lauterb., Fl. Schutzgeb. (1900) 420. — *Arytera geminata* Radlk. in K. Schum. & Lauterb., Nachtr. (1905) 308. — Type: *Lauterbach 2306* (holo B†; iso WRSL), Ssigauu, Papua New Guinea, 11 June 1896.

Arytera litoralis var. *major* King, J. As. Soc. Bengal. 65 (1896) 446. — *Arytera litoralis* f. *major* Radlk. in Gibbs, J. Linn. Soc. Bot. 42 (1914) 66. — Syntypes: *King's collector 695* (holo K; iso P), Gopeng, Malaya, Sep. 1880; *885* (holo K; iso; FI), Sunga Rijak, Malaya, Oct. 1880; *4456* (holo BM?; iso L, P), Gopeng, Malaya, June 1883; *Ridley 1609* (n.v.), Selangor, Malaya; *5995* (n.v.), Singapore; *Scortechini 20* (holo K; iso L), Perak, Malaya; *Wray 3163* (holo CAL, n.v.; iso FI), Perak, Malaya.

[*Arytera litoralis* f. *minor* Radlk. in Gibbs, J. Linn. Soc. Bot. 42 (1914) 66, nom. nud., nom. inval. (I.C.B.N. [1994] Art. 32.1.c).]

Moulinsia cupanioides auct. non Camb.: Camb., Mém. Mus. Hist. Nat. Paris 18 (1829) 40.

Nephelium mutabile auct. non Blume: Miq., Fl. Ind. Bat., Suppl. 1 (1861) 198, 508.

Tree, rarely *shrub*; indument of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth to slightly rough, puberulous when young; flowering twigs 1–7 mm thick. *Leaves* 1–3(–4)-jugate; petiole 1.3–9.5 cm long, lenticels present or absent; rachis 0.8–11.5 cm long, (hemi)terete, glabrous to puberulous when young. *Leaflets* opposite to subopposite, petioluled; petiolules pulvini only, 2–14 mm long, slightly to distinctly 1-grooved, lenticels usually present abaxially; blade ovate to elliptic (to obovate), 4.2–31.1 by 1.4–12 cm, index 1.6–4.5, not falcate, slightly coriaceous to chartaceous, not to densely punctate; base (rounded to) acute to slightly attenuate, sometimes oblique, then acroscopic (or basiscopic) side broader; margin entire to slightly repand, flat to slightly undulating, not revolute; apex acuminate to cuspidate (to retuse or rounded), very apex retuse to rounded, not mucronulate; upper surface glabrous (to puberulous on midrib); lower surface glabrous to puberulous, especially on venation, colour same as to (slightly) different from that of upper surface (brownish), domatia large to small pockets to (often pustular) sacs (to pits), opening in front (or on top), rarely completely absent; venation on upper surface approx. flat, midrib slightly raised, colour same as lamina to reddish brown or yellowish, on lower surface raised; nerves 3–35 mm apart, marginally open, intercalating veins sometimes present; veins (slightly) scalariform to almost reticulate, laxly reticulate, not distinct. *Inflorescences* axillary to pseudoterminal (to ramiflorous), branching along rachis (and in axil or not branching); rachis terete to slightly flattened, 1.5–17 cm long, puberulous when young; first-order branches up to 10 cm long; cymules dichasial (or monochasial), 1–7-flowered. *Bracts* and *bracteoles* triangular to slightly ovate, margin entire, abaxially puberulous, adaxially glabrous; bracts 0.3–1.2 mm long; bracteoles 0.1–0.6 mm long. *Pedicels* 1–5 mm long, elongating up to 10 mm in fruit, puberulous. *Flowers* 1–3.5 mm diam. *Calyx* 0.8–2 mm high, teeth 0.6–1.9 mm high, triangular to ovate, slightly imbricate, rarely punctate, margin entire, not membranaceous, apex acute to acuminate; outside puberulous, inside glabrous. *Petals* (2–)5(–6), triangular to rhomboideal to (ob)ovate, 0.5–2.2 by 0.3–1.9 mm, index 1–2.5, not punctate; claw 0.1–0.4 mm long, margin entire, apex obtuse to acuminate; blade usually gradually decurrent into claw, outside glabrous to pilose, inside (sub)glabrous (to subpilose), margin (sub)pilose; scales 0.2–1.2 mm long, free to basally adnate to margin, basally sometimes slightly auricled, apex broadened, sometimes irregular, slightly to densely pilose. *Disc* not lobed, glabrous to pilose. *Stamens* (male) 6–8(–10); filament 2–4 mm long, pilose; an-

ther 0.7–1.1 mm long, straight, pilose; connective not protruding. *Pistil* (female): ovary 2- (or 3-)locular, 0.6–1 mm long, puberulous, style and stigma 0.4–1.5 mm long, elongating up to 3 mm in fruit, not to slightly 2- (or 3-)lobed, in fruit upper 0.5–2.5 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 (or 3) well-developed lobes, 0.5–2.3 cm high by 0.7–3.6 cm broad, axil not thickened transversely, outside glabrous to subpuberulous, smooth to slightly rugose to verrucose, inside pilose on sutures; stipe up to 3 mm long, slender to broadly cuneate; edge of margin rounded to slightly keeled; angle between lobes c. 180° (c. 120°); blackish to reddish brown; lobes laterally not to slightly flattened, valves 5–21 mm high by 8–23 mm long; endocarp (pale) brown. *Seed* ellipsoid to orbicular, laterally not to slightly flattened, 6–24 by 5–19 mm, dull brown to blackish; arilloid covering seed 1/2 to completely, margin dentate to lobed, inside not to slightly folded towards base, thick towards base, coriaceous, consisting of 2 layers, outer layer thin, soft, yellowish, inner layer thick, firm, chocolate-brown; hilum elliptic, 1.5–7 by 1.5–5.5 mm; endotesta dark brown. *Embryo*: cotyledons dorsoventrally above to almost secondarily laterally beside each other, equal to slightly unequal, upper or lower larger, apices not elongated; radicle 0.5–3 mm long, glabrous.

Field notes — Tree 2–40 m high, 7–91 cm dbh, crown 7.5 m, buttresses up to 1.6 m high, 1.5 m wide, 10 cm thick. Bark smooth or scaly, greyish green to dark reddish to black, not fissured, not peeling; outer bark soft, purplish to brownish; inner bark pale greenish yellow to pale reddish to purplish to slightly brown, soft. Cambium brown to red to light yellow to white. Sapwood yellowish to (reddish) white, hard, surface slightly corrugated (in Papua New Guinea); heartwood brown to red to white. Young branches and petiole reddish. Leaves pale or dark green, glossy above. Flower buds yellowish; flower pale yellow to white green, once (*Kostermans & Wirawan 316*) reported as fragrant; anthers yellow. Fruit yellow to red; arilloid red; seed coat black.

Distribution — From India (Bay of Bengal) across Southeast Asia up to South China (Hainan), throughout Malesia up to the Solomon Islands.

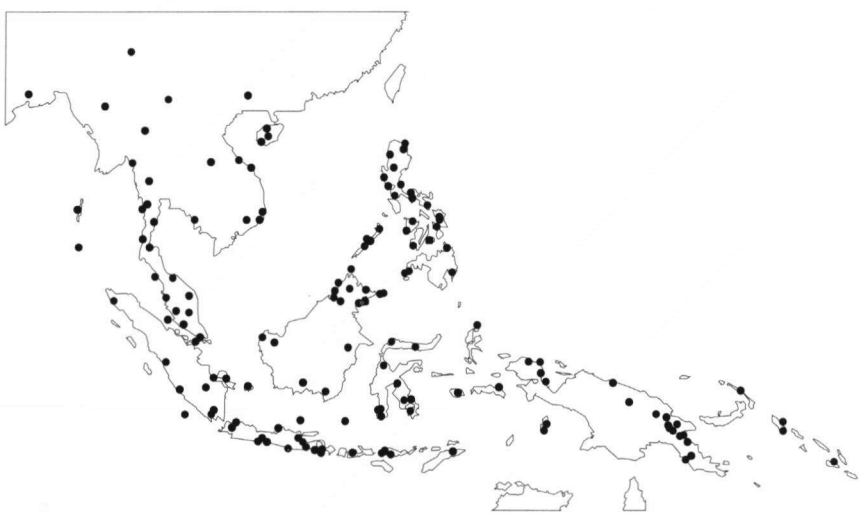

FIGURE 5.30. *Arytera litoralis* Blume. Distribution map.

Habitat & Ecology — In secondary and (disturbed) primary forests, on many different substrates. Altitude sea level to c. 1500 m. Flowering and fruiting throughout the year.

Vernacular names — *Malesia:* Rerak boesa. *Borneo:* Anging manuk (Kad. pa); Ampungit (Murut); Bangkor-bangkor (MuB); Mendjanganan; Nunuk-nunuk; Petinag (Sungei-Kinabatangan). *Sumatra:* Kajoe soegi; Oerat roesa; Pening-pening ramboetan; Ramboetan oetan; Toekoe biawa. *Bali:* Kajoe sampi. *Sumba:* Wihi koerang; Lindi kelaoe. *Timor:* Tie gotok (Buneq); Kai nato (Uindigui). *Flores:* Ndéér; Ndéér wina. *Irian Jaya:* Konggro (Sentani); Lowkwa (Manikiong); Bepan (Hattam); Fatjenie (Kebar). *Papua New Guinea:* Neiulei (Upper Waria).

Notes — (1) For a discussion of the synonymy of *Arytera litoralis*, see Turner (1993).

(2) In *SAN 33812* the scales of the petals appeared fused.

(3) This is an extremely variable species, which cannot, however, be divided into smaller entities, because intermediates between forms with different characters (such as sac-like, pustular domatia vs. pockets or pits; disc glabrous vs. pilose; leaflets punctate or not) can always be found; moreover, the different characters occur in different combinations. On the Lesser Sunda Islands east of Lombok and in New Guinea, however, a trend can be distinguished towards generally 2-jugate leaves with smaller domatia, and more reticulate (less scalariform) veins; also, the disc is usually rather densely pilose and the abaxial side of the leaflets often has a denser indument on the venation than in other areas. Here too, though, these characters are not consistent and more 'typical' forms also occur. Collections from Irian Jaya are reported to be buttressed.

(4) Rarely (e. g. *NGF 5238, 15418, 29771*) the fruits are almost completely pilose inside, with only a glabrous patch near the centre of the valves. These specimens have sometimes been identified as *A. brachyphylla*, from which they can be distinguished, however, by their abaxially prominent lateral veins and less oblong leaflets.

Specimens studied — INDIA: 10 specimens. — BURMA: 12 specimens. — THAILAND: 14 specimens. — CHINA: 39 specimens. — LAOS: 3 specimens. — CAMBODIA. 3 specimens. — VIETNAM: 29 specimens. — MALAYSIA. Malaya: 29 specimens; Sabah: 53 specimens. — SINGAPORE: 1 specimen. — PHILIPPINES: 98 specimens. — INDONESIA. Sumatra: 18 specimens; Borneo: 12 specimens; Java: 95 specimens; Sulawesi: 28 specimens; Lesser Sunda Islands: 24 specimens; Moluccas: 9 specimens; Irian Jaya: 12 specimens. — PAPUA NEW GUINEA: 21 specimens. — SOLOMON ISLANDS: 3 specimens.

A16 - Arytera microphylla (Benth.) Radlk. — Fig. 5.31, 5.32

Arytera microphylla (Benth.) Radlk., Sapind. Holl.-Ind. (1879) 44; Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9 (1879) 553; in Engl., Pflanzenr. 98 (1933) 1281; S.T. Reynolds, Fl. Austr. 25 (1985) 91; Austrobaileya 2 (1985) 161. — *Nephelium microphyllum* Benth., Fl. Austr. 1 (1863) 468. — Type: *Bidwill s. n.* (holo K; iso M, MEL), Wide Bay, Australia.

Tree or *shrub. Indument* on vegetative parts short, straight, patent, on reproductive parts longer, straight, appressed; glandular scales absent; buds not 'varnished.' *Branchlets* approx. smooth, puberulous to sericeous when young; flowering twigs 1–3 mm thick. *Leaves* 1- (or 2-)jugate; petiole 0.1–3 cm long, puberulous to tomentose, flattened, lenticels present abaxially. *Leaflets* opposite, sessile to subsessile; petiolules pulvini only, up to 2 mm long, not grooved, lenticels present abaxially; blade elliptic to obovate, 0.9–5.9 by 0.4–2.9 cm, index 1.6–2.7, not falcate, coriaceous, not punctate; base

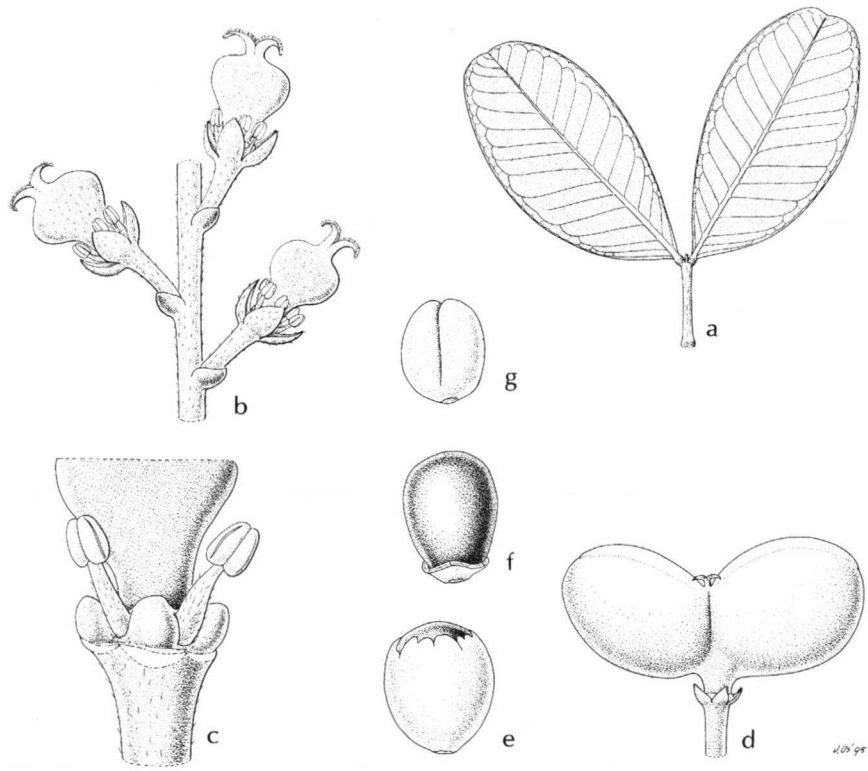

FIGURE 5.31. *Arytera microphylla* (Benth.) Radlk. (a) Leaf, × 1; (b) solitary female flowers with very young fruit, × 6; (c) dissected flower showing disc, × 12.5; (d) fruit, × 3; (e) seed with arilloid, × 3; (f) seed with the arilloid removed, × 3; (g) embryo, × 3. (a–c: *Randall & Young 630*; d–g: *Weston & Richards 1481*.)

attenuate, symmetric to slightly oblique, then acro- or basiscopic side broader; margin entire to slightly serrate near tip, flat to slightly undulating, not revolute; apex retuse to acute, not mucronulate; both surfaces glabrous, lower colour approx. same as that of upper surface, domatia absent; venation flat, midrib slightly raised, on upper surface colour same as lamina; nerves 1.5–6 mm apart, marginally looped; veins laxly reticulate, not distinct. *Inflorescences* axillary to pseudoterminal, branching in axil (and along rachis); rachis terete to flattened, 1–10 cm long, puberulous when young; first-order branches up to 2 cm long; cymules two-flowered basally, flowers solitary toward the apex. *Bracts* triangular, adaxially glabrous, abaxially puberulous; bracts 0.5–1 mm long; bracteoles absent. *Pedicels* 1–1.5 mm long, elongating up to 3 mm in fruit, (sub)puberulous to glabrescent. *Flowers* c. 2.5 mm diam. *Calyx* 5- (or 6-)dentate, 0.7–1.2 mm high, teeth 0.6–1.1 mm high, triangular to ovate, not punctate, margin entire, apex acute to acuminate; outside puberulous, inside (sub)glabrous. *Petals* usually absent, rarely 1 or 2 sepaloid petals present. *Disc* 5- or 6-lobed, glabrous. *Stamens* (male) 5 or 6; filament 1–2 mm long, pilose; anther 0.3–0.4 mm long, straight, pilose; connective

not protruding. *Pistil* (female): ovary 2- (or 3-)locular, c. 0.5 mm long, subglabrous; style and stigma c. 0.5 mm long, elongating up to 1–1.5 mm in fruit, 2-lobed, in fruit lobes recurved, upper 0.8–1.2 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 0.6–1.3 cm high by 0.7–1.4 cm broad, axil not thickened transversely, outside subglabrous, approx. smooth to slightly verrucose, inside velutinous to pilose; stipe 1–3 mm long, slender to broadly cuneate; edge of margin grooved to rounded; angle between lobes c. 180°; dark brown to blackish; lobes laterally not flattened, valves 4–8 mm high by 6–10 mm long; endocarp light yellowish brown. *Seed* ellipsoid, laterally not flattened, 6–7.5 by 5–6 mm, dark brown; arilloid covering seed 3/4 to completely, lobed, inside not folded towards base, thin, fleshy, membranaceous, consisting of 1 layer, drab yellow; hilum elliptic to orbicular, 1.3–1.5 by 1–1.4 mm; endotesta pale brown. *Embryo:* cotyledons secondarily laterally beside each other, equal, apices not elongated; radicle 0.5–0.8 mm long, glabrous.

