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A Systematic Revision of the Mangrove Genus *Avicennia* (Avicenniaceae) in Australasia*

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Abstract

In Australasia (including Australia, New Zealand, New Guinea and other islands in the south-western Pacific) the mangrove genus *Avicennia* L. consists of five species: *A. alba* Bl., *A. integra* N. C. Duke, *A. marina* (Forsk.) Vierh., *A. officinalis* L. and *A. rumphiana* Hallier f. Based on morphological characters and supported by allele patterns in isozyme studies (reported elsewhere), *A. marina* is divided into three varieties. Keys, descriptions, brief synonymy, descriptive figures and distribution maps are provided for each of the seven taxa.

Introduction

The genus *Avicennia* L. comprises a small group of tree species occurring chiefly within the mangrove zone of tropical sheltered coastlines of the world. In tropical regions this often includes a select group of coinhabitants, such as *Rhizophora* L. However, in subtropical and temperate tidal habitats *Avicennia* often occurs as the exclusive tree or shrub form, making it the most widely distributed of any mangrove. In addition, and again unlike other mangroves, it grows in a very wide range of salinities and intertidal topographic positions. These observations are very important in the present context, because recently such variations in habitat conditions were shown to correlate with morphologies of both leaves and floral parts in two species of *Avicennia* (Soto and Corrales 1987; Soto 1988; Duke 1990a). In view of these findings, systematic determinations need to be reassessed.

Tomlinson (1986) presented the most recent account summarising his findings and earlier treatments, particularly the detailed one by Moldenke (1960). *Avicennia* spp. were thus shown to be divided, with no species in common, into two biogeographic regions of the world; viz. Atlantic-eastern Pacific (New World), and Indo-western Pacific (Old World). The latter region, and Australasia in particular, will be assessed here.

According to Moldenke (1980b) this region included at least five species and five varieties, or eight taxa. Prior to this, Bakhuizen van den Brink (1921) grouped Indo-western Pacific taxa into two species, although one of them comprised four varieties (minus an Arabian one, which apparently corresponds to one of the Asian forms). In later Malaysian accounts, four species were recognised by Watson (1928) and Wyatt-Smith (1954). These four, along with a fifth taxon, *A. marina* var. *resinifera*, in southern Australasia, were similar to the Indo-western Pacific complement described by Bakhuizen van den Brink (1921). However, these five are not entirely consistent with five described for Papua New Guinea by Percival and Womersley (1975). Four taxa, *A. officinalis*, *A. alba*, *A. marina*, including the Asian and southern variety, are comparable. Differences, however, mainly surround the fifth taxon in each case, namely *A. lanata* in Wyatt-Smith (1954), and *A. eucalyptifolia* in Percival and

*Aust. Inst. Marine Sci. Contrib. No. 520.

Womersley (1975). They are not comparable, and the combination of both accounts again describe six taxa for the Indo-western Pacific.

Therefore, for this region, Moldenke (1960, 1967, 1968, 1975a, 1975b, 1976, 1977, 1978, 1980a) described few additional taxa, apart from some new combinations or varieties. Nevertheless, his detailed and exhaustive treatment did not resolve the troublesome systematics of this group, and specific distinctions and distributional records of all taxa remained uncertain. For example, around mainland Australia, he recognised at least seven taxa including five species: *A. alba* in the Northern Territory, *A. balanophora* in Queensland (Brisbane River only), *A. eucalyptifolia* in northern Australia, *A. marina* var. *anomala* in north-eastern Queensland (Low Isles only), var. *resinifera* (= var. *australasica*) all around mainland Australia, var. *marina* in Western Australia, and *A. officinalis* in New South Wales. This complex assessment was seriously questioned by several, mainly field-based accounts (Jones 1971;

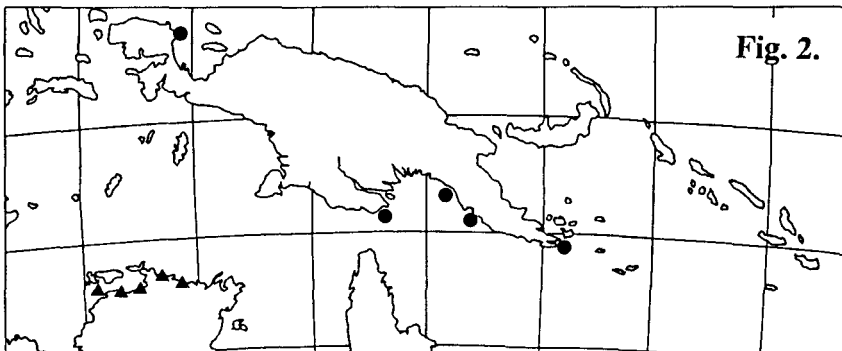
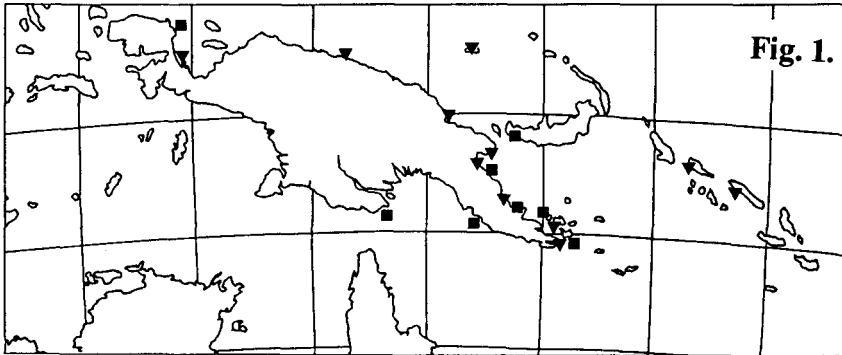


Fig. 1. Distribution of *Avicennia alba* Blume (●) and *A. rumphiana* Hallier f. (▲) in Australasia.

Fig. 2. Distribution of *Avicennia integra* N. C. Duke (●) and *A. officinalis* L. (▲) in Australasia.

Semeniuk *et al.* 1978; Wells 1982, 1983; Duke 1988) which in total recognised just two species in Australia. Firstly, *A. officinalis* was not recorded from the east coast, and the closely comparable *A. integra* was found only in the Northern Territory. Secondly, *A. marina* was widespread and extremely variable, and as such it presumably accounted for all determinations of putative species and varieties proposed by Moldenke.

Based on an extensive reassessment of morphological characters (Duke 1990a), and a study of allozyme variation (Duke, unpublished data), the present study found that *Avicennia* in Australasia comprised five species. Three of them, *A. alba* Bl., *A. officinalis* L., and *A. rumphiana* Hallier f., are confined to New Guinea and the western Pacific islands (Figs 1, 2); a fourth, *A. integra* N. C. Duke, is endemic to the Northern Territory of Australia (Fig. 2); and the fifth, *A. marina* (Forsk.) Vierh., is widespread (Fig. 3),

morphologically variable, and consists of three varieties. One corresponds with *A. marina* var. *australasica* (Walp.) Moldenke, previously known as var. *resinifera* (Forst.) Bakh., in south-eastern mainland Australia and northern New Zealand, the other two are less well defined. They include a 'south-western' Australian variety which appears referable to the Asian form and Arabian Type (hence, var. *marina*), and a 'north-eastern' Australia and New Guinea variety which in part includes *A. eucalyptifolia* Zipp. ex Miq., here reduced to var. *eucalyptifolia* (Zipp. ex Miq.) N. C. Duke. While var. *australasica* is distinguished chiefly by bark character and calyx pubescence, the other two differ mainly in flower dimensions and position of the stigma in relation to anthers.

Allozyme patterns in *A. marina* show primary separation of genes into two distinct geographic areas: those in south-eastern Australia, New Caledonia, Lord Howe Island and New Zealand; and those elsewhere, viz. northern and western Australia, Malaysia and Thailand. This observation demonstrates the greater difference of var. *australasica* from the other two, and this was supported by the importance of their morphological distinctions. Furthermore, infraspecific status was confirmed for those populations in suggested contact zones (Fig. 3)

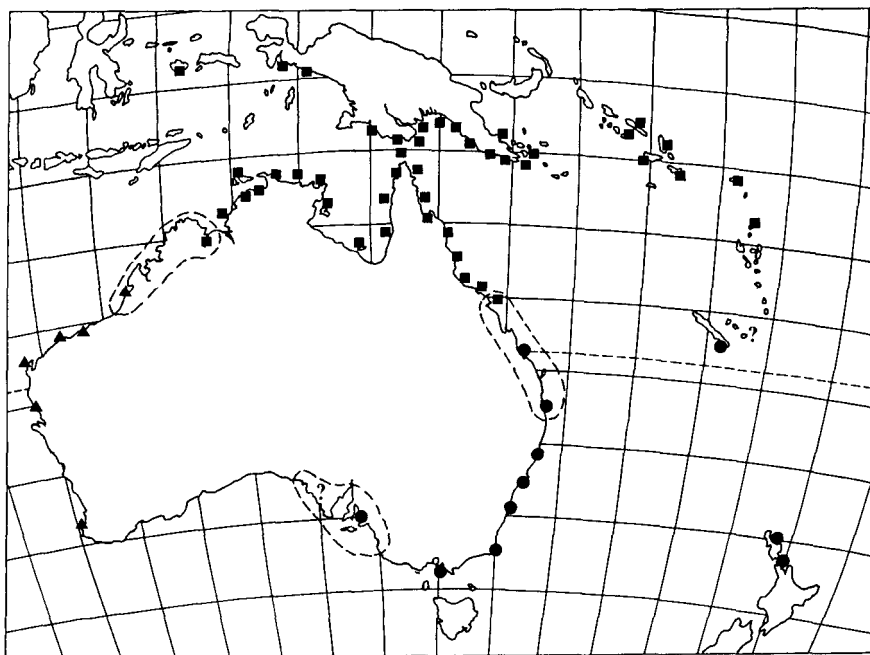


Fig. 3. Distribution of *Avicennia marina* (Forsk.) Vierh. varieties in Australasia: var. *australasica* (Walp.) Moldenke (n); var. *eucalyptifolia* (Zipp. ex Miq.) N. C. Duke (g); and, var. *marina* (5). Zones of major overlap and intergradation are indicated by dashed outlines.

by progeny from individual trees displaying Mendelian patterns and proportions of respective alleles. Therefore, in consideration of this mixing, diagnostic problems are expected because any relationship between morphological characters and allozyme patterns has not been established for these zones, covering several hundred kilometres. Specimens from New Caledonia and Lord Howe Island, however, were referred to var. *australasica* based on flower and leaf morphology, as well as on allozyme patterns. This conclusion is supported in part by Tomlinson (1986) who compared specimens in New Caledonia with those in New Zealand. Together, they suggest an extension of the Australian east coast zone of overlap, across to the island chain north of New Caledonia (Fig. 3).

Herbaria

This revision is based on both herbarium and field observations. Contributing herbaria (abbreviations from Holmgren and Keuken 1974): AIMS, Herbarium of the Australian Institute of Marine Science, Townsville (note: this collection is now lodged with BRI); BRI,

Queensland Herbarium, Brisbane; DNA, Herbarium of the Conservation Commission of the Northern Territory, Darwin; and LAE, Division of Botany, Office of Forests, Lae, Papua New Guinea.

Generic Circumscription and Synonymy

The synonymy is not exhaustive, but is an attempt to identify all names and authorities applied to taxa in Australasia. It was not possible to view most type specimens, but those reported are collated chiefly according to the various descriptive accounts. Problems with this approach are readily acknowledged, and a more rigorous appraisal is recommended. Observations on colour, texture and form are generally field-based. Detailed measurements were taken from dried herbarium specimens, unless otherwise stated. A complete list of specimens examined is lodged with the journal as an Accessory Publication*. In addition, mean values are often given in parentheses immediately following attribute ranges of specimen means listed in descriptions.

Avicennia L., Sp. Pl. 1 (1753) 110.

Type species: Avicennia officinalis L.

Bontia L. ex Loefl., Iter Hisp. (1758) 193.

Donatia Loefl., l.c. (1758).

Upata Rheede ex Adans., Fam. Pl. 2 (1763) 12 and 201.

Horau Adans., l.c. (1763) 80 and 585.

Sceura Forsk., Flor. Aegypt.-Arab. 2 (1775) 37.

Racua J.F. Gmel. in L., Syst. Nat. ed. 13, 1, 2 (1789) 1612.

Corna Noronha, Verh. Batav. Gen. 5 ed. 1, 4 (1790) 2.

Racka Bruce, Trav. Abyss. et Nub. 5 (1790) app. 44.

Halodendron Du Petit Thou., Gen. Nov. Madagas. (1806) 8.

Halodendron Roem. and Schult. in L., Syst. Veg., ed. 16, 3 (1818) 485.

Hilairanthus Van Tiegh., Jour. de Bot. (Morot) 12 (1898) 357-8.

