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# ADDITIONAL NOTES ON THE GENUS AVICENNIA. VI

Harold N. Moldenke

AVICENNIA L.

Additional & emended bibliography: Ernould, Mém. Acad. Roy. Belg. Cl. Scienc., ser. 2, 6: [3], 5, 7, 8, 10, 12, 24--29, & fig. 15--17, 30, 37, 38, 40, 42, & 43. 1921; Zahran, Bull. Inst. Désert Egypt. 15: 7--12. 1967; Täckholm & Boulos, Suppl. Notes Stud. Fl. Egypt [Publ. Cairo Univ. Herb. 5:] 8. 1974; Moldenke, Phytologia 32: 343--370. 1975.

It is worth noting that Täckholm & Boulos (1974) also accept the Avicenniaceae as a distinct family. Their work, cited above, bears the date "1972" on the title-page, but was not actually published until 1974.

AVICENNIA AFRICANA P. Beauv.

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Recent collectors describe this plant as a tree or shrub, 2--22 m. tall, with numerous pneumatophores, which, according to Jenik (1967) are exactly similar to those seen in Laguncularia racemosa Gaertn. The corollas are said to have been "white with yellow center" on Morton A.494, while Irvine (1961) describes them as "dull-white, thin purplish stripes inside". Other collectors say "corolla-lobes white, pubescent inside". Irvine (1961) reports that the flowers are "bird-pollinated". This is interesting because the American species, great nectar-producers, are obviously insect-pollinated.

Avicennia africana has been collected in anthesis from September to July and in fruit in January and April. Sowunmi (1973) describes the pollen, on the basis of "Ikorodu 1966. Okafor and Macaulay, FHI", as follows: "Pollen grains isopolar, radially sym-

metrical; 3-colporate; peritreme-subprolate (P 31.2 ± 0.4 µm, E 25.2 ± 2.0 µm). Sexine subtectate, reticulate. NPC: 345. Colpi provided with granulate membranes which often protrude very conspicuously beyond the surface of the grain, especially after acetolysis. Apocolpium diameter 6.8 µm. Ora more or less circular, faintly delimited. (The apertures in this species could not be measured as they were not well displayed). Exine 1.6 µm thick, tapering towards the apertures. Sexine reticulate. Muri 0.5 µm wide, supported generally by one, but sometimes by two rows of bacula. Lumina 1.0 µm wide. Tectal part of muri 0.5 ± 0.1 µm, infratectal baculate zone 0.6 ± 0.2 µm thick, some bacula appear to be branched apically, and foot layer 0.5 ± 0.1 µm thick. Erdtman (1952, 1966) referred to the pollen as being (2-)-3 colporoidate, sexine reticulate. No 2-colporoidate grains have been observed by the present author. Such grains probably occur only rarely and might have been missed. The conspicuously protruding colpal membranes were not mentioned in Erdtman's (ibid.) short description."

It is worth noting here that the leaves on Berhaut 6418 are extremely large, while those on Compère 1834 and Dalziel 970 are remarkably small.

The original Palisot de Beauvois reference in the bibliography of this species is often cited as "1805" or "1809", but the actual date of publication seems to have been 1806.

Avicennia africana is very widely regarded as being the same species as the Avicennia found so abundantly in the New World, whether this be called A. nitida Jacq. or A. germinans (L.) L. Among the authors to so regard it may be mentioned Dalziel (1937) Roberty (1954), and Gibson (1970). Clarke (1885) notes that "Mr. Bentham considers the American and African A. tomentosa not specifically distinct". Hooker & Bentham (1849), while using the name, A. africana, comment that it is "Probably not distinct from the American A. nitida Jacq." Kohlmeyer, in a personal communication to me, informs me that two species of fungi endemic to the pneumatophores of Avicennia occur on both the west African and the American hosts and suggests that this may also point to the conspecificity of the hosts. The Kohlmeyers (1971) record Rhabdospora avicenniae from A. africana. Kuntze (1891) reduces what he refers to as "A. africana Beauv. non Schauer" to the synonymy of A. germinans.