Field notes — Small tree or shrub 2.5–5.5 m high. Fruits orange. Seeds brown with red arilloid.

Distribution — Australia: Queensland, Wide Bay and Burnett districts.

Habitat & Ecology — In microphyll vine thicket, depauperate rainforest remnants, and along roadsides. On alluvial soils, basalt and dark brown loam. Altitude 280–460 m. Flowering Aug.; fruiting Sep.–Jan.

Note — Occasionally 2-jugate leaves and 3-locular ovaries can be found.

Specimens studied — AUSTRALIA. Queensland: 12 specimens.

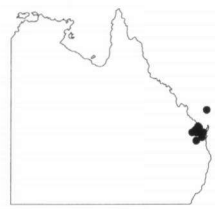

FIGURE 5.32. *Arytera microphylla* (Benth.) Radlk. Distribution map.

A17 - Arytera miniata H. Turner — Fig. 5.33, 5.34

Arytera miniata H. Turner, Blumea 38 (1993) 138; Fl. Males. I, 11 (3) (1994) 475. — Type: *Carr 11554* (holo L; iso A, CANB, K), Kanosia, Papua New Guinea, 28 Feb. 1935.

Tree or *shrub*. *Indument* of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth to somewhat rough, puberulous when young; flowering twigs 1.5–2 mm thick. *Leaves* 1- or 2-jugate; petiole 1–5 cm long, lenticels often present abaxially; rachis 1.5–3.5 cm long, terete to hemiterete, sometimes with a slight to distinct longitudinal ridge, puberulous. *Leaflets* opposite to subopposite, petioluled; petiolules pulvini only, 3–9 mm long, not to slightly 1-grooved, lenticels often present abaxially; blade ovate to elliptic, 4–11.6 by 1.9–6 cm, index 1.4–2.5, not falcate, (slightly) coriaceous to somewhat chartaceous, not to slightly punctate; base slightly attenuate to acute, symmetric (to basiscopic side broader); margin entire to slightly repand, flat to slightly undulating, not revolute; apex retuse to rounded to slightly acuminate, very apex retuse to rounded, not mucronulate; upper surface glabrous; lower surface (sub)puberulous especially on venation, colour slightly more brown than that of upper surface, domatia somewhat pustulate (pockets to) sacs opening in front; venation on upper surface flat, midrib slightly raised, colour same as lamina to reddish yellow, on lower surface raised; nerves 4–22 mm apart, marginally approx. open to weakly looped distally; veins more or less scalariform, laxly reticulate, distinct.

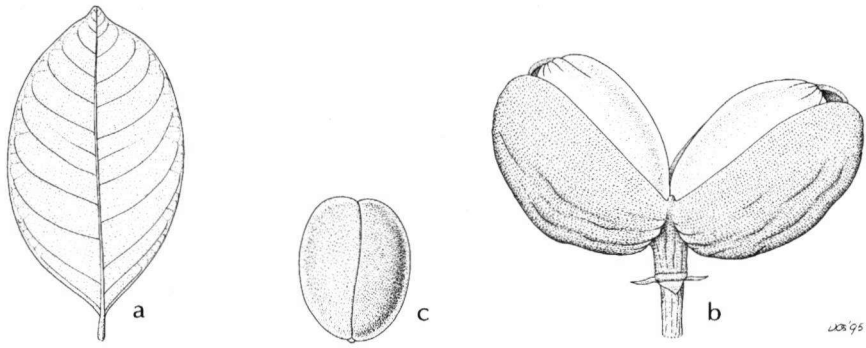

FIGURE 5.33. *Arytera miniata* H. Turner. (a) Leaflet, × 0.5; (b) fruit, × 3; (c) embryo, × 3. (a–c: *Carr 11554*.)

Infructescence axillary to pseudoterminal, branching along rachis; rachis terete, 3–10 cm long, puberulous when young; first-order branches up to 9 cm long. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous, adaxially glabrous; bracts 0.4–0.8 mm long; bracteoles 0.2–0.3 mm long. *Pedicels* 1.5–4 mm long in fruit, subpuberulous. *Flowers* not observed. *Calyx* 0.6–1.5 mm high, teeth 0.4–1.1 mm high, triangular, not punctate, margin entire, not membranaceous, apex acute; outside puberulous, inside glabrous. *Petals* (only remains beneath fruits seen) obovate, c. 1 by 0.6 mm, index 1.7, not punctate; claw 0.3 mm long, margin entire, apex obtuse; blade gradually decurrent into claw, outside glabrous, inside glabrous, margin pilose; scales c. 0.5 mm long, adnate to margin, basally not auricled, apex broadened. *Disc* not lobed, probably glabrous. *Stamens* (female): filament c. 1 mm long, basally pilose; anther c. 0.6 mm long, straight, pilose; connective not protruding. *Pistil* (female): ovary 2-locular; style and stigma elongating up to 1–2 mm in fruit, apically minutely 2-lobed, in fruit upper 1–1.5 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 0.7–1.3 cm high by 0.7–1.7 cm broad, axil not thickened transversely, outside subpuberulous, slightly rugose to verrucose, inside pilose along sutures; stipe 1–3 mm long, slender; edge of margin rounded; angle between lobes c. 180°; blackish to reddish brown; lobes laterally not to slightly flattened, valves 4–7 mm high by 7–10 mm long; endocarp pale brown. *Seed* ellipsoid to slightly ovoid, laterally not flattened, 8–9 by 5–6 mm, blackish brown; arilloid covering seed completely, lobed, inside not folded towards base, thin to slightly thickened towards base, coriaceous, consisting of 2 layers, outer layer thin, soft, drab yellowish, inner layer thick, firm, chocolate brown; hilum elliptic, c. 2 by 1.7 mm; endotesta pale brown. *Embryo:* cotyledons laterally beside each other (to somewhat obliquely above each other), equal to slightly unequal, upper or lower larger, apices not elongated; radicle 0.5–1 mm long, glabrous.

Field notes — Tree (slender or straggling and crooked) or shrub 2–10 m high, 2.5–12.5 cm dbh. Bark gray to pale brown, slightly suberose, closely corrugated and slightly darker within. Leaves stiff, dull, dark green above, slightly blueish-glaucous beneath, with pale venation. Flower buds cream. Fruit green when young, golden yellow to orange when ripe; arilloid scarlet.

Distribution — Papua New Guinea: Central Province.

Habitat & Ecology — In (rain)forest, on edge of mangrove swamp, and in dry, semi-deciduous monsoon thickets with *Eucalyptus*. Often described as rare or infrequent. Altitude sea level to 30 m. Budding Aug.; fruiting Jan., Feb., Apr.

Specimens studied — PAPUA NEW GUINEA. Central Province: *Brass 3760*; *Carr 11080, 11554*; *Kwapena (WLL) 123, 127*; *UPNG (Frodin, Katik & Mabberley) 4316.*

FIGURE 5.34. *Arytera miniata* H. Turner. Distribution map.

A18 - Arytera morobeana H. Turner — Fig. 5.35, 5.36

Arytera morobeana H. Turner, Blumea 38 (1993) 139; Fl. Males. I, 11 (3) (1994) 476. — Type: *LAE (Katik & Taho) 74816* (holo L; iso A, BRI, CANB, LAE), Oomsis logging area, Morobe Prov., Lae Subprov., Papua New Guinea, 6 Apr. 1980.

Tree. Indument of long, crispate, patent hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, crispate-hirsute when young; flowering twigs 1.5–5 mm thick. *Leaves* 1- or 2-jugate; petiole 2.5–7 cm long, lenticels sometimes present abaxially; rachis 1.8–3.5 cm long, (hemi)terete, crispate-hirsute. *Leaflets* opposite, petioluled; petiolules pulvini only, 4–9 mm long, 1-grooved, lenticels present abaxially; blade slightly (ob)ovate, 9.3–21.6 by 3.8–7.2 cm, index 2.1–3.2, not falcate, chartaceous, punctate; base slightly attenuate to acute, symmetric (to acroscopic side slightly broader); margin entire to slightly repand, flat, not revolute; apex acute to acuminate (to slightly retuse), very apex retuse to obtuse, not mucronulate; upper surface (sub)glabrous; lower surface subglabrous to crispate-hirsute especially on venation, colour slightly to distinctly different from that of upper surface (more olive-brown to brown), domatia

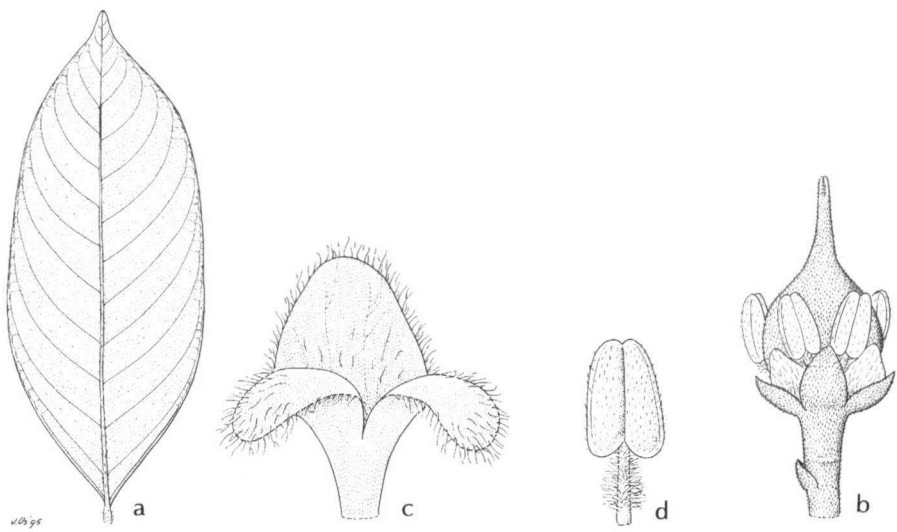

FIGURE 5.35. *Arytera morobeana* H. Turner. (a) Leaflet, × 0.5; (b) flower, × 6; (c) petal, × 25; (d) stamen, × 12.5. (a–d: *LAE 74816*.)

pockets to sacs opening in front; venation on upper surface flat, midrib slightly raised, colour same as lamina, midrib reddish, on lower surface raised; nerves 5–25 mm apart, marginally open; veins scalariform, laxly reticulate, distinct. *Inflorescences* axillary to pseudoterminal, branching in axil and along rachis; rachis terete to slightly flattened, 3–5 cm long, crispate-hirsute when young; first-order branches up to 1.5–2 cm long; cymules monochasial, 1- or 2-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially crispate-hirsute, adaxially glabrous; bracts 0.3–0.9 mm long; bracteoles 0.2–0.4 mm long. *Pedicels* 1.5–2 mm long, crispate-hirsute. *Flowers* 2–2.5 mm diam. *Calyx* 1–1.5 mm high, teeth 0.9–1.4 mm high, triangular to slightly ovate, not punctate, margin entire, not membranaceous, apex acute; outside crispate-hirsute, inside (sub)glabrous. *Petals* 5, elliptic, 1.5–1.8 by 0.8–1.2 mm, index 1.2–2, not punctate; claw 0.3–0.4 mm long, margin entire, apex obtuse to acute; blade gradually decurrent into claw, outside rather densely pilose, inside subglabrous to pilose, margin pilose; scales 0.8–1.2 mm long, free, basally not auricled, apex broadened, rather densely pilose. *Disc* not lobed, subglabrous to pilose on rim. *Stamens* (female) 8 or 9; filament 0.8-1.4 mm long, densely pilose; anther 1–1.5 mm long, curved inward, densely pilose; connective not protruding. *Pistil* (female): ovary 2-locular, 0.4–1 mm long, pilose; style and stigma 1.5 mm long, elongating up to 3 mm in fruit, minutely 2-lobed, in fruit upper c. 2 mm stigmatic. Mature *fruit* not observed.

Field notes — Tree 6–8 m high, 8 cm dbh. Bark light grey to brown, underbark brownish straw to reddish brown. Wood creamy orange. Leaves dark green. Flowers creamy orange.

Distribution — Papua New Guinea: Morobe Province.

Habitat & Ecology — Lowland rainforest. Altitude c. 100 m. Flowering March, Apr.

FIGURE 5.36. *Arytera morobeana* H. Turner. Distribution map.

Specimens studied — PAPUA NEW GUINEA. Morobe Province: *Hartley 11354*; *LAE (Katik & Taho) 74816.*

A19 - Arytera multijuga H. Turner — Fig. 5.37, 5.38

Arytera multijuga H. Turner, Blumea 38 (1993) 140; Fl. Males. I, 11 (3) (1994) 476. — Type: *ANU (Flenley) 2846* (holo L; iso A, BRI, CANB, K, LAE), Pokaris near Kompian, Western Highlands Distr., Wabag subdistr., Papua New Guinea, 15 June 1965.

Tree. Indument of long, crispate, patent hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, crispate-hirsute when young; flowering twigs 5–10 mm thick. *Leaves* 4-jugate; petiole 9.5–13 cm long, lenticels absent abaxially; rachis 13.5–18.5 cm long, terete, slightly 2-grooved, crispate-hirsute. *Leaflets* subopposite to alternate, subsessile to petioluled; petiolules pulvini only, 3–10 mm long, not to indistinctly 2-grooved, lenticels present; blade elliptic to slightly obovate, 10.6–20.4 by 4.7–7.2 cm, index 2.3–3, not falcate, coriaceous, slightly punctate; base acute, oblique, basiscopic side broader; margin slightly repand, flat, not revolute; apex slightly cuspidate, very apex rounded, not mucronulate; upper surface slightly to densely crispate-hirsute on venation; lower surface crispate-hirsute, especially on venation, colour approx. same as that of upper surface, domatia minute pockets opening in front; venation on upper surface flat, midrib slightly raised, colour same as lamina, on lower surface

FIGURE 5.37. *Arytera multijuga* H. Turner. (a) Habit, × 0.5; (b) flower, × 6; (c) petal, × 12.5. (a–c: *ANU (Flenley) 2846.*)

raised; nerves 6–19 mm apart, marginally looped, intercalating veins often present; veins scalariform, laxly reticulate, distinct. *Inflorescences* axillary, branching along rachis; rachis terete, 4–6 cm long, crispate-hirsute when young; first-order branches up to 7.5 cm long; cymules dichasial, 1–3-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially crispate-hirsute, adaxially subglabrous to pilose; bracts 0.7–1 mm long, bracteoles 0.2–0.5 mm long. *Pedicels* 1.5–3 mm long, crispate-hirsute. *Flowers* 2.5–3 mm diam. *Calyx* slightly dimorphic: 2 outer smaller ones 1.1–1.4 mm high, 3 inner larger ones 1.7–2 mm high, teeth 1–1.3 resp. 1.6–1.9 mm high, ovate, not punctate, margin entire, apex obtuse; outside crispate-hirsute, inside densely puberulous. *Petals* 5, elliptic to ovate, 1.1–1.9 by 0.8–1.2 mm, index 1.1–2.1, not punctate; claw 0.1 mm long, margin entire (to slightly denticulate near apex), pilose, apex obtuse to acute; blade gradually decurrent into claw, outside (sub)glabrous, inside subglabrous to subpuberulous; scales 0.4–0.9 mm long, adnate to margin, basally not auricled, apex broadened, densely pilose. *Disc* not lobed, glabrous. *Stamens* (male) 7 or 8; filament 2–3 mm long, pilose; anther (male) 1.1–1.4 mm long, straight, glabrous; connective slightly protruding. *Pistil* (male): ovary 3-locular, c. 0.9 mm long, puberulous; style and stigma c. 0.2 mm long. *Fruit* not observed.