Tree, shrub-like, about 1-2 m high, or spreading to columnar, 30 m high, canopy moderately open; trunk base simple, occasionally with low placed aerial roots; bark either white, smooth, flaky, or grey-brown, fissured, pustular, with many short longitudinal fissures or reticulate lines forming very small scales; subsurface roots radiating, horizontal; pneumatophores vertical, finger-like, unbranched, flaky, soft spongy light wood, 10-30 cm above substrate, 0.5-1 cm wide near distal tip. Branchlets and twigs with jointed appearance from swollen nodes and subterminal vegetative growth, surfaces of dense grey, white or brownish, short, dense hairs. Leaves simple, opposite, decussate, entire, coriaceous, mostly inconspicuous veins, midrib prominent below, young apical bud enclosed in petiolar groove of terminal leaf pair; petiole, 1-3 cm long, often pubescent on lower surface (indumentum of uniform dense palisade of microscopic club-shaped hairs), mostly semi-amplexicaul, decurrent tapering canaliculate along half of length as petiolar groove, remainder semi-terete to leaf blade; lamina obovate, ovate-elliptic to narrowly lanceolate, 4-17 cm long, green above, dull pale pubescent below; apex pointed or rounded. Inflorescences borne in upper axils, terminal or subterminal, pedunculate, usually umbellate or paniculate, capitate or spicate with 2-7 opposite, decussate bud pairs along a single mostly unbranched peduncle, lower units subtended by foliage leaves, upper by involute foliaceous or simplebracts, in all about 1-3 cm long at anthesis. Flowers sessile, bisexual, protandrous, 0.3-1.3 cm long, scented, mostly globose in bud, each subtended by one bract and two lateral bracteoles enclosing the calyx base; bract solitary, convex, triangular to oblong, sometimes foliaceous; bracteoles convex, elongate triangular to oblong; calyx 5-merous, outer surface pubescent or glabrous, lobes quincuncial, ovate; bracts and calyx edges ciliate to hairy, or entire; corolla actinomorphic or variably zygomorphic, tubular at base, lobes inner surface dull glabrous or pubescent, outer surface pubescent, mostly 4 (uncommonly 5 or 6), equal or slightly unequal, with rounded or obtuse distal apices, entire, often revolute, reflexed; stamens mostly 4 (uncommonly 5 or 6), either equal or unequal pairs, alternate with corolla lobes, inserted basally or around corolla tube mouth; anthers bilobed, dorsifixed, dehiscing introrsely by longitudinal slits, pollen adherent; ovary, ampulla-shaped or elongate conical, variably pubescent, superior, unilocular; style prominent; stigma bilobed, pointed arms

*Available from the Managing Editor, *Australian Systematic Botany*, 314 Albert St, East Melbourne, Vic. 3002, Australia.

equal or unequal, glabrous, often reflexed. Fruit cryptoviviparous, compressed ellipsoid or ovoid capsule, often with narrow persistent stylar beak, 1-4 cm long; pericarp thin (< 0.5 mm thick), outer surface variably pubescent, dull pale green, suture line green, bilateral, slightly indented; bract, bracteoles and calyx persistent on pericarp; pre-seedling solitary (rarely 2) in capsule, two large fleshy bright green (often purple tinted, rarely the yellow 'albino' form) cotyledons folded, one abaxially, the other adaxially around the plumular axis, mostly glabrous but often pubescent on concave, flat, or the least convex outer lobe surface; radicle elongate, terete, fully or partly hairy along length, about half propagule length; plumule pubescent, hairy about base, cryptic, not always present in propagule.

Distribution

Eight species in two widely separate, mostly tropical regions: three in the Atlantic, Caribbean and eastern Pacific (New World; note Tomlinson 1986); and five in the Indo-western Pacific (Old World). Fig. 4.

Ecology

Found commonly in mangrove swamps and salt pans, along tidal creeks, fringing sheltered bays and coastlines, and within coral reef ramparts and atoll lagoons. Trees may develop on virtually any substrate, but greatest expression is evident in firm black estuarine mud influenced by frequent tidal flooding and riverine outflow. *Avicennia* species are generally considered to be pioneers of mangrove forests, but this view must be qualified. Their common occurrence on newly accreting banks appears to be opportunistic because later on, if these banks are eroded, the trees will be uprooted. Their role in retarding bank erosion is more likely to be related directly with short-term factors such as episodic storm surges and riverine flooding. In this case any sustained damage is quickly rectified by rapid redevelopment of both undermined root systems and remaining above-ground structure. Plants have been observed to coppice from fractured trunks, and develop adventitious root systems from partly severed fallen trunks. This genus also shows a wide range of salinity tolerance, exemplified by *A. marina* being able to live in fresh stagnant water, and, in seasonally dry conditions where salinities of ground water approach 80‰. Similarly a wide tolerance to temperature is shown by the wide latitudinal range. In view of these diverse physiological tolerances the genus would be expected to be more dominant in tropical mangrove forests. However, this potential is substantially repressed by a combination of some shade intolerance of saplings, and by propagule-eating small crabs (Smith 1988). In the latter case, it is a lesson, firstly, to record the absence of *Avicennia* saplings where these crabs occur across the tidal profile and, secondly, to watch the scurrying and scavenging activity as propagules (and leaves) fall.

Notes

The position of *Avicennia* as a monogeneric family, Avicenniaceae Engl., is supported by at least 40 different authors from 1826 to 1974, as asserted by Moldenke (1960-1980a), and reaffirmed by Tomlinson (1986). I follow their view in this treatment, although others maintain that the genus belongs with the Verbenaceae (e.g. Kanis 1981). I believe more serious problems presently pertain to specific names than to familial classifications, especially with regard to the increasing number of studies on the role of individual species in trophodynamic interrelationships of intertidal and near-shore ecosystems. This account therefore concentrates on specific and infraspecific variation in the genus as found in the Indo-western Pacific region.

Brief Evaluation of Diagnostic Characters

Habitat

Most taxa occupy low intertidal positions, but *A. marina* is located virtually throughout the tidal range of mangroves (i.e. from around mean sea level to high spring level). Another taxon, *A. rumphiana*, occurs chiefly in high to mid intertidal sites. Furthermore, Australian species, *A. marina* and *A. integra*, express quite different upriver ranges with the latter having a very restricted occurrence within the range of the other.

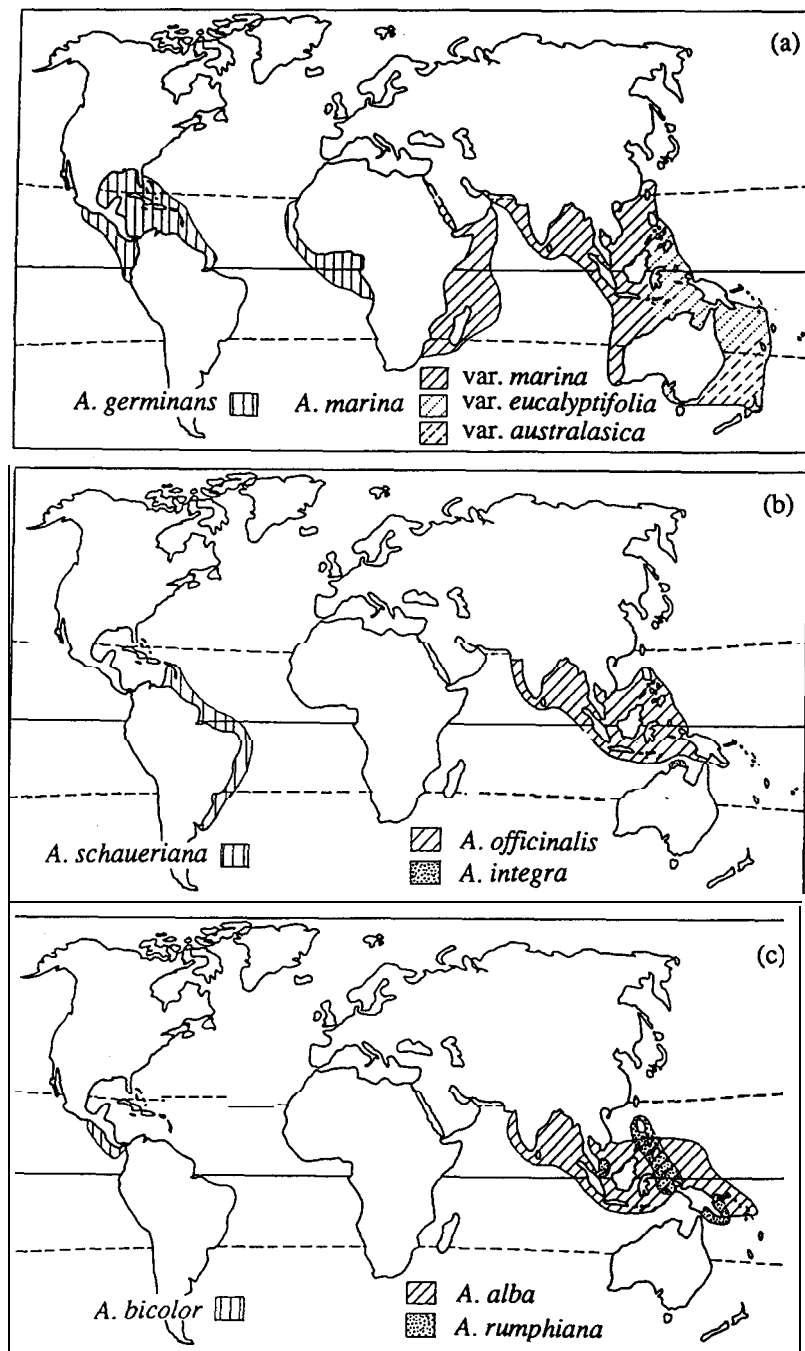


Fig. 4. World distribution of *Avicennia* taxa: (a) *A. germinans* (L.) L., *A. marina* (Forsk.) Vierh. var. *australasica* (Walp.) Moldenke, *A. marina* var. *eucalyptifolia* (Zipp. ex Miq.) N. C. Duke and *A. marina* var. *marina*; (b) *A. schaueriana* Stapf & Leechman ex Moldenke, *A. officinalis* L. and *A. integra* N. C. Duke; and (c) *A. bicolor* Standley, *A. alba* Blume and *A. rumphiana* Hallier f.

Habit

General foliage characteristics change subtly with each species. They all have mostly open spreading canopies with pale undersurfaces of leaves, but differ in coloration and leaf shape. They are bright green (slightly yellowish) as in *A. officinalis* and *A. integra*, greyish green as in *A. marina* and *A. rumphiana* or tend to be darker green as in *A. alba*. Leaf shape and apices also influence general canopy appearance; thus for species with round **apices the** canopy takes on a rounded softer look while acute apices present a sharp, spiked appearance. Such characteristics are useful to the field observer whereas differences in tree or shrub form are not, because most species have a notably variable habit, depending on site of occurrence.

Bark

In most taxa, trunk bark is fissured tending to pustular, and not flaky. However, for two varieties of *A. marina* in northern and western Australia, and New Guinea, the bark is smooth (chalky white when dry, green and blotchy brown when wet) and frequently thinly flaky.

Aerial Roots

Most species have some aerial or prop root development: this appears to be relatively prolific in both *A. officinalis* and *A. integra* but apparently absent in *A. rumphiana*. The roots tend to be woody not corky like pneumatophores. They are also placed low on the trunk, mostly within 1m of the substrate.

Pneumatophores

There are no apparent differences between taxa in pneumatophore length, thickness, distance from the trunk or frequency.

Leaves

Shape and size of leaves have previously been used as major taxonomic characters, but have now been found to be extremely unreliable and diagnostically confusing because they reflect environmental factors (Duke 1990a). This was particularly evident in samples from the same tree of *A. marina* where sun and shade leaf morphologies differed significantly. It therefore appears that unwarranted attention was directed towards leaf form of understandably limited herbarium specimens. Such potential problems did not escape the attention of recent field observers (e.g. Semeniuk *et al.* 1978; Wells 1982) or earlier descriptive botanists (e.g. Bakhuijzen van den Brink 1921). In view of these comments, such differences, noted earlier (*Habit*), can still be useful in specific determinations. Colour is less valuable in herbarium samples but leaf apices and general shape (note, ratios of L/W and L/'distance from blade-base to greatest width') are important characters when viewed conservatively.

Petiole

Lengths of petioles are of little use because ranges largely overlap for each species.

Inflorescence

One species, *A. alba*, is characterised by an inflorescence that tends to be spicate while all others are capitate. Other variation in inflorescences is mostly shared with ranges in numbers of buds overlapping significantly between species. Pubescence on peduncles, while present in all species, differs in texture and hairiness in sufficient amounts to provide additional support for some diagnoses. Thus at one extreme *A. officinalis* and *A. integra* are notably puberulent, while at the other *A. rumphiana* is tomentose.

Calyx and Bracts

There are important differences in pubescence of outer calyx surface and edges which assist in distinguishing between species, and the varieties of *A. marina*. Thus *A. marina* is observed to be variable in calyx pubescence but other Australasian taxa are either virtually glabrous (*A. officinalis* and *A. integra*) or largely pubescent. *Avicennia integra* is characterised by entire calyx lobes while all others have ciliate or hairy edges.

Corolla

Old World taxa are characterised by glabrous inner and pubescent outer surfaces of the corolla. However, there are marked differences between the sizes of the lobes, and their diameters at anthesis. The corolla lobes of *A. officinalis* and *A. integra* are twice as large as those of other species with roughly the same lobes. Furthermore, all taxa are chiefly actinomorphic, although *A. officinalis* and *A. integra* are variably zygomorphic, differing within individual inflorescences.

Anthers, Style and Ovary

The length of filaments, the placement of their attachment in the corolla mouth, the size of anthers, the position of anthers in relation to stigma, the shape of the style, and the amount and type of pubescence are all important supplementary characters. Briefly *A. officinalis* and *A. integra* have an elongate flask- or ampulla-shaped style exerted above or equal to the upper edge of long-stalked (> anther length) large anthers, while other Australasian taxa generally have short thick styles ending either well below the anthers or barely at the upper edge of short-stalked (\leq anther length) small anthers.

Propagule

The surface of the pericarp is different between species. It varies from tomentose or woolly in *A. rumphiana*, to velvety in *A. officinalis* and *A. integra*, to puberulent in *A. alba* and *A. marina*. Propagule shape is useful as well, being rounded in *A. rumphiana* and *A. marina*, elongate in *A. officinalis* and *A. integra* and very elongate in *A. alba*. The amount of hair along the radicle (hypocotyl) may also be used to distinguish species. Thus the short woolly collars about the root tip of *A. marina* and *A. alba* are distinct from the more extended woolly collar of *A. integra* and the fully hairy radicles of *A. officinalis* and *A. rumphiana*. *Avicennia alba* is further distinguished by hooked hairs on the radicle while others have straight or wavy hairs.

