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A SYSTEMATIC REVISION OF THE MANGROVE GENUS SONNERATIA (SONNERATIACEAE) IN AUSTRALASIA*

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SUMMARY

In Australia, New Guinea and the southwestern Pacific seven taxa are recognised in *Sonneratia*, of which three species are redescribed in view of their Indo-Malesian counterparts (*S. alba, S. caseolaris, S. ovata*), one species is redescribed from its most likely Indo-Malesian equivalent (*S. lanceolata*, being distinct from *S. caseolaris*), one widespread hybrid is fully described (*S.* x *gulngai* being the putative synonym of *S. alba* x *S. caseolaris*), and two other hybrids (*S. alba* x *S. gulngai, S. alba* x *S. lanceolata*) of very limited occurrence are described as sub-units of their closest 'parental' forms. A key, descriptions and full synonymy are given as well as 2 distribution maps, 6 other figures and one table.

TAXONOMIC STATUS AND DISTRIBUTION

Backer & Van Steenis (1951) compiled a thorough review of the Sonneratiaceae, a family of the order Myrtales. Two genera were described and include *Duabanga*, a small evergreen rainforest genus, and Sonneratia. The latter was made up of five mangrove tree species: *S. alba, S. caseolaris, S. ovata, S. apetala* , and *S. griffithii*. Their distributions were described as tropical and ranging through the Indo-West Pacific region.

However, the account was not complete and new observations were reported in various appendices up to 1972. Some observations included those of additional characters, e.g., leaf mucronate tips or stamen colour; but most importantly there was the possibility of undescribed taxa. These included putative hybrids discovered in NW. Borneo (Muller & Hou-Liu, 1966). In Australia, only one taxon (*S. alba*) was initially reported (Backer & Van Steenis, 1951; Jones, 1971), although there was some evidence that suggested the presence of others, including hybrids (Van Steenis, 1968; Muller & Van Steenis, 1968). Additional taxa were later discovered in extensive field surveys across northern Australia (Wells, 1982; Bunt et al., 1982). However, problems were encountered in classifying them using keys of Backer & Van Steenis (1951). These problems (Bunt et al., 1982; Duke et al., 1984) included: 1)

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presence or absence of petals used to distinguish *S. alba* and *S. ovata*; 2) the occurrence of two forms of *S. caseolaris*; and 3) the possibility of a hybrid between one of the *S. caseolaris* forms and *S. alba* (or *S. ovata*?). Therefore classification of *Sonneratia* species in the study region (described as Australia, New Guinea and the southwestern Pacific) was incomplete, and no taxa were adequately defined.

The most widespread species, *S. alba* (fig. 1), was considered always to have

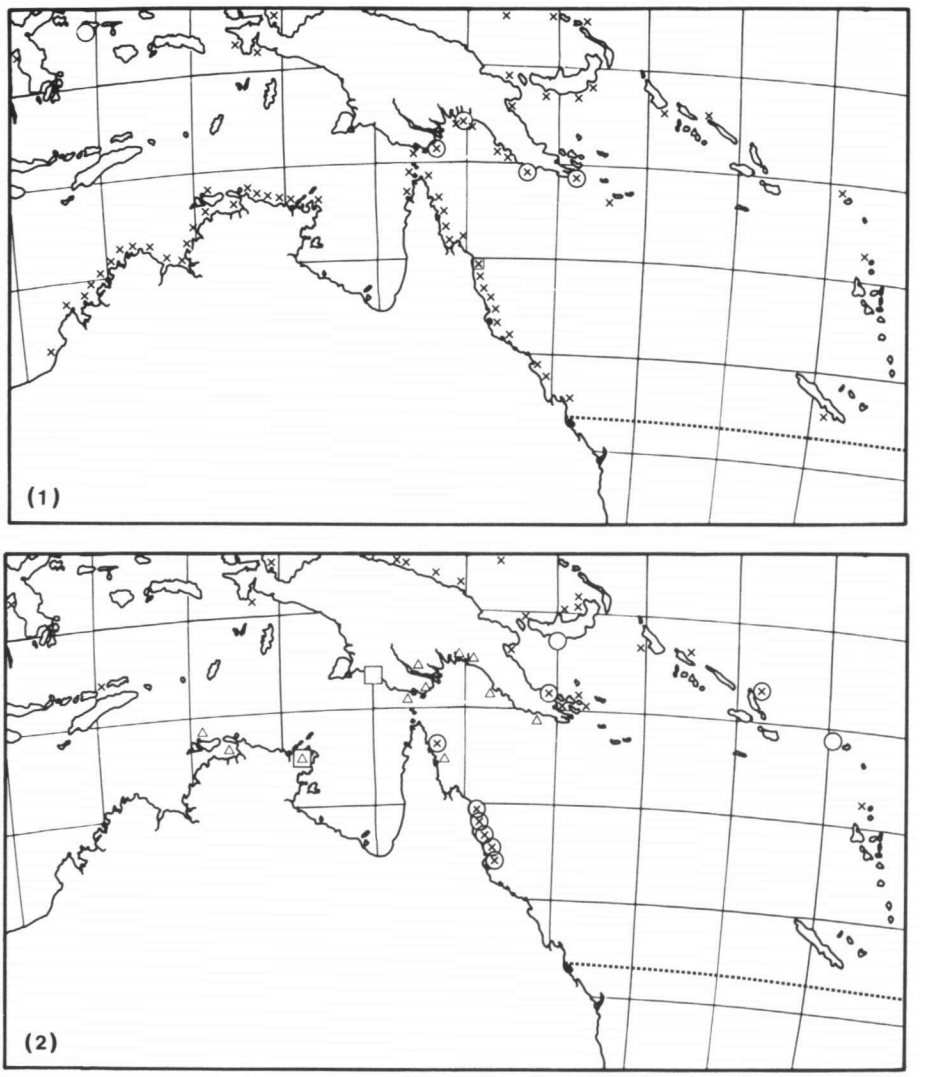

Fig. 1. Distribution of *Sonneratia* in Australia, New Guinea and the southwestern Pacific region: (1) *S. alba* J. Smith (cross), *S. ovata* Backer (circle), and *S. alba* x *S. gulngai* (square); (2) *S. caseolaris* (L.) Engl.(cross), *S.* x *gulngai* N.C. Duke (circle), *S. lanceolata* Blume (triangle) and *S. alba* x *S. lanceolata* (square).

petals, although these may have been hard to discern (Backer & Van Steenis, 1951). Exhaustive searches of both fresh and herbarium material from the region have revealed that the petalous condition of *S. alba* is variable. It is now known to occur in three forms: petalous, apetalous, and semipetalous (the latter term applies to those forms where petal numbers are less than the number of calyx lobes, commonly six).

These three forms were also observed to have a disjunct distribution. Apetalous varieties predominate at the southern limits of the species on the east and west coasts of Australia. In New Guinea, there is no discernible geographical pattern. However, ecologically, apetalous forms predominate in small offshore island populations, and petalled forms are chiefly estuarine throughout their range.

The use of petal presence or absence by Backer & Van Steenis (1951) to distinguish between apetalous *S. alba* and the less common, normally apetalous, *S. ovata* created problems. Although both species possess white filaments, many other characters appeared to be quite distinctive. Characters unique to *S. ovata* include the lack of a mucronate leaf apex, a finely verruculose calyx, and its common occurrence in higher topographic (tidal) positions near the terrestrial fringe. The known distribution of *S. ovata* (fig. 1) was extended, and it occurs along the southern Papua New Guinea coastline to Milne Bay (10°23'S, 150°31'E). The species was not recorded in Australia, but it was located on Daru Island (9°05'S, 143° 10'E) in the northern Torres Strait.

Van Steenis (1968) indicated that he expected a greater variety of forms of *Sonneratia* in Australia and New Guinea, including some of the putative hybrids observed in NW. Borneo (Muller & Van Steenis, 1968). Since then three other major taxa have been discovered. These five taxa and their diagnostic characters are presented in table 1.

Sonneratia lanceolata and *S. caseolaris* have never been observed to co-inhabit the same estuary, although their geographical ranges overlap. *Sonneratia caseolaris* is only found on the northeast coast of Australia (fig. 1), but *S. lanceolata* also occurs in the Northern Territory (although it is limited to three separate areas). In New Guinea the distribution of these two taxa is also disjunct, with *S. lanceolata* occupying most larger estuaries on the mainland south coast, and *S. caseolaris* in similar habitats on the north coast.

Features which characterise populations of the hybrid *S.* × *gulngai* (Duke, 1984) include morphological attributes which are either intermediate or alternately shared between *S. alba* and *S. caseolaris*. These characters include: high levels of pollen infertility and poor fruit set; a floral development cycle which is complex; generally luxuriant foliage and greater tree size. This latter factor allows this common hybrid form to be easily recognised in the field. The regional distribution of the hybrid and the least common parent, *S. caseolaris*, are equivalent in Australia. Both taxa are found on the east coast from the southern limit, Murray River (18°05'S, 146°01'E), north to the Olive River (12°10'S, 143°05'E). It is anticipated that in New Guinea additional populations will be located where the parental ranges also overlap.

This revision is based on both herbarium material and field observations. Contributing herbaria (abbreviations from Holmgren & Keuken, 1974): AIMS, Herbarium of the Australian Institute of Marine Science, Townsville; BRI, Queensland Herba-

Table 1. Diagnostic characters of major *Sonneratia* in Australia, New Guinea and the southwestern Pacific region.

	S. alba	*S. caseolaris*	*S. x gulngai*	*S. lanceolata*	*S. ovata*
Leaves	elliptic	elliptic	elliptic	elliptic lanceolate	broadly ovate
Leaf apices	rounded, mucro fold	apiculate, mucronate	apiculate, mucronate	apiculate, mucronate	rounded, mucro absent
Leaf base	attenuate oblique	attenuate oblique	attenuate oblique	attenuate oblique	reniform
Peduncle/branchlets	terete	terete or tetragonous	terete	terete or tetragonous	terete
Petals	white, linear-spathulate, often absent	red, linear	red, linear	red, linear, rarely double	absent
Stamen	white	red, rarely white	red	white	white
Calyx	smooth, shiny	coriaceous-warty, shiny	smooth, dull shiny	coriaceous-smooth, dull	smooth, dull coriaceous
Fruit calyx (hypanthium)	cup-shaped	flat-expanded	cup-shaped	flat-expanded	flat-expanded
Fruit	width = corolla width	width 5 mm > corolla width	width = corolla width	width 5 mm > corolla width	width 5 mm > corolla width
Seeds	falcate	angular irregular	angular irregular	angular irregular	rounded irregular
Inflorescence	1–5 (2)	1–3 (1 or 2)	1–3 (1 or 2)	1–2 (1)	1–3 (2)
Pollen					
shape	triporate	variable	variable	triporate	
size	50–80 µmP 40–50 µmE	40–60 µmP 30–40 µmE	60–100 µmP 40–65 µmE	40–65 µmP 30–55 µmE	—

rium, Brisbane; DNA, Herbarium of the Conservation Commission of the Northern Territory, Darwin; LAE, Division of Botany, Department of Forests, Lae; PERTH, Western Australian Herbarium, Department of Agriculture, Perth; QRS, Queensland Research Station, Forest Research Institute, Atherton; and UPNG, Herbarium of the University of Papua New Guinea, Port Moresby.