Field notes — Tree 8 m high, 10 cm dbh. Bark brown, underbark green to orange, inner bark green to white. Wood white to light brown. Flowers pink.

Distribution — Papua New Guinea: Western Highlands Province.

Habitat & Ecology — Rainforest, on slope, SE aspect, in strong shade. Soil latosol. Altitude 2200 m. Flowering June.

Vernacular name — Palya (Enga language).

Notes — (1) Only known from the type locality.

(2) In *ANU (Flenley) 2846* a single flower with a 6-merous calyx was found.

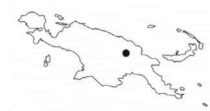

FIGURE 5.38. *Arytera multijuga* H. Turner. Distribution map.

Specimens studied — PAPUA NEW GUINEA. Western Highlands Province: *ANU (Flenley) 2846, 2875.*

A20 - Arytera musca H. Turner — Fig. 5.39, 5.40

Arytera musca H. Turner, Blumea 38 (1993) 140; Fl. Males. I, 11 (3) (1994) 478. — Type: *Brass 7620* (holo L; iso A, BM, BO), Lake Daviumbu, Middle Fly River, Papua New Guinea, Aug. 1936.
Arytera divaricata auct. non F. Muell.: Merr. & Perry, J. Arnold Arbor. 21 (1940) 522.

Tree. Indument of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, puberulous when young; flowering twigs 3–7 mm thick. *Leaves* 2-jugate; petiole 2.5–10.5 cm long, lenticels usually present abaxially; rachis 1.5–5 cm long, (hemi)terete to flattened with 2 more or less distinct longitudinal grooves, puberulous to glabrescent. *Leaflets* opposite to subopposite, petioluled; petiolules pulvini only, 4–9 mm long, 1-grooved, lenticels present abaxially; blade elliptic to slightly obovate, 4.5–19 by 2.2–8.8 cm, index 1.8–2.9, not falcate, thinly coriaceous to chartaceous, usually not punctate; base acute to slightly attenuate, symmetric to slightly oblique, then basiscopic side broader; margin entire to slightly repand, approx. flat, not revolute, apex obtuse to acute to slightly acuminate, very apex retuse to obtuse, not mucronulate;

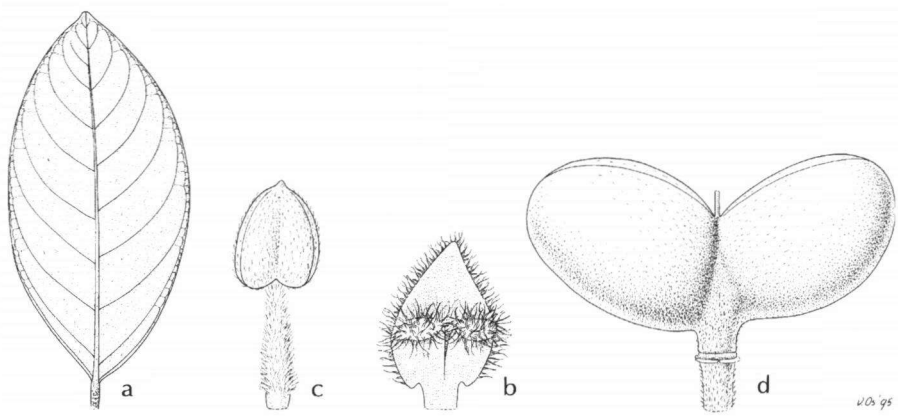

FIGURE 5.39. *Arytera musca* H. Turner. (a) Leaflet, × 0.5; (b) petal, × 25; (c) stamen, × 12.5; (d) fruit, × 3. (a–c: *Brass 7743*; d: *Brass 8483*.)

upper surface glabrous; lower surface subpuberulous on venation, colour slightly different from that of upper surface (brownish), domatia pockets (to sacs) opening in front; venation on upper surface flat, midrib slightly raised, colour yellowish to reddish, on lower surface raised; nerves 6–32 mm apart, marginally open; veins indistinctly scalariform, laxly reticulate, distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis (and in axil); rachis terete to slightly flattened, 4–12.5 cm long, puberulous when young; first-order branches up to 6 cm long; cymules dichasial, 1–7-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous, adaxially glabrous; bracts 0.3–0.7 mm long; bracteoles 0.2–0.3 mm long. *Pedicels* 1–4.5 mm long, puberulous. *Flowers* 1.5–2 mm diam. *Calyx* 5- (or 6-)dentate, 0.7–1.2 mm high, teeth 0.5–1.1 mm high, triangular to slightly ovate, not punctate, margin entire, apex approx. acute; outside puberulous, inside glabrous. *Petals* 2–5(–6), elliptic (to orbicular), 0.9–1.3 by 0.4–1 mm, index 1.3–2.6, not punctate; claw 0.1–0.3 mm long, margin entire, apex obtuse to acute (to slightly acuminate); blade gradually decurrent into claw, outside subpilose, inside subpilose, margin pilose; scales 0.5–0.8 mm long, free, basally not auricled to slightly auricled, apex (slightly) broadened, densely pilose. *Disc* not lobed, glabrous. *Stamens* (male) 8; filament 1.5–2.5 mm long, pilose; anther 1.1–1.3 mm long, curved inward, pilose; connective protruding. *Pistil* (male): ovary 2- (or 3-)locular, c. 0.5 mm long, puberulous; (female) style and stigma elongating up to 1.5–3 mm in fruit, with a distinct thickening between style and stigma, not to slightly 2-lobed, in fruit upper 0.5–1 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 0.7–1.3 cm high by 0.7–2.6 cm broad, axil not thickened transversely, outside subpuberulous, smooth to slightly rugose, inside pilose on sutures; stipe 0.5–2 mm long, slender; edge of margin rounded; angle between lobes c. 180°; dark brown to blackish; lobes laterally sometimes flattened, valves 6–10 mm high by 9–15 mm long; endocarp pale brown. *Seed* orbicular, laterally flattened, c. 6 by 6 mm, blackish; arilloid covering seed completely, lobed, inside slightly folded towards base, thick towards base, coriaceous, consisting of 2 layers, outer layer thin,

soft, pale yellow, inner layer thick, firm, chocolate brown; hilum elliptic, c. 3 by 2 mm; endotesta brown. *Embryo*: cotyledons obliquely dorsoventrally to almost secondarily laterally beside each other, equal to unequal, upper larger, apices not elongated; radicle 0.5–1 mm long, glabrous.

Field notes — Tree 8–15 m high, 12.5 cm dbh. Bark thin, brown and grey, shedding in small hard scales or fairly smooth. Blaze thin, light pinky brown. Flowers creamy yellow when young, white when mature. Fruits yellow; aril red; seeds purple.

Distribution — Papua New Guinea: Western Province.

Habitat & Ecology — Rain and monsoon forests; on imperfectly drained plain. Altitude 15 – 30 m. Flowering Sep.; fruiting Dec.

Specimens studied — PAPUA NEW GUINEA. Western Province: *Brass 7620, 7743, 8422, 8483*; *Paijmans 386*; *Pullen 7229*.

FIGURE 5.40. *Arytera musca* H. Turner. Distribution map.

A21 - Arytera nekorensis H. Turner, *spec. nov.* — Fig. 5.41, 5.42

A. chartacea et *A. collina* similissima, in foliis bifoliolatis dense punctatis, foliolorum marginibus distincte revolutis differt. — Typus: *MacKee 42137* (holo L; iso P), Poya, Forêt de Nékoro, New Caledonia, 16 Aug. 1984.

Tree. Indument of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, subpuberulous when young; flowering twigs 1–2.5 mm thick. *Leaves* 1-jugate; petiole 0.5–1.1 cm long, hemiterete, subpuberulous, lenticels rarely present abaxially; apical process of rachis distinct, 1.5–4 mm long. *Leaflets* opposite, subsessile; petiolules 1.5–5 mm long, 1-grooved, lenticels rarely present abaxially; blade elliptic, 2.4–10.3 by 1–4.6 cm, index 1.5–3.2, not falcate, very coriaceous, punctate; base slightly attenuate to acute, symmetric to slightly oblique, then basiscopic side broader; margin entire, flat to slightly undulating, strongly revolute; apex retuse to obtuse, not mucronulate; upper surface glabrous to slightly puberulous on base of midrib; lower surface (sub)glabrous, colour same as to slightly more olive than that of upper surface, domatia absent; venation on upper surface flat, colour same as lamina, midrib reddish brown to straw, on lower surface flat, midrib raised; nerves 2–10 mm apart, marginally looped; veins densely reticulate, not distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis; rachis (slightly) flattened, 5.5–13.2 cm long, subpuberulous when young; first-order branches up to 4.3 cm long; cymules dichasial, 1–3-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially subpuberulous, adaxially puberulous; bracts 0.4–0.8 mm long; bracteoles minute. *Pedicels* 2–3 mm long, elongating up to 4–7 mm in fruit, subpuberulous, especially on articulation. *Flowers* c. 2 mm diam. *Calyx* 1–1.1 mm high, teeth 0.3–0.4 mm high, triangular, not punctate, margin entire, not membranaceous, apex obtuse; outside subpuberulous, inside puberulous on teeth. *Petals* 5, obovate, 0.9–1.6 by 0.4–0.8 mm, index 2–2.5, punctate; claw 0.4–0.5 mm long, margin entire, apex obtuse to acute; blade gradually decurrent into claw, outside subpilose, inside pilose basally, margin pilose, apex glabrous; scales 0.1–0.5 mm long, enation of margin, basally not auricled, apex not broadened. *Disc* 5-lobed, rim subpilose. *Stamens* (female) 8(–10); filament 0.9–1.4 mm long, basally

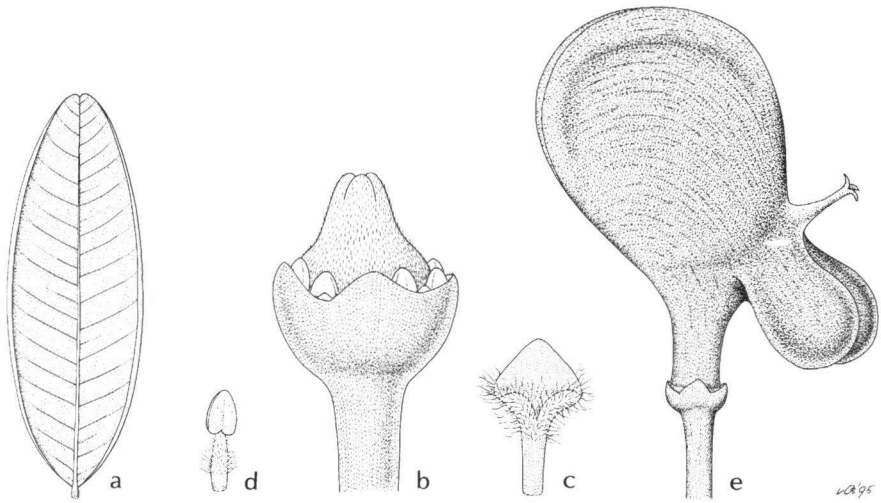

FIGURE 5.41. *Arytera nekorensis* H. Turner. (a) Leaflet, × 0.5; (b) flower, × 12.5; (c) petal, × 25; (d) stamen, × 12.5; (e) fruit, × 3. (a, e: *Veillon 6905*; b–d: *MacKee 42137*.)

pilose; anther 0.5–0.6 mm long, straight, subpilose; connective not protruding. *Pistil* (female): ovary 3-locular, c. 1.2 mm long, pilose; style and stigma c. 0.4 mm long, elongating up to 2.5 mm in fruit, 3-lobed, in fruit upper 0.3–0.5 mm stigmatic. *Fruit* slightly obcordate, with 1–3 well-developed lobes, 1.1–1.8 cm high by 1–2.1 cm broad, axil thickened transversely, outside shortly puberulous, rugose, inside pilose, especially along sutures; stipe 3–4 mm long, slender; edge of margin rounded; angle between lobes 45–180°; pale brown; lobes laterally not flattened, valves 9–10 mm high by 9–11 mm long; endocarp pale brown. *Seed* not properly developed.

Field notes — Tree 10–12 m high, 30 cm dbh. Bark pale grey, rough, detaching in thin flakes. Leaves dark shiny green above, bright green below.

Distribution — New Caledonia: Poya, Nékoro forest.

Habitat & Ecology — Sclerophyll forest and dense coastal forest, on black clayey soil, thick alluvial soil on basalt, and limestone. Altitude 2–10 m. Hydromorphie temporaire. Flowering June; fruiting Aug., Sep.

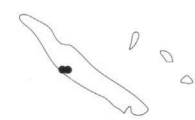

FIGURE 5.42. *Arytera nekorensis* H. Turner. Distribution map.

Note — Differs from *A. chartacea* and *A. collina* in the number of leaflets, the strongly revolute margin of the leaflets and the distinct apical process of the leaf rachis.

Specimens studied — NEW CALEDONIA: *MacKee 42137*; *Morat 8642*; *Veillon 6905, 7380*.

A22 - Arytera neoebudensis (Guillaumin) H. Turner, *comb. nov.* — Fig. 5.43, 5.44

Cupaniopsis neoebudensis Guillaumin, J. Arnold Arbor. 12 (1931) 241. — Type: *Kajewski 381* (holo A; iso BISH, BRI, K, NY, P), Eromanga Island, Dillon Bay, Vanuatu, 8 June 1928.