Key to the Australasian Species of *Avicennia*

- 1a. Leaf apex usually pointed; radicle glabrous except for short hairy collar about distal tip; pericarp puberulent; flower small 3-8 mm long, corolla diameter 3-7 mm, calyx 3-6 mm long; inflorescence spicate or capitate 2
- b. Leaf apex usually rounded; radicle hairy along most, if not entire length; pericarp velvety or densely tomentose; flower variable in size 3-13 mm long, corolla diameter 4-12 mm, calyx 2-10 mm long; inflorescence capitate 3
- 2a. Inflorescence usually spicate; propagule very elongate with pointed distal end; style barely extended from ovary, minute; stigma positioned below lower edge of anthers; ovary glabrous on upper surface near style, pubescent below. *Northern New Guinea, western Pacific, Indo-Malesia to western India* 1. *A. alba*
- b. Inflorescence capitate; propagule ovoid with rounded distal end; style erect, short; stigma positioned between upper and lower edge of anthers; ovary pubescent below style. *New Zealand, mainland Australia, southern New Guinea, south-western Pacific, Indo-Malesia, to southern China, to India, Persian Gulf, Red Sea and eastern Africa* 3. *A. marina*
- 3a. Flower small, < 7 mm long, calyx < 4 mm long; style short; stigma positioned at lower edge of small (0.5 mm long) anthers; peduncle, small twigs and leaf undersurface yellowish to russet tomentose; propagule ovoid with rounded distal end; pericarp densely tomentose. *New Guinea, Indo-Malesia and the Philippines* 5. *A. rumphiana*
- b. Flower large, > 7 mm long, calyx \geq 5 mm long; style elongate; stigma exerted or positioned at upper edge of large (> 1 mm long) anthers; peduncle, small twigs and leaf undersurface pale puberulent; propagule elongate with pointed distal end; pericarp velvety 4
- 4a. Sepal, bracteole and bract edges ciliate, or hairy; calyx small, < 7 mm long, \leq 5 mm wide. *Southern New Guinea, Indo-Malesia, the Philippines to western India* 4. *A. officinalis*
- b. Sepal, bracteole and bract edges entire; calyx large, \geq 8 mm long, > 5 mm wide. *Australia (Northern Territory)* 2. *A. integra*

Species Descriptions

1. *Avicennia alba* Bl., Bijdr. Flor. Ned. Ind. 14 (1826) 821. Type: Blume 1700 (L, lecto). Indonesia. Java, Nusa Kambangan.

In part, var. *latifolia* Moldenke, Phytologia 1 (1940) 410. Type: Noerkas 58 (L, holo, BO 16934-6, -iso, NY-iso), Indonesia, Celebes.

Avicennia resinifera non Forst. f. *sensu* W. Griff., Trans. Linn. Soc. 20 (1846) 6, t. 1; Not. Pl. Asiat. 4 (1854) 186-8.

Avicennia officinalis non L. *sensu* Kurz. ex C. B. Clarke in Hook. f., Flor. Brit. Ind. 4 (1885) 604.

Sensu var. *alba* (Bl.) Hook. ex Jafri, Flor. Karachi (1966) 290.

Avicennia spicata Kuntze, Rev. Gen. Pl. 2 (1891) 502. Type: Kuntze 6045 (NY, lecto), Singapore.

Avicennia marina non (Forsk.) Vierh. *sensu* var. *alba* (Bl.) Bakh., Bull. Jard. Bot. Buitenz. 3 (1921) 207.

Tree, or shrub, to 25m high, often about 10m; trunk base simple, low-placed aerial roots rare; bark dark brown to black, warty or smooth, often with many short longitudinal fissures or reticulate lines forming very small scales; pneumatophores about 20 cm high, 5-10 mm wide near distal tip. Leaf lamina ovate-elliptic, apex mostly bluntly acute, 73-111 (93) mm long, 20-46 (33)mm wide, 34-63 (48)mm from base to greatest width, upper surface dark green satiny, undersurface pale finely pubescent; petiole 4-21 (14)mm long, glabrous above, often pubescent below. Inflorescence mostly spicate with 3-7 opposite, decussate bud-pairs positioned about bud length apart, around 20-30 mm long at anthesis. Flower 3-5mm long; bract narrowly triangular, often curved, asymmetric, edge ciliate, apex acute; bracteoles triangular, edges ciliate, apices acute; calyx lobes ovate, 3-4mm long, 2-4mm wide, edges ciliate or hairy, outer surface mostly pubescent except for glabrous distal margin about 0.5 mm wide; corolla actinomorphic, 4-6 mm diameter, lobes mostly 4, orange, slightly revolute, slightly reflexed, slightly unequal, 2-3 mm long, 2-3 mm wide, apices rounded, outer surface pubescent except for minute (much <0.5 mm wide) glabrous distal margin, inner surface dull glabrous; stamens mostly 4, alternate with corolla lobes, positioned equally around corolla mouth, about 0.5 mm long; anthers about 0.5 mm long; stigma glabrous, bilobed pointed arms equal, positioned about 0.5 mm below anthers; style minute, around 0.2 mm long, glabrous; ovary depressed conical, around 1.5 mm long, narrow distal surface glabrous, middle densely tomentose, base glabrous. Fruit compressed elongate ellipsoid, 19-27 (22) mm long, 10-15 (12) mm wide, 5-8 (6) mm thick, distal tip sharply acute with narrow (c. 0.2 mm) persistent stylar beak, about 0.5 mm long; pericarp outer surface dull pale green, puberulent; calyx persistent on pericarp, 2-3 mm long from base, 4-5 mm diameter; radicle about 9 mm long, mostly glabrous with densely hairy collar c. 2 mm wide, distal tip glabrous, hairs wavy, distally hooked; plumule about 4 mm long, puberulent, slightly hairy about base. Fig. 5.

Floral phenology: in New Guinea flowering occurs chiefly in December and January and propagules mature predominantly in March.

Distribution: *Avicennia alba* occurs from western India, through Indo-Malesia, south-eastern Asia, southern Philippines, Palau and Yap Islands of the western Pacific to northern Australasia. In this region it is apparently restricted to the north coast of New Guinea and islands immediately east. The eastern extent of the taxon is around the Solomon Islands, and its southern limit is around Milne Bay. The species is unknown in Australia. Figs. 1 and 4.

Ecology: this taxon is found along tidal river banks and about entrances of tidal inlets in Papua New Guinea. In these sites it generally occupies the lower tidal position of mangroves and it is commonly observed on newly formed mud banks.

Notes

Avicennia alba is readily distinguished by relatively spicate inflorescences, small flowers, and very elongate propagules. However, while these features have usually identified this taxon, there were some doubts regarding its specific status. Nevertheless, this was last shown when it was described as a variety of *A. marina* by Bakhuizen van den Brink (1921). Since then Moldenke (1960-80) has re-affirmed the specific status of Blume's original description.

On another matter, however, the variety *latifolia* proposed by Moldenke (1940) is presently rejected in the absence of more suitable evidence, because distinguishing attributes of leaf morphology may be influenced by environmental factors, as observed in *A. germinans* (L.) L. (Soto and Corrales 1987; Soto 1988) and *A. marina* (Duke 1990a).

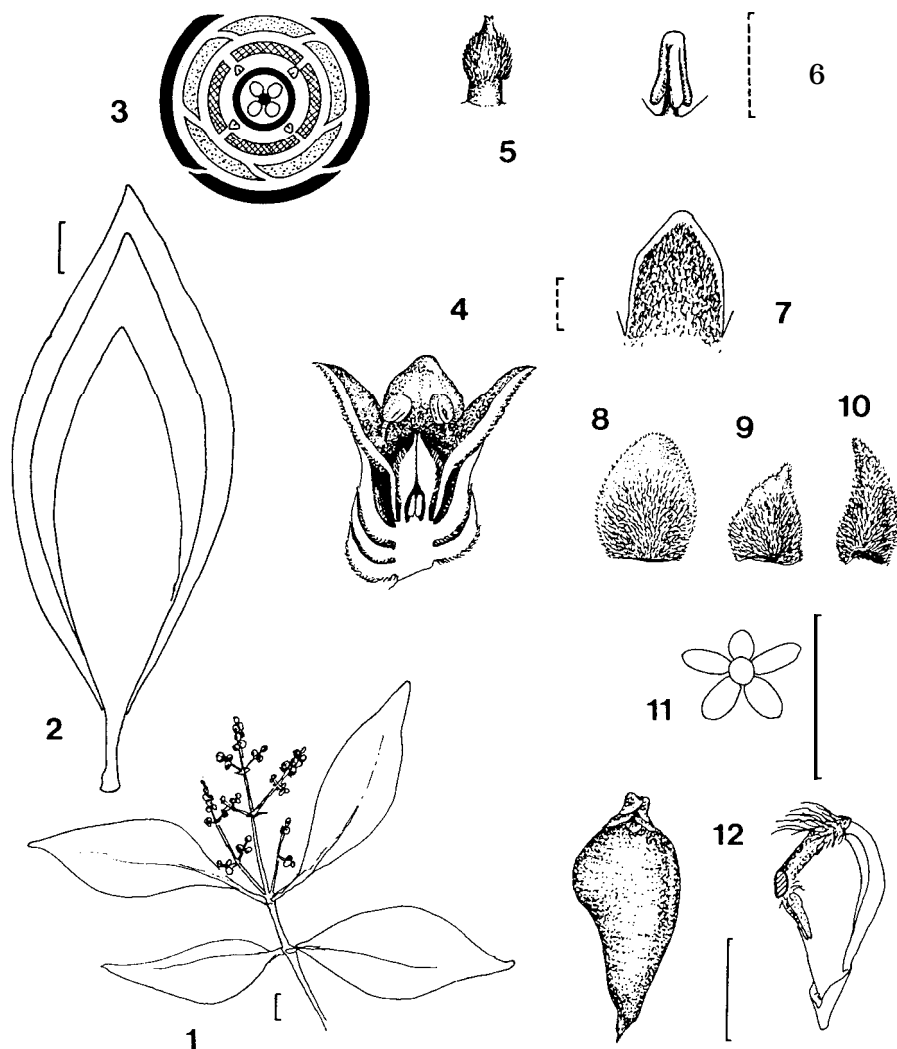


Fig. 5. *Avicennia alba* Blume. 1, Flowering branchlet; 2, mean range of leaf outlines; 3, floral diagram; 4, flower (longitudinal section) showing general internal anatomy at anthesis; 5, ovary and style; 6, isolated four-lobed placenta; 7, undersurface of single corolla lobe; 8, calyx lobe (from lower position in floral diagram), exterior surface; 9, bracteole, exterior surface; 10, bract, exterior surface; 11, diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12, mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal radicle and plumule. Solid scales = 1 cm, dashed scales = 1 mm. (Reference: 4-11, K. Mair NGF1808 12, D. Foreman LAE59275.)

Representative Specimens (33 collections examined)

THAILAND: Samut Prakan, Ban Bang Pu (13° 31' N, 100° 39' E), *H. h4.v.d. Kevie 1* (BRI 185667). MALAYSIA: Lahad Datu (5° 02' N, 118° 19' E), *G. H. S. Wood SAN16165* (BRI 254051); Brunei Town (4° 56' N, 114° 55' E), *B. E. Smythies s.n.* (BRI 254050); Tawao (4° 15' N, 117° 54' E), *A. D. E. Elmer 21250* (BRI); Salak R. (2° 30' N, 113° 30' E), *A. G. Wells s.n.* (DNA 12660). SINGAPORE: Changi

(1°23'N, 103°59'E), Hardail 129 (BRI). INDONESIA. Pulau Panaitan (6°36'S, 105° 12'E), *J. v. Borssum Waalkes* 747 (BRI). Java: Batavi (6° 05' S, 106° 48' E), *Bakhuizen van den Brink* 1191 (BRI). Irian Djaya: Geelvink Bay, Job I. (2° 38' S, 134° 27' E), *F. A. W. Schram BW15026* (LAE). PAPUA NEW GUINEA. Sepik: Vanimo Stn. (2° 40' S, 141° 20' E), *A. Gillison NGF25237* (BRI, LAE). Manus: Metaphor Village, Manus I. (2° 10' S, 146° 45' E), *D. Foreman & Katik LAE59275* (LAE). Madang: Madang (5° 13' S, 145° 47' E), *K. Muir NGF1808* (LAE). Morobe: Sisilia R., Umboi I. (5° 29' S, 147° 47' E), *B. Conn LAE66065* (BRI, LAE). Labu (6° 45' S, 146° 57' E), *T. G. Hartley 10293* (LAE). Northern: Komabun Village (9° 21' S, 149° 11' E), *R. D. Hoogland 4184* (LAE). Papuan Islands: Sewa Bay, Normanby I. (10° 00' S, 150° 55' E), *Y. Lelean LAE 52545* (LAE). Milne: Mime Bay northern (10° 24' S, 150° 32' E), *L. S. Smith NGF1370* (BRI, LAE); Modewa Bay, Gara R (10° 39' S, 105° 19' E), *L. J. Brass 28889* (LAE). SOLOMON ISLANDS. Choiseul: Pemba (7° 00' S, 157° 00'E), *I. Gafui BSIP18767* (LAE). Santa Ysabel: Allardyce Harbour (8° 20'S, 159° 44' E), *J. Sone BSIP2613A* (LAE 56288).

2. *Avicennia integra* N. C. Duke, Austral. Syst. Bot. 1 (1988) 177-80. Type: *A. G. Wells s.n.* (DNA14909, holo), *D. Hearne* 192 (DNA, topo), Australia, Northern Territory, Adelaide River (13° 15'S, 131° 07' E).

Avicennia officinalis non L. *sensu* A. G. Wells in B. F. Clough, Mangrove Ecosyst. Austral. (1982) 65; in H. J. Teas, Tasks Veg. Scien. 8 (1983) 61.

Tree, or shrub, to 2-7 m high; trunk base simple, low-placed aerial roots common; bark reddish brown, smooth in smaller forms, grey brown, pustular in larger trees; pneumatophores about 20-30 cm high. Leaf lamina ovate-elliptic, apex mostly rounded, slightly revolute, 59-129 (88) mm long, 26-53 (35) mm wide, 30-66 (44) mm from base to greatest width, upper surface bright satiny green, undersurface pale finely pubescent; petiole 11-26 (16) mm long, glabrous above, often pubescent below. Inflorescence mostly capitate with 1-3 opposite, decussate bud-pairs (often including a solitary terminal bud), about 20-30 mm long at anthesis. Flower 11-13 mm long, slightly scented; bract triangular, entire, sometimes foliaceous or absent; bracteoles oblong, entire; calyx lobes ovate, 8-10 mm long, 5-6 mm wide, entire, outer surface shiny, mostly glabrous, some pubescence at base; corolla variably zygomorphic, 7-11 mm diameter, lobes mostly 4 (sometimes 5 or 6), golden yellow, tending revolute, reflexed, unequal, 3-5 mm long, 3-4 mm wide, apices rounded, outer surface pubescent except for glabrous border about 1 mm wide, inner surface dull glabrous; stamens mostly 4, alternate with corolla lobes, positioned equally around corolla tube mouth, about 1.5 mm long for shorter pair, about 2.5 mm long for longer pair, anthers about 1.5 mm long; stigma narrow, glabrous, about 2 mm long, bilobed pointed arms unequal, not exceeding anthers or calyx; style elongate, about 4 mm long, distal half glabrous, lower densely tomentose; ovary, ampulla-shaped, about 2 mm long, densely tomentose. Fruit ellipsoidal, 21-23 mm long, 12-15 mm wide, 8-10 mm thick, distal tip mostly acute with very narrow (c. 0.5 mm) persistent stylar beak, to 4 mm long; pericarp outer surface pale grey-green, velvety pubescence; calyx persistent on pericarp, 6-10 mm long from base, 11-12 mm diameter, bract often absent; radicle about half propagule length, mostly densely hairy, basal portion c. 2 mm long, glabrous, distal tip blunt, glabrous; plumule about 6 mm long, finely pubescent, hairy about base. Fig. 6.