A BRIEF EVALUATION OF DIAGNOSTIC CHARACTERS *

Habitat — Most species of this region may be distinguished by the habitat in which they commonly occur. Further details shall be reported by Duke (a; in preparation). Only two species, *S. lanceolata* and *S. caseolaris,* were found in the same, or a similar, habitat.

Habit — Tree form and foliage colour may be used to distinguish the species. However, the differences are subtle but they are useful to the experienced field observer.

Pneumatophores — Length, diameter and shape are useful characters in the field.

Leaves — Subtle differences of surface texture, colour and shape may be used to distinguish most species. However, only *S. lanceolata* (with lanceolate leaves) and *S. ovata* (with broadly ovate leaves and no apical mucro) may be readily separated.

Petiole — Relative length, and degrees of lamina extensions may be used to categorise subgroupings or support other diagnostic characters.

Inflorescence — The numbers of buds per inflorescence vary but are not generally considered diagnostic.

Hypanthium — Surface texture of the calyx tube is diagnostic although populations of some species vary slightly. The degree of red coloration is variable on the inner calyx lobe surfaces.

Corolla — Presence or absence of petals is of little assistance in distinguishing the species because this character is variable in *S. alba.* Petal colour may be useful in separating subgroups.

Stamens — Colour of the filaments is generally consistent and useful in separating subgroups of the genus, unlike length and thickness.

Ovary — Structure of the ovary generally is not diagnostic. Subtle differences are observed in the position of placental material on the septa. The number of locules is variable.

Pollen — Muller (1969, 1978) and Wright (1977) reported some differences in shape, size and ornamentation.

Cytology — Muller & Hou-Liu (1966) reported chromosome counts of n = 11 for the major Indo-Malesian taxa and associated hybrids. In Australasia, one of us (Duke) observed counts of n = 12 in the four major taxa described (1–4). Methods used were similar to those described earlier by Muller & Hou-Liu (1966), except that acid orcein stain was found more suitable. These latter results concur with the findings of Sidhu (1962) for *S. apetala,* and Weiss (1973) for *S. alba.*

* Unless otherwise stated, all characters are more fully described in the specific descriptions.

Fruit — Characteristics of the mature fruit are very important in distinguishing between the species. Some characters enable generic subgroups to be delimited, others may be used to confirm species identification. Diagnostic characters include calyx tube shape, the relative widths of fruit and hypanthium, and surface texture and colour.

Seeds — Shape and size of seeds are generally not useful as diagnostic tools, but one species, *S. alba*, is readily distinguished from the others.

MORPHOMETRIC ANALYSES

Classification of taxa in this revision was supported by morphometric analyses. Full details of these studies are to be reported by Duke (b, in preparation). In summary, 283 specimens from 43 Australasian sites were examined. Collections were obtained both fresh and from various herbaria including LAE, DNA, QRS, BRI, and AIMS. Observations on collections covered up to 42 numeric and 18 multistate attributes of a wide range of vegetative and reproductive part morphological characters – including those commonly used in earlier specific descriptions. The study showed *S. alba* as having a central generalised affinity with five of the six other taxa considered (fig. 2). *Sonneratia lanceolata* was notably seen as the taxon with the last affinities with *S. alba*. It was also quite separate from *S. caseolaris*. Putative hybrids are clearly portrayed in their intermediate positions. Thus overall in the scheme there are basically three wings branching from the central axis of *S. alba* and *S. caseolaris*.

Intraspecific results demonstrate the possible ecotypic expression of the petalous condition of *S. alba*. This species is found to be apetalous chiefly in marine offshore situations and in higher latitudes. Other characters are less variable and this species along with *S. caseolaris*, *S.* × *gulngai* and *S. ovata* are seen to be generally morphologically homogeneous. In contrast, *S. lanceolata* has well defined infraspecific groups based on geographic occurrence.

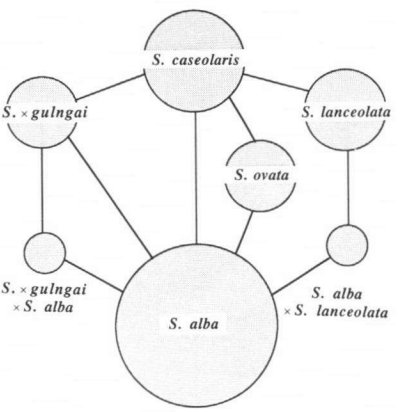

Fig. 2. Schematic diagram of Australasian *Sonneratia* taxa and their inter-specific affinities deduced from morphometric analyses. Choice of circle size and line length is arbitrary.

ACKNOWLEDGEMENTS

This revision is part of a larger study of the genus *Sonneratia* in Australasia. The study was undertaken part-time towards a thesis with the James Cook University of North Queensland whilst the senior author was employed by the Australian Institute of Marine Science. We wish to note our gratitude to both these institutions and Dr. John Bunt (A.I.M.S.). We also wish to thank the directors and curators of the herbaria listed for making specimens in their care available to us.

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— (b) Morphometric analysis of the mangrove genus Sonneratia in Australasia. In preparation.

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Tree medium, columnar to spreading, c. 20 m, trunk not buttressed; bark flaky, grey pale brown; roots radiating, horizontal, subsurface. *Pneumatophores* numerous, vertical, stout, elongate, cone-shaped, often branching, soft flaky surface, soft spongy light wood, length 0.2–2.5 m above substrate. *Leaves* simple, opposite, entire, smooth, glabrous, leathery; apex mucronate, either extended (minutely) and thickened, or obscure, or rarely non-existent. Stipules absent. *Flowers* bisexual, terminal, either singly or in groups of 2 or 3, 4–8-merous; calyx tube of mature bud obconical or cup-shaped, lobes ovate-oblong-triangular, surface green, leathery, sometimes coloured red on the inside. Disc saucer-shaped. *Petals* when present red, white, or white with slight green or red coloration near base, filamentous, spathulate, thinly lanceolate or narrowly linear, early caducous. *Stamens* numerous (approximately 300), inflexed in closed bud, straight in open flower, early caducous; filaments filiform, red or white; anthers reniform, pale yellow. *Ovary* superior, sessile, depressed, 10–20 locules. *Style* folded twice, contracted in mature bud, straight and extended in open flower; stigma entire, capitate. *Fruit*, when mature, rests on the persistent calyx as an indehiscent, green, smooth, depressed-globose berry with leathery pericarp, crowned by style base; style sometimes persistent but withered. *Seeds* c. 5 mm long, numerous, embedded in firm pulp, released after fruit has fallen from the tree.

Distribution. Seven species, extending from East Africa to Indo-Malesia, Australia, New Guinea and the western Pacific.

Ecology. Found throughout northern Australia, New Guinea, and the south-western Pacific region in mangrove swamps, on the banks of tidal rivers and creeks, and within sheltered bays of offshore islands and reef cays along the Great Barrier Reef. *Sonneratia* species along with *Avicennia* are usually regarded as pioneers of the mangrove swamp. The seeds are intolerant of shade, germinating on bare or near bare mud banks. Consequently their occurrence is usually at the waters edge of the mangrove forest (frontal). There is one exception, *S. ovata*, which is an uncommon species not yet observed in great detail, but noted to occur closer to the terrestrial margin.

Notes. Several vernacular names appeared in prior revisions. 'Pagapate' was the vernacular term used by Sonnerat, Voy. Nouv. Guinée (1776) 16, t. 10 & 11, to describe what is now called *Sonneratia caseolaris*. Sonnerat did not present an acceptable name. Linnaeus fil. (1781: l.c.) recognised the value of the description and figure, and named the taxon *Sonneratia acida*. However, the problem was compounded because the species had already been named *Rhizophora caseolaris* by Lin-

naeus (1754: l.c.). Additional problems (discussed later for respective species) arose because this single epithet was based on the dual description '*Mangium caseolare album/rubrum*' by Rumphius, Herb. Amboin. 3 (1743) 111, t. 73–75. Furthermore, the generic name of *Rhizophora* was found to be inappropriate, and several subsequent treatments listed other epithets: e.g., *Blatti* was proposed by Adanson (1763: l.c.) based presumably on a description by Rheede, Hort. Malab. 3 (1682) 43, t. 40. Other treatments followed Linnaeus filius. Engler (1897: l.c.) proposed an agreeable solution by conserving *Sonneratia* L. f. as the name of the genus, and, *S. caseolaris* (L.) Engl. as the type species. However, there was continued confusion with specific epitheton, notably *S. caseolaris*. These will be discussed later for respective taxa. The name '*Tombea*', referred to in earlier treatments (notably Backer & Van Steenis, l.c.), was not listed in synonymy. It was also believed to be vernacular (New Caledonia). Brongniart & Gris (1864: l. c.) believed the entity was *Chiratia* Montrouzier, although they later synonymised it under *Sonneratia* (Brongn. & Gris, 1866: l.c.).

KEY TO THE SPECIES*

1 a. Calyx smooth, usually shiny; mature fruiting receptacle cup-shaped, the fruit diameter usually < 4 cm, width ≤ hypanthium width; petioles usually > 0.7 cm long 2

b. Calyx coriaceous, often warty and shiny or finely textured; mature fruiting receptacle flat-expanded, fruit diameter usually > 4 cm, width mostly 0.5 cm (or more) greater than hypanthium width; petioles usually < 0.7 cm long 3

2 a. Petals white (maybe tinged green or pink at base) and linear, spathulate or absent; staminal filaments white; style length (shortly after anthesis) < 4.5 cm; calyx tube often distinctly ribbed beneath lobe fusion points; fruit surface dull; seeds falcate and smooth. *Northern Australia, New Guinea, western Pacific, through Indo-Malesia to China, India and southeastern Africa* ..... **1. S. alba**

b. Petals red, linear; staminal filaments red; style length (shortly after anthesis) > 4.5 cm; calyx tube not ribbed beneath lobe fusion points; fruit surface satiny; seeds angular and rugose. *Northeastern Australia, northern New Guinea, southwestern Pacific to at least northwestern Borneo* ..... **3. S. × gulngai**

3 a. Petals red, linear; staminal filaments red or white; style length shortly after anthesis > 5 cm; peduncle often tetragonous; calyx lobes flat, expanded; calyx surface shiny, slightly coriaceous; leaf base attenuate to shortly so; leaf mucronate apex distinct 4

b. Petals absent; staminal filaments white; style length shortly after anthesis < 4.5 cm; peduncle terete; calyx lobes distinctly reflexed, adpressed; calyx surface verruculose; leaf base rounded to truncate to subcordate; leaf mucronate apex absent or minute. *Southern New Guinea, Indo-Malesia to Thailand and China* **5. S. ovata**

* Observations on colour, texture and form are generally field based. Detailed measurements were taken from dried specimens, unless otherwise stated. Mean values are often given in brackets immediately following attribute ranges of specimen means listed in the specific descriptions.