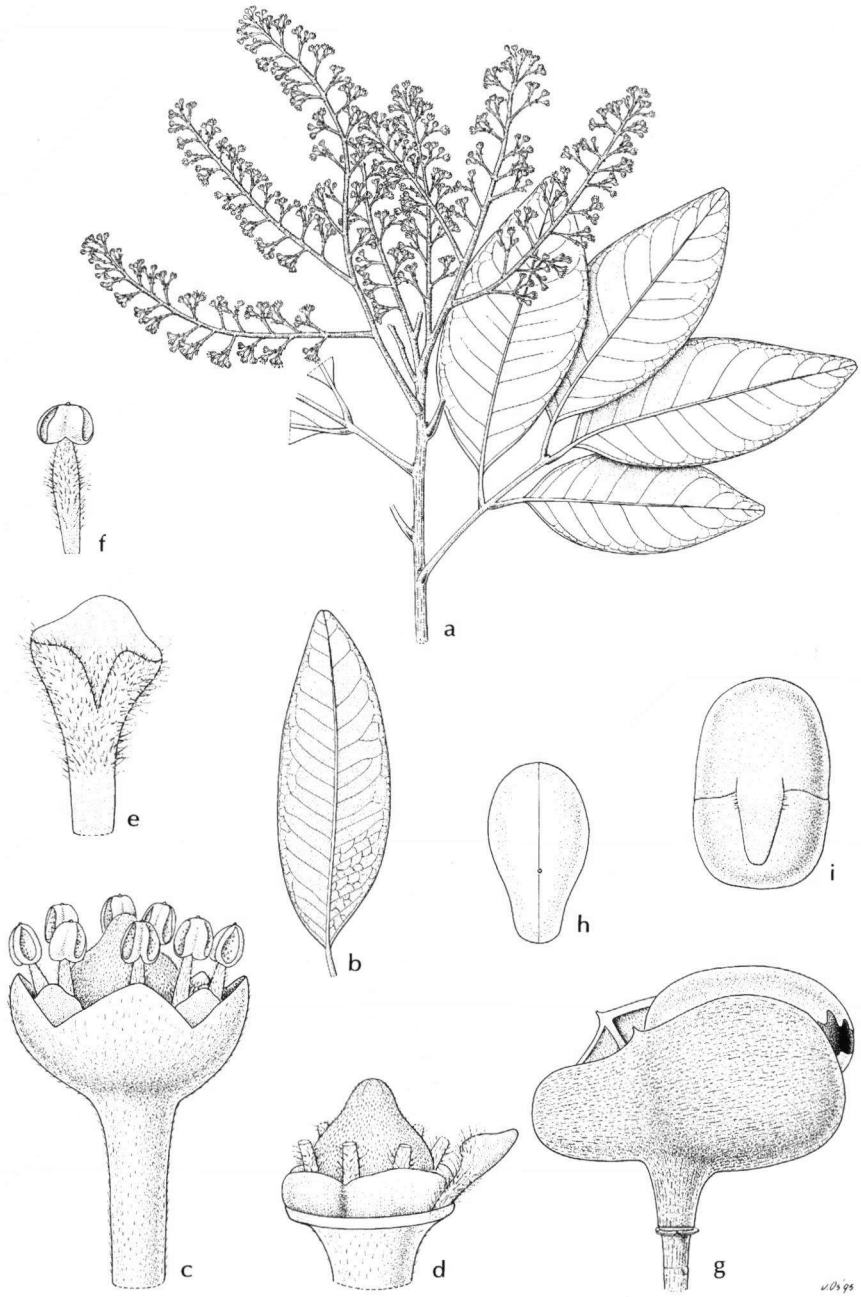

FIGURE 5.43. *Arytera neoebudensis* (Guillaumin) H. Turner. (a) Habit, × 0.5; (b) leaflet, lower part on one side with detail of tertiary venation pattern, × 0.5; (c) flower, × 12.5; (d) dissected flower showing disc, × 12.5; (e) petal, × 25; (f) stamen, × 12.5; (g) fruit, × 1.5; (h) schematic top view of fruit, × 1.5; (i) embryo, × 1.5. (a–f: *MacKee 18939*; g–i: *Wheatley JWV 746*.)

Tree or *shrub*. *Indument* of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth to slightly rough, puberulous when young; flowering twigs 2–5 mm thick. *Leaves* 2–4-jugate; petiole 0.9–4.5 cm long, lenticels absent abaxially; rachis 0.8–6 cm long, hemiterete, glabrous to puberulous. *Leaflets* opposite to subopposite, petioluled; petiolules 3–13 mm long, 1-grooved, lenticels absent abaxially; blade ovate to elliptic, 2.7–12 by 1.5–4.2 cm, index 1.5–3.4, not falcate, coriaceous to chartaceous, usually punctate; base slightly attenuate to acute, symmetric (to basiscopic side broader); margin entire, flat to slightly undulating, not to slightly revolute; apex rounded to slightly acuminate, very apex retuse to obtuse, not mucronulate; upper surface glabrous to subpuberulous on base of midrib; lower surface glabrous to subpuberulous on base of midrib, colour different from that of upper surface, domatia absent; venation on upper surface flat, midrib flat to slightly raised, colour same as lamina to yellowish, midrib usually yellow to reddish brown, on lower surface flat, midrib raised; nerves 2–13 mm apart, marginally looped; veins laxly reticulate, not distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis (and in axil); rachis flattened, 3.1–15 cm long, puberulous when young; first-order branches up to 8.5 cm long; cymules dichasial, 1–3-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous, adaxially glabrous; bracts 0.4–1 mm long; bracteoles 0.1–0.3 mm long. *Pedicels* 0.5–2.2 mm long, elongating up to 4 mm in fruit, (sub)puberulous. *Flowers* 1.8–2.2 mm diam. *Calyx* 0.8–1.2 mm high, teeth 0.4–0.8 mm high, triangular, not punctate, margin entire, not membranaceous, apex acute; outside puberulous, inside (sub)puberulous on teeth. *Petals* 5, obovate to rhomboid, 0.9–1.9 by 0.6–1 mm, index 1.3–2.3, not punctate; claw 0.5–1.2 mm long in male flowers, 0.2 mm long in female flowers, margin entire, slightly denticulate apically, apex rounded to obtuse; blade gradually decurrent into claw, outside subglabrous, inside pilose, margin pilose, apex completely glabrous; scales 0.3–0.5 mm long, enation of margin, basally not auricled, apex not broadened, pilose. *Disc* 5-lobed, glabrous to subpilose on rim. *Stamens* (male) 6–8; filament 2–2.6 mm long, slightly flattened dorsoventrally, pilose; anther 0.6–0.8 mm long, straight, subpilose; connective slightly protruding. *Pistil* (female): ovary 3- (or 2-)locular, c. 1.5 mm long, lower half longitudinally grooved, upper half smooth, puberulous; style and stigma c. 0.8 mm long, elongating up to 0.8 mm in fruit, 3- (or 2-)lobed, in fruit upper c. 0.3 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 2–3.2 cm high by 2.4–4.4 cm broad, axil thickened transversely, outside glabrous to subpuberulous, rugose to verrucose, inside crispately pilose, especially along margins; stipe 2–7.5 mm long, slender; edge of margin rounded; angle between lobes c. 120°; bright brown to blackish brown; lobes laterally not flattened, valves 15–19 mm high by 16–25 mm long; endocarp pale straw. *Seed* ellipsoid, laterally not to slightly flattened, 18–22 by 15 mm, dark brown to blackish brown; arilloid covering seed 1/2 to completely, lobed, inside not folded towards base, thin to slightly thickened towards base, fleshy membranaceous, consisting of 1 layer, soft, pale yellow to orange-brown; hilum elliptic, 6–7 by c. 4.5 mm; endotesta dark brown. *Embryo:* cotyledons dorsoventrally above each other, equal to slightly unequal, then upper larger, apices not elongated; radicle 5.5–6.5 mm long, margin pilose at base.

Field notes — Tree or shrub 2–25 m tall; canopy variable but not dense. Buttresses small, low, steep, curved, thin. Bark light grey-brown, smooth with slight horizontal banding, sometimes appearing speckled with brown spots on white background; outer bark light pinkish brown, fibrous, slightly wavy grain; inner bark very pale pinkish brown to white, staining rusty brown on exposure to air; the whole 1 cm thick (cork very thin). Sapwood white; heartwood dark red brown, hard, durable. Leaves mid-, slightly yellowish green with yellow midrib and margin shiny above; lighter mid-green with yellow midrib and margin, dull below. Panicles lax. Flowers whitish yellow to white. Fruits green turning light yellow green. Arilloid red. Seed black.

Distribution — Vanuatu: Aneityum, Erromanga, Malekula. New Caledonia: New Caledonia, Île Walpole, Loyalty Islands.

Habitat & Ecology — On rocky slopes near lagoon. On red clay over weathered volcanics. On volcanic soil. In lowland primary rainforest, together with *Agathis obtusa Calophyllum neoebudicum, Hernandia* cf. *cordigera*. Altitude 120–300 m. Visited by many blue flies. Flowering May, June; fruiting Aug.–Nov.

Uses — Wood used for constructions.

Vernacular names — Vanuatu: M'tap (Erromanga); Nar-vu-vat (Erromanga); Nembangar (Malekula).

Specimens studied — VANUATU. Aneityum: *Bernardi 13030*; *Kajewski 842*; *Wheatley JWV 746*; Erromanga: *Bernardi 13222, 13367*; *Bourdy 187*; *Kajewski 381*; *RSNH (Chew Wee-Lek) 111*; Malekula: *RSNH (Hallé) 6458*; Mallieolo: *Bourdy 803*. — NEW CALEDONIA. New Caledonia: *Deplanche s.n.*, Oct. 1864; *MacKee 17081, 28591, 39765, 41497, 43786, 44085*; *Suprin 827*; *Veillon 7309*; Loyalty Islands: 11 specimens.

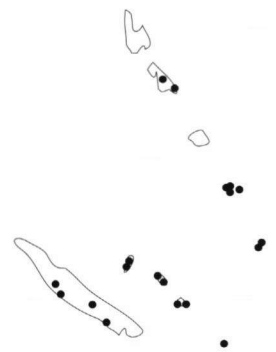

FIGURE 5.44. *Arytera neoebudensis* (Guillaumin) H. Turner. Distribution map.

A23 - **Arytera novaebrittanniae** H. Turner — Fig. 5.45, 5.46

Arytera novaebrittanniae H. Turner, Blumea 38 (1993) 141; Fl. Males. I, 11 (3) (1994) 478. — Type: *LAE (Stevens et al.) 58188* (holo L; iso A, BRI, CANB, E, K, LAE, M, NSW), Fullebourn Harbour, hill overlooking bay, West New Britain Distr., Gasmata subdistr., Papua New Guinea, 3 May 1973.

Tree. Indument of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, puberulous when young; flowering twigs 2–3 mm thick, in fruit 3.5–7 mm thick. *Leaves* 2–4-jugate; petiole 1–9 cm long, lenticels sometimes present; rachis 1.5–10.5 cm long, hemiterete, often with a ridge adaxially, glabrous to subpuberulous when young. *Leaflets* opposite to subopposite, subsessile to petioluled; petiolules pulvini only, 1–7 mm long, not to 1-grooved, wrinkled, lenticels usually present; blade ovate, 4.4–17.8 by 1.4–5.9 cm, index (2.3–)3–4.9, not to slightly falcate, coriaceous to chartaceous, sometimes punctate; base acute, symmetric; margin entire, approx. flat, not revolute; apex acuminate to caudate, very apex rounded, not mucronulate; upper surface glabrous; lower surface glabrous to subpuberulous on venation, colour same as to slightly more olive than that of upper surface, domatia few to many large sacs opening on top; venation on upper surface flat, colour same as lamina, on

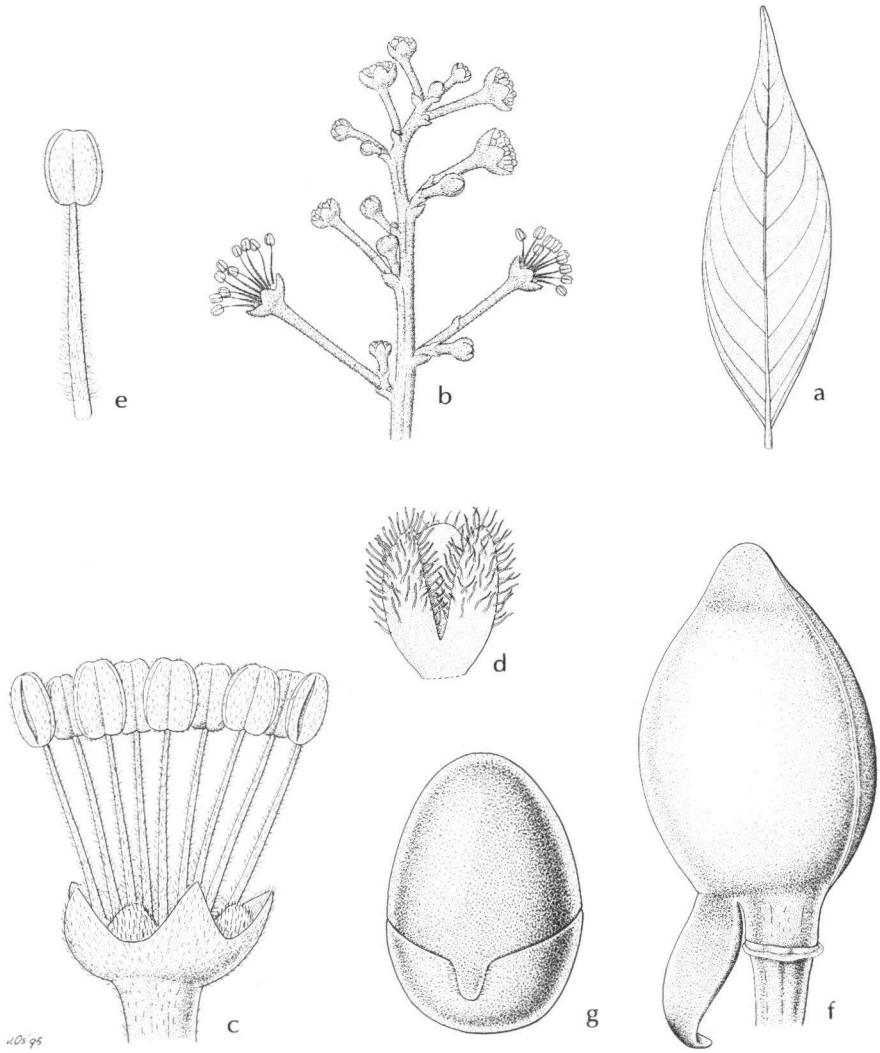

FIGURE 5.45. *Arytera novaebrittanniae* H. Turner. (a) Leaflet, × 0.5; (b) detail of inflorescence, × 3; (c) flower, × 12.5; (d) petal, × 25; (e) stamen, × 12.5; (f) fruit, × 3; (g) embryo, × 3. (a, f, g: *NGF 58188*; b–e: *NGF 26789*.)

lower surface raised; nerves 5–22 mm apart, marginally open; veins weakly scalariform, laxly reticulate, distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis; rachis flattened when young, terete when in fruit, 3–18 cm long, puberulous when young; first-order branches up to 4 cm long; cymules dichasial with one branch often moved upward along petiole of first flower, 1–7-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially puberulous, adaxially glabrous; bracts 0.3–1 mm long; bracteoles 0.1–0.3 mm long. *Pedicels* 3–5 mm long, elongating up to 5–8 mm

in fruit, puberulous when young. *Flowers* 2 mm diam. *Calyx* 0.8–1.1 mm high, teeth 0.6–1 mm high, triangular, not punctate, margin entire, not membranaceous, apex acute; outside puberulous, inside glabrous. *Petals* 5, rhomboid to obovoid, 0.6–0.8 by 0.5–0.6 mm, index 1.2–1.6, not punctate; claw 0.1–0.3 mm long, margin entire, apex obtuse; blade gradually decurrent into claw, outside pilose, inside subglabrous to pilose, margin pilose; scales 0.6–0.7 mm long, free, basally not auricled, apex broadened, densely pilose. *Disc* not lobed, swollen spoke-like between filaments, puberulous to pilose. *Stamens* (male) 7 or 8; filament 2.2–2.8 mm long, pilose; anther 0.8–0.9 mm long, straight, puberulous; connective not protruding. *Pistil* (male): ovary 2- (or 3)-locular, 0.6–0.7 mm long, puberulous; (female) style and stigma elongating up to 1.2–2.2 mm in fruit, not lobed, in fruit upper 0.6–1 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 1.5–2.2 cm high by 1–2.9 cm broad, axil not thickened transversely, outside subglabrous to subpuberulous, smooth, inside (sub)puberulous along margins; stipe 1.5–2.5 mm long, slender; edge of margin sharp; angle between lobes c. 180°; dark brown; lobes laterally not flattened, valves 10–12 mm high by 15–19 mm long; endocarp pale brown. *Seed* ovoid, laterally not flattened, c. 14 by 9 mm, blackish brown; arilloid covering seed 1/2–3/4, lobed, inside not folded towards base, thick towards base, coriaceous, consisting of 2 layers, outer layer thin, soft, drab yellow, inner layer thick, firm, chocolate brown; hilum elliptic, c. 7 by 5 mm; endotesta dark brown. *Embryo:* cotyledons dorsoventrally above each other, unequal, upper larger, apices not elongated; radicle c. 1 mm long, margin pilose.

Field notes — Tree, height 7–21 m, 25–30 cm dbh; buttresses absent. Bark (dark grey) brown, rugose, somewhat scaly, not to slightly fissured; inner bark orange to dark red-brown. Wood orange to cream, odourless; watery exudate sometimes present (*NGF 26789*). Leaves shiny green above and below. Flower buds pale yellow, flowers cream, stamens white. Fruit brownish to yellowish green; arilloid red; seed black.