Floral phenology: flowering occurs chiefly from September to November and fruiting in December and January.

Distribution: *Avicennia integra* is located in 15 mainly riverine estuaries of the Northern Territory, Australia (Wells 1982, 1983), from Buffalo Creek (Shoal Bay, near Darwin; 12° 20' S, 130° 57' E) in the west to an eastern limit of the Glyde River (eastern Arnhem Land; 12° 16'S, 135° 03'E). Figs 2 and 4.

Ecology: Wells (1982) describes the habitat as soft low-intertidal mud banks along convex meanders of river estuaries that remain brackish for most of the year. In this situation it is considered a coloniser, in association with *Sonneratia alba* Smith and *Acanthus ilicifolius* L. A lack of seedlings beneath established trees was taken to be an indication of shade intolerance in *A. integra* but, as recently shown (Smith 1988), it may also be the result of propagule-eating small crabs which inhabit shaded sites. Upriver distribution is also restricted, and *A. integra* is confined to the middle third of the riverine range of *A. marina*. By contrast, the latter cosmopolitan taxon occurs out on the sea shore and well upstream toward the tidal limit.

Notes

Avicennia integra has only recently been distinguished from *A. officinalis*. This was mostly due to the lack of a full description for the Northern Territory plant. However, general confusion surrounding *A. officinalis* in Australia and the region also meant that a full comparative base was unavailable anyway. This treatment found *A. integra* distinguished by calyx edges which are entire rather than ciliate or hairy, as noted for *A. officinalis*. Supportive characters include larger dimensions of the flower in *A. integra* compared with *A. officinalis*, particularly those of calyx width (5.3-6.4 mm; 4.0-5.3 mm) and length (8.0-9.8 mm; 5.0-6.7 mm) and length of anthers (about 1.5 and 2.5 mm; about 0.8

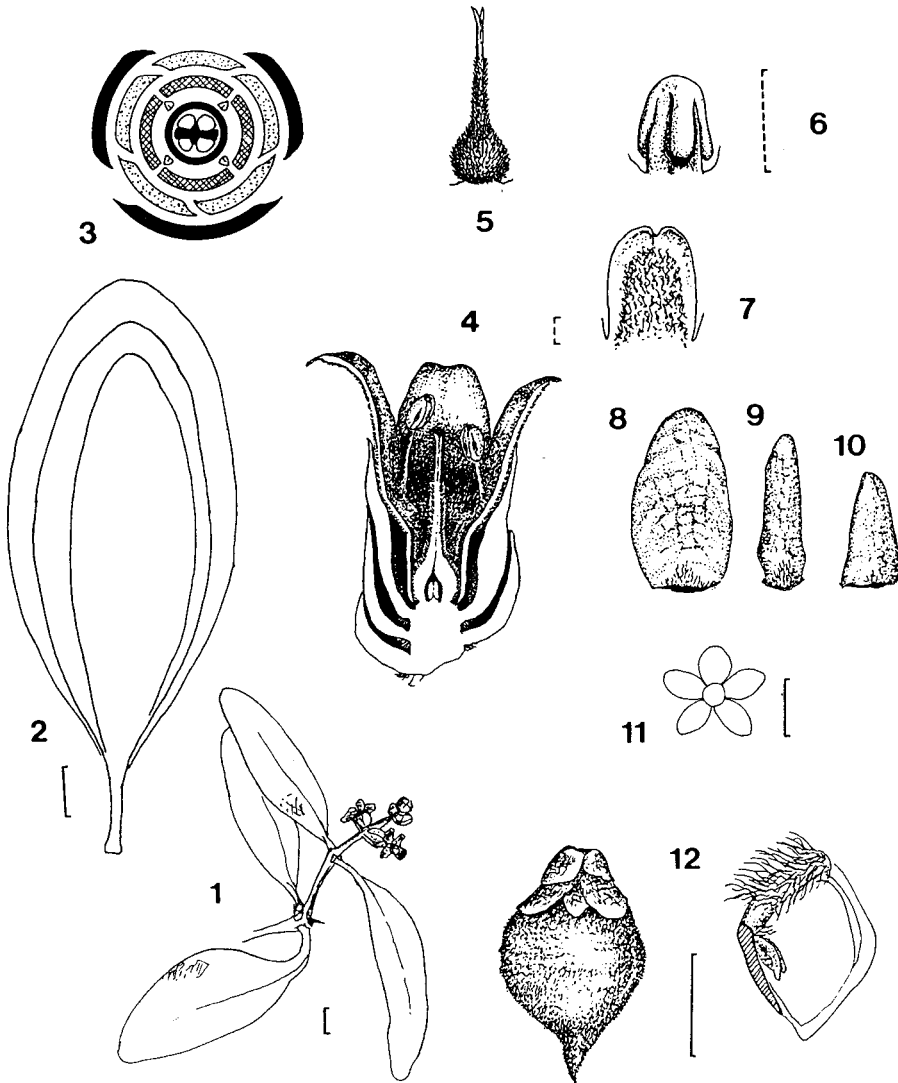


Fig. 6. *Avicennia integra* N. C. Duke. 1, Flowering branchlet; 2, mean range of leaf outlines; 3, floral diagram; 4, flower (longitudinal section) showing general internal anatomy at anthesis; 5, ovary and style; 6, isolated four-lobed placenta; 7, undersurface of single corolla lobe; 8, calyx lobe (from lower position in floral diagram), exterior surface; 9, bracteole, exterior surface; 10, bract, exterior surface; 11, diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12, mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal radicle and plumule. Solid scales = 1 cm, dashed scales = 1 mm. (Reference: 4-11, N. C. Duke AIMS778; 12, G. M. Wightman AIMS1130.)

and 1.8 mm). Less apparent is the wider glabrous border on the undersurface of corolla lobes (about 1 mm compared with about 0.5 mm).

All Specimens Examined (24 collections)

AUSTRALIA. Northern Territory: Buffalo Ck. (12° 21'S 130° 54' E), T. Turner (BRI 228626), G. M. Wightman 450 (DNA); Micket Ck. (12° 12'S 130° 57' E), N. C. Duke (AIMS 1054-5), G. M. Wightman 822, 976 (DNA); Micket Ck., vicinity (12° 25'S, 131° 18' E), G. M. Wightman 3297 (DNA); Micket Ck., vicinity (12° 21'S, 130° 56'E), G. M. Wightman 377 (DNA), G. M. Wightman (AIMS 1130); Adelaide R. (12° 29'S, 131° 16'E), G. M. Wightman 2111 (DNA); Adelaide R., vicinity (12° 25'S, 131° 18'E), G. M. Wightman 3297 (DNA); Adelaide R., vicinity (13° 15'S, 131° 07'E), D. Hearne 192 (DNA), A. G. Wells (DNA 14909, 14916); South Alligator R. (12° 40'S, 132° 20'E), J. S. Bunt (AIMS 1028, 1034), G. M. Wightman 530 (DNA); South Alligator R., road bridge (12° 11' S, 132° 23'E), N. C. Duke (AIMS 778, 1047-9, 1115); Hutchinson Strait (12° 08 S, 132° 35'E), G. M. Wightman 2462 (DNA); Liverpool River (12° 10' S, 134° 10' E), A. G. Wells (DNA 13672).

3. *Avicennia marina* (Forsk.) Vierh., Denkschr. Akad. Wiss. Wien Math.-Nat. 71 (1907) 435; in part, var. *typica* Bakh., Bull. Jard. Bot. Buitenz. 3 (1921) 20.5. *Type*: see *Sceura marina* Forsk.

In part, var. *intermedia* (W. Griff.) Bakh., l.c. (1921) 211; f. *intermedia* (W. Griff.) Moldenke, Phytologia 50 (1982) 310. *Type*: see *Avicennia intermedia* W. Griff.

In part, var. *resinifera* (Forst. f.) Bakh., l.c. (1921) 210; name retained apparently because of common usage, although new combination proposed as var. *australasica* (Walp.) Moldenke, Phytologia 7 (1960) 231. *Type*: see *Avicennia resinifera* Forst. f.

In part, var. *acutissima* Stapf & Moldenke in Moldenke, l.c. (1940). *Type*: R. K. Bhide s.n. (K, holo; NY, iso), India, Bombay, Salsette Island.

In part, var. *anomala* Moldenke, l.c. (1940) 411. *Type*: D. Henne and C. Wilhelmi s.n. (B, Bernhadi, holo; NY, iso), Australia, Queensland, Low Isles.

In part, f. *angustata* Moldenke, Phytologia 23 (1972) 425. *Type*: P. Chai S.29949 (LL) Sarawak, First Division, Buntal River, Buntal village.

Sceura marina Forsk., l.c. (1775). *Type*: *Forskål s.n.* (BM), Arabia, Yemen.

Avicennia resinifera Forst. f., Pl. Escul. Ins. Ocean. Austral. (1786) 72-3. *Type*: J.G.A.

Forster, s.n. (BM, Pallas, iso; UPSV, holo), New Zealand, North Island.

Racka torrida J. F. Gmel., Syst. Nat. 2 (1,791) 245. *Type*: not located.

Halodendron thouarsi Roem. & Schult. in L., l.c. (1818). *Type*: *Herb. Petit-Thouars s.n.* (P), site undetermined.

Racka ovata Roem. & Schult., Syst. Veg. 4 (1819) 207. *Type*: not located.

Avicennia nitida non Jacq. *sensu* Thunb., Flor. Java (1825) 15.

Avicennia tomentosa non Jacq. *sensu* Sieber (in part) ex Presl, Bot. Bemerk (1844) 99.

In part, var. *arabica* Walp., Rep. Bot. Syst. 4 (1845) 133. *Type*: not located.

In part, var. *australasica* Walp., Rep. Bot. Syst. 4 (1845) 133. *Type*: J. G. A. Forster (BM, Pallas, iso; UPSV, holo), New Zealand, North Island.

Avicennia intermedia W. Griff., l.c. (1846) 6, t. 1; and, l.c. (1854) 188. *Type*: W. Griffith s.n. (K, holo; P, iso), Malaysia, Malay Peninsula, Malacca, Pulau Jawa.

Avicennia officinalis non L. *sensu* Schau: DC., Prod. Syst. Nat. 11 (1847) 700.

In part, var. *ovatifolia* Kuntze, l.c. (1891); includes f. *flaviflora* Kuntze, Rev. Gen. Pl. 3, 3 (1898) 249. *Type*: Kuntze s.n. (B), Zanzibar; and f. *tomentosa* Kuntze, l.c. (1898). *Type*: Kuntze s.n. (US), Zanzibar.

In part, var. *eucalyptifolia* (Zipp.) Val., Bull. Dep. Agric. Ind. Néérl. 10 (1907) 53.

Type: see *Avicennia eucalyptifolia* Zipp. ex Miq.

In part, var. *acuminata* Domin, Bibl. Bot. 89, 6 (1928) 1116. *Type*: Domin s.n. (not located), Australia, Queensland, Russell River.

Avicennia eucalyptifolia Zipp. ex Miq., Flor. Ned. Ind. 2 (1856) 912, in syn.; ex Moldenke, l.c. (1960) 162-5. *Type*: *Spanoghe s.n.* (L 908.265-613, cotype); *Zippelius s.n.* (L 908.265-623, cotype), Indonesia, Timor.

Avicennia alba non Bl. *sensu* Val., l.c. (1907) 53; *sensu* Jafri, Flor. Karachi (1966) 290 and 351, fig. 285.

In part, var. *acuminatissima* Merr., Philipp. J. Sc. C. Bot. 11, 6 (1916) 311. *Type*: C. B. Robinson 1862 (B, BM, BO, CAL, F, K, L, P, US, holo), Indonesia, Mollucca Is., Amboina.

- Avicennia mindanaense* Elm., Leaflet. Philipp. Bot. 8 (1915) 2868. Type: *Elmer 11990*, in part (G, CAL, E, L, W, US, holo), Philippines, Mindanao.
- Avicennia sphaerocarpa* Stapf ex Ridley, J. Fed. Malay States Mus. 10 (1920) 151; and Flor. Malay Penin. 3 (1923) 640. Type: *C. Curtis 3533* (K), Malaysia, Malay Peninsula, Penang, Sungai Pinang.
- Avicennia balanophora* Stapf & Moldenke in Moldenke, l.c. (1940) 409-10. Type: *F. Mueller s.n.* (K, holo; BRI, photo), Australia, Queensland, Brisbane River.
- Trichorhiza lechenaultii* Miq. ex Moldenke, Prelim. Alph. List Invalid Names (1940) 43, in syn. Type: *Preiss 1298* (LD, holo, B, iso), Western Australia, Fort Leschenault.
- Avicennia maritima* Naurois & Roux, Bull. Inst. Fond. Afr. Noire 27 (1965) 851. Type: not located.