Among the botanists, however, who have maintained A. africana as distinct may be mentioned Palisot de Beauvois (1804), Baker (1900), deWildeman (1923), Irvine (1961), Erdtman (1962), Keay (1963), Hepper (1963, 1973), Chapman (1970), Bazilovskaya (1972), Letouzey (1972), and Sowunmi (1973). Considering the great importance which many modern botanists attach to pollen morphology as an indication of taxonomic relationship, it is interesting to note that Erdtman (1952, 1966, 1971) describes the pollen-grains of A. africana as 32 x 26 mu and the reticulate sexine as thick as

the nexine, while in A. germinans they are 39 x 29 mu and the reticulate sexine is considerably thicker than the nexine. Unfortunately, I do not know what herbarium specimens he used as the basis for his A. germinans description, nor do I know exactly where in its supposed range Kohlmeyer secured the material on which his fungi grew. It is quite obvious to me that the west African plant is not identical with the true A. germinans as this occurs in southern Florida and the more northern portions of the West Indies nor with the northern South American A. germinans var. cumanensis (H.B.K.) Moldenke. Nor do I think it conspecific with A. elliptica Thunb. or its var. martii Moldenke of northeastern South America. It could, however, prove to be the same as, or, if the pollen is actually different, very closely related to or derived from A. germinans var. guayaquilensis (H.B.K.) Moldenke or A. tonduzii Moldenke of northern and northeastern South America and southern Central America.

Hooker & Bentham (1849) give the overall distribution of A. africana as "Senegal to Bonin"; Irvine (1961) says "Senegambia to Gaboon and B. Congo"; while Hepper (1963) asserts that the species "extends along the coast of western Africa to Cabinda and Longo; also in S. Tomé". Berhaut (1967) records it from Diable Island, Sénégal. Naurois (1965) discovered it on Tidre Island off the coast of Mauritania at 19°50' N., the most northerly position known for the species.

Giglioli & King (1966) have studied the connection between this plant and the malaria vector, Anopheles melas. The insect breeds in these mangrove swamps during the long dry season in Gambia. These swamps are flooded by the spring tides only. The soils have high salinity. The haloseral succession appears to begin with the colonization of fresh alluvium by Rhizophora racemosa which is replaced, in time, by Avicennia africana. With further accretion of soil, this species eventually dies out, leaving the large barren flats which are so typical of the region. Avicennia, they note, has a greater ability to take up and excrete salts than most mangrove swamp plants.

Irvine (1930) says that in Ghana (Gold Coast) A. africana grows in association with Sesuvium portulacastrum, that the bark yields tannin employed in tanning leather, and that the wood is used as firewood and, when in sufficient abundance, for building. "The wood stands well under water". He reports that "The tree grows in communities in the shallow lagoons near the sea. It is one of the tallest trees in the Mangrove association....and may reach 40 feet in height." His description of the tree is of special interest: "roots sticking up from the mud of lagoons in great numbers, probably for breathing purposes, also slender stilt-roots near the base of the trunk." This is the first reference in literature (known to me) of the occurrence of stilt-roots in the Avicenniaceae. In this connection, see my following discussion under A. alba Blume and the photograph there reproduced.

Villiers (1973) studied a mangrove swamp in the north littoral region of Gabon which is characterized by an outcropping rocky substratum over most of its surface. The vegetation here is noteworthy because of the absence of the normal association zones and has a mosaic appearance. Associated with Avicennia africana are Acrostichum aureum, Phymatodes scolopendria, Philoxerus vermicularis, Conocarpus erectus, Laguncularia racemosa, Rhizophora spp., Dalbergia ecastophyllum, Ormocarpum verrucosum, Loranthus sp., Flagellaria guineensis, Asparagus warneckei, Phoenix reclinata, Pandanus candelabrum, Fimbristylis spp., Eleocharis geniculata, Paspalum vaginatum, and Bulbophyllum sp. Th abundance of New World species in this assemblage is worthy of note.

Chapman (1970) proposes the ecologic association, Avicennietum africanum. Hansford (1961) records the fungus, Asteridiella sepulta (Pat.) Hansf. [Meliola sepulta Pat., Irene sepulta (Pat.) Toro, Irenina sepulta (Pat.) Stevens] from Avicennia africana as host in Sierra Leone, based on Deighton 358.