Distribution — Papua New Guinea: New Britain. Solomon Islands: Guadalcanal.

Habitat & Ecology — Forest on coral limestone and montane forest together with *Podocarpus*. Altitude 125–1200 m. Flowering May; fruiting Apr., May.

Uses — Wood used for house-building on the Solomon Islands.

Vernacular names — *New Britain:* Narekereke, naulanga; *Solomon Islands:* Ketsarah.

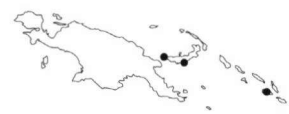

FIGURE 5.46. *Arytera novae-brittanniae* H. Turner. Distribution map.

Specimens studied — PAPUA NEW GUINEA. West New Britain Province: *LAE (Stevens et al.) 58188*; *NGF (Frodin) 26789, 26856.* — SOLOMON ISLANDS. Guadalcanal: *Kajewski 2573.*

A24 - **Arytera pauciflora** S.T. Reynolds — Fig. 5.47, 5.48

Arytera pauciflora S.T. Reynolds, Fl. Austr. 25 (1985) 91, 198; Austrobaileya 2 (1985) 163. — Type: *Michael s.n.* (holo BRI sheet no. 170246, n.v.; iso BRI sheet no. 170247, n.v.), Johnstone River, Australia, March 1915.

Tree. Indument of short, straight, appressed hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth to rather rough, sericeous when young; flowering twigs

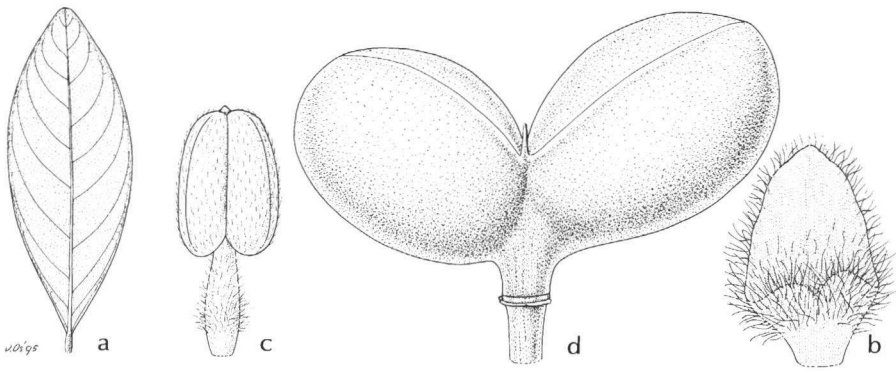

FIGURE 5.47. *Arytera pauciflora* S.T. Reynolds. (a) Leaflet, × 0.5; (b) petal, × 25; (c) stamen, × 12.5; (d) fruit, × 3. (a–c: *Graham 2488*; d: *Stocker 1484*.)

1–2 mm thick. *Leaves* 1- or 2-jugate; petiole 0.7–4.2 cm long, lenticels present abaxially; rachis 0.7–2.6 cm long, hemiterete, not to slightly winged, glabrous to subsericeous. *Leaflets* opposite, petioluled; petiolules pulvini only, 2–8 mm long, 1-grooved, lenticels present abaxially; blade ovate to elliptic, 2.8–10.6 by 1–5.3 cm, index 2–3.2, not to slightly falcate, slightly bullate, chartaceous, usually minutely punctate; base attenuate to obtuse, symmetric to slightly oblique, then basiscopic side broader; margin entire, flat, not revolute; apex obtuse to acuminate, very apex retuse to rounded, not mucronulate; upper surface glabrous; lower surface glabrous to subsericeous on venation, colour same as to slightly lighter than that of upper surface, domatia small pockets opening in front; venation on upper surface flat, midrib slightly raised, colour same as lamina, on lower surface raised; nerves 3–14 mm apart, marginally open; veins densely reticulate, scalariform, not distinct. *Inflorescences* axillary or (pseudo)terminal, branching in axil and along rachis; rachis terete to flattened, 1–3.5 cm long, sericeous when young; first-order branches up to 1.5 cm long; cymules dichasial, 1–3-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially sericeous, adaxially glabrous; bracts 0.7–1 mm long; bracteoles 0.3–0.8 mm long. *Pedicels* 2–4 mm long, in fruit up to 12 mm long, (sub)sericeous. *Flowers* 2–2.5 mm diam. *Calyx* 1.3–2 mm high, teeth 0.8–1.5 mm high, triangular to ovate, not punctate, margin entire, not membranaceous, apex acute; outside puberulous, inside glabrous. *Petals* 5, triangular to ovate to rhomboid, 0.7–1.3 by 0.5–1 mm, index 1–1.3, not punctate; claw up to 0.1 mm long, margin entire, apex acute to slightly acuminate; blade abruptly decurrent into claw, outside pilose, inside subglabrous to pilose, margin pilose; scales 0.1–0.3 mm long, free to adnate to margin, basally not auricled, apex broadened. *Disc* not lobed, glabrous. *Stamens* (male) 7–9; filament 0.4–1 mm long, pilose; anther 1.6–1.7 mm long, curved inward, pilose; connective slightly protruding. *Pistil* (male) ovary 2-locular, 0.6–0.9 mm long, smooth, sericeous; (female) style and stigma elongating up to 1–1.2 mm in fruit, not lobed, in fruit upper c. 0.7 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 0.9–1.1 cm high by 1.5–2.3 cm broad, axil not thickened transversely, outside glabrous, rugose to verrucose, often scaly, inside pilose on sutures;

stipe 0.1–1 mm long, broadly cuneate; edge of margin rounded to sharp to keeled; angle between lobes c. 180°; dull blackish brown; lobes laterally slightly flattened, valves 7–9 mm high by 9–12 mm long; endocarp light brown. *Seed* ellipsoid to ovoid, laterally flattened, 4–9 by 2.5–5 mm, blackish to dark brown; arilloid covering seed 3/4 to completely, slightly lobed, inside not folded towards base, thick towards base, fleshy, consisting of 2 layers, outer layer thin, soft, light coloured, inner layer thick, firm, dark brown; hilum elliptic, 1.5–2.5 by 1–2 mm; endotesta light brown. *Embryo:* cotyledons obliquely dorsoventrally above each other, equal to unequal, then lower larger, apices not elongated; radicle 0.5–0.8 mm long, glabrous.

Field notes — Trees 6–15 m high, 25 cm dbh. Bark smooth, mid-grey. Wood hard. Leaves mid-glossy green above, only duller below; young leaves pink. Flowers cream to yellow. Fruit dull brown.

Distribution — Australia: N Queensland, Atherton Tableland.

Habitat & Ecology — In rainforest or rainforest remnants. In subcanopy layer. On sandy grey soil. Altitude 450–900 m. Flowering Sep., Nov.; fruiting June, Aug., Sep.

Specimens studied — AUSTRALIA. Queensland: 13 specimens.

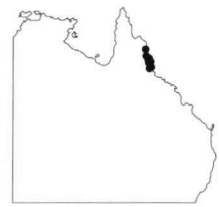

FIGURE 5.48. *Arytera pauciflora* S.T. Reynolds. Distribution map.

A25 - Arytera pseudofoveolata H. Turner — Fig. 5.49, 5.50

Arytera pseudofoveolata H. Turner, Blumea 38 (1993) 142; Fl. Males. I, 11 (3) (1994) 479. — Type: *Brass 5560* (holo A; iso BM, BO, NY, US), Kubuna, Central distr., Papua New Guinea, Nov. 1933.
Arytera sp. S.T. Reynolds, Fl. Austr. 25 (1985) 93; Austrobaileya 2 (1985) 165.
Arytera foveolata auct. non F. Muell.: Merr. & Perry, J. Arnold Arbor. 21 (1940) 523.

Tree. Indument of long, crispate, patent hairs; glandular scales absent; buds not 'varnished.' *Branchlets* smooth, crispate-hirsute when young; flowering twigs 2.5–3 mm thick. *Leaves* 2-jugate; petiole 3.8–7.5 cm long, lenticels absent abaxially; rachis (hemi)terete, 1.8–4.8 cm long, sometimes with 2 longitudinal grooves, crispate-hirsute. *Leaflets* opposite, petioluled; petiolules pulvini only, 3–10 mm long, 1-grooved, lenticels usually present abaxially; blade ovate to elliptic, 5.4–17.7 by 2–7.4 cm, index 2–3.2, not falcate, coriaceous to chartaceous, not punctate; base slightly attenuate to acute, symmetric to slightly oblique, then basiscopic (or acroscopic) side broader; margin entire to slightly repand, flat, not revolute; apex rounded to slightly acuminate, very apex retuse to rounded, not mucronulate; upper surface glabrous; lower surface crispate-hirsute on venation, colour different from that of upper surface (brown); domatia small, few pockets to (pustular) sacs opening in front, situated in axils of nerves; venation on upper surface flat, midrib usually slightly raised, colour same as lamina to reddish or yellowish, on lower surface raised; nerves 6–20 mm apart, marginally open; veins scalariform, laxly reticulate, distinct. *Inflorescences* axillary to pseudoterminal, branching along rachis or not branching; rachis terete to slightly flattened, 3.5–14 cm long, crispate-hirsute when young; first-order branches up to 5.5 cm long; cymules dichasial, 1–5-flowered. *Bracts* and *bracteoles* triangular, margin entire, abaxially crispate-hirsute,

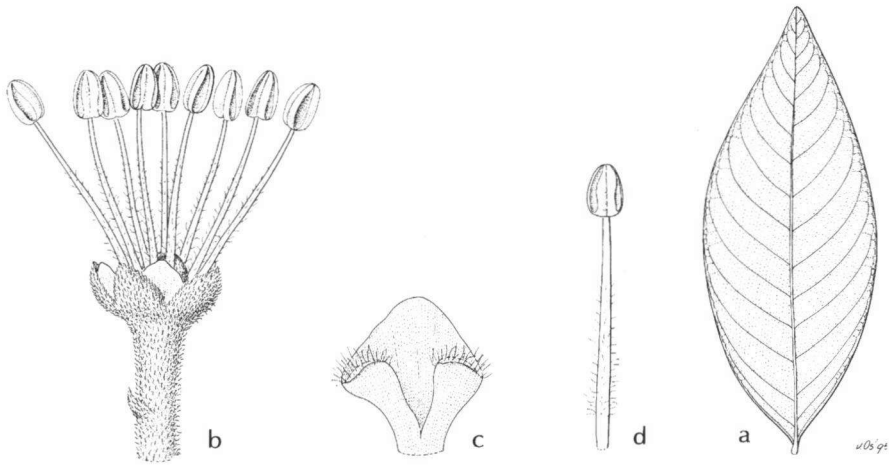

FIGURE 5.49. *Arytera pseudofoveolata* H. Turner. (a) Leaflet, × 0.5; (b) flower, × 12.5; (c) petal, × 25; (d) stamen, × 12.5. (a–d: *Brass 5560.*)

adaxially glabrous; bracts 0.3–0.7 mm long; bracteoles 0.1–0.2 mm long. *Pedicels* 1.5–3 mm long, crispate-hirsute. *Flowers* 1.5–2 mm diam. *Calyx* 0.7–0.9 mm high, teeth 0.5–0.7 mm high, (triangular to) ovate, not punctate, margin entire, not membranaceous, apex acute to obtuse; outside crispate-hirsute, inside glabrous. *Petals* 3–5, elliptic to almost semiorbicular, 0.6–1 by 0.5–0.7 mm, index 1.1–2, not punctate; claw 0.1–0.4 mm long, margin entire, apex obtuse; blade gradually decurrent into claw, outside glabrous, inside glabrous, margin subglabrous to subpilose; scales 0.3–0.7 mm long, adnate to margin up to halfway, basally not auricled, apex slightly broadened, sparsely pilose. *Disc* not lobed, pilose on rim and between stamens. *Stamens* (male) 6–8; filament 3–3.7 mm long, sparsely pilose; anther 0.5–0.6 mm long, straight, subglabrous to subpilose; connective not protruding. *Pistil* (male): 2-locular, ovary 0.5 mm long, puberulous. *Fruit* not observed.

Field notes — Small substage tree 30 ft. Leaves greyish underneath. Flowers white.

Distribution — Papua New Guinea: Central Province. Australia: Cape York area.

Habitat & Ecology — In semi-evergreen mesophyll vine forest and scrub, on ridges and hillsides; on latosols derived from lateritised basalt and from basic volcanic rocks among granite. Rainfall 160 cm annually average and monsoonal. Altitude up to 100 m. Flowering Nov.

Uses — Used for firewood (Murray Island).

Vernacular name — Ur sekerseker (Murray Island).

Specimens studied — PAPUA NEW GUINEA. Central Province: *Brass 5560.* — AUSTRALIA. N Queensland: *Jones 2551*; *Lawrie 104*; *L.S. Smith 2551, 12579*; *Webb & Tracey 6960, 7884.*

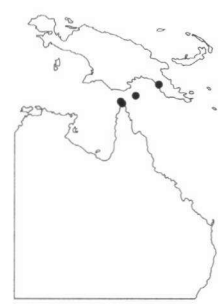

FIGURE 5.50. *Arytera pseudofoveolata* H. Turner. Distribution map.

5.3.5 – Incompletely known species

A26 – ***Arytera exostemonea*** Domin, Bibl. Bot. 22 (1927) 908; S.T. Reynolds, Austrobaileya 2 (1985) 166. — Type: *Domin s.n.*, Russel River, Australia, Jan. 1910 (n.v.).

I have not seen material of this species, but I agree with Reynolds that from the description it seems to be close to, if not identical with, *Arytera divaricata*.

5.3.6 – Excluded species

E1 – *Arytera concolor* (Gillespie) A.C. Smith, J. Arnold Arbor. 31 (1950) 298. — Type: *Gillespie 4794* (holo BISH; iso A, B, K, NY), Taveuni, Fiji, 3 March 1928 = **Cupaniopsis concolor** (Gillespie) R.W. Ham.
See: F.A.C.B. Adema, Leiden Bot. Ser. 15 (1991) 94.

E2 – *Arytera karang* Miq., Fl. Ind. Bat., Suppl. (1861) 510. — Type: *Diepenhorst HB 2487* (holo U; iso L), Priaman Prov., Sumatra, Indonesia = **Guioa diplopetala** (Hassk.) Radlk.
See: P.C. van Welzen, Leiden Bot. Ser. 12 (1989) 197.

E3 – *Arytera leichhardtii* (Benth.) Radlk., Sapind. Holl.-Ind. (1879) 44. — Type: *Leichhardt s.n.* (holo MEL sheet no. 74654), Queensland, Australia = **Dimocarpus leichhardtii** (Benth.) S.T. Reynolds.
See: S.T. Reynolds, Austrobaileya 1 (1983) 495.

E4 – *Arytera? macrocarpa* Miq., Fl. Ind. Bat., Suppl. (1861) 510. — Type: *Teijsmann s.n.*, Tarabangi, Lampong, Sumatra, Indonesia = **Triomma malaccensis** Hook. f. (Burseraceae).
See: P.W. Leenhouts, Fl. Males. ser. I, 5 (1956) 218.

E5 – *Arytera montana* Blume, Rumphia 3 (1849) 171. — Type: *Korthals s.n.* (holo L sheet no. 908.272-341), Sumatra, Indonesia = **Lepidopetalum montanum** (Blume) Radlk.
See: P.C. van Welzen et al., Blumea 36 (1992) 457.

E6 – *Arytera morocarpa* Walp., Ann. 7 (1869) 627 (printing error for *A. macrocarpa*, see there).

E7 – *Arytera semiglauca* F. Muell., Trans. Phil. Inst. Vict. 3 (1859) 25. — Type: *Hill & Mueller s.n.* (holo K), Moreton Bay, Australia = **Guioa semiglauca** (F. Muell.) Radlk.
See: P.C. van Welzen, Leiden Bot. Ser. 12 (1989) 285.