Tree, or shrub, to 30 m high, often about 5-10 m but extremely variable; trunk base simple, occasionally with low-placed aerial roots; bark variable, white smooth flaky or, brown fissured pustular with many short longitudinal fissures or reticulate lines forming very small scales; pneumatophores about 20-30 cm high, 5-10 mm wide near distal tip. Leaf lamina ovate-elliptic to narrowly lanceolate, apex variably pointed, 43-164 (87) mm long, 12-49 (25) mm wide, 19-56 (36) mm from base to greatest width, upper surface shiny green, undersurface dull pale finely pubescent; petiole 3-23 (11) mm long, glabrous above, often pubescent below. Inflorescence capitate with 2-5 opposite, decussate bud-pairs very closely placed, about 10-30 mm long at anthesis. Flower 4-8 mm long, sweetly scented; bract triangular or ovate, generally symmetric, edge ciliate, apex acute; bracteoles ovate, edges ciliate, apices acute; calyx lobes ovate, 3-6 mm long, 2-4 mm wide, edges ciliate, outer surface fully or partly pubescent; corolla actinomorphic, 3-7 mm diameter, lobes mostly 4, orange, revolute, reflexed, slightly unequal, 1-3 mm long, 2-3 mm wide, apices rounded, outer surface pubescent except for minute glabrous margin, inner surface dull glabrous; stamens mostly 4, alternate with corolla lobes, positioned equally around corolla mouth, about 0.5 mm long; anthers about 1 mm long; stigma glabrous, bilobed pointed arms equal, positioned below anthers or barely exerted; style around 0.5 mm long, glabrous; ovary conical, around 2.5 mm long, upper portion densely tomentose, base glabrous. Fruit compressed ovoid, 14-31 (22) mm long, 11-27 (17) mm wide, 4-10 (6) mm thick, distal tip bluntly acute with narrow persistent stylar beak, c. 1 mm long; pericarp outer surface pale grey green, puberulent; calyx persistent on pericarp, 3-7 mm long from base, 5-10 mm diameter; radicle about 10 mm in length, mostly glabrous with short densely hairy collar c. 2 mm wide, hairs straight or wavy, distal tip glabrous; plumule about 5 mm long, pubescent, hairy about base. Figs 7-9.

Floral phenology: timing of flowering and maturation of propagules varies considerably with latitude (Duke 1990b), although each is relatively consistent at any site. In latitudes around 10°S flowering occurs chiefly from November to December and propagules mature mainly in March and April. In sites further south there is a progressive shift in phenological events to the southern limit of the species. Thus around 38°S flowering occurs chiefly in May and June while propagules mature in January and February. Trends in equatorial sites have not been fully established.

Distribution: *Avicennia marina* occurs widely from eastern Africa to the Persian Gulf, through Indo-Malesia, India, south-east Asia to China and Japan, and south through the Philippines and western Pacific islands to Australasia. The species is dominant, or at least common, in most mangrove assemblages from New Guinea to southern Australia and New Zealand. It is limited on only part of this region, notably the north coast of New Guinea and equatorial western Pacific, where it appears to be replaced by *A. alba*. Figs 3 and 4.

Ecology: the occurrence of this taxon is widely variable. As discussed earlier in relation to the genus, this species has a wide physiological tolerance to salinity, intertidal position, and temperature. However, it is apparently restricted by a certain degree of shade intolerance, as well as crabs which consume its propagules. Therefore occurrence is not a true indication of its preferred habitat, and its common absence in median intertidal positions is more a reflection of crab presence in these locations (Smith 1988). Over its full geographic range, however, this taxon may be found in monotypic stands across the entire intertidal profile above mean sea level. Its wide tolerances also enable it to occupy offshore reefal lagoons as well as sandy or rocky sheltered embayments. This feature provides this species with a significant dispersal advantage over other less adaptable taxa.

Notes

As Moldenke apparently did not view specimens of the Northern Territory species, all variation attributed to Australian *Avicennia*, notably in his five species, must presumably be found in *Avicennia marina sensu lato*. The species is distinguished by puberulent surfaces of apical stems, leaf undersurfaces, floral parts and fruit, plus acute leaf apices, capitate inflorescence, small flowers, mostly glabrous radicle and rounded fruit. Other binomials applied to this species tend to reflect the confusion in identifying true *A. marina*. Thus, while the name has been generally prominent in the region and the Old World since 1907, other names were proposed to explain regional differences. Some of these now provide varietal basionyms. The present treatment recognises three varieties in Australasia. Furthermore, these have been shown to freely interbreed where they occur in sympatry, confirming their subspecific status, but causing problems with diagnoses in overlap zones (Fig. 3).

Specimens Examined

Representative specimens are listed for each variety. In all, 395 herbarium (see Accessory Publication) and 45 field collections were examined. Dimensions and descriptions of the different varieties were based on dried litter fall collections made over one full year (Duke 1990a), while the specific description was taken from herbarium collections.

Key to Varieties of *Avicennia marina*

- 1a. Calyx outer surface fully pubescent, occasionally with a minute, < 0.5 mm wide, glabrous peripheral margin; trunk bark grey, fissured, pustular 3a. var. *australasica*
- b. Calyx outer surface pubescent near base, peripheral surface glabrous, width much > 0.5 mm; trunk bark green, chalky smooth, often thinly flaky in patches (note: bark on smaller trees and shrubs < 1.5 m tall, often similar to mature specimens of var. *australasica*) 2
- 2a. Stigma subequal with upper edge of anthers; corolla diameter mostly < 5 mm at anthesis, lobes mostly ≤ 2.2 mm wide; leaf blade mostly lanceolate, or narrowly so 3b. var. *eucalyptifolia*
- b. Stigma equal with lower edge of anthers; corolla diameter mostly > 5 mm at anthesis, lobes mostly > 2.2 mm wide; leaf blade mostly ovate-elliptic 3c. var. *marina*

3a. *Avicennia marina* (Forsk.) Vierh. var. *australasica* (Walp.) Moldenke, Phytologia 7 (1960) 231.

Avicennia tomentosa Sieber var. *australasica* Walp., l.c. (1845); *sensu Avicennia marina* (Forsk.) Vierh. var. *resinifera* (Forst. f.) Bakh., l.c. (1921) 210; Moldenke, l.c. (1960), name retained apparently because of common usage. Type; *J. G. A. Forster* (BM, Pallas, iso; UPSV, holo), New Zealand, North Island.

Tree, or shrub, to 10 m high, often about 5 m; bark brown or grey fissured, pustular, with many short longitudinal fissures or reticulate lines forming very small scales. Leaf lamina ovate-elliptic, 40–70 (57) mm long, 18–36 (28) mm wide, 22–35 (29) mm from base to greatest width, upper surface green satiny, undersurface pale finely pubescent; petiole tending amplexicaul, 7–13 (11) mm long, often pubescent under. Flower 5–7 mm long; bract broadly triangular, apex acute; bracteoles ovate, apices acute; calyx lobes ovate, 4–5 mm long, 3–4 mm wide, outer surfaces fully pubescent, or nearly so, with glabrous margin to 0.5 mm wide; corolla 3–7 mm diameter, lobes mostly 4, orange, revolute, reflexed, slightly unequal, 2–3 mm long, 2 mm wide, apices rounded, outer surface pubescent except for minute glabrous distal margin, inner surface dull glabrous; stamens about 0.5 mm long; anthers about 1 mm long; stigma thick, about 2 mm long, bilobed pointed arms equal, positioned level with middle of anthers; ovary conical, upper surface tomentose, base 0.7 mm high, glabrous. Fruit 15–26 (20) mm long, 12–21 (17) mm wide, 6–12 (9) mm thick; calyx persistent on pericarp, 3–6 mm long from base, 5–8 mm diameter; radicle 5–16 (10) mm long, mostly glabrous with short densely hairy collar, c. 2 mm long, hairs straight or wavy; plumule about 5 mm long, fully pubescent, hairy about base. Fig. 7.

Floral phenology: timing of flowering and maturation of propagules varies considerably with latitude, although each is repeated annually for particular sites. In latitudes around 25° S flowering occurs chiefly in January and February and propagules mature mainly in April and May. In sites further south there is a progressive shift in phenological events to the southern limit of the species. Thus around 38° S flowering occurs chiefly in May and June while propagules mature in January and February.

Distribution: the var. *australasica* is restricted to temperate and subtropical latitudes. It is dominant, or at least common, in most mangrove assemblages from Rockhampton to Adelaide on the south-eastern coast of mainland Australia, and northern New Zealand. Figs 3 and 4.

Notes

Varietal descriptions by Walper and Bakhuizen van den Brink each refer to *A. resinifera* Forst. f. in synonymy. The former therefore has priority, although it was with the incorrect

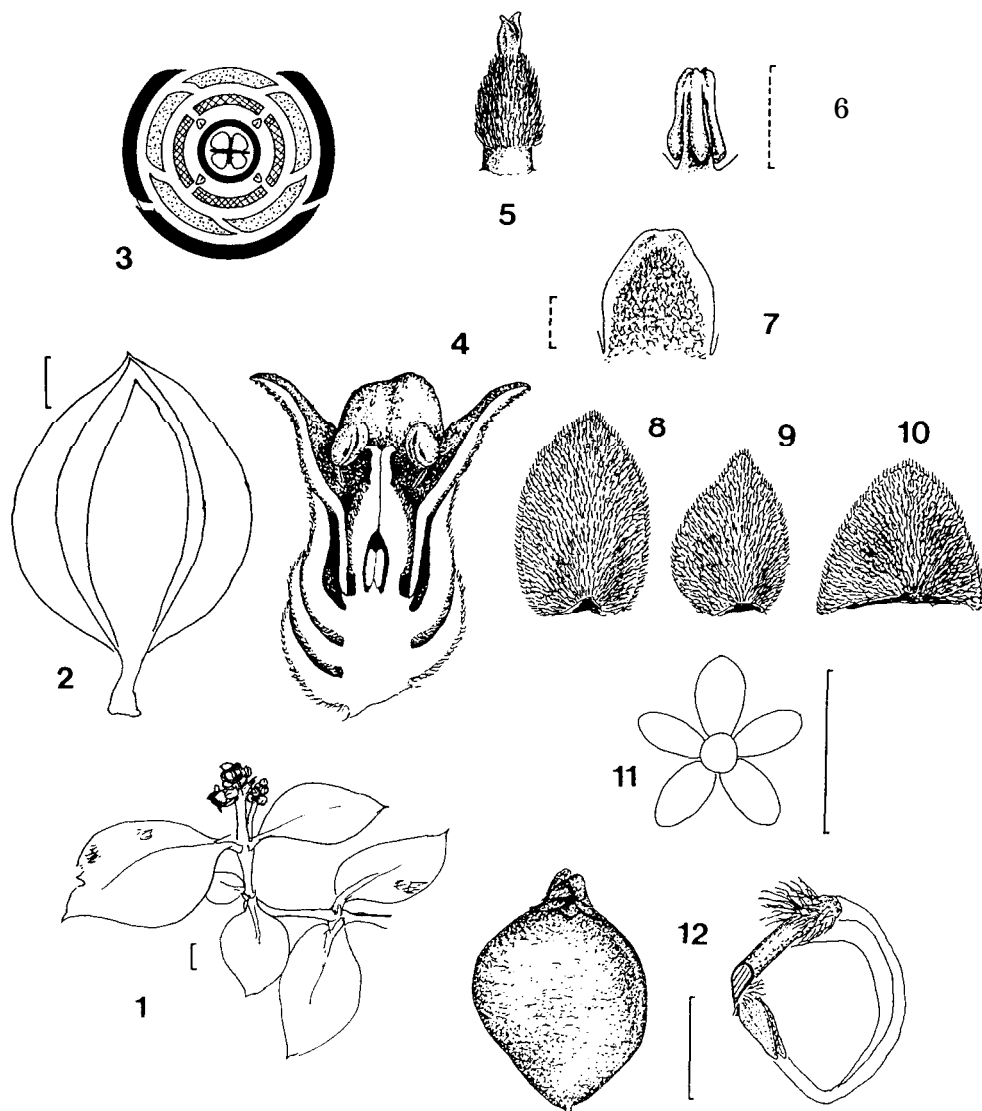


Fig. 7. *Avicennia marina* (Forsk.) Vierh. var. *australasica* (Walp.) Moldenke. 1, Flowering branchlet; 2, mean range of leaf outlines; 3, floral diagram; 4, flower (longitudinal section) showing general internal anatomy at anthesis; 5, ovary and style; 6, isolated four-lobed placenta; 7, undersurface of single corolla lobe; 8, calyx lobe (from lower position in floral diagram), exterior surface; 9, bracteole, exterior surface; 10, bract, exterior surface; 11, diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12, mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal radicle and plumule. Solid scales = 1 cm, dashed scales = 1 mm. (Reference: 4-12, N. C. Duke AIMS1096-8.)

species name. In recognition of this occurrence, Moldenke formally made his new combination with *A. marina* but curiously never offered the correction in subsequent writings, preferring to use the Bakhuizen van den Brink name. This variety may be distinguished by fully, or nearly so, pubescent calyces and bracts and grey fissured bark. In the field, distinctions between sympatric varieties recognised in this treatment are expected to be difficult (notably around Rockhampton and Adelaide, particularly the former) because different varieties freely interbreed.

Representative Specimens

AUSTRALIA. Queensland: Bribie I. (27° 00' S, 153° 08' E), *C. T. White s.n.* (BRI 254068); Pine R., mouth (27° 17' S, 153° 04' E), *L. S. Smith 11434*, -6 (BRI); Brisbane R. (27° 35' S, 152° 53' E), *F. Mueller s.n.* (K, photo BRI); Stradbroke I. (27° --' S, 153° --' E), *T. E. Hunf. s.n.* (BRI 33971); Mainland near southern Fraser I. (27° 5'-S, 153° 2'-E), *S. F. Kajewski 80* (BRI); Moreton Bay (27° 51' S, 153° 24' E), *L. Durrington 751* (BRI); Tallebudgera (28° 0'-S, 153° 2'-E), *C. T. White 1880* (BRI). New South Wales: Tweed R. (28° 1'-S, 153° 2'-E), *W. T. Jones s.n.* (BRI 249511, -2); Tweed R. (28° 1'-S, 153° 2'-E), *W. T. Jones s.n.* (BRI 249501); Brunswick R. (28° --' S, 153° --' E), *W. T. Jones s.n.* (BRI 249509); N. of Brunswick Heads (28° 32' S, 153° 33' E), *R. Coveny 4389* (BRI); Nambucca R. (30° 42' S, 152° 57' E), *W. G. Allaway s.n.* (AIMS 949); Hexham swamp (32° 4'-S, 151° 4'-E), *R. Story 7224* (BRI); Long Beach (35° 42' S, 150° 14' E), *J. Beeton 4* (BRI); Merimbula Lake (36° 54' S, 149° 53' E), *W. G. Allaway s.n.* (AIMS 952). Victoria: Westernport Bay (38° 21' S, 145° 13' E), *J. S. Bunt s.n.* (AIMS 945, 1149); Mornington Penin., Sandy Pt. (38° 5'-S, 146° 01' E), *M. A. Todd 44* (BRI); Tooradin, Cardinia Ck. (38° 5'-S, 141° 3'-E), *H. C. Beaglehole s.n.* (BRI 257052). South Australia: Port Gawler (34° 42' S, 138° 28' E), *M. M. Retallick s.n.* (AIMS 955, 1017-8). NEW ZEALAND. Bay of Islands, Parekura Bay (35° 16' S, 174° 07' E), *E. J. Godley s.n.* (BRI 203529).