Avicennia africana is variously employed by natives in the lands where it occurs, as we have noted previously. Villiers (1973) says: "Le bois dur et blanc est utilisé comme combustible et pour la fabrication des poteaux de cases ou des membranures des embarcations. La poudre de l'écorce entre dans la composition d'une pommade à base d'huile de palme contre la galle, les poux et les chiques. L'écorce sort au tannage. Les graines sont mangées en cas de famine (mais une longue préparation est nécessaire pour les rendre comestibles)." This statement is repeated for the natives of Sénégal by Chevalier (1931) in at least most of its details. Bazilovskaya (1972) reports the plant is "important" to the native economy of Guinea. Dalziel (1937) asserts that "The sapwood is white, the heart light brown, darkening, fairly hard and durable, said to be termite-proof. It is used on the coast for boat and house-building, piles, wharves, gun-stocks, etc. It yields firewood, and charcoal for fish ovens, and is used in the Niger Delta to prepare salt, chiefly from the leaves and roots; the salt.....is better than that from other mangroves.....It is also said to be used as a red dye. The bark is used to treat parasitic skin diseases, itch, etc. In western Senegal some island people are said to use the germinating seeds of Avicennia as a famine food, but these, when uncooked or improperly prepared, are actually poisonous." Irvine (1961) repeats practically the same information, adding that the wood is used for furniture (e.g. chair-legs) and the bark yields 12.5 percent tannin, used to tan leather. He notes that "The dry pulverized bark in warm water is used as a paste for parasitic skin diseases, itch, and dermatitis. The pulverized bark, with palm-oil, is made into an ointment which is used in Fr. Equat. Africa for itch, lice, and 'flesh worms' (Abbé Walker). The leaves are said to be used as an enema in Liberia for piles."

In addition to the many vernacular names for this plant previously recorded by me (1960, 1970) the following are also reported:

"aguirigui", "aligiri", "aligitsi", "bakèlè", "balumbu", "benga", "béséki", "bu hek", "bukélék", "buran", "burhan", "chrodo", "diligitsi", "dilitsi", "diubukumâ", "egirigi", "élowè", "fang du Como", "fang du Rio Muni", "ibuâdé", "igiri", "loango", "mangle boton", "mbagé", "maglé", "mbuan", "mbugâd", "mbugan", "mbugând", "mbhurhan", "mpongwè", "mugiri", "muandi", "ndar", "ngowè", "nkomi", "olive mangrove", "orungu", "paletuvier blanc", and "sanar". Some of these names are applied also to other mangrove species in the area not differentiated by the natives.

Bentham & Hooker (1849) cite unnumbered Vogel collections from Grand Bassa and Cape Palmas. Baker (1900), Dalziel (1937), Irvine (1930, 1961), and Villiers (1973) together cite the following collections: SÉNÉGAL: Baldwin 5753; Chevalier 2759 & 2760; Döllinger 73, in part; Roger 75; Unwin 397. GAMBIA: Fox 106; Frith 34; Pitt 693; Ruxton s.n. PORTUGUESE GUINEA: Esp. Santo 1219. REPUBLIC OF GUINEA: Debeaux s.n. SIERRA LEONE: Don 168 & s.n.; Glanville 246; T. S. Jones 410; Lane-Poole 320; Mann vii; Scott-Elliot 4120; Thomas 7070. TURTLE ISLANDS: Deighton 2362. ST. LOUIS ISLAND: Brunner 1; Döllinger 73, in part. JAFAL ISLAND: Leprieur s.n. LIBERIA: Dinklage 1910; T. Vogel 101 & s.n.; Whyte s.n. BUSHROD ISLAND: Baldwin 13050. IVORY COAST: Chevalier 19908. GHANA: Andoh 5604; Chipp 175; Deakin 24; deWit & Morton A.2971; Foggie 4942; Irvine 754; Johnson 984; Morton A.494. TOGO: Warnecke 63. NIGERIA: Southern: Barter 46; MacGregor 341; Rosvear 16; Rowland s.n.; Talbot s.n.; Unwin 56; Vogel 101. CAMEROONS: Bates 195; Maitland 30. FERNANDO PO: Mann 231; Milne s.n. GABON: Chevalier 4343, 26815, & 27142; Debeaux 102; Dupanquet s.n.; Dybowski 170; Griffon du Bellay s.n.; Hallé N.1551; Klaine 85 & 1836; Leroy s.n.; Poběquin 7; Thollon 138, 208, & 638; Villiers 8, 23, 89, 143, & 262. PORTUGUESE CONGO: Soyaux 60. ZAIRE: Dupuis s.n. ANGOLA: Welwitsch 5641, 5709, & 5726.