E8 – *Arytera silaka* Miq., Fl. Ind. Bat., Suppl. (1861) 510. — Type: *Teijsmann HB 610* (holo U; iso BO), Singkara, Sumatra, Indonesia = **Guioa pubescens** (Zoll. & Mor.) Radlk.
See: P.C. van Welzen, Leiden Bot. Ser. 12 (1989) 272.

E9 – *Arytera sordida* Radlk., Bot. Jahrb. 56 (1920) 301. — Type: *Ledermann 12492* (holo B†; iso M), Kaiserin-Augusta-Fluss Exp., Felsspitze, Papua New Guinea, Aug. 1913 = **Sarcopteryx rigida** Radlk.
See: P.C. van Welzen, Blumea 36 (1991) 98.

E10 – *Arytera subnitida* C.T. White, Proc. Roy. Soc. Queensl. 47 (1936) 56. — Type: *Brass 2345* (holo A; iso BRI, SING), Daintree R., Queensland, Australia, March 1932 = **Mischocarpus exangulatus** (F. Muell.) Radlk.
See: R.W.J.M. van der Ham, Blumea 23 (1977) 266.

5.4 – *MISCHARYTERA*

5.4.1 – Generic description

MISCHARYTERA (Radlk.) H. Turner, *gen. nov., stat. nov.*

Arytera sect. *Mischarytera* Radlk. in Engl., Pflanzenr. 98 (1933) 1271. — Type species: *Mischarytera lautereriana* (F.M. Bailey) H. Turner.

Trees. Indument consisting of rather short, appressed, straight hairs; glandular scales absent; buds not 'varnished.' *Branchlets* terete, smooth, hairy when young. *Leaves* paripinnate, (2–)3–11-jugate; petiole pulvinate, lenticels present or absent; rachis hemiterete to flattened, not, rarely (*M. lautereriana*) slightly, winged, approx. glabrous. *Leaflets* opposite to alternate, petioluled; petiolules pulvinate, lenticels present; blade ovate to elliptic to obovate, not to slightly falcate, very coriaceous to chartaceous, punctate; base attenuate to acute, symmetric; margin entire to slightly serrate near apex, flat to slightly revolute; apex obtuse to acuminate, very apex retuse, rarely (*M. lautereriana*) rounded, mucronulate or not; upper surface smooth, (sub)glabrous; lower surface smooth, without papillae, (sub)glabrous, domatia sacs or pits in axils of nerves, opening on top; venation on upper surface flat or slightly sunken (*M. bullata*), midrib slightly raised, on lower surface usually raised, sometimes only midrib so; nerves marginally looped; veins laxly reticulate. *Inflorescences* thyrsoid, axillary to pseudoterminal, branching along rachis; rachis terete to flattened, puberulous when young; cymules dichasial or cincinnate (*M. lautereriana*). *Bracts* and *bracteoles* triangular to ovate, margin entire to slightly dentate, abaxially puberulous, adaxially glabrous. *Flowers* actinomorphic, seemingly hermaphrodite, but presumably functionally unisexual, male flowers with an underdeveloped pistil and relatively long stamens, female flowers with a well-developed pistil and short stamens; male and female flowers presumably (although rarely actually observed in herbarium specimens) usually in same inflorescence. *Calyx* 5-dentate to -partite, persistent in fruit; teeth equal, teeth triangular to ovate, (slightly) punctate, margin entire to slightly dentate, membranaceous; outside glabrous to puberulous, inside glabrous. *Petals* 5, equal, with a distinct claw; blade outside (sub)glabrous; scales absent or minute, not crested. *Disc* annular, complete, glabrous. *Stamens* 7 or 8; filament at least basally pilose; anther basifix, straight, glabrous; thecae latrorsely opening with a longitudinal slit; connective not protruding

beyond thecae. *Pistil:* ovary 3-locular, smooth, subglabrous to puberulous; ovules one per locule, ascending, apotropous, campylotropous; style and stigma elongating in fruit, usually (sub)persistent; stigma shortly 3-lobed. *Fruit* a slightly obcordate to almost globose capsule, with 1–3 well-developed lobes, opening loculicidally or loculifragally, axil thickened transversely; outside glabrescent when ripe, usually smooth, inside glabrous; stipe distinct, slender; edge of margin rounded; dissepiments complete; lobes laterally not flattened; exocarp thick, coriaceous, mesocarp thick, coraceous to woody, endocarp thin, chartaceous, with an extra sclerenchymatic layer radiating from attachment of seed, leaving axis and suture free, reaching up to 1/2–2/3 of height of lobe, detaching from fruit wall in mature fruit. *Seed* orbicular to ellipsoid; arilloid apically open, covering entire seed, sometimes slightly alate, consisting of 1 layer; hilum (sub)basal; micropylar wart usually indistinct; exotesta thin, coriaceous; endotesta thin, more membranaceous. *Embryo* notorrhizal, cotyledons obliquely dorsoventrally above or laterally beside each other, apices not or slightly elongated (*M. macrobotrys*), surface smooth or irregular; radicle dorsoventrally flattened, inserted in a pocket formed by endotesta, margin glabrous; plumule inconspicuous.

5.4.2 – Key to the species

1 a. Bracts up to 1.5 mm long; leaves up to 11-jugate; leaflets narrow (index 3–6.2); lateral veins 1.5–7 mm apart [Australia] ..... **M2: M. lautereriana**
b. Bracts shorter than 1 mm; leaves up to 7-jugate; leaflets broader (index 2–3.4); lateral veins 5–18 mm apart **2**
2 a. Fruit large (2.5–3 cm high); stipe long (5–6 mm); inflorescence with 7–15 flowers per cymule; petiole 4–5.5 cm long; leaf rachis 4.5–9.5 cm long; leaflets very coriaceous, slightly bullate [Papua New Guinea] ..... **M1: M. bullata**
b. Fruit smaller (1.8–2 cm high); stipe short (2–3 mm); inflorescence with 3–7 flowers per cymule; petiole more than 6 cm long; leaf rachis 8.5–32.5 cm long; leaflets chartaceous, not bullate [Australia, Papua New Guinea] . **M3: M. macrobotrys**

5.4.3 – Species descriptions

M1 - Mischarytera bullata (H. Turner) H. Turner, *comb. nov.* — Fig. 5.51, 5.52

Arytera bullata H. Turner, Blumea 38 (1993) 137; Fl. Males. I, 11 (3) (1994) 471. — Type: *Hartley 12077* (holo A; iso CANB, K, L, LAE), five miles S of Sassaura, Eastern Highlands Province, Papua New Guinea, 23 July 1963.

Tree. Branchlets smooth, shortly puberulous when young; flowering twigs 6 mm thick. *Leaves* 3–6-jugate; petiole 4–5.5 cm long, lenticels present abaxially; rachis 4.5–9.5 cm long, hemiterete. *Leaflets* subopposite to alternate, petioluled; petiolules 6–9 mm long, 2-grooved; blade oblong-elliptic, 6.7–10.9 by 3–4 cm, index 2.2–2.9, slightly falcate, slightly bullate, very coriaceous, punctate; margin entire, flat, slightly revolute; apex obtuse to slightly acuminate, very apex retuse, not to minutely mucronulate; lower surface colour slightly different from that of upper surface, domatia large pits to sacs; venation on upper surface slightly sunken, colour same as lamina, on

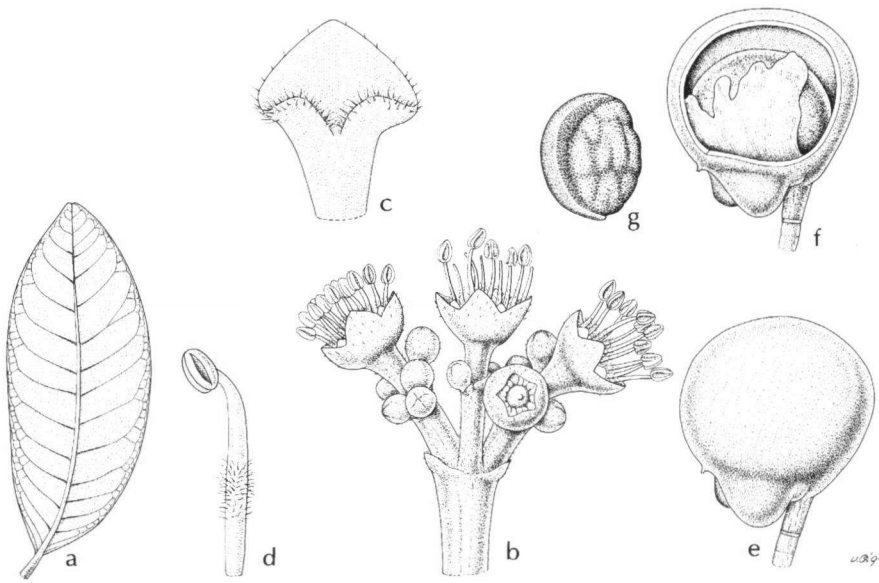

FIGURE 5.51. *Mischarytera bullata* H. Turner. (a) Leaflet, × 0.5; (b) cymule, × 6; (c) petal, × 25; (d) stamen, × 6; (e) fruit, × 1; (f) partly dissected fruit showing extra layer of endocarp, × 1; (g) embryo, × 1. (a–g: *Hartley 12077*.)

lower surface raised; nerves 5–12 mm apart; veins distinct. *Inflorescences* pseudoterminal; rachis flattened, 17–22.5 cm long; first-order branches up to 10 cm long; cymules dichasial, 7–15-flowered. *Bracts* and *bracteoles* triangular, margin entire, slightly punctate; bracts 0.3–0.8 mm long; bracteoles 0.2–0.3 mm long. *Pedicels* 0.6–1 mm long, elongating up to 3 mm in fruit, puberulous. *Flowers* c. 2 mm diam. *Calyx* 0.8–1 mm high, teeth 0.6–0.8 mm high, triangular, margin entire, apex acute to obtuse; outside puberulous. *Petals* oblong-elliptic, 0.9–1 by 0.7–1 mm, index 1–1.4, slightly punctate; claw 0.4–0.6 mm long, margin entire, apex rounded; blade abruptly decurrent into claw, inside subpuberulous, margin puberulous at base of blade; scales absent or present, up to 0.2 mm long, enation of margin, basally auricled, apex not broadened. *Stamens* (male) 7 or 8; filament 2–2.3 mm long, basally pilose; anther c. 0.3 mm long. *Pistil* (female): ovary c. 0.6 mm long, subpuberulous; style and stigma c. 0.3 mm long, elongating up to 0.7–1 mm in fruit, in fruit upper 0.2–0.3 mm stigmatic. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 2.7–3 cm high by 2.6–4.5 cm broad, opening loculifragally, outside smooth to slightly rugose; stipe 5–6 mm long; angle between lobes c. 120°; blackish brown; lobes laterally not flattened, valves c. 24 mm high by 17–18 mm long; endocarp dark brown. *Seed* orbicular, laterally not flattened, c. 17 by 19 mm, blackish; arilloid not alate, very thick especially towards base, fleshy, drab brown; hilum approx. orbicular, c. 3 by 3 mm; endotesta blackish. *Embryo:* cotyledons secondarily laterally beside each other, slightly unequal, lower larger, apices not elongated, surface irregular with a knobby appearance; radicle 3–4.5 mm long.

Field notes — Tree c. 36 m high, 90 cm dbh. Outer bark light grey, smooth; inner bark reddish brown. Petals and stamens white. Fruit hard, green.

Distribution — Papua New Guinea: Eastern Highlands Province.

Habitat & Ecology — In oak forest. Altitude c. 1500 m. Flowering July.

Note — Only known from the type collection.

FIGURE 5.52. *Mischarytera bullata* H. Turner. Distribution map.

M2 - Mischarytera lautereriana (F.M. Bailey) H. Turner, *comb. nov.* — Fig. 5.53, 5.54

Nephelium lautererianum F.M. Bailey, Bot. Bull. Queensl. Dep. Agric. 4 (1891) 8; Queensl. Fl. 1 (1899) 304. — *Arytera lautereriana* Radlk., Fedde Rep. 20 (1924) 37; W.D. Francis, Proc. Roy. Soc. Queensl. 38 (1927) 67, fig. 2–4, t. 13: 3–6; Radlk. in Engl., Pflanzenr. 98 (1933) 1283; W.D. Francis, Austr. Rain For. Trees (1951) 260, figs. 5: 3–6, 7, 152, 153; R.W. Ham, Blumea 23 (1977) 291; S.T. Reynolds, Fl. Austr. 25 (1985) 89; Austrobaileya 2 (1985) 159. —Type: *Simmonds & Bailey s. n.* (holo BRI sheet no. 25328, n.v.; iso BM, K), Eudlo Scrub, Queensland, Australia, Nov. 1891.

Tree. Branchlets smooth, puberulous to sericeous when young; flowering twigs 2–5 mm thick. *Leaves* (2–)3–11-jugate; petiole 2.5–11.3 cm long, lenticels present abaxially; rachis 3.2–24 cm long, flattened, not to slightly winged. *Leaflets* opposite to subopposite (to alternate), subsessile to petioluled; petiolules 2–15 mm long, distinctly 1-grooved; blade narrowly ovate to oblong elliptic, 3.2–16.9 by 0.9–3.7 cm, index 3–6.2, not to slightly falcate, coriaceous, densely punctate; margin entire to slightly serrate near apex, flat to slightly undulating, sometimes revolute; apex obtuse to acuminate, very apex retuse (to rounded), usually mucronulate; lower surface colour same as to more reddish than that of upper surface, domatia few to many pits or sacs, situated mostly on basiscopic side of midrib, not near tip; venation on upper surface flat, colour same as lamina, on lower surface flat, midrib raised; nerves 1.5–7 mm apart; veins not distinct. *Inflorescences* axillary to pseudoterminal; rachis terete to flattened, 4–23.5 cm long; first-order branches up to 7.5 cm long; cymules dichasial to cincinnate, 1–5-flowered. *Bracts* and *bracteoles* triangular to ovate, margin entire to slightly dentate; bracts 0.8–1.5 mm long; bracteoles 0.3–0.5 mm long. *Pedicels* 0.5–3 mm long, subglabrous to puberulous. *Flowers* 1.5–2.5 mm diam. *Calyx* 0.4–1 mm high, teeth 0.3–0.9 mm high, triangular to ovate, margin entire to dentate, apex acute to acuminate; outside glabrous to subpuberulous. *Petals* ovate to triangular, (male) 0.8–1.7 by 0.6–1 mm, index 1.2–2, (female) 0.4–1 by 0.4–0.8 mm, index 1–1.4, not punctate; claw (male) 0.3–1.1, (female) up to 0.3 mm long, margin slightly dentate near apex, apex obtuse to acute; blade abruptly decurrent into claw, inside puberulous, margin glabrous; scales 0.1–0.3 mm long, enation of margin, basally sometimes auricled, apex not broadened, membranaceous margin absent. *Stamens* (male) 7 or 8; filament 2.5–3.5 mm long, basally pilose; anther 0.6–0.8 mm long. *Pistil* (female): ovary 0.7–1 mm long, subglabrous; style and stigma 0.4–0.7 mm long, elongating up to 1.5–2 mm in fruit, in fruit upper 0.1–0.2 mm stigmatic. *Fruit* slightly obcordate to almost globose,