4 a. Staminal filaments red, rarely white; calyx tube grooved; leaves mostly obovate, length to breadth ratio usually < 2; flower buds medially constricted; fruit surface shiny, coriaceous. *Northeastern Australia, northern New Guinea, southwestern Pacific, through Indo-Malesia to China and India* ..... **2. S. caseolaris**

b. Staminal filaments white; calyx tube not grooved or ridged; leaves mostly lanceolate, length to breadth ratio usually > 2; flower buds with no distinct medial constriction; fruit surface shiny, smooth. *Northern Australia, southern New Guinea, to at least Borneo and Celebes* ..... **4. S. lanceolata**

Additional, but rare taxa:

(a) Solitary tree distinguished from *S.* × *gulngai* by absence of petals. *Northeastern Australia* ..... **3a. S. alba** × **S. gulngai**

(b) Two specimens distinguished from *S. lanceolata* by cup-shaped calyx tube on mature fruit. *Northern Australia, southern New Guinea*
4a. S. alba × **S. lanceolata**

1. Sonneratia alba J.Smith – Fig. 3.

Sonneratia alba J.Smith in Rees, Cycl. 33, 2 (1819); DC., Prod. 3 (1828) 231; Blume, Mus. Bot. Lugd.-Bat. 1 (1851) 338; Miq., Fl. Ned. Ind. 1, 1 (1855) 497; Brongn. & Gris, Ann. Sci. Nat. Bot. 6 (1866) 266; Bull. Soc. Bot. France 13 (1866) 479; Kurz, For. Fl. Burma 1 (1877) 526; C.B.Clarke, Fl. Brit. India 2 (1879) 580; Fern.-Vill., Nov. App. (1880) 92; Bisschop Grevelink, Pl. Ned. Ind. (1883) 163; Ceron, Cat. Pl. Herb. Manila (1892) 86; Koord. & Valeton, Bijdr. Booms. Java 1 (1894) 200; Koord., Versl. Minahasa (1898) 470; F.M.Bailey, Queensl. Fl. (1900) 679; Ann. Rep. Brit. New Guinea (1901) 143; Becc., Nelle For. di Born. (1902) 579; Koord., Exk. Fl. Java 2 (1912) 663; F.M.Bailey, Compr. Cat. Queensl. Pl. (1913) 214; Merr., Interpr. Herb. Amboin. (1917) 383; Backer, Bull. Jard. Bot. Buitenz. III, 2 (1920) 330; E.G. Baker, J. Linn. Soc. Bot. 15 (1921) 307; Engl. & Drude, Veg. Erde 9 (1921) 655; Gagnep. & Guillaumin, Fl. Gén. Indo-Chine 2 (1921) 980; Merr., Enum. Born. Pl. (1921) 418; C.T. White, Proc. Roy. Soc. Queensl. 34 (1922) 45; Meindersma, Tectona 15 (1922) 573, f. 17; Trop. Natuur 12 (1923) 77, f. 17; R.Parker, Indian For. 51 (1925) 507; C.T. White, J. Bot. 64 (1926) 217; K.Heyne, Nutt. Pl. Ned.-Ind. (1927) 1156; Ridley, Disp. Pl. (1930) 293; Troll, Trop. Natuur 22 (1933) 33, cum ic.; Kint, Trop. Natuur 23 (1934) 173, f. 9; Kaneh., J. Jap. Bot. 14 (1938) 421, f. 1–3; Brenan & Greenway, Checkl. For. Trees Brit. Emp., Tangany. Terr. V, 2 (1949) 592; Steenis, Fl. Scholen Indonesië (1949) 292; Backer & Steenis, Fl. Males. I, 4 (1951) 285, f. 3b; Wyatt-Smith, Malayan For. 16 (1953) 214, t. 1, f. 3; H. Perrier, Fl. Madag. (1954) fam. 148, 2, f. 1; Mahabale & Deshpande, Palaeobotanist 6 (1957) 52, t. 1; Cuf., Bull. Jard. Bot. État Brux. 29, Suppl. (1959) 612; Dale & Greenway, Kenya Trees Shrubs (1961) 539, f. 98; Backer & Bakh. f., Fl. Java 1 (1963) 257; Vu Van Cuong, Fl. Cambodia Laos Vietnam 4 (1965) 196, pl. 1; Muller & Hou-Liu, Blumea 14 (1966) 337, t. 1, f. 1c & 3c; Steenis, N. Queensl. Naturalist 35 (1968) 5, cum ic.; Muller & Steenis, ibid. 35 (1968) 7; G.Williams Sangai, Fl. Trop. E. Africa (1968) 1, f. 1; J.E.D.Fox, Ann. Rep. For. Res. Malay. (1970) 99; W.T.Jones, N. Queensl. Naturalist 20 (1971) 50; Backer & Steenis, Fl. Males. I, 6 (1972) 973, f. 17e–g & 18c; Whitm., Malayan For. Rec. 26 (1972) 445; Lind & Morrison, East Afr. Veg. (1974) f. 4 (2d); Chai, Malaysian For. 38 (1975) 202; Frodin et al., Univ. Papua New Guinea Occas. Pap. 3 (1975) 42; Percival & Womersley, Bot. Bull., Dept. For., Papua New Guinea 8 (1975) 85, 88, f. 65; Chapman, Mangrove Veg. (1976) 388, f. 291c; Floyd, Ecol. Rep., Dept. For. Papua New Guinea 4 (1977) 45, 47; Semeniuk et al., Mangroves W. Austral. (1978) 73, pl. 30; A.G.Wells in Clough, Mangrove Ecosyst. Austral. (1982) 74; in Teas, Tasks Veg. Sci. 8 (1983) 71; Ko, Acta Phytotax. Sin. 23 (1985) 313. – *Rhizophora caseolaris* L., Herb. Amb.

(1754) 13, p.p. – *Sonneratia acida* auct. non L. f.: Benth., Fl. Austral. 3 (1866) 301, p.p.; Hiern, Fl. Trop. Afr. 2 (1871) 483; Baker, Fl. Mauritius (1877) 102; Volkens, Bot. Jahrb. Syst. 31 (1901) 47; Dupont, Rep. Invest. St. Pierre Astove, Kew Libr. (1907) 24; Hemsley, Kew Bull. (1919) 122. – *Blatti alba* Kuntze, Rev. Gen. Pl. 1 (1891) 238; Niedenzu in E. & P., Nat. Pfl. Fam. 3, 7 (1892) 21, f. 7h & j. – *Sonneratia caseolaris* auct. non (L.) Engl.: Engl., Pflanzenwelt Ost-Afrikas C (1895) 286; in E. & P., Nat. Pfl. Fam. Nachtr. 1 (1897) 261, ex parte; sensu Merr., Enum. Philipp. Flow. Pl. 3 (1923) 139; Panshin, Philipp. J. Sci. 48 (1932) 161, pl. 7; Kaneh., Fl. Micron. (1933) 251, f. 117; Enum. Micron. Pl. (1935) 375; R. Williams, Useful Orn. Pl. Zanzibar Pemba (1949) 449, cum ic., ex parte; Blake, Austral. J. Bot. 2 (1954) 136; Fernando & Pancho, Sylvatrop. Philipp. For. Res. J. 5 (1980) 52. – *Sonneratia pagatpat* auct. non Blanco: Merr., Bull. Bur. For. Philipp. 1 (1903) 42; Philipp. J. Sci. 1 (1906) Suppl. 101; Fl. Manila (1912) 344. – *Sonneratia griffithii* auct. non Kurz: Watson, Malayan For. Rec. 6 (1928) 50,55,120, f.24; Burkill, Dict.2 (1935) 2053. – Type: Rumphius, Herb. Amboin. 3 (1743) 111, t. 73!, Indonesia, Amboina.

Chiratia leucantha Montr., Mém. Acad. Sci. Lyon, Sect. Sci. 10 (1860) 203; Brongn. & Gris, Ann. Sci. Nat. Bot. 1 (1864) 364; Bull. Soc. Bot. France 11 (1864) 71. – Types: *Vieillard 432, Pancher s.n., Deplanche 505* (syn.; n.v.), New Caledonia.

Sonneratia mossambicensis Klotzsch in W. Peters, Naturw. Reise Mossambique 1 (1862) 66, pl. 12. – *Sonneratia acida* var. *mossambicensis* (Klotzsch) Mattei, Boll. Reale Orto Bot. Giard. Colon. Palermo 7 (1908) 108. – Type: *Peters s.n.* (B, holo; K, iso; n.v.), Africa, Mozambique.

Sonneratia iriomotensis Masam., Syokubutu-tirigaku (1936) f. 71; Trans. Nat. Hist. Soc. Taiwan 29 (1939) 272. – *Sonneratia alba* J. Smith var. *iriomotensis* (Masam.) Yamamoto, J. Soc. Trop. Agric. 12 (1940) 162. – Type: unknown, Japan?

Sprawling to erect tree c. 20 m high. Trunk base not buttressed. Bark smooth or lightly fissured and flaky, dark grey to pale fleshy coloured. *Pneumatophores* stocky, bluntly pointed, c. 25 cm high. *Leaves:* lamina elliptic or ovate (often widely so), 48–107 (74) mm long, 25–76 (47) mm wide, pale green, dull on upper surface, satin lustre on lower surface, midvein rarely reddened, lamina not decurrent on petiole; apex broad, mucro recurved, adpressed to leaf undersurface; petiole 6–15 (9) mm long, terete. *Inflorescence* with 1–5 (2) buds; stems beneath mostly terete. Mature bud: apex acute to obtuse, attenuate to obtuse at base, medially constricted, upper portion 13–15 (14) mm wide, lower portion 12–22 (16) mm wide, in all 20–33 (28) mm long. *Flowers:* hypanthium glossy, smooth, often ribbed beneath fusion point of calyx lobes; calyx lobes 5–8 (6 or 7), 13–19 (16) mm long, acute apex, inner surface often reddish; petal numbers and presence variable, linear, 14–30 (20) mm long, 1–2 (1) mm wide when fresh, to spathulate or stamen-like, mostly white, often tinged red or green at base; staminal filaments 15–45 (29) mm long when fresh, entirely white; anthers dorsifixed, pale yellow; petals and stamens fall within hours of anthesis; ovary 12–20-(16-)locular; style c. 43 mm long, stigma fungiform, c. 3 mm wide. *Berry* erect, globose, 4–27 (14) mm long, 22–46 (32) mm wide, pericarp coriaceous, dull without ribs; calyx persistent, hypanthium cup-shaped, 25–41 (32) mm wide, 27–46 (37) mm from calyx base to lobe apex, lobes erect, spreading 17–26 (20) mm long. *Seeds* numerous, c. 12 mm long, falcate.

Phenology. Leaf fall peaks in January. Flowering is common in October and November. Fruiting (in the Murray River, Queensland, c. 40% of units attains maturity from immature bud stages; c. 30% are aborted at the immature fruit stage) occurs mainly around February (ranging from January to March).