Additional citations: SÉNÉGAL: J. T. Baldwin 5753 (W--2070037); Berhaut 6418 (Mu). LIBERIAN ISLANDS: Bushrod: J. T. Baldwin 13050 (N, W--2672582). IVORY COAST: F. R. Fosberg 40637 (W--2580423A). GHANA: J. K. Morton A.494 (Ba); Vigne 353 (W--1758635). NIGERIA: Southern: Dalziel 970 (Mu). GABON: Bogner 611 (Mu). ZAIRE: Compère 1834 (Mu); Wagemans 587 (Mu).

AVICENNIA ALBA Blume

Additional & emended synonymy: Avicennia officinalis Kurz apud C. B. Clarke in Hook. f., Fl. Brit. India 4: 604, in syn. 1885 [not A. officinalis L., 1753, nor Maxim., 1932, nor Millsp., 1930, nor Schau., 1856]. Avicennia alba Miq. ex Kuntze, Rev. Gen. Pl. 2: 502, in syn. 1891 [not A. alba Karst., 1907, nor Wight, 1921]. Avicennia officinalis Watt apud Cooke, Fl. Presid. Bomb., ed. 2, imp. 1, 517, in syn. 1958. Avicennia officinalis var. alba (Bl.) Hook. ex Jafri, Fl. Karachi 290, in syn. 1966.

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Additional & emended illustrations: Bakh., Bull. Jard. Bot. Buitenz., ser. 3, 3: pl. 14 & 15. 1921; Janssonius, Mikrogr. Holz. Jav. 832, fig. 296. 1926; Janssonius, Key Javan. Woods 214, fig. 296. 1952; Chowdhury & Ghosh, Indian Woods 1: pl. C. 1958; Chandhri, Veg. Act. Geobot. 10: ph. 2. 1961; Brunig, Malayan Forest. 32: 151. 1969; Corner & Watanabe, Illustr. Guide Trop. Pl. 750. 1969; Grümmer, Pfl. & Tiere Trop. Geb. 135. 1969.

The illustration labeled as A. alba by Jafri (1966) is actually a depiction of A. marina var. acutissima Stapf & Moldenke and the

plant which he describes as being very common in the Karachi area of Pakistan is also A. marina var. acutissima. The true A. alba is not known from present Pakistan (but does occur in what is now Bangladesh). The A. resinifera of Griffith (1854), on the other hand, actually is A. alba. The illustration given by Meijer (1968) as A. alba actually depicts A. marina var. rumphiana (H. Hallier) Bakh.

It should also be noted here that Blume's original description of A. alba is often cited as "1825", but was not actually published until 1826.

It is also worth noting here that the "A. tomentosa Roxb." is usually regarded as a synonym of A. officinalis L., but Kurz (1877) maintains it as a taxon different and distinct from A. officinalis. He and some other authors who use this homonym probably are referring to A. alba. The reference, "Rheed. 4. t. 45", is sometimes cited for A. alba, but I am unable to find any such illustration of A. alba in the works of Reede tot Drakestein.

Corner & Watanabe (1969) describe A. alba as a "Mangrove tree with peg-like pneumatophores. Leaf dark green above, silvery grey beneath. Flowers 4--5 mm. wide, in spikes, yellow". Recent collectors describe it as a gregarious shrub or tree at water fringes, 15--70 feet tall, the trunk 1--5 feet in girth, with aerial roots above the water surface, the bark surface subject to tide action black and rough, above tide action gray or pinkish-gray and smooth or dark glaucous-brown, lenticellate, the lenticels small, the soft wood whitish, the leaves glaucous beneath, the inflorescence indeterminate, in spike-heads, the peduncles brown-tomentose, the flowers fragrant, the calyx green, the petals 4, the stamens 4, alternating with the petals, the filaments short, orange-yellow, the anthers cream-colored or darker colored and turning black, the pistil very light-yellow, the stigma bifid, and the fruit glaucous-green, the sutures on both sides of the pericarp purplish. The corollas are said to have been "orange" in color on Orolfo 690, "orange-yellow" on Chai S.26764, S.27535, & S.29944, and "yellow" on Chai S.30626. Chai S.29936 exhibits some leaves like those of var. latifolia Moldenke on the same branch with typical ones. Wood vouchers accompany R. M. King 5588 & 5601 and Chai S.26764 & S.30667. The species has been found in flower from March to June, as well as in August, December, and January.

Raghaven & Arora (1958) and Cave (1959) report the haploid chromosome number as 33 and the diploid number as 66, but Löve (1968) reports n = 30, based on Ghosh E.331 from Jambu Island, Orissa, India. An additional vernacular name reported (besides those previously reported by me) is "báen". A very detailed description of the wood anatomy is given by Janssonius (1926).