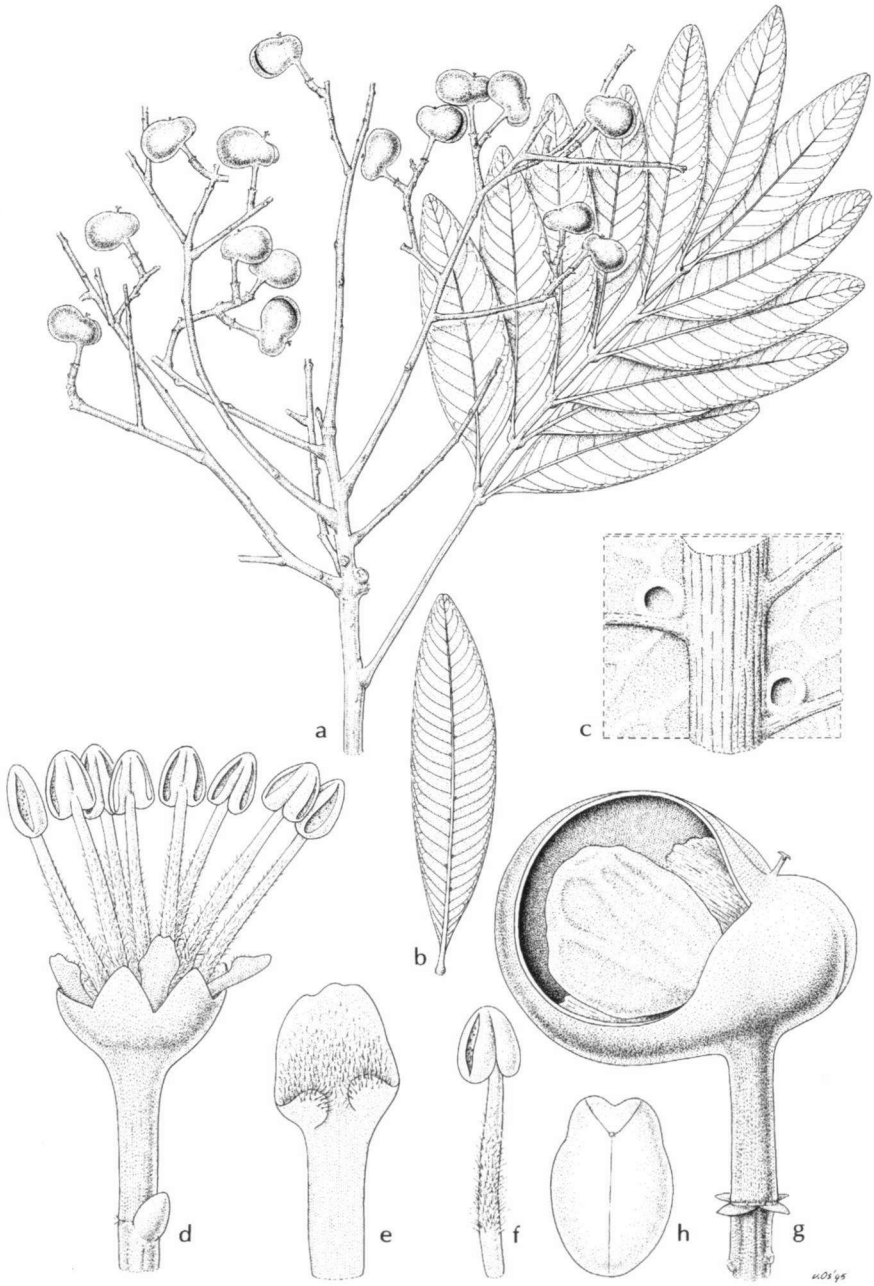

FIGURE 5.53. *Mischarytera lautereriana* (F.M. Bailey) H. Turner. (a) Habit, × 0.5; (b) leaflet, × 0.5; (c) domatia, × 12.5; (d) flower, × 25; (e) petal, × 25; (f) stamen, × 12.5; (g) partly dissected fruit, showing extra layer of endocarp, and immature seed enclosed in arilloid, × 3; (h) schematic top view of fruit, × 1.5. (a–c, g, h: *Clemens s.n.*; d–f: *W.J.F. McDonald, Fisher & Ryan 3183.*)

with 1–3 well-developed lobes, 0.9–1.9 cm high by 0.5–2 cm broad, opening loculifragally, outside smooth, inside sometimes pilose around attachment of seed; stipe 3–8 mm long; angle between lobes c. 120–180°; blackish to dark reddish brown; valves 10–13 mm high by 10–13 mm long; endocarp light brown. *Seed* ellipsoid, laterally flattened, 6.5–12 by 4.5–8 mm, brown; arilloid alate, thin, membranaceous to chartaceous, pale brownish; hilum somewhat lateral, elliptic, 1.2–2 by 0.9–1 mm; endotesta blackish to light brown. *Embryo:* cotyledons laterally beside each other, equal, apices not elongated, surface smooth; radicle 1–1.7 mm long.

Field notes — Tree, 8–30 m high, 15–50 cm dbh. Stem deeply fluted, sometimes buttressed. Outer bark brown to mid-grey; inner bark (subrhytidome layer) green on the outside, within with a narrow yellow-brown layer and a broader pinkish brown layer near the sapwood. Sapwood corrugated, whitish, c. 1.2 cm thick; heartwood pinkish. Leaves dark glossy green above, duller below. Flowers with a marked perfume; sepals green, petals cream. Young fruit light green. Fruits sought by forest creatures (Clemens).

Distribution — Australia: Queensland.

Habitat & Ecology — In rainforest and complex notophyll vine forest together with *Ficus macrophylla* and *Tristania conferta*. On soils derived from basalt and greenstone. Altitude 680–1100 m. Flowering Apr.–July; fruiting July–Nov.

Uses — The arilloid is sometimes used to make jam. The wood is said to be suitable for flooring and scantlings (cf. Francis, l. c.).

Vernacular names — Corduroy tamarind, Rose tamarind.

Note — *Moore s. n.*, 1868, head of MacLeay River, NSW, is somewhat aberrant in the shape and venation of the leaflets, and in the shape of the domatia. It was also collected somewhat more southerly than the other specimen.

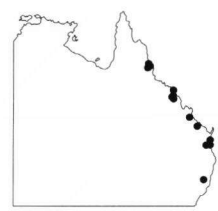

FIGURE 5.54. *Mischarytera lautereriana* (F. M. Bailey) H. Turner. Distribution map.

Specimens studied — AUSTRALIA. Queensland: 24 specimens. New South Wales: 1 specimen.

M3 - Mischarytera macrobotrys (Merr. & Perry) H. Turner, *comb. nov.* — Fig. 5.55, 5.56

Mischocarpus macrobotrys Merr. & Perry, J. Arnold Arbor. 21 (1940) 524. — *Arytera macrobotrys* R.W. Ham, Blumea 23 (1977) 291; S.T. Reynolds, Fl. Austr. 25 (1985) 90; Austrobaileya 2 (1985) 160; H. Turner, Fl. Males. I, 11 (3) (1994) 474. — Type: *Brass 7618* (holo A; iso BRI, L), Lake Daviumbu, Middle Fly River, Papua New Guinea, Aug. 1936.

Tree. Branchlets smooth, puberulous when young; flowering twigs 5–8 mm thick. *Leaves* 3–6-jugate; petiole 6–10.5 cm long, lenticels absent abaxially; rachis 8.5–32.5 cm long, (hemi)terete. *Leaflets* subopposite to alternate, petioluled; petiolules 6–12 mm long, not to slightly 1-grooved; blade elliptic to slightly obovate, 7.7–18 by 3.3–5.9 cm, index 2.1–3.4, not falcate, subcoriaceous to chartaceous, densely punctate; margin entire, flat, not to slightly revolute; apex acuminate, very apex retuse, minutely mucronulate; lower surface colour approx. same as that of upper surface, domatia sacs; venation on upper surface flat, colour yellowish to same as lamina, on lower surface

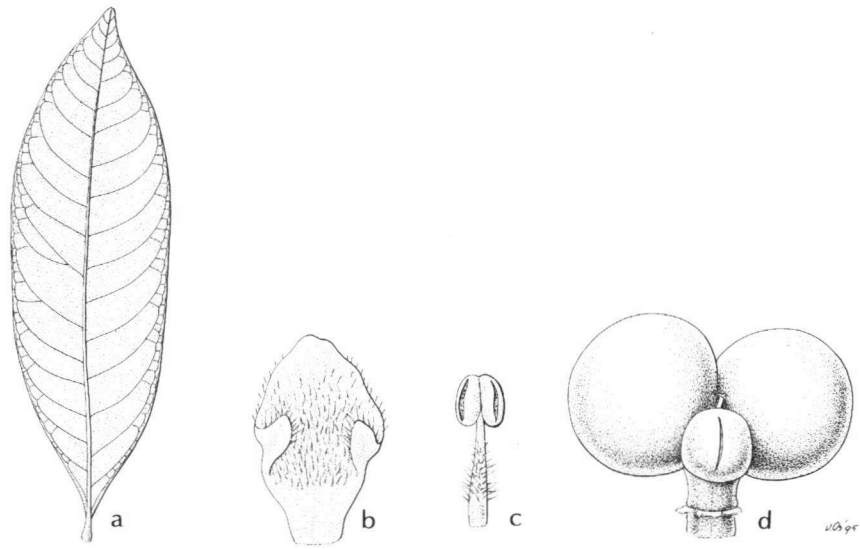

FIGURE 5.55. *Mischarytera macrobotrys* (Merr. & Perry) H. Turner. (a) Leaflet, × 0.5; (b) petal, × 25; (c) stamen, × 12.5; (d) fruit, × 1.5. (a–c: *Brass 7618*; d: *Brass 8057*.)

raised; nerves 5–20 mm apart; veins distinct. *Inflorescences* axillary to pseudoterminal; rachis flattened, 17–40 cm long; first-order branches up to 20 cm long; cymules dichasial, 3–7-flowered. *Bracts* and *bracteoles* triangular, punctate; bracts 0.3–1 mm long; bracteoles 0.1–0.4 mm long. *Pedicels* 1.5–2 mm long, puberulous. *Flowers* 1.5–1.7 mm diam. *Calyx* 0.5–0.9 mm high, teeth 0.3–0.6 mm high, triangular to ovate, margin entire, apex acute to obtuse; outside (sub)puberulous. *Petals* ovate, 0.8–1.1 by 0.6–1 mm, index 1–1.5, punctate; claw 0.2–0.3 mm long, margin entire to slightly denticulate, apex rounded to acute; blade gradually decurrent into claw, inside pilose, margin pilose; scales minute or absent, adnate to or enation of margin, up to 0.4 mm long, basally sometimes auricled, apex sometimes slightly broadened and forked, sparsely pilose. *Stamens* (male) 7 or 8; filament 1.8–2.5 mm long, pilose; anther 0.3–0.6 mm long. *Pistil* (female): ovary c. 1 mm long, puberulous; style and stigma 1–1.2 mm long, elongating up to at least 2 mm in fruit, in fruit upper c. 0.5 mm stigmatic, papillose. *Fruit* slightly obcordate, with 1 or 2 well-developed lobes, 1.8–3 cm high by 1.8–2.8 cm broad, opening loculicidally or loculifragally, axil thickened transversely, outside smooth; stipe 2–3 mm long; angle between lobes c. 120°; blackish; valves 1.8–3 cm high by 1.8–2.8 cm long; endocarp dark brown to greyish brown. *Seed* ovoid to orbicular, laterally slightly flattened, c. 13 by 12 mm, pale brown; arilloid not alate, very thick, especially towards base, fleshy to spongy, drab brown; hilum elliptic, c. 5 by 4–5 mm; endotesta dark brown. *Embryo:* cotyledons obliquely dorsoventrally above each other, unequal, upper larger, apices slightly elongated, surface irregular with a knobby appearance; radicle c. 2.5 mm long.

Field notes — Tree 7–20 m high, 20 cm dbh, buttressed. Bark brown, lenticellate, slightly fissured. Sapwood surface corrugated. Leaves up to 70 cm long, smooth and shiny; venation pale. Flowers cream-coloured to white. Fruits green, dehiscent; arilloid translucent or yellow, acidic.

Distribution — Papua New Guinea: Along middle and lower Fly River; Australia: Cape York area.

Habitat & Ecology — Substage or canopy tree, common on ridges, also in rainforest margin. Altitude 75–80 m. Flowering July, Aug.; fruiting Oct., Nov.

Specimens studied — PAPUA NEW GUINEA. Western Province: *Brass 7464, 7618, 8057.* — AUSTRALIA. Queensland: *Dockrill 467*; *Hyland 3574RFK.*

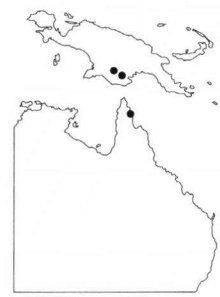

FIGURE 5.56. *Mischarytera macrobotrys* (Merr. & Perry) H. Turner. Distribution map.

5.5 – IDENTIFICATION LIST

The numbers in **bold** are the species numbers as given in Sections 5.3 and 5.4.

A 4605: **A15**; 4642: **A15**; NC3173: **A15** — Achmad (F.G.) 4066: **A15** — Adduru 141: **A15** — Afriastini 1496: **A15** — Ahern 295: **A15** — Ahern's collector 274: **A15** — Angian 7732: **A15** — Anning 367: **A11** — ANU 2846: **A19**; 2875: **A19**.

Backer 74: **A15**; 24869: **A15**; 33406: **A15**; 33407: **A15**; 33408: **A15**; 33409: **A15**; 33410: **A15** — Balajadia 3740: **A15**; 3760: **A15**; 3806: **A15** — Balansa 147: **A5**; 148: **A6**; 150: **A1**; 151: **A1**; 1442: **A5**; 1445: **A13**; 2264: **A1**; 2264a: **A1**; 2841: **A13** — van Balgooy 6009: **A15** — van Balgooy & Mamesah 6486: **A15** — Bartlett 13929: **A15** — Baudouin 134a: **A13**; 689: **A1**; 690: **A6** — Bäuerlen 504: **A9**; 510: **A9**; 512: **A9**; 854: **A9**; 22350: **A9**; 22385: **A9** — Baumann-Bodenheim 5031: **A1**; 5876: **A13**; 6053: **A1**; 7365: **A1** — bb 2852: **A15**; 4182: **A15**; 8670: **A15**; 14345: **A15**; 24990: **A15**; 25337: **A15** — Beccari 1: **A15**; FI 2799, a, b: **A15**; FI 2800, a, b: **A15**; FI 2801a, b, c: **A15**; FI 2842: **A15** — den Berger 661: **A15** — Bernardi 9538: **A12**; 9539: **A12**; 9680: **A1**; 13030: **A22**; 13057: **A4**; 13081: **A4**; 13103: **A4**; 13222: **A22**; 13260: **A4**; 13315: **A4**; 13367: **A22** — Bernier 190: **A5**; 12028: **A6** — Berry K40: **A4** — van Beusekom & Santisuk 2878: **A15**; 2929: **A15** — Blake (S.T.) 2776: **A9** — Blanch 118: **A15** — Blume 1314: **A15** — de Boer 6630: **A15** — Bogle & Bogle 570: **A15** — Boorman 22384: **A10** — Bourdy 187: **A22**; 803: **A22** — Bourret 1178: **A1** — Brascamp VI: **A15** — Brass 3760: **A17**; 5560: **A25**; 7464: **M3**; 7618: **M3**; 7620: **A20**; 7743: **A20**; 8057: **M3**; 8422: **A20**; 8483: **A20**; 19157: **A10**; 20251: **A24** — Brousmiche 354: **A1** — Bryan 413: **A4** — BS 5219: **A15**; 6189: **A15**; 14061: **A15**; 20901: **A15**; 21753: **A15**; 23370: **A15**; 26276: **A15**; 42634: **A15**; 44061: **A15**; 48336: **A15**; 48952: **A15**; 49100: **A15**; 78227: **A15**; 78594: **A15** — BSIP 711: **A15**; 4066: **A4**; 5645: **A4**; 5691: **A4**; 5726: **A4**; 6113: **A4**; 9004: **A4**; 13339: **A4**; 13772: **A4**; 13844: **A4**; 13967: **A4**; 14019: **A4**; 14968: **A4**; 15020: **A4**; 15839: **A4**; 16538: **A4**; 17519: **A4**; 18152: **A4** — Burger 2055: **A15**; 2075: **A15** — Burley, Turikin et al. 2705: **A15** — Buwalda 5107: **A15** — BW 431: **A15**; 505: **A15**; 558: **A15**; 2871: **A15**; 5254: **A15**; 9542: **A15**; 10439: **A15**; 10747: **A15**; 10794: **A15**; 10873: **A15**; 15616: **A15** — Byrnes 3490: **A10**.