Distribution. The species is found from southeastern Africa to India and southern China to the western islands of the Pacific Ocean. In Australia the species is found from Port Clinton (22°35'S, 150°45'E) on the east coast, across northern

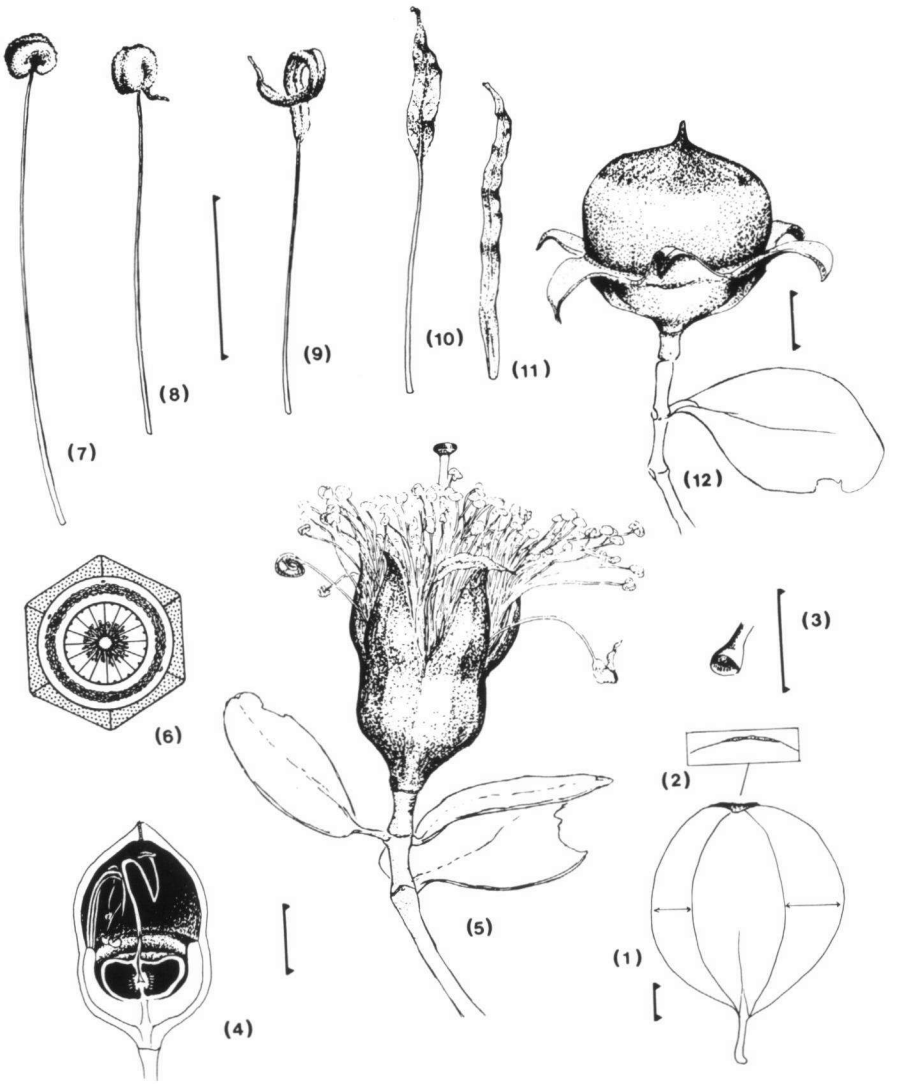

Fig. 3. *Sonneratia alba* J. Smith. 1. Mean range of leaf outlines; 2. 'lip'-like leaf mucronate apex; 3. petiole base; 4. mature flower bud (longitudinal section) showing general internal anatomy just prior to anthesis; 5. flower at anthesis (petalled form); 6. floral diagram (semi-petalled form); 7. stamen; 8 & 9. two forms of staminal-form petals; 10. spathulate petal; 11. linear petal; 12. mature fruit. Scale = 1 cm.

Australia to Cape Bossut (18°43'S, 121°38'E) on the west coast. The species was similarly widespread about New Guinea, although it is less common on the northern coast. Other locations include: New Caledonia, New Hebrides, Solomon Islands, and generally throughout SW. Oceania. Fig. 1.

Ecology. This species occurs at lower tidal contours in frontal stands, as isolated trees in downstream lower estuarine situations or about offshore islands in areas of high to moderate rainfall and tidal range greater than one metre. Commonly associated with *Rhizophora stylosa, Aegiceras corniculatum* and *Avicennia marina*, and usually growing in either sand, gravel or soft mud.

Notes. Since J. Smith described *S. alba* (1819: l.c.) from the figure and description of *'Mangium caseolare album'* Rumphius (1743: l.c.), our view of this taxon has been relatively stable. However, one aspect has altered significantly. In earlier keys (e.g., Backer & Steenis, 1951: l.c.), the presence or absence of petals was used as a definitive key attribute. Unfortunately, there were a variety of petalous conditions in *S. alba*. Furthermore, the occurrence of less-petalled forms was related to marginal habitats resulting from both climatic and localised factors. Thus in colder climates, towards the southern latitudinal limits, apetalous and semipetalous forms were more common. In more equatorial areas, petalled forms were common in riverine estuaries and less-petalled forms were found more frequently offshore on smaller rocky islands and coral cays. This apparent ecotypic variability precluded even the use of intraspecific epitheton based on petallous condition in this taxon.

2. Sonneratia caseolaris (L.) Engl. – Fig. 4.

Sonneratia caseolaris (L.) Engl. in E. & P., Nat.Pfl.Fam.Nachtr. 1 (1897) 261; Koord. & Valeton, Bijdr. Booms. Java 8 (1902) 156; Merr., Fl. Manila (1912) 344; Druce, Bot. Exch. Club Brit. Isles 3 (1914) 424; Merr., Interpr. Herb. Amboin. (1917) 383; Enum. Born. Pl. (1921) 418; R. Parker, Indian For. 51 (1925) 507; Panshin, Philipp. J. Sci. 48 (1932) 143; Burkill, Dict. 2 (1935) 2052; Kaneh., J.Jap.Bot. 14 (1938) 423, f. 3 1–n; Steenis, Fl. Scholen Indonesië (1949) 291; Merr., J.Arnold Arbor. 31 (1950) 285; Backer & Steenis, Fl. Males. I, 4 (1951) 283, f. 3c; Wyatt-Smith, Malayan For. 16 (1953) 214, t. 1, f. 1; Backer & Steenis, Fl. Males. I, 5 (1958) 537; Steenis, Nova Guinea n.s. 12 (1963) 189; Vu Van Cuong, Fl. Cambodia Laos Vietnam 4 (1965) 199, pl. 1; Muller & Hou-Liu, Blumea 14 (1966) 337, t. 1, f. 1e & 3e; Steenis, N. Queensland Naturalist 35 (1968) 3, cum ic.; Muller & Steenis, ibid. 35 (1968) 8; J.E.D. Fox, Ann. Rep. For. Res. Malay. (1970) 99; Backer & Steenis, Fl. Males. I, 6 (1972) 973, f. 17a–d & 18e; Whitm., Malayan For. Rec. 26 (1972) 445; Chai, Malaysian For. 38 (1975) 203; Perci - val & Womersley, Bot. Bull., Dept. For., Papua New Guinea 8 (1975) 88, f. 66; Chapman, Mangrove Veg. (1976) 388, f. 291e; Floyd, Ecol. Rep., Dept. For., Papua New Guinea 4 (1977) 44 ic. only; A.G. Wells in Teas, Tasks Veg. Sci. 8 (1983) 72, ex parte; Ko, Acta Phytotax. Sin. 23 (1985) 313. – *Rhizophora caseolaris* L., Herb. Amb. (1754) 13, ex parte; Amoen. Acad. 4 (1759) 123; Syst. Nat. ed. 10 (1759) 1043; Sp. Pl. ed. 2 (1762) 635; Burm. f., Fl. Indica (1768) 108; Lour., Fl. Cochinch. ed. 2 (1793) 296, 363. – *Sonneratia acida* auct. non L. f.: Lam., Encycl. 1 (1785) 429; Tabl. Encycl. 2 (1794) t. 420; J.Smith in Rees, Cycl. 33, 2 (1819); Roth, Nov. Pl. Sp. (1821) 233; Sprengel, Syst. Veg. 2 (1825) 493; DC., Prod. 3 (1828) 231; Roxb., Fl. Ind. ed. 2 (1832) 506; Wight & Arn., Prod. Fl. Penins. Ind. Or. 1 (1834) 327; Decne., Nouv. Ann. Mus. Hist. Nat. 3 (1835) 454; Spanoghe, Linnaea 15 (1841) 203; Wight, Icon. Pl. 2 (1843) 340; Korth., Ned. Kruidk. Arch. 1 (1846) 198; Blume, Mus. Bot. Lugd.-Bat. 1 (1851) 336; A. Gray, U.S. Expl. Exp., Phan. 15 (1854) 550; Griff., Not. Pl.

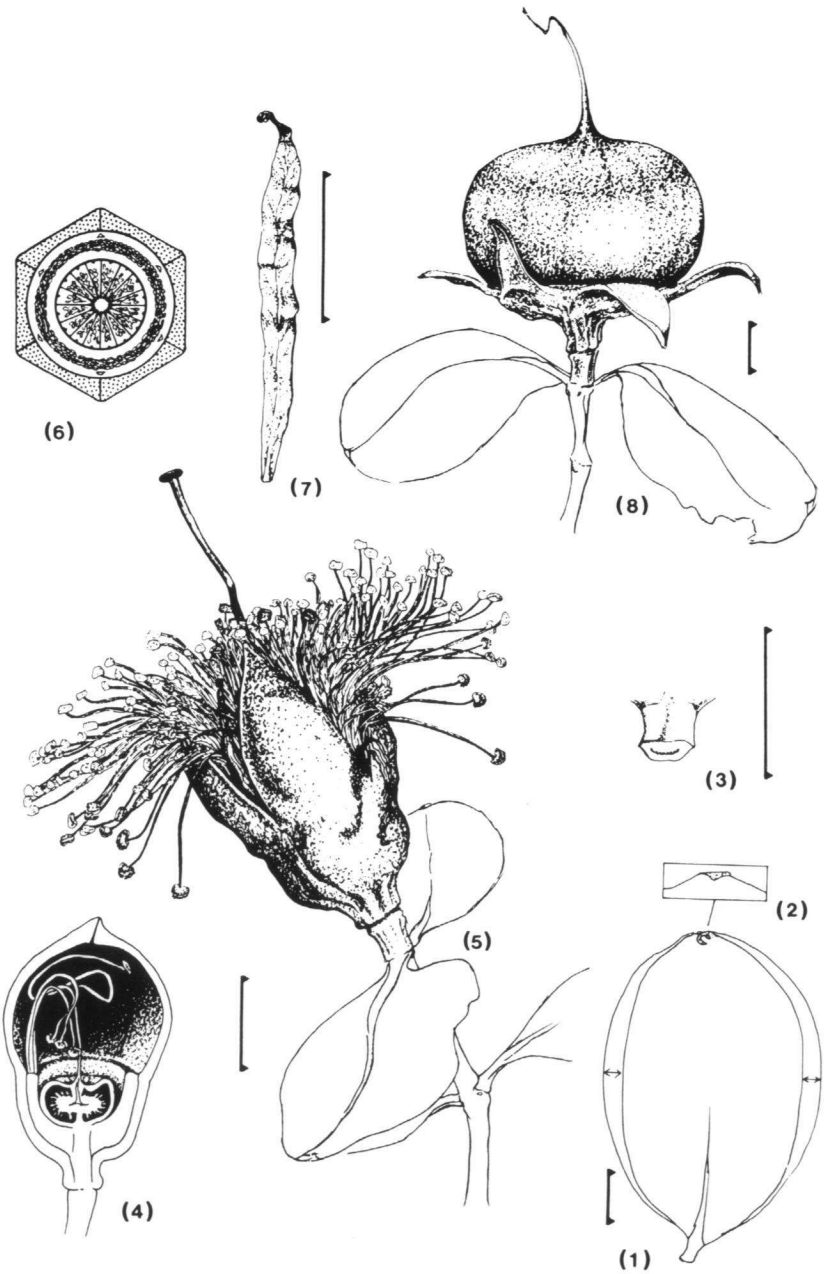

Fig. 4. *Sonneratia caseolaris* (L.) Engl. 1. Mean range of leaf outlines; 2. variable shaped leaf mucronate apex; 3. petiole base; 4. mature flower bud (longitudinal section) showing general internal anatomy just prior to anthesis; 5. flower at anthesis; 6. floral diagram; 7. petal; 8. mature fruit. Scale = 1 cm.