3b. *Avicennia marina* (Forsk.) Vierh. var. *eucalyptifolia* (Zipp.) N. C. Duke, comb. nov.
Avicennia officinalis Schau. var. *eucalyptifolia* (Zipp. ex Miq.) Val., l.c. (1907). Type: see *Avicennia eucalyptifolia* Zipp. ex Miq. in 3. *Avicennia marina* (Forsk.) Vierh.
Avicennia alba Val. var. *acuminatissima* Merr. l.c. (1916). Type: *C. B. Robinson 1862* (B, BM, BO, CAL, F, K, L, P, US, holo), Indonesia, Mollucca Is., Amboina.
Avicennia officinalis Schau. var. *acuminata* Domin. l.c. (1928). Type: *Domin s.n.* (not located), Australia, Queensland, Russell River.
Avicennia marina (Forsk.) Vierh. var. *anomala* Moldenke, l.c. (1940) 411. Type: *D. Henne and C. Wilhelmi s.n.* (B, Bernhardt, holo; NY, iso), Australia, Queensland, Low Isles.
Avicennia marina (Forsk.) Vierh. f. *angustata* Moldenke, l.c. (1972). Type: *P. Chai S.29949* (LL) Sarawak, First Division, Buntal River, Buntal village.

Tree, or shrub, to 30 m high, often about 10 m; bark smooth green when wet, chalky white when dry, often thinly flaky in patches. Leaf lamina mostly lanceolate to narrowly lanceolate, 55-93 (76) mm long, 17-32 (23) mm wide, 21-41 (32) mm from base to greatest width, upper surface shiny green, undersurface dull pale finely pubescent; petiole semi-amplexicaul, 7-14 (11) mm long. Flower 5-7 mm long; bract triangular, apex acute; bracteoles ovate, apices bluntly acute; calyx lobes ovate, 3-5 mm long, 2-3 mm wide, outer surface mostly pubescent, glabrous margin about 1 mm wide; corolla 3-5 mm diameter, lobes 4, orange, revolute, reflexed, slightly unequal, 2-3 mm long, 1-2 mm wide, apices rounded, outer surface pubescent except for minute glabrous distal margin, inner surface dull glabrous; stamens about 0.5 mm long; anthers about 0.8 mm long; stigma, about 2 mm long, glabrous, bilobed pointed arms equal, level with lower edge of anthers; ovary conical, upper surface tomentose, base c. 0.3 mm high, glabrous. Fruit 10-21 (16) mm long, 9-19 (15) mm wide, 6-11 (8) mm thick; calyx persistent on pericarp, 4-6 mm long from base, 4-7 mm diameter; radicle 5-13 mm long, mostly glabrous with short densely hairy collar, c. 2 mm wide, hairs straight or wavy; plumule about 5 mm long, fully pubescent, hairy about base. Fig. 8.

Floral phenology: timing of flowering and maturation of propagules varies considerably with latitude, although each is repeated annually for particular sites. In latitudes around 10°S flowering occurs chiefly in November to December and propagules mature mainly in March and April. In sites further south there is a progressive shift in phenological events to the southern limit of the variety. Thus around 22°S flowering occurs chiefly in January and February while propagules mature in April. Trends in equatorial sites have not been fully established.

Distribution: the global extent of var. *eucalyptifolia* is unknown. However, based on the character of narrow lanceolate leaves (= *A. eucalyptifolia*) it apparently ranges from the southern Philippines, western Indonesia to Australasia. In this region it is restricted to tropical latitudes from around Mackay to Wyndham in Australia to southern New Guinea and the southern Solomon Islands. Figs 3 and 4.

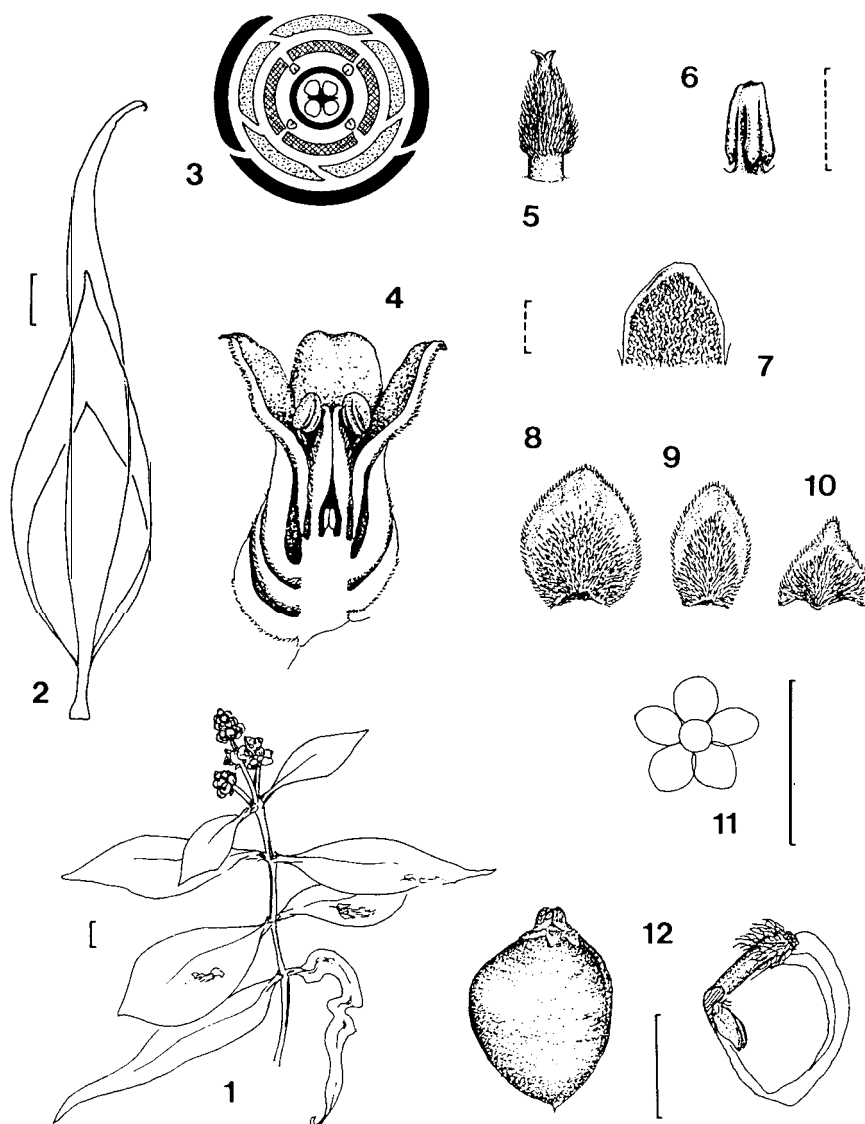


Fig. 8. *Avicennia marina* (Forsk.) Vierh. var. *eucalyptifolia* (Val. ex Miq.) N. C. Duke. 1, Flowering branchlet; 2, mean range of leaf outlines; 3, floral diagram; 4, flower (longitudinal section) showing general internal anatomy at anthesis; 5, ovary and style; 6, isolated four-lobed placenta; 7, undersurface of single corolla lobe; 8, calyx lobe (from lower position in floral diagram), exterior surface; 9, bracteole, exterior surface; 10, bract, exterior surface; 11, diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12, mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal radicle and plumule. Solid scales = 1 cm, dashed scales = 1 mm. (Reference: 4-12, N. C. Duke AIMS1062-3.)

Notes

The description of *A. officinalis* var. *eucalyptifolia* (Val. ex Miq.) Val. appears appropriate in view of its narrow lanceolate leaves and location, but it was made under the wrong specific name. The variety is further distinguished by the stigma positioned equal to the top edge of, or slightly above anthers in anthesis. In the field, varietal distinctions are expected to be less clear in zones where two varieties overlap (notably around Rockhampton to Mackay, Broome to Wyndham) because they freely interbreed.

Representative Specimens

INDONESIA. Irian Djaya: FakFak, Kembala (2°55'S, 132°77'E), *C. J. Stefels* BW3199 (LAE). PAPUA NEW GUINEA. Northern: Tufi, Uiaku (Unguhu?) (8° 43'S, 148° 07'E), *W. Moi* 9 (LAE). Milne: Medino Village, Milne Bay (9° 40'S, 150° 01' E), *R. D. Hoogland* 4699 (BRI, LAE). Western: Daru I. (9° 05' S, 143° 15' E), *L. J. Brass* 6215 (BRI, LAE). Gulf: Amo (7° 51' S, 145° 26' E), *M. Galore* NGF41116 (BRI, LAE). Central: Fairfax Harbour (9° 30'S, 147° 10' E), *A. N. Gillison* NGF22163 (BRI, LAE). SOLOMON ISLANDS. Malaita: Malaita I. (9° 00'S, 161° 00'E), *S. F. Kajewski* 2344 (BRI). AUSTRALIA. Western Australia: Wyndham (15° 22' S, 128° 23' E), *R. A. Perry* 2547 (BRI). Northern Territory: Darwin Harbour, East Arm (12° 25'S, 130° 50'E), *J. Must* 881 (BRI, DNA); Darwin, Nightcliff (12° 35'S, 130° 49' E), *M. O. Parker* 688 (DNA); South Alligator R., road bridge (12° 11' S, 132° 23'E). *N. C. Duke* s.n. (AIMS 777, 1051-2); East Alligator R. (12° 30'S, 133° 00'E), *Martensz* AE691 (BRI, DNA); Hutchinson Strait (12° 08'S, 135° 32' E), *G. M. Wightman* 2461 (DNA); Groote Eylandt (14° 00' S, 136° 25' E), *J. Waddy* 463 (DNA). Queensland: Andoom Ck. (12° 34' S, 141° 52' E), *A. Morton* 1013 (BRI); Jardine R. (10° 55' S, 142° 13' E), *N. C. Duke* s.n. (AIMS 476); Cape York (10° 4'-S, 142° 3'-E), *L. S. Smith* 12616 (BRI, LAE); Endeavour R. (15° 28' S, 145° 15' E), *V. Scarth-Johnson* 1282A (BRI); Cairns (16° 55' S, 145° 46' E), *W. Macnae* s.n. (BRI); Hinchinbrook I., Missionary Bay (18° 16'S, 146° 13' E), *N. C. Duke* s.n. (AIMS 559); Lucinda Pt. (18° 3'-S, 146° 2'-E), *C. T. White* s.n. (BRI 383354-5).

3c. *Avicennia marina* (Forsk.) Vierh. var. *marina*.

Avicennia tomentosa Sieber var. *arabica* Walp., l.c. (1845). *Type*: not located.

Avicennia officinalis Schau. var. *ovatifolia* Kuntze, l.c. (1891). *Type*: not located.

In part, f. *flaviflora* Kuntze, Rev. Gen. Pl. 3, 3 (1898) 249. *Type*: *Kuntze* s.n. (B), Zanzibar.

In part, f. *tomentosa* Kuntze, l.c. (1898). *Type*: *Kuntze* s.n. (US), Zanzibar.

Avicennia marina (Forsk.) Vierh. var. *typica* Bakh., l.c. (1921) 205. *Type*: see *Sceura marina* Forsk in 3. *Avicennia marina* (Forsk.) Vierh.

Avicennia marina (Forsk.) Vierh. var. *intermedia* (W. Griff.) Bakh., l.c. (1921) 211. *Type*: see *Avicennia intermedia* W. Griff., in 3. *Avicennia marina* (Forsk.) Vierh.

Avicennia marina (Forsk.) Vierh. var. *acutissima* Stapf & Moldenke in Moldenke, l.c. (1940). *Type*: *R. K. Bhide* s.n. (K, holo; NY, iso), India, Bombay, Salsette Island.

Tree, or shrub, to about 10 m high; bark smooth green when wet, chalky white when dry, often thinly flaky in patches. Leaf lamina ovate-elliptic, 37-84 (69) mm long, 19-27 (24) mm wide, 18-41 (34) mm from base to greatest width, upper surface green satiny, undersurface pale finely pubescent below; petiole amplexicaul, 4-14 (11) mm long, often pubescent under. Flower 6-8 mm, scented; bract ovate, apex rounded; bracteoles ovate, apices rounded; calyx lobes ovate, 4-6 mm long, 3-4 mm wide, outer surfaces hairy pubescent about base, glabrous margin about 1.5 mm wide; corolla 5-6 mm diameter, lobes revolute, reflexed, 2-3 mm long, 2 mm wide, apices rounded, outer surface pubescent except for minute glabrous distal margin, inner surface dull glabrous; stamens about 0.8 mm long; anthers about 1.3 mm long; stigma thick, about 3 mm long, bilobed pointed arms equal, positioned level with lower edge of anthers; ovary conical, upper surface tomentose, base c. 1 mm high, glabrous. Fruit 12-23 (18) mm long, 13-22 (17) mm wide, 8-12 (10) mm thick; calyx persistent on pericarp, 5-6 mm long from base, 7-8 mm diameter; radicle 7-13 mm long, mostly glabrous with short densely hairy collar, c. 2 mm wide, hairs straight or wavy; plumule about 5 mm long, fully pubescent, hairy about base. Fig. 9.

Floral phenology: timing of flowering and maturation of propagules varies considerably with latitude, although each is repeated annually for particular sites. In latitudes around 17°S flowering occurs chiefly in December and January and propagules mature mainly in March. In sites further south there is a progressive shift in phenological events to the

southern limit of the variety. Thus around 33° S flowering occurs chiefly in March while propagules mature in October and November.

Distribution: in this region var. *marina* is restricted to Western Australia, particularly from Bunbury in the south to around Broome in the north. This northern limit is not precise and significant overlap is expected between this variety and var. *eucalyptifolia* observed in Wyndham. Figs 3 and 4.