Cabalion 1520: **A4** — Carr 11080: **A17**; 11554: **A17**; 13406: **A15**; 13502: **A5**; 13522: **A15**; 14969: **A14** — Carron 25: **A9** — Castro & Melegrito 1623: **A15** — Cel /V-142: **A15**; I 93: **A15** — Chanel 151: **A4** — Chevalier 38350: **A15**; 41205: **A15** — Chow 70864: **A15** — Christophersen 462: **A4**; 1142: **A4** — Christophersen & Hume 1895: **A4**; 1906: **A4** — Chun & Tso 43612: **A15**; 43633: **A15**; 43840: **A15**; 44711: **A15** — Clark, Pickard & Coveny 1301: **A9** — Clemens (J. & M.S.) 4000: **A15** — Clemens (M.S.) 10657: **A15** — Compton 777: **A1**; 915: **A12** — Constable 3591:

A10 — Craven & Schodde 267: **A15** — Cribs 680: **A1** — Crosby 32: **A4** — Cult. BO IL 32(a): **A15** — Cuming 1761: **A15** — Cunningham 27: **A10**; 28: **A10**; 128: **A10**.

Däniker 2702: **A5** — D'Alleizette 1458: **A15** — Dallachy 14480: **A10** — Degener 15346: **A4**; 32135: **A4** — Degener & Ordonez 13565: **A4** — Deplanche 57: **A22**; 280: **A6**; 447: **A6** — Dietrich 243: **A9**; 318: **A10**; 549: **A10**; 623: **A10**; 870: **A10**; 1370: **A10**; 1775: **A10**; 2426: **A10** — Dockrill 467: **M3** — Docters van Leeuwen 1921: **A15** — Domin 6261: **A10**; 6262: **A10**; 6263: **A10**.

Ebalo 499: **A15** — Edeling 14441: **A15** — Elbert 3406: **A15** — Elmer 7136: **A15**; 13772: **A15**; 17165: **A15**; 17430: **A15**; 22006: **A15** — Elsol & Stanley 501: **A11** — Endert 5105: **A15**.

Fawcett 173: **A9**; 213: **A9**; 22351: **A9**; 185-24-173: **A9**; A63: **A10**; E22: **A10** — FB 217: **A15**; 295: **A15**; 477: **A15**; 772: **A15**; 863: **A15**; 1136: **A15**; 1466: **A15**; 1476: **A15**; 2529: **A15**; 2589: **A15**; 2976: **A15**; 5663: **A15**; 9216: **A15**; 9306: **A15**; 9361: **A15**; 9394: **A15**; 14760: **A15**; 17709: **A15**; 24038: **A15**; 24650: **A15**; 24678: **A15**; 25478: **A15**; 26257: **A15**; 26893: **A15**; 26998: **A15**; 27067: **A15**; 27084: **A15**; 27773: **A15**; 28832: **A15** — Fleury 38943: **A15**; 39047: **A15** — Floyd 1882: **A10** — Forbes 2624: **A15** — Forster PIF 4799: **A16**; PIF 6663: **A11** — Forster & Bean 5800: **A8** — Fox 11287: **A15** — Franc 825: **A6**; 1189: **A1**; 2104: **A6** — Francis 22359: **M2** — Fraser 91: **A15** — FRI (KEP) 3529: **A15**; 21556: **A15**; 21658: **A15**; 26230: **A15**; 27640: **A15**; 29242: **A15**; 71397: **A15**; 98719: **A15**; 98726: **A15**; 115677: **A15** — Friedberg 532: **A15**; 1060: **A15** — Fung 20433: **A15**.

Garrett 145: **A15** — Geesink, Hattink & Charoenphol 7366: **A15** — Geesink, Phanichapol & Santisuk 5675: **A15** — Gibbs 2664: **A15**; 2697: **A15**; 4332: **A15** — Gillespie 3924: **A4** — Godwin C2322: **A2** — Goklin 2958: **A15** — Goodenough 1491: **A15** — Graham 2488: **A24** — Gray 1352: **A10**; 1354: **A10**; 3545: **A10**; 4454: **A10**; 4850: **M2** — Gray & Gray 3910: **A10** — Greenwood 478: **A4**; 478: **A4** — Griffith 988: **A15**; 990: **A15**; 14324: **A15** — Guillaumin 12026: **A1** — Guillaumin & Baumann-Bodenheim 11109: **A1**; 11155: **A1**; 12114: **A12**; 12176: **A12** — Guppy 273: **A4**.

Hallier 918: **A15**; 1161: **A15** — Haniff 372: **A15** — Hartley 11354: **A18**; 12077: **M1**; 13124: **A15** — Helfer 33: **A15**; 51: **A15**; 989: **A15** — Henry (A.) 8391: **A15**; 8395: **A15**; 8547: **A15** — Henry (B.C.) 140: **A15** — Hoff 958: **A1**; 1218: **A5**; 2126: **A6** — Hoogerwerf 144: **A15** — Hopkins & Graham 3191: **A10** — Horsfield 5(bis): **A15**; 7(bis): **A15** — How 70404: **A15**; 70864: **A15**; 71758: **A15**; 72992: **A15**; 73368: **A15** — Howard 374: **A4** — Hyland 1353: **A10**; 2533: **A2**; 2926: **A2**; 3574: **M3**; 4168: **M2**; 4218: **M2**; 10854: **A2**; AFO2847: **A10**.

Iboet 419: **A15**; 529: **A15** — Irby 280: **A9**.

Ja 45: **A15**; 2267: **A15**; 3830: **A15** — Jacobs 4976: **A15**; 8071: **A15**; 9509: **A7** — Jaffré 1010: **A12**; 1131: **A12**; 2980: **A6** — Jessup 79: **A10**; 266: **A9** — Jessup & Reynolds 164: **A9** — Jones 1682: **A9**; 2551: **A25**; 3476: **A10**; C243: **A11** — Jonker 304: **A15**.

Kajewski 219: **A4**; 381: **A22**; 386: **A4**; 742: **A4**; 827a: **A4**; 842: **A22**; 1050: **M2**; 1129: **A10**; 2013: **A15**; 2573: **A23** — Kalshoven 1652: **A15** — Karta 276: **A15** — Kato, Ueda, Okamoto, Sunarno & Mahjar C8350: **A15** — Keith 9884: **A15** — Kerr 7264: **A15** — Kheon Winit 631: **A15** — King's collector 695: **A15**; 885: **A15**; 4456: **A15** — Kjellberg 782: **A15**; 2286: **A15** — KL 1766: **A15**; 1822: **A15** — de Kok 541: **A1**; 541a: **A13** — Koorders 3056b: **A15**; 7271b: **A15**; 7283b: **A15**; 7284b: **A15**; 7285b: **A15**; 7330b: **A15**; 7335b: **A15**; 7336b: **A15**; 7337b: **A15**; 7338b: **A15**; 7343b: **A15**; 7346b: **A15**; 7358b: **A15**; 7410b: **A15**; 7574b: **A15**; 7575b: **A15**; 7585b: **A15**; 7586b: **A15**; 7593b: **A15**; 7594b: **A15**; 7595b: **A15**; 7598b: **A15**; 7602b: **A15**; 12802b: **A15**; 14693b: **A15**; 14701b: **A15**; 18852b: **A15**; 20180b: **A15**; 21869b: **A15**; 21876b: **A15**; 24645b: **A15**; 24767b: **A15**; 24893b: **A15**; 25327b: **A15**; 25402b: **A15**; 25462b: **A15**; 26237b: **A15**; 26575b: **A15**; 27003b: **A15**; 28402b: **A15**; 28669b: **A15**; 29070b: **A15**; 29121b: **A15**; 29921b: **A15**; 30423b: **A15**; 33306b: **A15**; 33724b: **A15**; 33730b: **A15**; 34108b: **A15**; 34960b: **A15**; 36106b: **A15**; 36423b: **A15**; 39122b: **A15**; 39711b: **A15**; 39714b: **A15**; 47770b: **A15**; 47772b: **A15** — Koroiveibau & Qoro 14767: **A4** — Kostermans 319: **A15**; 1572: **A15**; 4652: **A15**; 18303: **A15**; 18519: **A15**; 19105: **A15**; 19134: **A15**; 19193: **A15**; 22005: **A15** — Kostermans & Wirawan 60: **A15**; 316: **A15** — Kramer 14: **A15** — Krempf 1657: **A15** — Kwapena 123: **A17**; 127: **A17**.

Labohm 1182: **A15** — Lace 4788: **A15**; 5182: **A15** — LAE 51560: **A15**; 58188: **A23**; 74816: **A18** — Lakshminarasimhan 20702: **A15** — Lam 7631: **A11**; 7673: **A11** — Lambach 1241: **A15**; 1304: **A15** — Latz 3506: **A2** — Lau 14: **A15** — Laumonier 6932: **A15** — Lauterbach 2305: **A15** — Lawrie 104: **A25** — Le Rat 110: **A13**; 570: **A1**; 576: **A1** — Lécard 107: **A6**; 168: **A5** — Ledermann 9555: **A7** — Lei 14: **A15**; 740: **A15** — Liang 61987: **A15**; 62199: **A15**; 64531: **A15**; 65433: **A15**; 66244: **A15**; 66311: **A15**; 69349: **A15** — Loher 2072: **A15**; 2073: **A15**; 5883: **A15**; 5884: **A15**; 12313: **A15**; 12462: **A15**; 12749: **A15**; 12767: **A15**; 12861: **A15**; 13250: **A15** — Lütjeharms 4470: **A15**.

MacDaniels 2017: **A6** — McClure 7703: **A15** — MacDonald (W.) 146: **A10** — MacDonald (W.J.F.) 3439: **A8** — MacDonald, Fisher & Ryan 3183: **M2** — MacKee 995: **A1**; 2434: **A6**; 2437: **A1**; 3792: **A6**; 4204: **A12**; 4564: **A12**; 7839: **A6**; 12489: **A6**; 12520: **A12**; 12944: **A12**; 12950: **A12**; 13282: **A13**; 14524: **A1**; 14553: **A1**; 15255: **A12**; 15527: **A12**; 15643: **A1**; 17081: **A22**; 18381: **A5**; 18939: **A22**; 18973: **A22**; 18988: **A1**; 20384: **A12**; 20444: **A12**; 20670: **A6**; 20686: **A12**; 21758: **A1**; 22074: **A6**; 22273: **A13**; 22324: **A1**; 23434: **A13**; 23674: **A1**; 23910: **A12**; 24708: **A5**; 24709: **A6**; 24968: **A5**; 24986: **A5**; 25078: **A5**; 25149: **A1**; 25313: **A5**; 25410: **A22**; 25434: **A22**; 25499: **A22**; 25510: **A6**; 26330: **A5**; 26975: **A6**; 27089: **A1**; 27160: **A12**; 27701: **A12**; 28156: **A5**; 28567: **A12**; 28591: **A22**; 28861: **A1**; 29747: **A5**; 30066: **A1**; 30770: **A6**; 33345: **A12**; 33563: **A6**; 34377: **A6**; 34897: **A5**; 34909: **A1**; 35051: **A6**; 35054: **A1**; 35132: **A1**; 35458: **A6**; 35760: **A5**; 37881: **A1**; 37882: **A5**; 37887: **A5**; 38028: **A12**; 38953: **A1**; 39170: **A6**; 39174: **A5**; 39765: **A22**; 39767: **A1**; 40425: **A1**; 40428: **A5**; 40653: **A12**; 40979: **A6**; 41134: **A5**; 41368: **A1**; 41472: **A5**; 41497: **A22**; 42130: **A1**; 42137: **A21**; 42286: **A22**; 42449: **A5**; 42524: **A13**; 43786: **A22**; 43887: **A6**; 44085: **A22**; 44857: **A5**; 44885: **A22** — MacMillan 5049: **A6** — MacPherson 2452: **A13**; 2838: **A13**; 4647: **A5**; 5590: **A1**; 5667: **A13**; 6506: **A12** — Mail 2713: **A15** — Maingay 439: **A15** — Maradjo 53: **A15** — Martin 750: **A15** — Maxwell 85-585: **A15**; 86-292: **A15** — Meebold 3420: **A10**; 16668: **A4** — Merrill 1367: **A15**; 2971: **A15**; 5079: **A15**; 9446: **A15** — Metzner 266: **A15** — Michael 990: **A10** — Michael (N.) 3029: **A16** — Moore 21: **A10**; 22: **A10** — Morat 6003: **A4**; 6222: **A1**; 8642: **A21** — Mousset 1094: **A15** — Mueller 1463: **A10** — Mus. Neocal. 215: **A6**; 222: **A13**; 281: **A1**.

Nair 2614: **A15** — Naitau K16: **A4** — NGF 1308: **A15**; 2522: **A15**; 3771: **A15**; 4045: **A15**; 5238: **A15**; 7362: **A15**; 15418: **A15**; 15490: **A15**; 26789: **A23**; 26856: **A23**; 29771: **A15**; 45006: **A15** — Niyondham et al. 347: **A15** — Nothis 80: **A1**; 137: **A13** — Nur 1371: **A15**.

Orolfo 3804: **A15** — Otik 4242: **A15**.

Paijmans 386: **A20** — Pancher 77: **A1**; 79: **A6**; 138: **A1**; 149: **A1**; 215: **A6**; 222: **A13**; 610: **A5**; 734: **A1**; 778: **A6** — Parham 454: **A4** — Parham & Kuruvoli 13911: **A4** — Parham, Koroiveibau et al. 16691: **A4** — Parish 285: **A15** — Parkinson 507: **A15** — Parks 16317: **A1**? — Persietz 21: **A2**; 87: **A2**; 925: **A2** — Petit 83: **A6** — Pierre 5938: **A10** — de Pirey 37: **A15** — PNH 12334: **A15**; 15708: **A15**; 17569: **A15** — Poilane 444: **A15**; 972: **A15**; 1312: **A15**; 2732: **A15**; 4506: **A15**; 4553: **A15**; 7451: **A15**; 7812: **A15**; 7913: **A15**; 7926: **A15**; 7940: **A15**; 8359: **A15**; 9642: **A15**; 11958: **A15**; 11992: **A15**; 12009: **A15**; 15404: **A15**; 22160: **A15**; 22411: **A15**; 22668: **A15**; 24864: **A15**; 25356: **A15**; 30331: **A15** — Powell 23: **A4**; 348: **A4** — Prance 26651: **A4** — Pratt 79-1064: **A15** — Prawiroatmodjo & Soewoko 1782: **A15** — Puasa-Angian 3880: **A15** — Pullen 7229: **A20**.

Quadras 295: **A15**.

Ramos 363: **A15**; 861: **A15**; 1438: **A15** — Randall & Young 630: **A16** — Rechinger (K. & L.) 675: **A4** — Rechinger (K.) 1616: **A4** — Regalado & Vodonaivalu 839: **A4** — Reid 1: **M2** — Ridley 2162: **A15**; 5995: **A15** — Robinson 1317: **A15**; 1445: **A15**; 1484: **A15** — Rock 2628: **A15** — RSNH 33: **A4**; 111: **A22**; 6458: **A22**; 16065: **A4** — Russel-Smith & Lucas 4515: **A2**.

Saakov 98: **A15** — SAN 19911: **A15**; 21134: **A15**; 26289: **A15**; 27376: **A15**; 28781: **A15**; 31360: **A15**; 31956: **A15**; 33641: **A15**; 33812: **A15**; 33815: **A15**; 35056: **A15**; 35060: **A15**; 40484: **A15**; 43909: **A15**; 44555: **A15**; 47259: **A15**; 49139: **A15**; 49470: **A15**; 51725: **A15**; 56180: **A15**; 73309: **A15**; 80090: **A15**; 80765: **A15**; 80787: **A15**; 83769: **A15**; 83927: **A15**; 84316: **A15**; 92530: **A15**; 92566: **A15**; 95517: **A15**; 110972: **A15**; 113229: **A15**; 116181: **A15**; 116616: **A15**; 118930: **A15**;

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INDEX TO SCIENTIFIC NAMES

References are only made to taxa treated in Chapter 5. Accepted names are printed in Roman type, new names and combinations in **bold**, and synonyms in *italics*. Numbers preceded by a letter refer to those of the accepted species names under *Arytera* (A) or *Mischarytera* (M) and to those of the excluded species (E). Other references are by page number.