Asiat. 4 (1854) 652; Miq., Fl. Ned. Ind. 1, 1 (1855) 496, p.p.; Dalzell, Bombay Fl. (1861) 98; Miq., Sumatra (1862) 120, 316; Brandis, For. Fl. N.W. India (1874) 242; Kurz, For. Fl. Burma 1 (1877) 526; C.B. Clarke, Fl. Brit. India 2 (1879) 579; Fern.-Vill., Nov. App. (1880) 92; Vidal, Sin. Gen. Pl. Lenos. Filip., Atlas 27 (1883) t. 52, f. G; Boerl., Handl. Fl. Ned. Ind. 1 (1890) 538; Koord. & Valeton, Bijdr. Booms. Java 1 (1894) 198; Merr., Philipp. J. Sci. 3 (1908) Bot. 83; Pulle, Nova Guinea, Bot. 8 (1911) 677, 679; Whitford, Bull. Bur. For. Philipp. 10 (1911) Sonn.; Koord., Exk. Fl. Java 2 (1912) 663; Atlas Baumart. Java (1915) t. 592-4; Moll & Janssonius, Mikrogr. Holz. 3 (1918) 603; Gamble, Fl. Madras (1918/19) 363, 515; N. Brown, For. Products (1919) Sonn.; Backer, Bull. Jard. Bot. Buitenz. III, 2 (1920) 330; Foxw., Malayan For. Rec. 1 (1921) 117; Gagnep. & Guillaumin, Fl. Gén. Indo-Chine 2 (1921) 979; Troup, Silvic. Ind. Trees (1921) 2, f. 228; Ridley, Fl. Malay. Penins. 1 (1922) 825; Meindersma, Tectona 15 (1922) 573, f. 18; Trop. Natuur 12 (1923) 77, f. 18; Merr., Enum. Philipp. Flow. Pl. 3 (1923) 138; C.T. White, J. Bot. 64 (1926) 217; K. Heyne, Nutt. Pl. Ned.-Ind. (1927) 1156; Watson, Malayan For. Rec. 6 (1928) 50, 55, 120, f. 22; Ridley, Disp. Pl. (1930) 293; Panshin, Philipp. J. Sci. 48 (1932) 163, pl. 8; Kint, Trop. Natuur 23 (1934) 182; Mahabale & Deshpande, Palaeobotanist 6 (1957) 52, t. 1; Backer & Bakh. f., Fl. Java 1 (1963) 257. – *Aubletia caseolaris* Gaertn., De Fruct. Sem. Pl. 1 (1788) 379, t. 78, f. 2, p.p. – *Sonneratia rubra* Oken, Allg. Naturgesch. 3 (1841) 1952. – *Blatti caseolaris* Kuntze, Rev. Gen. Pl. 1 (1891) 238; Niedenzu in E. & P., Nat. Pfl. Fam. 3, 7 (1892) 21, f. 7a–g, p.p. – *Sonneratia alba* non J. Smith: Fernando & Pancho, Silvatrop. Philipp. For. Res. J. 5 (1980) 51. – Type: Rumphius, Herb. Amboin. 3 (1743) 112, t. 74 – 5!, Indonesia, Amboina.

Sonneratia acida L. f., Suppl. Pl. (1781) 252. – *Sonneratia pagatpat* Blanco, Fl. Filip. (1837) 424; ed. 2 (1845) 296; Blume, Mus. Bot. Lugd.-Bat. 1 (1851) 337; Miq., Fl. Ned. Ind. 1, 1 (1855) 496; Blanco, Fl. Filip. ed. 3 (1878) 186. – *Blatti pagatpat* Niedenzu in E. & P., Nat. Pfl. Fam. 3, 7 (1892) 21. – Type: *Sonnerat s.n.* (LINN, iso), New Guinea.

Sonneratia ovalis Korth., Ned. Kruidk. Arch. 1 (1846) 198; Miq., Anal. Bot. Ind. 1 (1850) 28. – Type: *Korthals s.n.* in herb. L (sh. nr. 908.128-980), Borneo, Bandjermasin.

Sonneratia neglecta Blume, Mus. Bot. Lugd.-Bat. 1 (1851) 338; Miq., Fl. Ned. Ind. 1, 1 (1855) 498. – Type: *herb. P. Royen* in herb. L (sh. nr. 908.128-961), Ceylon?

Sonneratia evenia Blume, Mus. Bot. Lugd.-Bat. 1 (1851) 337; Miq., Fl. Ned. Ind. 1, 1 (1855) 497. – Type: *Blume s.n.* in herb. L (sh. nr. 908.128-971), Indonesia, Timor.

Sonneratia obovata Blume, Mus. Bot. Lugd.-Bat. 1 (1851) 337; Miq., Fl. Ned. Ind. 1, 1 (1855) 497; Koord. & Valeton, Bijdr. Booms. Java 1 (1894) 198. – Type: *Blume s.n.* in herb. L (sh. nr. 908.128-990), Indonesia, Java, Tjilakahan.

Sonneratia acida auct. non L. f. var. *mucronata* Miq., Fl. Ned. Ind. 1, 1 (1855) 496, p.p.; R. Parker, Indian For. 51 (1925) 507. – Type: unknown, Indonesia, Java.

Columnar tree c. 20 m high, canopy generally sparse. Trunk base not buttressed. Bark smooth or lightly fissured and flaky, grey or flesh coloured. *Pneumatophores* thin, pointed and often branched, c. 1 m high. *Leaves:* lamina elliptic, 45–113 (79) mm long, 20–71 (52) mm wide, deep green satiny upper surface, lower surface shiny, midvein prominent with reddish coloration often on upper surface towards petiole base; apex acute, thickened, mucro recurved; petiole 2–9 (5) mm long, lamina decurrent. *Inflorescences* with 1–3 (mostly 1 or 2) buds; peduncles terete or tetragonous. Mature bud: apex mostly acute, attenuate to obtuse base, medially constricted, upper portion c. 15 mm wide, lower portion 13–17 (15) mm wide, in all 24–27 (25) mm long. *Flowers:* hypanthium satiny, coriaceous, tending to warty with pronounced ribs along calyx lobe margins, deep grooves beneath junctures; calyx lobes 5–7 (6), 14–19 (17) mm long, apex acute, inner surface often streaked with red coloration; petals always present, linear, 19–29 (25) mm long, 1–3 (2) mm wide when

fresh, red; staminal filaments c. 37 mm long when fresh, red, rarely white; anthers dorsifixed, pale yellow; petals and stamens fall within hours after anthesis; ovary 13–20- (16-)locular; style c. 62 mm long, stigma fungiform, c. 3 mm wide. *Berry* globose, 7–32 (20) mm long, 17–54 (41) mm wide; pericarp leathery, glossy with slight ribs; calyx persistent, hypanthium flat-expanded, 20–46 (34) mm wide, 27–46 (37) mm from calyx base to lobe apex, lobes erect, spreading, 18–30 (25) mm in length. *Seeds* numerous, irregularly angular, c. 7 mm long.

Phenology. Leaf fall occurs chiefly from October to January. Flowering occurs mainly around January. Along the Murray River, only 6% of the buds develop to mature fruit, about 60% of fruit set reach maturity. Fruit maturation occurs predominantly in June and July.

Distribution. The species is found from the west coast of India to southern China and through the western islands of the Pacific Ocean. Distribution in Australia is limited, occurring only on the northeast coast where it is associated with areas of higher rainfall and large river estuaries from the Murray River (18°05' S, 146°01'E) in the south to the Olive River (12°10' S, 143°05' E) in the north. In New Guinea, the taxon is only found on the north coast and on larger islands. Fig. 1.

Ecology. The species occurs in frontal stands often in upstream estuarine positions of rivers subjected to high levels of freshwater runoff. An alliance is observed with *Aegiceras corniculatum, Barringtonia racemosa* and *Rhizophora mucronata.* Substrate was usually soft river silt and mud of the accreting inside bank of estuarine meanders.

Notes. There was some confusion in attaching an epithet to this species. This confusion was based on at least two major errors or omissions in the original type description. Firstly, Linnaeus (1754: l.c.) named only one taxon from the Rumphius descriptions (1743: l.c.) of *'Mangium caseolare'* – being made up of two distinct forms, viz., *'album'* and *'rubrum'*. The latter form was generally believed to be that which Linnaeus had described, but it is impossible to be sure. J. Smith (1819: l.c.) partially clarified the situation by separately identifying the two taxa, and in naming *'f. album'* as *S. alba.* The second confusing aspect was in regard to the other form, *'f. rubrum'*, and, in the Linnaeus fil. (1781: l.c.) description of *S. acida.* This latter description (as already noted in the generic section) was based on different type material, and subsequent authors apparently used a mixture, viz., Linnaeus type material and Linnaeus fil. epithet. This confusion generally continued until the major revision by Backer & Van Steenis (1951: l.c.). These authors rightly reduced the Linnaeus fil. name to synonymy, and used *'Mangium caseolare rubrum'* ' as the type description. We follow Backer & Van Steenis in this, and for other type material not seen by us.

Sonneratia × gulngai N.C. Duke – Fig. 5.

Sonneratia x *gulngai* N.C. Duke, Austrobaileya 2 (1984) 103. – *Sonneratia alba* x *S. caseolaris* Muller & Hou-Liu, Blumea 14 (1966) 337, t. 1, f. 1d, 2b & 3d; Muller & Steenis, N. Queensl. Naturalist 35 (1968) 8; Backer & Steenis, Fl. Males. I, 6 (1972) 974, f. 18d; Chapman, Mangrove Veg. (1976) f. 291d. – Type: *N.C.Duke AIMS 547* (BRI, holo!; AIMS, CANB, JCT, K, L, iso!), Australia, Queensland, McIvor River.