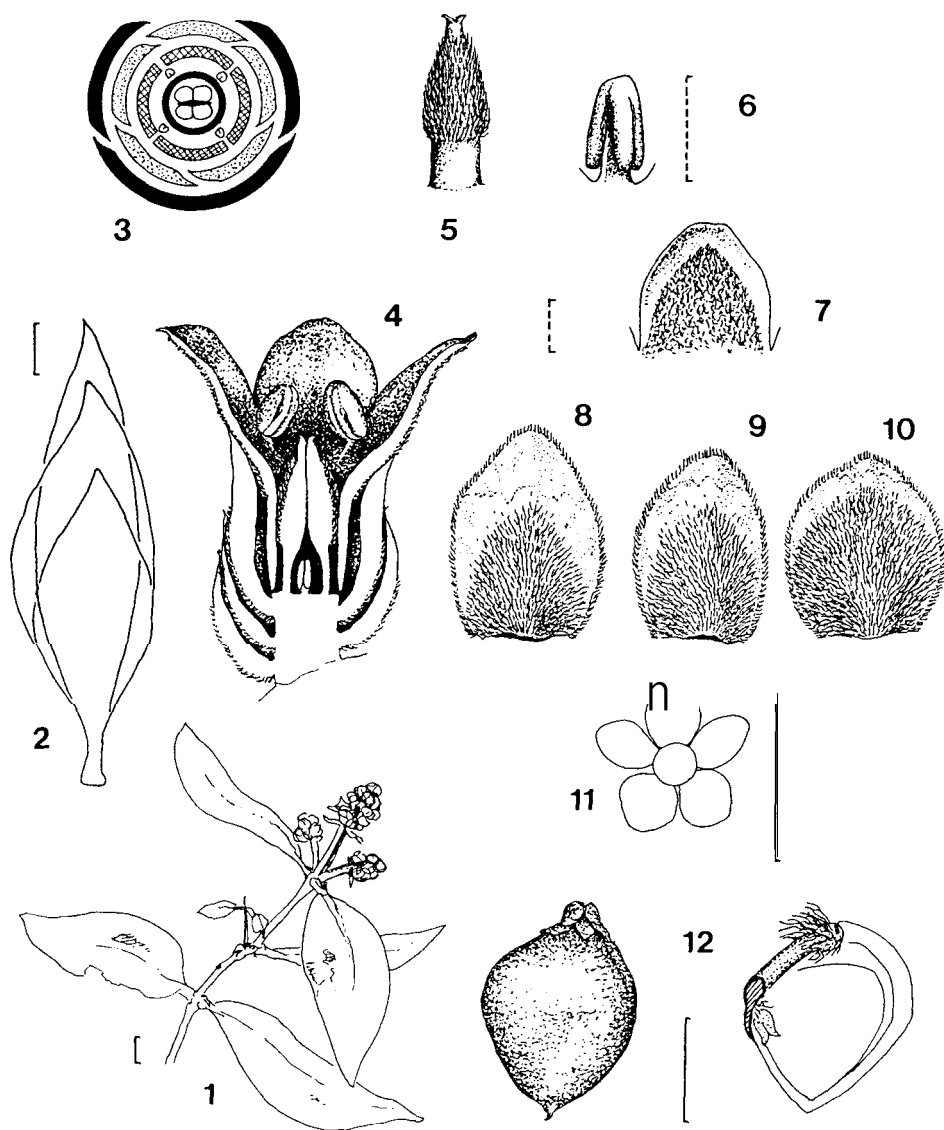


Fig. 9. *Avicennia marina* (Forsk.) Vierh. var. *marina* I, Flowering branchlet; 2, mean range of leaf outlines; 3, floral diagram; 4, flower (longitudinal section) showing general internal anatomy at anthesis; 5, ovary and style; 6, isolated four-lobed placenta; 7, undersurface of single corolla lobe; 8, calyx lobe (from lower position in floral diagram), exterior surface; 9, bracteole, exterior surface; 10, bract, exterior surface; 11, diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12, mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal radicle and plumule. Solid scales = 1 cm, dashed scales = 1 mm. (Reference: 4-12, G. S. McCutcheon AIMS1077-9.)

Notes

Asian material is referable to var. *marina* (Moldenke 1960) and this is referable to south-western Australian collections, with minimal ambiguity. The variety is distinguished by a short stigma positioned below or at the lower edge of anthers in anthesis. Material in south-western Australia was further distinguished by slightly larger flowers and thicker leaves, but these characters were possibly influenced by environmental factors because they were not reflected in isozyme patterns. In the field varietal distinctions are expected to be problematic in overlap zones between varieties (notably between Broome and Wyndham, and west of Adelaide) because they freely interbreed.

Representative Specimens

AUSTRALIA. Western Australia: King Sound, Derby (17° 19' S 123° 38' E), *N. C. Duke s.n.* (AIMS 790, 798); Cape Leveque (16° 24' S, 122° 55' E), *N. C. Duke s.n.* (AIMS 804); Cape Leveque (16° 24' S, 122° 55' E), *N. C. Duke s.n.* (AIMS 803); Purracamurra, near Port Hedland (20° 20' S, 118° 25' E), *T. Rose s.n.* (AIMS 1007, 1143); Karratha, near Dampier (20° 44' S, 116° 37' E), *C. Nicholson s.n.* (AIMS 1000, 1133); Carnarvon, vicinity (24° 28' S, 113° 41' E), *J. S. Bunt s.n.* (AIMS 947); Bunbury (33° 20' S, 115° 40' E), *S. L. Everist 9045* (BRI), *D. H. Smith s.n.* (AIMS 1011).

4. *Avicennia officinalis* L., Sp. Pl. 1 (1753) 110. Type: Herb. Linnaeus G.813, S.4 (LINN, holotype), G.813, S.5 (LINN, iso), India, southern coast.

Sensu var. *spatulata* f. *glandulosa* Kuntze, l.c. (1891). **Type:** undetermined, Java.

Sensu var. *tomentosa* (Willd.) Cowen, Rec. Bot. Surv. India 11 (1928) 199, 220.

Avicennia tomentosa non Jacq. *sensu* Willd., Sp. Pl. 3, 1 (1800) 395.

Sensu var. *asiatica* Walp., l.c. (1844). **Type:** undetermined, India.

Avicennia oepata Hamilt., Trans. Linn. Soc. 17 (1835) 221. **Type:** Rheede, Hort. Ind.

Malab. 4 (1683) 5, t. 45, India, southern coast.

Avicennia obovata W. Ciriff., l.c. (1854) 189-90. **Type:** not located.

Avicennia obtusifolia Wall. ex Moldenke, Prelim. Alph. List Invalid Names (1940) 5, in syn.

Type: Wallich s.n. (C), India, West Bengal, Sunderbund and Insula Gangis.

Tree, or shrub, to 25 m high, often about 5-10 m; trunk base simple, low-placed aerial roots common; bark reddish brown, smooth in smaller forms, grey-brown, finely fissured, sparsely pustular in larger trees; pneumatophores about 20-30 cm high. Leaf lamina ovate-elliptic, apex rounded, slightly revolute, 52-118 (90) mm long, 24-58 (41) mm wide, 27-64 (46) mm from base to greatest width, upper surface bright satiny green, undersurface pale finely pubescent; petiole 8-17 (13) mm long, glabrous above, often pubescent below. Inflorescence mostly capitate with 2-4 opposite, decussate bud-pairs, about 20-30 mm long at anthesis. Flower 8-12 mm long, sweet scented; bract circular, edge ciliate or hairy; bracteoles oblong, apices rounded, edges ciliate or hairy; calyx lobes ovate, 5-7 mm long, 4-5 mm wide, edges ciliate or hairy, outer surface shiny, mostly glabrous; corolla variably zygomorphic, 4-12 mm diameter, lobes 4, pale yellow-orange, tending revolute, reflexed, unequal, 3-5 mm long, 2-4 mm wide, apices rounded, outer surface pubescent except for minute (< 0.5 mm wide) glabrous distal margin, inner surface dull glabrous; stamens mostly 4, alternate with corolla lobes, positioned equally around corolla mouth, about 0.8 mm long for shorter pair, about 1.8 mm long for longer pair; anthers about 1 mm long; stigma narrow, glabrous, bilobed pointed arms slightly unequal, not exceeding anthers, but exceeding calyx; style elongate, about 2 mm long, glabrous; ovary ampulla-shaped, about 4 mm long, densely tomentose. Fruit compressed elongate ellipsoid, 14-38 (27) mm long, 8-27 (18) mm wide, 4-13 (7) mm thick, distal tip acute, with narrow (c. 3 mm wide) persistent styler beak, c. 5-10 mm long; pericarp outer surface pale grey-green, velvety pubescence; calyx persistent on pericarp, 5-8 mm long from base, 8-13 mm diameter; radicle about 13 mm long, densely hairy along full length, hairs wavy or straight, distal tip glabrous; plumule about 10 mm long, pubescent, hairy about base. Fig. 10.

Floral phenology: in New Guinea flowering occurs from September to November and propagules mature chiefly in January and February.

Distribution: *Avicennia officinalis* occurs commonly from western India through Indo-Malesia, south-eastern Asia and the Philippines to Australasia. In this region it is restricted mostly to the southern coastline of New Guinea. Its southern and eastern limits are

synchronous around the Milne Bay district of Papua New Guinea. The species is unknown in Australia. Figs 2 and 4.

Ecology: in New Guinea this taxon is frequently found in lower intertidal positions on soft recently consolidated mud banks, accreting banks of river meanders and at river mouths.

Notes

The binomial applied to this taxon represents one of the most troublesome in the genus, for which it is the type species. For example, in this region, all five species have been

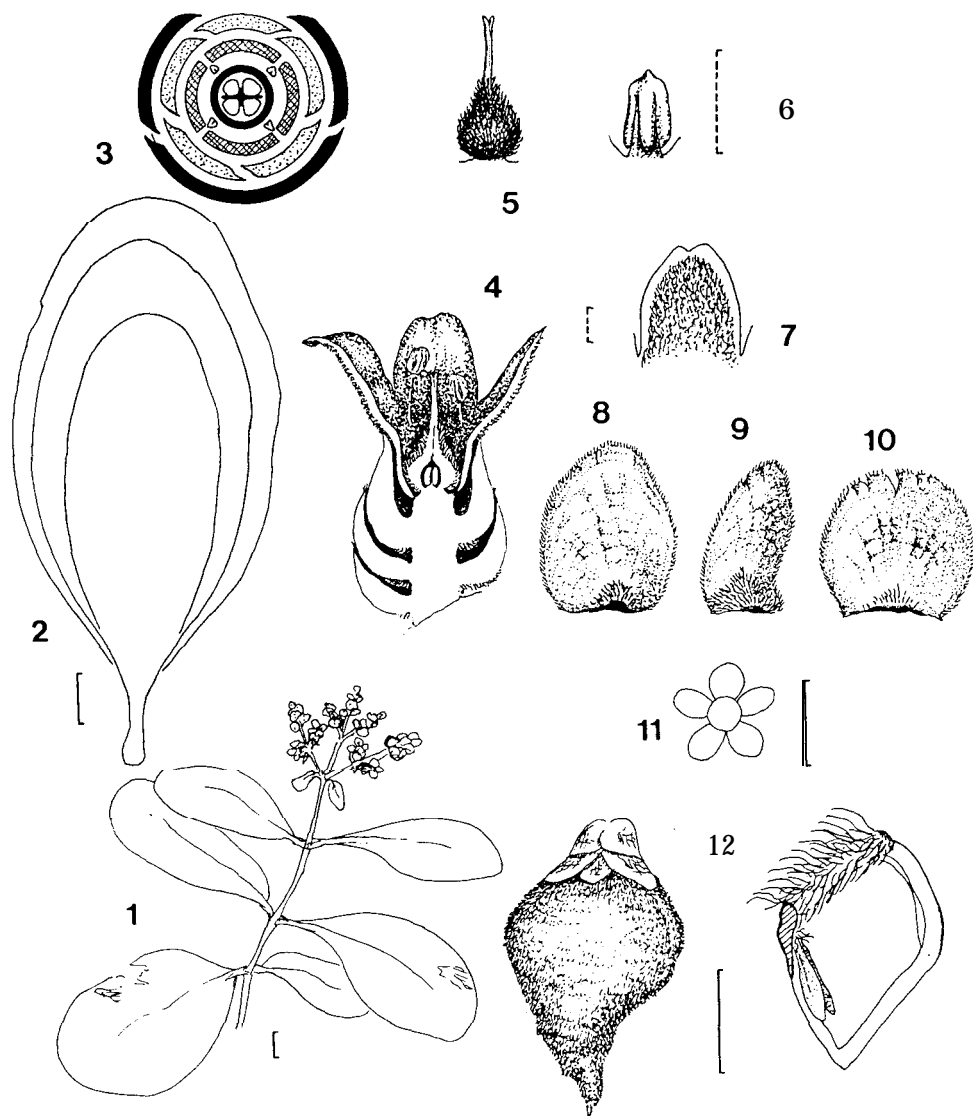


Fig. 10. *Avicennia officinalis* L. 1, Flowering branchlet; 2, mean range of leaf outlines; 3, floral diagram; 4, flower (longitudinal section) showing general internal anatomy at anthesis; 5, ovary and style; 6, isolated four-lobed placenta; 7, undersurface of single corolla lobe; 8, calyx lobe (from lower position in floral diagram), exterior surface; 9, bracteole, exterior surface; 10, bract, exterior surface; 11, diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12, mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal radicle and plumule. Solid scales = 1 cm, dashed scales = 1 mm. (Reference: 4-11, N. C. Duke AIMS757; 12, N. C. Duke AIMS1114.)

mistakenly referred to it by various authors. *Avicennia officinalis*, however, may be distinguished by its rounded leaf apices, ciliate or hairy calyx edges, large flowers, flask- or ampulla-shaped style and ovary, and hairy radicle. It is apparently closely related to *A. integra* and, although their occurrence is allopatric, their morphological characteristics are uniform throughout respective ranges. In Australia much confusion stems from the misapplication of this epithet to *A. marina* by Bailey (1913) and others. This may partly explain the observation by Moldenke (1960), recording this taxon on the east coast of Australia 'south to New South Wales'!