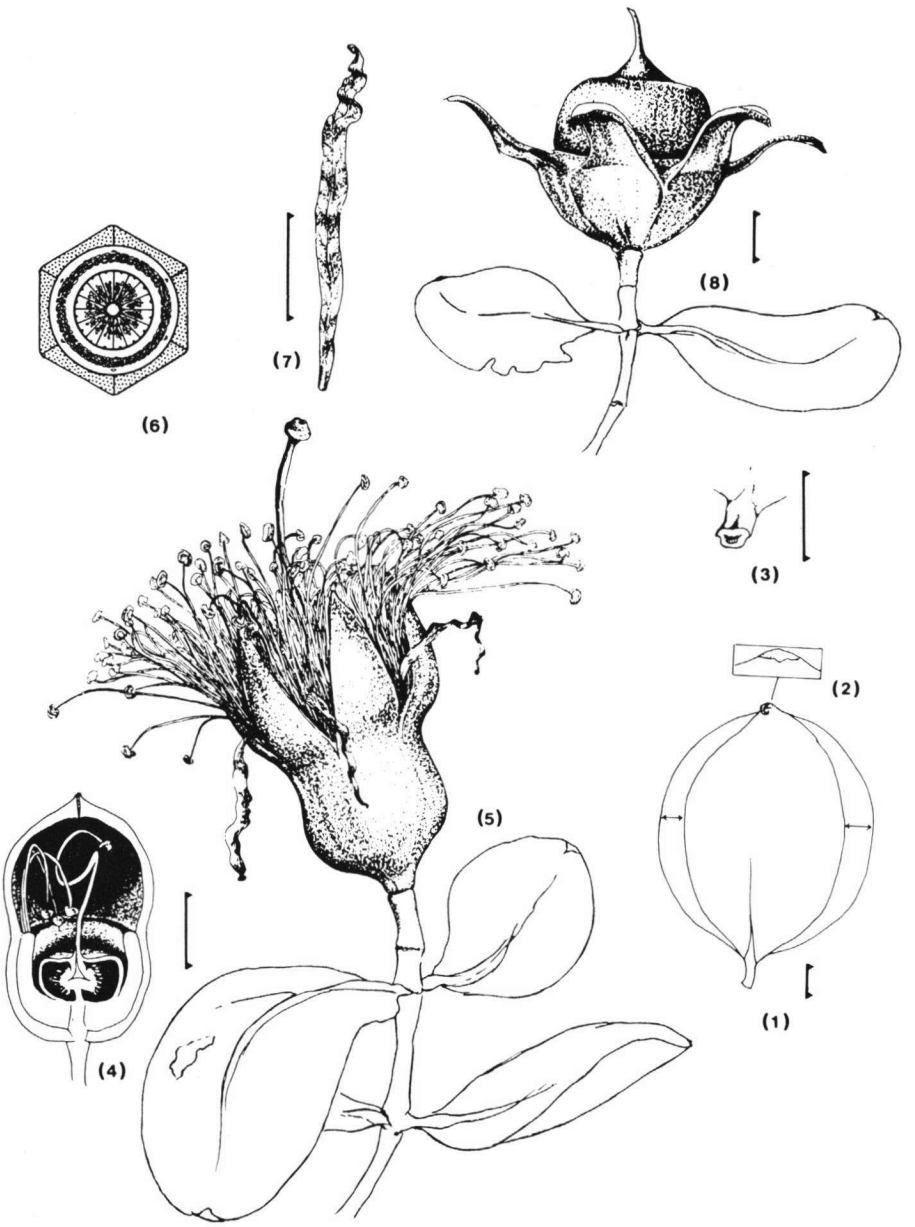

Fig. 5. *Sonneratia* x *gulngai* N.C. Duke. 1. Mean range of leaf outlines; 2. variable shaped leaf mucronate apex; 3. petiole base; 4. mature flower bud (longitudinal section) showing general internal anatomy just prior to anthesis; 5. flower at anthesis; 6. floral diagram; 7. petal; 8. mature fruit. Scale = 1 cm.

Spreading tree c. 25 m high; canopy rather dense. Trunk base not buttressed. Bark smooth or fissured and flaky, grey. *Pneumatophores* thin, pointed and often branched, c. 80 cm high. *Leaves:* lamina obovate, 52–85 (80) mm long, 38–64 (54) mm wide, dull green upper surface, satin lustre on lower surface, midvein often tinged red towards petiole; apex acute, thickened, mucro recurved; petiole 6–14 (11) mm long, lamina decurrent. *Inflorescences* with one or two buds; stems beneath mostly terete. Mature bud: apex acute to obtuse, attenuate to obtuse at base, medially constricted, the upper and lower portions often similar, in all 25–35 (31) mm long, 10–20 mm wide. *Flower:* hypanthium dull, smooth, without ribs; calyx lobes 5–7 (6), 15–23 (18) mm long, acute apex, often reddish on inner surface; petals always present, linear, 20–41 (33) mm long, 1–3 (2) mm wide when fresh, red; staminal filaments c. 37 mm long when fresh, red; anthers pale yellow; petals and stamens fall within hours after anthesis; ovary 13–17- (15-)locular; style c. 30 mm long, stigma fungiform, c. 1.7 mm wide. *Berry* erect, globose, 10–20 (12) mm long, 29–48 (39) mm wide, sometimes indented around style base; pericarp leathery, smooth, satiny lustre, without ribs; calyx persistent, hypanthium cup-shaped, 31–45 (38) mm wide, 41–47 (44) mm from calyx base to lobe apex, lobes erect, 23–28 (27) mm long. *Seeds* numerous, angular.

Phenology. Leaf fall peaks twice, in August to September and March to May. Floral development of the hybrid is complex and is coupled with observations of high levels of aborted pollen (c. 30% collapsed grains) and low fruit set and maturation (along the Murray River, c. 1% of the potential crop attain maturity). The dual character of the hybrid is briefly summarised by the apparent bimodal peak of flowering and fruiting periods which coincide in this region with those of *S. alba* and *S. caseolaris*, respectively. Flowering occurs as two peaks based on December and also in March. Mature fruits fall mainly in March and August.

Distribution. This putative hybrid has been reported (Muller & Hou-Liu, 1966) to occur in northwestern Borneo. In Australia, *S.* × *gulngai* is found on the northeastern coast from the Murray River (18°05'S, 146°01'E) in the south, to the Olive River (12°10'S, 143°05'E) in the north. It is limited to estuaries which have both *S. caseolaris* and *S. alba*. The latter species is widespread, therefore the possible limitations on the distribution in Australia of the hybrid are linked to the occurrence of the less common *S. caseolaris*. Occurrence is more frequent in estuaries where the distributions of *S. alba* and *S. caseolaris* overlap. Distribution throughout Indo-Malesia is expected to be widespread while subject to the constraints already outlined. Fig. 1.

Ecology. *Sonneratia* × *gulngai* is easily distinguished in the field by its size and luxuriant foliage (i.e., darker green canopy appearance with larger leaves and flower buds). It is found commonly at the downstream limits of *S. caseolaris* which often places it centrally within Australian estuaries. In this position the species occurs in lower to middle tidal contours; i.e., above and behind *S. caseolaris*. Here it is commonly associated with *Bruguiera parviflora* and *Xylocarpus granatum*. To a lesser extent the species is also associated with *Rhizophora mucronata* and *Nypa fruticans*. *Sonneratia* × *gulngai* is usually found on firm mud or silt.

Notes. *Sonneratia* × *gulngai* is comparable with *S. alba* × *S. caseolaris* Mul-ler & Hou-Liu (1966: l.c.), but there are some differences. However, the Austra-lian taxon has consistent morphological characteristics throughout the region; particularly in northeastern Australia. The taxon is therefore recognised as a distinct hybrid species. Its hybrid status is supported by the following evidence:

— intermediate and shared morphological characters;
— reduced fertility and distinctive shape and character of the pollen;
— poor fruit maturation;
— complex floral phenology, apparently taking characteristics of each of the putative parental cycles;
— luxuriant growth of tree form and foliage;
— distribution in Australia limited to those estuaries where *S. caseolaris* also occurs;
— number of individuals usually quite low; more plants are found in those estuaries where the distributions of *S. alba* and *S. caseolaris* overlap.

3a. Sonneratia alba × Sonneratia gulngai

Spreading tree c. 15 m high. Trunk base not buttressed. Bark smooth or lightly fissured and flaky, pale grey coloured. *Leaves:* lamina elliptic or ovate, 63 mm long, 37 mm wide, pale green dull on upper surface, satin lustre on lower surface, midvein green, lamina decurrent on petiole; apex broadly acute, mucro recurved, adpressed to leaf undersurface; petiole 7 mm long, terete. *Inflorescences* with only one bud; stems beneath terete. Mature bud: apex acute to obtuse, attenuate to obtuse at base, medially constricted, upper portion 12 mm wide, lower portion 11 mm wide, in all 22 mm long. *Flowers:* hypanthium dull, smooth, without ribs or grooves; calyx lobes 5–7 (6), 13 mm long, apex acute, inner surface green tinged red at base; petals absent; staminal filaments entirely red; anthers dorsifixed, pale yellow; stamens fall within hours of anthesis; ovary 12–17- (15-)locular; style c. 39 mm long, stigma fungiform, c. 3 mm wide. *Berry* erect, globose, 15 mm long, 31 mm wide, pericarp coriaceous, dull, without ribs; calyx persistent, hypanthium cup-shaped, 31 mm wide, 33 mm from calyx base to lobe apex, lobes erect, spreading, 20 mm long. *Seeds* numerous, angular.

Phenology. Mature buds and fruit were collected in August and September.

Distribution. Only one tree was observed throughout the region. This tree is located in the McIvor River (15°08'S, 145°14'E), Australia, around 8 km upstream from the estuary mouth and on the waters' edge. Reference collections held at AIMS include *N.C. Duke AIMS 702*.

Notes. This taxon is distinguished by its red staminal filaments and lack of petals on specimens which otherwise resembled *S. alba*. This latter species (the downstream form) and *S. caseolaris* (the upstream form) are common in the McIvor River estuary. *Sonneratia* × *gulngai*, the predominant hybrid form, is well represented and there are numerous specimens in the overlap zone. As all these forms occur in close proximity it is considered that opportunities for hybridization are high. This significant overlap in *Sonneratia* taxa is not observed elsewhere in Australia.

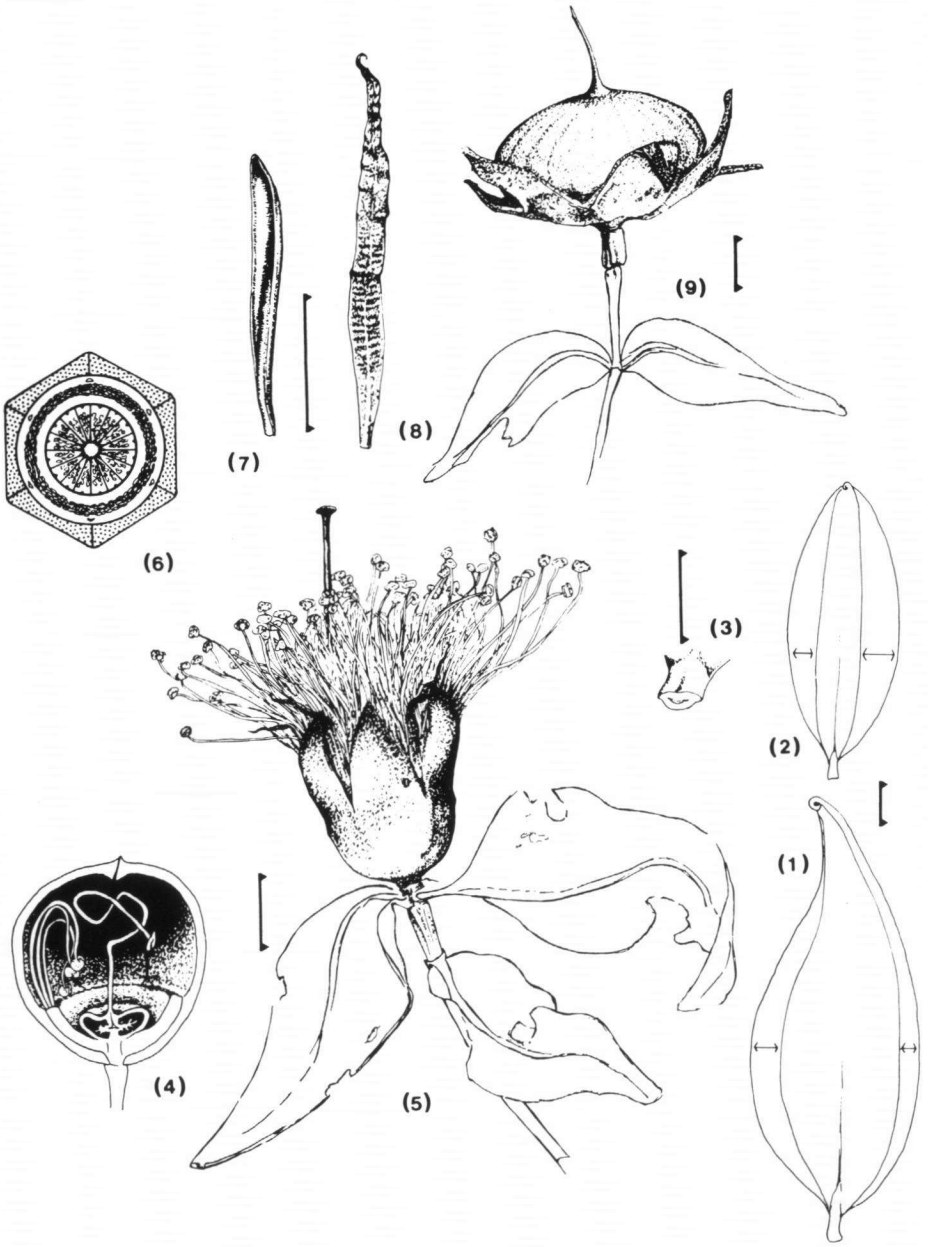

Fig. 6. *Sonneratia lanceolata* Blume. 1. Mean range of lanceolate leaf outline; 2. ibid. of ovate leaf outline; 3. petiole base; 4. mature flower bud (longitudinal section) showing general internal anatomy just prior to anthesis; 5. flower at anthesis (common single petal form); 6. floral diagram; 7. thickened second petal of the uncommon double-petalled form; 8. normal linear petal; 9. mature fruit. Scale = 1 cm.

4. Sonneratia lanceolata Blume – Fig. 6.

Sonneratia lanceolata Blume, Mus. Bot. Lugd.-Bat. 1 (1851) 337; Miq., Fl. Ned. Ind. 1, 1 (1855) 497; Koord., Versl. Minahasa (1898) 471; Becc., Nelle Foreste di Born. (1902) 579; C.T. White, Proc. Roy. Soc. Queensl. 34 (1922) 45; R. Parker, Indian For. 51 (1925) 505. – *Sonneratia acida* auct. non L. f.: Benth., Fl. Austral. 3 (1866) 301, p. p.; Ewart & Davies, Fl. North. Terr. Austral. (1917) 199; Blake, Austral. J. Bot. 2 (1954) 137. – *Sonneratia alba* auct. non J.Smith: Merr., Enum. Born. Pl. (1921) 418. – *Sonneratia caseolaris* auct. non (L.) Engl., ex parte: Ridley, Fl. Malay. Penins. 1 (1922) 825; Backer & Steenis, Fl. Males. I, 4 (1951) 283, ex parte; Percival & Womersley, Bot. Bull., Dept. For., Papua New Guinea 8 (1975) 88, ex parte; Frodin et al., Univ. Papua New Guinea Occas. Pap. 3 (1975) 44; Floyd, Ecol. Rep., Dept. For., Papua New Guinea 4 (1977) 47, non ic.; A.G. Wells in Clough, Mangrove Ecosyst. Austral. (1982) 75; in Teas, Tasks Veg. Sci. 8 (1983) 72, ex parte. – T y p e : *Blume s.n.* in herb. L (sh. nr. 908.128-988), Indonesia, Borneo.

Columnar tree c. 20 m high, canopy generally sparse. Trunk base not buttressed. Bark smooth or lightly fissured and flaky, grey to pale fleshy colour. *Pneumatophores* thin, pointed, c. 20 cm high. *Leaves:* lamina elliptic to lanceolate, 61–124 (86) mm long, 12–38 (25) mm wide, dull pale green, upper and lower surfaces similar, midvein rarely reddened; apex acute, slightly thickened, mucro recurved; petiole 2–7 (4) mm long, lamina decurrent. *Inflorescences* with mostly one but sometimes two buds; peduncles terete or tetragonous. Mature bud: apex acute to obtuse, base mostly obtuse, no medial constriction, 20–26 (23) mm long, 12–18 (15) mm wide. *Flowers:* hypanthium dull, slight leathery with no ribs or grooves; calyx lobes 5–7 (6), 13–14 (14) mm long, apex acute, inner surface rarely with reddish streaks; petals always present, rarely doubled, linear, 12–38 (29) mm long, 2–4 (3) mm wide when fresh, red; staminal filaments c. 45 mm long when fresh, always white; anthers dorsifixed, yellow; petals and stamens fall within hours after anthesis; ovary 12–17- (15-)locular; style c. 56 mm long, stigma fungiform, c. 3 mm wide. *Berry* globose, 9–18 (14) mm long, 25–38 (31) mm wide; pericarp smooth, glossy, with slight ribs; calyx persistent, hypanthium flat-expanded, 24–30 (26) mm wide, 24–30 (27) mm from calyx base to lobe apex, lobes erect, spreading, 14–19 (16) mm in length. *Seeds* numerous, angular, c. 7 mm long.

Phenology. No information exists on leaf fall periodicity. Flowering was observed in September to October and in March. Fruits were numerous in specimens collected during December to March.

Distribution. Except for the type record, there are few records of this species in countries other than Australia and New Guinea. In Australia this species occurs in the Pascoe (12°30'S, 143°16'E) and Claudie (12°50'S, 143°21'E) Rivers of northeastern Queensland, and several rivers in three separate locations in the Northern Territory; viz. Arnhem Bay (12°00'S, 136°00'E), Bonaparte Gulf (12°00'S, 132°00'E), and Melville Island (11°01'S, 130°01'E). It is known only on the southern coast of New Guinea. Fig. 1.

Ecology. The species occurs at lower tidal contours in frontal stands or as isolated trees in upstream estuarine positions in rivers subjected to relatively high levels of freshwater runoff. Associated species include *Avicennia marina, Nypa fru-*

ticans and *Bruguiera sexangula*. Substrate is usually fine soft silt on the accreting inside banks of river meanders.

Notes. In this study there were two taxa referable to *S. caseolaris* described by Backer & Van Steenis (1951: l.c.). We had to decide which taxon was consistent

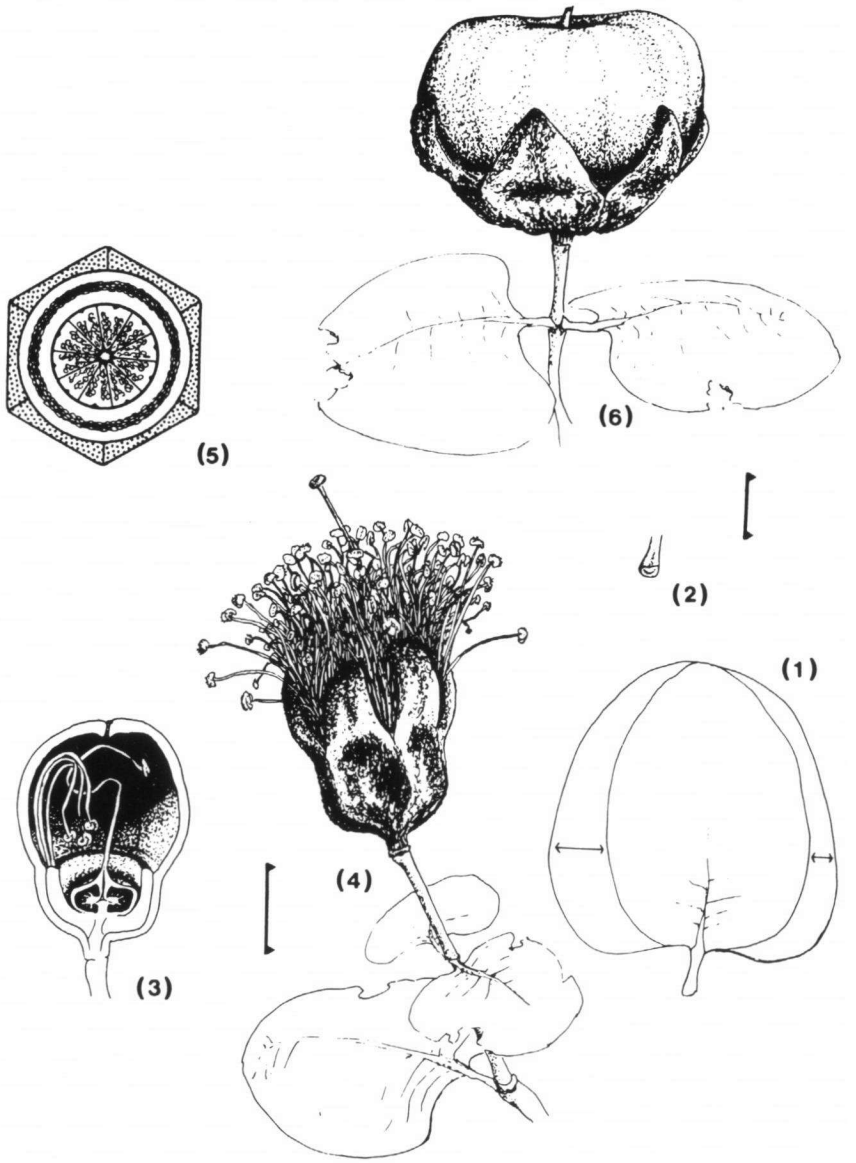

Fig. 7. *Sonneratia ovata* Backer. 1. Mean range of leaf outlines; 2. petiole base; 3. mature flower bud (longitudinal section) showing general internal anatomy just prior to anthesis; 4. flower at anthesis; 5. floral diagram; 6. mature fruit. Scale = 1 cm.

with that epithet. Our problem was resolved by comparing these taxa with the respective Rumphius description and figures (1743: l.c.). The shape of the leaves was a major diagnostic character. We now recognise the ovate-leaf entity from northeast Australia and northern New Guinea as *S. caseolaris*. The remaining form had lanceolate leaves and was comparable with *S. lanceolata* Blume (1851: l.c.).

Populations of *S. lanceolata* from neighbouring rivers often exhibit distinct morphological differences. One population isolated from the main estuary of the Wildman River (12°18' S, 132°04' E) has leaves which are typically linear rather than lanceolate, and the petal numbers are often double.

4a. Sonneratia alba × Sonneratia lanceolata

Tree to 8 m high. *Leaves:* lamina elliptic, 77–101 (89) mm long, 35–54 (41) mm wide, midvein prominent under; apex acute, slightly thickened, mucro recurved; petiole 7–12 (10) mm long, lamina not always decurrent. *Inflorescence:* stems beneath mostly terete. *Mature bud:* apex acute to mostly obtuse, attenuate to obtuse at base, slight medial constriction, in all 31 mm long, 19 mm wide. *Flowers:* hypanthium dull, slightly leathery, with no ribs or grooves; calyx lobes 6, 19 mm long, apex acute; petals lanceolate, red; staminal filaments possibly white; style c. 56 mm long, stigma fungiform, c. 1–2 mm wide. *Berry* erect, globose, 7 mm long, 26 mm wide, not indented about style base; pericarp smooth, glossy, with slight ribs; calyx persistent, hypanthium cup-shaped, 28 mm wide, 39 mm from calyx base to lobe apex, lobes erect, spreading, 23 mm long.