Representative Specimens (36 collections examined)

SRI LANKA. Trincomalee, NW. of Batticaloa (8° 00' N, 81° 40' E), *G. Davidse* 8978 (BRI). MALAYSIA. Selangor: Kuala Selangor (3° 00' N, 101° 20' E), *Samsuai Ahmad SA1119* (LAE); Sarawak R. (2° 30' N, 113° 30' E), *A. G. Wells s.n.* (DNA 12668). N. Borneo: Kedayan, Kudat (6° 53' N, 116° 50' E), *A. Cuadra A3187* (BRI 387183, -4). SINGAPORE. Ulu Pandau N.R. (1° 19' N, 103° 47' E), *Hardial 125* (LAE). PHILIPPINES. Negros (10° 00' N, 123° 00' E), *K. M. Curran 19386* (BRI). INDONESIA. Sumatra: Belawan (3° 47' N, 98° 41' E), *Horthing 6028* (BRI 387182). Seroei: Sei Papoma (1° 53' S, 136° 14' E), *Aet et Idjan 706* (BRI, LAE). Mollucas: Weda (0° 21' N, 127° 52' E), anon. NIFS24925 (BRI 111266). Irian Djaya: Vogelkop, Wosi (0° 52' S, 134° 05' E), *Ch. Koster BW6850* (LAE). PAPUA NEW GUINEA. Milne: Alotau, Gibara Village (10° 24' S, 150° 20' E), *G. Larivita LAE70516* (BRI, LAE). Western: Daru I. (9° 05' S, 143° 15' E), *L. J. Brass 6224* (BRI, LAE); Parama I. (9° 01' S, 143° 24' E), *O. Gideon LAE76194* (LAE). Gulf: Omati R. (7° 40' S, 144° 09' E), *J. S. Womersley NGF5054* (BRI, LAE); Wapo R. (7° 32' S, 144° 39' E), *J. S. Womersley NGF46469* (BRI, LAE); Port Romilly (7° 45' S, 144° 50' E), *A. J. Hart NGF4530* (BRI, LAE); Purari R. delta (7° 45' S, 144° 05' E), *N. C. Duke s.n.* (AIMS 764); Apiopie (7° 50' S, 145° 10' E), *L. A. Craven 823* (BRI, LAE). Central: Kerema Bay (7° 58' S, 145° 44' E), *R. Schodde 4201* (BRI, LAE); Galley Reach (9° 06' S, 146° 57' E), *K. Paijmans Pj1790a* (LAE); Kanudi (9° 26' S, 147° 09' E), *W. K. Kirina 9* (LAE 211162).

5. *Avicennia rumphiana* Hallier f., Meded. Rijksherb. Leiden 37 (1918) 89. *Type: H. Hallier* 3522 (L, lecto), Philippines, Luzon [not, 'Mangium album' Rumphius, Herb. Amboin. 3 (1750) 116, t. 76, as this = *Avicennia marina* var. *eucalyptifolia*].

Avicennia nitida non Jacq. *sensu* Blanco, Flor. Filip., ed. 1 (1837) 504.

Avicennia tomentosa non Jacq. *sensu* Blanco, Flor. Filip., ed. 2 (1845) 353.

Avicennia officinalis non L. *sensu* Schau. ex Miq., Flor. Ind. Bat. 2 (1856) 912.

Sensu var. *spathulata* f. *tomentosa* Kuntze, l.c. (1891). *Type: Kuntze* 6046 (NY), Singapore.

Avicennia lanata Ridley, J. Fed. Malay States Mus. 10 (1920) 151-2. *Type: Watson and Burkill* 3793 (K, cotype; NY, iso), *Burkill* 3797 (K, cotype), Singapore, River Valley Road; *Watson* 2767 (K, cotype), Malay Peninsula, Pahang, Kuatan.

Avicennia marina non (Forsk.) Vierh. *sensu* var. *rumphiana* (Hallier f.) Bakh., l.c. (1921) 213.

Tree, or shrub, to 20 m high, often about 5-10 m; trunk base simple, aerial roots absent; bark dark brown to black, warty or smooth, often with many short longitudinal fissures or reticulate lines forming very small scales; pneumatophores around 20-30 cm high. Leaf lamina ovate-elliptic, apex rounded, 61-99 (79) mm long, 28-47 (36) mm wide, 36-53 (44) mm from base to greatest width, upper surface dark green satiny, undersurface dull pale russet, densely pubescent; petiole 11-18 (14) mm long, glabrous above, densely pubescent below. Inflorescence capitate with 2-4 opposite, decussate bud-pairs, around 10-20 mm long at anthesis. Flower 3-6 mm long, scented; bract triangular, often asymmetric, edge ciliate, apex bluntly acute; bracteoles depressed triangular, edges ciliate or hairy, apices rounded; calyx lobes ovate, 2-4 mm long, 2-5 mm wide, edges ciliate, outer surface densely pubescent except for glabrous distal margin of width c. half calyx length; corolla actinomorphic, 3-9 mm diameter, lobes mostly 4, golden yellow, revolute, reflexed, slightly unequal, 2-3 mm long, 2-3 mm wide, apices rounded, outer surface pubescent except for minute (much < 0.5 mm wide) glabrous distal margin, inner surface dull glabrous; stamens mostly 4, alternate with corolla lobes, positioned equally around corolla mouth, about 0.5 mm long; anthers about 0.5 mm long; stigma glabrous, bilobed pointed arms equal, positioned below anthers; style narrow, around 0.4 mm long, glabrous; ovary domed, about 1.1 mm long,

upper surface densely tomentose, base glabrous (c. 0.5 mm high). Fruit compressed ovoid, 13-18 (16) mm long, 10-18 (14) mm wide, 4-7 (6) mm thick, distal tip rounded, stylar beak absent; pericarp outer surface light green to russet, woolly tomentose, variably wrinkled; calyx persistent on pericarp, 2-4 mm long from base, 5-7 mm diameter; radicle about 10 mm long, densely hairy along full length, hairs straight or wavy, distal tip glabrous; plumule about 4 mm long, pubescent, hairy about base. Fig. 11.

Floral phenology: in New Guinea flowering occurs during October and November and propagules mature chiefly in December.

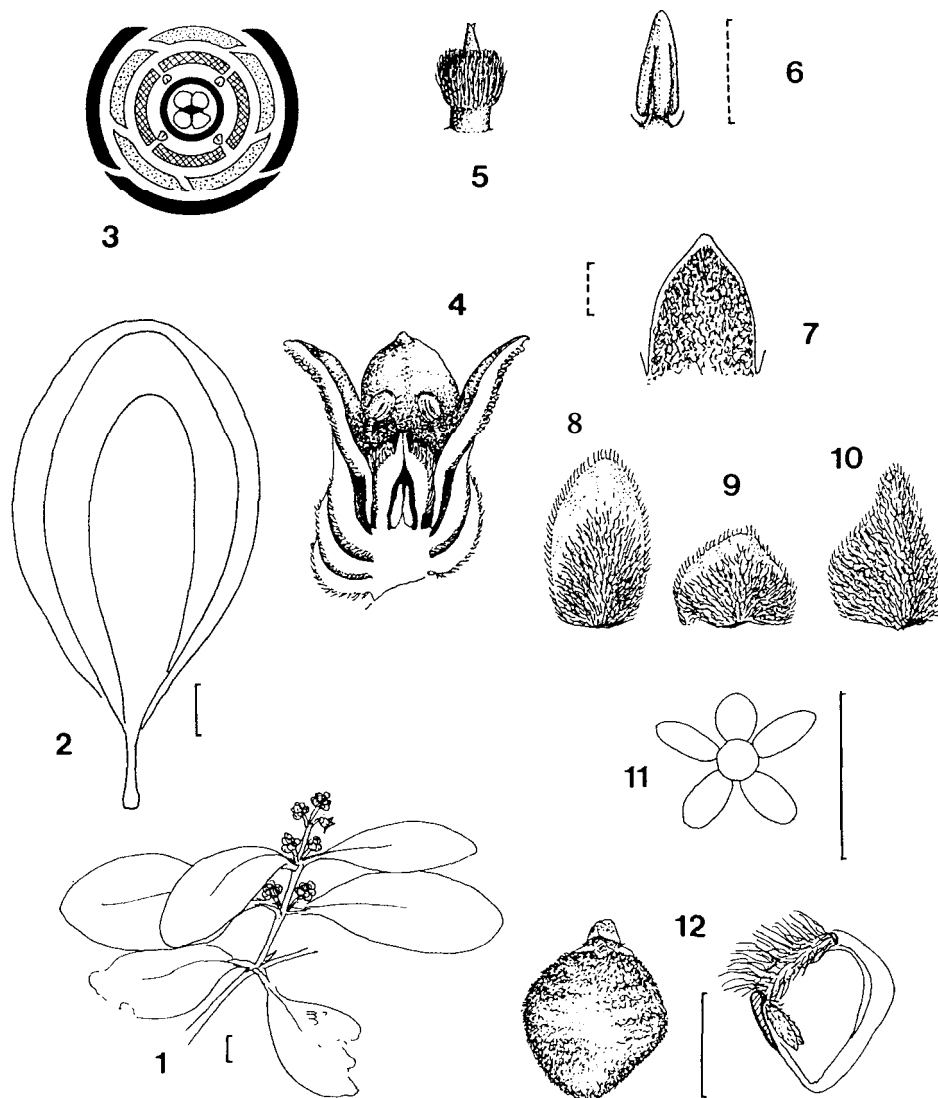


Fig. 11. *Avicennia rumphiana* Hallier f. 1, Flowering branchlet; 2, mean range of leaf outlines; 3, floral diagram; 4, flower (longitudinal section) showing general internal anatomy at anthesis; 5, ovary and style; 6, isolated four-lobed placenta; 7, undersurface of single corolla lobe; 8, calyx lobe (from lower position in floral diagram), exterior surface; 9, bracteole, exterior surface; 10, bract, exterior surface; 11, diagram showing arrangement and dimension of calyx lobes (orientation as in floral diagram); 12, mature propagule, both intact and with pericarp and outer cotyledonary lobe removed to reveal radicle and plumule. Solid scales = 1 cm, dashed scales = 1 mm. (Reference: 4-11, *Main et Aden* 1618; 12, N. C. Duke AIMS1067.)

Distribution: *Avicennia rumphiana* is relatively uncommon but occurs widely through Malaysia, Philippines and western Indonesia to Australasia. In this region it is apparently restricted to mainland New Guinea, particularly but not exclusively the north coast. Its southern and eastern limits are synchronous around the Milne Bay District. The species is unknown in Australia. Figs 1 and 4.

Ecology: limited field observations in Papua New Guinea and herbarium annotations indicate that this taxon is located chiefly in sand or firm silt substrate of middle to higher intertidal positions about coastal embayments.

Notes

This species appears to be relatively infrequent, although individual trees can be quite large. In addition, it has the distinction of not often occurring in low intertidal sites, where all others chiefly are found. The main distinguishing character for *A. rumphiana* includes the dense, rusty brown, tomentose pubescence on apical stems, leaf undersurfaces, flower parts and fruit. Other important attributes include rounded leaf apices, small flowers, a hairy radicle and rounded fruit. Despite these distinctive characteristics, but in-keeping with its infrequent occurrence, *A. rumphiana* was virtually unknown from this region. The present description was supplemented with information from the Malay Peninsula and Singapore (Watson 1928; Tan and Keng 1965). It is of interest that local specimens were determined as *A. marina* var. *rumphiana* at LAE, but their New Guinea occurrence was not reported by Percival and Womersley (1975, and only in passing by Frodin *et al.* (1975). There were also problems with the choice of the correct name for this taxon, and this involves several important considerations. Initially, two forms accepted by Moldenke (1960) appeared applicable, including *A. lanata* and *A. marina* var. *rumphiana*. I have carefully assessed the respective descriptions and find them indistinguishable. Furthermore, as the taxon deserved specific status, it came down to a choice between two binomials, *A. lanata* or *A. rumphiana*. The latter description by Hallier f. predated Ridley's by two years, but I was not satisfied that the Rumphius plate and description could be used as the Type. I found the Rumphius *Avicennia* (i.e. 'Mangium album') more like *A. marina*, possibly var. *eucalyptifolia*. Nevertheless, the description by Hallier f. is unmistakably that of the present species, *A. rumphiana*. Therefore, I have nominated as lectotype one of the specimens he collected and, with this proviso, the name used by Hallier f. stands.

All Specimens Examined (22 collections)

SINGAPORE. Pulau Senang (1° 11' N, 103° 44' E), *Sidek biu Kiah S85* (LAE); Changi (1° 23' N, 103° 59' E), *Hardial 128* (LAE). PHILIPPINES. Mindanao: Davao (7° 04' N, 125° 36' E), *C. Ferraris 20800* (BRI). INDONESIA. Irian Jaya: Oransbari, Vogelkop (1° 16' S, 134° 18' E), *V. W. Moll BW9758* (LAE), *Chr. Versteegh BW4787* (LAE). Moluccas: Morotai (2° 20' N, 128° 25' E), *Main et Aden 1618* (BRI, LAE). PAPUA NEW GUINEA. Western: Daru I. (9° 05' S, 143° 10' E), *L. J. Brass 6225* (BRI, LAE), *N. C. Duke* (AIMS 1122-3), *J. S. Womersley NGF43809* (LAE). Central: Galley Reach (9° 06' S, 146° 57' E), *J. S. Bunt* (AIMS 1183); Tahira (9° 44' S, 147° 30' E), *G. Leach* (LAE 246733); Wai (10° 10' S, 148° 00' E), *K. Rau 244* (LAE). Milne: Salamo R. (9° 38' S, 150° 47' E), *J. Buderus NGF24054* (LAE). Papuan Islands: Goodenough I., Kalimatabutabu (9° 16' S, 150° 18' E), *J. R. Croft LAE71286* (BRI, LAE); Sideia I., near Samarai (10° 37' S, 150° 40' E), *N. C. Duke* (AIMS 1067); Logea I., near Samarai (10° 37' S, 150° 40' E), *N. C. Duke* (AIMS 1066). Northern: Oro Bay (8° 53' S, 148° 30' E), *J. Cavanaugh NGF2402* or -4 (BRI, LAE); Dobodura (8° 47' S, 148° 21' E), *anon. NGF2404?* (LAE 6500). Morobe: Mo R. (7° 45' S, 147° 35' E), *H. Streimann NGF23996* (BRI, LAE). West New Britain: Kilenge (5° 25' S, 148° 25' E), *C. E. Ridsdale NGF30480* (BRI, LAE).

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