Phenology. Flowers were collected in June and mature fruit in December.

Distribution. Only two herbaria specimens were seen. In addition there are tentative sightings from the Kikori region of Papua New Guinea. It is expected, however, that the distribution of this taxon would reflect that of the putative parents.

AUSTRALIA. Northern Territory: Goromura River (12°28'S, 136°13'E),*Wells s.n.* (DNA 15228). INDONESIA. West Irian: Merauke (8°30'S, 140°22'E), *McKee 1701* (LAE).

Notes. This taxon is distinguished chiefly by its *S. alba*-like fruit on specimens which otherwise resemble *S. lanceolata*. However, the leaves are not so long in relation to their width.

Foliage characteristics are expected to be somewhat reminiscent of *S.* × *gulngai* with larger leaves and buds and a more luxuriant crown.

5. Sonneratia ovata Backer – Fig. 7.

Sonneratia ovata Backer, Bull. Jard. Bot. Buitenz. III, 2 (1920) 329; Meindersma, Tectona 15 (1922) 573, f. 19; Trop. Natuur 12 (1923) 77, f. 19; Steenis, Bull. Jard. Bot. Buitenz. III, 12 (1932) 162; Merr. & Perry, J. Arnold Arbor. 22 (1941) 269; Backer & Steenis, Fl. Males. I, 4 (1951) 285, f. 3a; Wyatt-Smith, Malayan For. 16 (1953) 214, t. 1, f. 2; Mahabale & Deshpande, Palaeobotanist 6 (1957) 52, t. 1; Backer & Bakh. f., Fl. Java 1 (1963) 257; Vu Van Cuong, Adansonia 4 (1964) 346; Fl. Cambodia Laos Vietnam 4 (1965) 202, pl. 1; Muller & Hou-Liu, Blumea 14 (1966) 337, t. 1, f. 1a & 3a; Backer & Steenis, Fl. Males. I, 6 (1972) 974; Whitm., Malayan For. Rec. 26 (1972) 445; Chai, Malaysian For. 38 (1975) 203; Percival & Womersley,

Bot. Bull., Dept. For., Papua New Guinea 8 (1975) 85, f. 64; Frodin et al., Univ. Papua New Guinea Occas. Pap. 3 (1975) 44; Chapman, Mangrove Veg. (1976) 388, f. 291a; Floyd, Ecol. Rep., Dept. For., Papua New Guinea 4 (1977) 47 & 49, cum ic.; Ko, Acta Phytotax. Sin. 23 (1985) 313. – *Sonneratia alba* auct. non J. Smith: Watson, Malayan For. Rec. 6 (1928) 50, 55, 122, f. 23; Burkill, Dict. 2 (1935) 2051. – Type: *Backer 21422* (L, lecto ex Vu Van Cuong, 1965), Indonesia, Java.

Columnar tree c. 20 m high. Trunk base not buttressed. Bark slightly flaky, pale brown to grey. *Pneumatophores* thin, pointed, c. 20 cm high. *Leaves:* lamina very widely ovate, 43–56 (45) mm long, 36–47 (38) mm wide, green, base reniform, upper surface glossy, lower surface satiny, midvein not reddened, leaf apex obtuse, mucro absent; petiole 5–6 (5) mm long, terete. *Inflorescence* with 1–3 (2) buds; peduncle terete. Mature bud: apex obtuse, base mostly attenuate, medially constricted, with upper portion c. 17 mm wide, lower portion 13–17 (15) mm wide, in all 23–31 (27) mm long. *Flowers:* hypanthium dull, verruculose, with grooves beneath each calyx lobe juncture; calyx lobes always 6, 14–15 (15) mm long, obtuse apex, inner surface sometimes tinged with red at base; petals absent; staminal filaments c. 19 mm long when fresh, entirely white; anthers dorsifixed, yellow; petals and stamens fall within hours of anthesis; ovary ± 10-locular; style c. 26 mm long, stigma fungiform, c. 2 mm wide when fresh. *Berry* globose, 20–21 (21) mm long, 42–53 (47) mm wide, pericarp leathery, satiny, without ribs; calyx persistent, hypanthium flat-expanded, 26–27 (27) mm wide, 27–30 (29) mm from calyx base to lobe apex adpressed to pericarp, 18–20 (19) mm long. *Seeds* numerous, rounded irregular, c. 5 mm long.

Phenology. Flowers were observed and collected from March to October, and fruits from April to October.

Distribution. This species is uncommon, but occurs from China through Malaysia to New Guinea. In Papua New Guinea it is located in several sites from Daru Island (9°05'S, 143°00'E) to the Gulf of Papua (7°05'S, 144°00'E) and to Milne Bay (10°03'S, 150°31'E). It is unknown in Australia. Fig. 1.

Ecology. The species occurs on the landward edge of mangrove swamps in brackish water and muddy soil.

Notes. The acceptance of petalous variability for *S. alba* removed the only real problem in *S. ovata* determinations. Therefore, without the pseudo-reliance on this character, more diagnostic characters were used. *Sonneratia ovata* was distinguished by several attributes including: the presence of a fine verruculose texture on the calyx surface; leaf shape and texture; absence of a leaf mucronate apex; and, habitat. Therefore, while the species was found infrequently in this region, it had a very different morphology from other taxa.

IDENTIFICATION LIST OF COLLECTIONS
(Anonymous collections were omitted)

Sonneratia

1. *alba* J. Smith
2. *caseolaris* (L.) Engl.
3. x *gulngai* N.C. Duke (= *alba* x *caseolaris*)

3a. *alba* x *gulngai*

4. *lanceolata* Blume

4a. *alba* x *lanceolata*

5. *ovata* Backer

Adair 203: 1 – AIMS series 80, 156, 157, 180, 203, 213: 1; 235: 4; 242, 244, 255–257: 1; 262: 2; 263: 1; 264: 3; 270, 272, 276, 277: 1; 278: 2; 279, 294: 3; 296–299, 306: 2; 307: 3; 308, 313–317: 1; 318, 319: 2; 329, 330: 3; 331, 332: 1; 339: 2; 345, 348: 1; 362: 3a; 363: 3; 365: 1; 366: 3a; 368: 1; 369: 3; 371, 372: 1; 377, 380, 381: 4; 387–389, 393, 396–401, 406–420, 422, 432: 1; 434: 4; 435, 436: 1; 437: 4; 445, 482, 497: 1; 510, 511: 2; 524: 4; 530, 535, 545, 546: 1; 547: 3; 548: 2; 549, 563, 577, 580: 1; 593: 3; 604: 1; 608–613: 2; 614, 615: 3; 616: 1; 617: 4; 618, 620: 2; 629, 631, 632: 3; 633, 634: 1; 636: 4; 642: 1; 644: 4; 645, 646: 1; 651, 652: 4; 653: 1; 654, 662–664: 4; 665, 666, 672, 673, 679: 1; 686: 2; 688: 1; 689: 2; 690: 1; 692: 3; 693, 696, 697: 2; 698: 3; 699: 1; 700: 3; 701: 1; 702: 3a; 707, 721: 4; 723: 1; 731: 4; 734: 1; 735: 4; 736: 2; 737, 738: 3; 739: 1; 740, 741: 4; 742: 1; 743–745: 3a; 746, 749, 750: 4; 752–755: 1; 756, 761, 770–772: 4; 775: 1; 776, 779: 4; 783, 784: 2; 785: 3; 799, 800, 805, 812–820: 1; 825: 4; 826: 1; 827: 2; 828: 3; 829: 4; 830: 3; 831: 4; 832: 2; 833–837: 1; 838: 2; 845–847: 1; 849: 1.

Blake 16953, 18838: 1 – Boyland 353: 1 – Brass 790, 891: 1; 980: 4; 1350: 1; 1617, 5775: 4; 6264: 5; 6268: 1; 7968, 8204, 8633: 4; 21923: 5; 28160: 1; 33818: 2 – BRI series 33205, 33207, 63632, 63636, 63638: 1; 63645, 63648, 63649: 2; 63651: 1; 87411: 2; 140263: 4; 230424: 1 – BSIP series 2600, 2628: 1; 5676: 2; 6544, 7095, 10435: 1; 10635: 2; 10894, 13322: 1; 16575, 17183: 3; 18002, 19269: 1 – BW series 28: 2; 2445, 3198: 1; 3410: 2; 3575: 1; 4241, 4259: 2; 4586: 1; 5249, 5346, 7569, 7591: 2; 8576, 9814: 1; 14861: 2 – Byrnes NB501, NB895: 1.

Cameron 2409: 1 – Clarkson 2211, 2313: 1 – Craven 812: 1.

Darbyshire 798: 1 – DNA series 9869, 9875, 9876: 4; 13666: 1; 13674, 13679, 13689, 15227: 4; 15228: 4a.

Flecker 7787: 2; 8352: 1 – Franc 2295: 1.

Gill M25: 1.

Hanson 1539: 1 – T.G. Hartley 10254, 10254B, 10354A: 2 – Henshall 813: 1 – Hoogland 4193, 4419: 2 – Hyland 8896: 1; 9348: 2.

Jones 4026: 1 – Juncosa 23x81h: 5.

Kajewski 442: 2 – Kirina 4, 12: 1.

Lütjeharms 5399: 1.

McDonald 1632: 1 – KcKean B49: 1 – McKee 1701: 4a – Moi 115: 1 – Must 882: 1.

NGF series 1382: 1; 1597: 2; 1833, 4105: 1; 4118: 4; 5026: 1; 5045: 4; 6543: 2; 7199: 1; 8012: 4; 8022: 5; 8040: 4; 8683: 2; 9104: 4; 11107: 1; 15307, 16319, 17198: 2; 17688: 1; 18056: 2; 18422, 22171: 1; 22303: 2; 22434: 1; 24053, 25236: 2; 27259: 1; 29425: 2; 29856: 1; 30487: 2; 30781: 1; 37554, 39407: 2; 41115: 1; 41161: 3; 41215: 1; 41496: 2; 43323: 1; 43740: 2; 43797, 43814: 1; 43821: 5; 48638: 2; 49443, 49446: 1; 52139: 2; 59104: 4; 59295: 2; 61201: 4; 61219: 1; 62170: 4; 65553, 66068, 70530: 1.

Paijmans 1796: 1; 1878: 4 – Panoff 264: 1 – Parker 690: 1 – PERTH series 2817/B, 2849/C: 1 – Pullen 6431: 4.

QRS series 41350, 41351: 1.

Rankin 1169, 1817, 2218: 1 – Rau S4: 5 – Rijkers 14800: 1 – Robinson 9285: 1 – van Royen 3100, 5429: 1.

Saunders 161, 968: 2 – Scarth-Johnson 949A: 2 – Schodde 4444: 4 – Sharpe 20: 1 – Smith 4009, 10670, 12506: 1 – Stocker 1339: 1 – Stoddart 4640, 4773, 4839, 4852, 4905, 5043, 5104: 1 – Stone 10485: 1.

Thom 4161, 4167: 1 – Thorne 37898: 1.

UPNG series 57: 1; 804: 1.

White 131: 1; 689: 4.

INDEX

Numbers refer to the specific taxon codes. Synonyms are in *italics*.