Burkill (1966) calls the species "A tree attaining, not infrequently, a height of 70 feet, and sometimes more, which likes rich soil and takes possession of newly formed mud-banks, generally where it obtains a good deal of fresh water from a river flowing to the

sea past it; inland it occurs on the banks of such a river. Outside of Malaya, it extends from India to Polynesia."

Fig. 1. A. alba, showing trunk and pneumatophores

My good friend, Paul Chai, in a letter to me dated May 25, 1973, asserts that "I found in Sarawak that some individuals of all three species (A. alba, A. marina and A. officinalis) occurring here possess stilt roots. These individuals were found to be confined to soft muddy soil.....Unlike the stilt roots of Rhizophora, stilt roots of Avicennia are more slender and soft. They arise in the same way as aerial roots which extend and reach the mud eventually." To see examples of this condition, see the figure 5 here and the similar figure to be presented in my discussion of A. marina. These are probably the "aerial roots above the water level" referred to by some collectors. I am grateful to Paul Chai for his permission to use the photographs here presented, in all cases depicting trees growing in Sarawak.

Gaussen and his associates (1965) refer to A. alba as a "colonizer on mangrove deltas". Chandhri (1961) reports that it "secretes hygroscopic salts which have the ability to absorb water from the

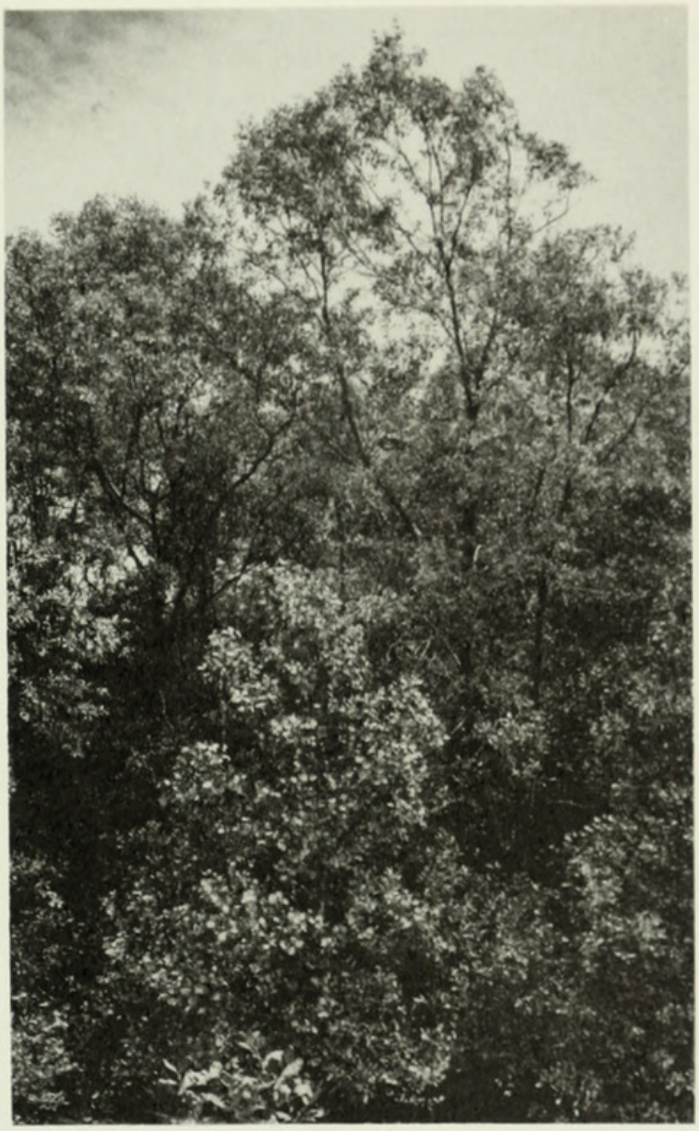

Fig. 2. A. alba forest with Sonneratia alba in foreground

atmosphere and so replenishes its water supply during the night and cooler parts of the day when the relative humidity is high; it grows in pure mangrove forests in protected creeks and the mouths of rivers in shallow seas". Chapman (1970) proposes the ecologic associations Avicennietum album and Avicennieto albae - A. marinae.

Stone (1970) gives a good description of this species as it occurs in Guam: "A tree (ours rather small) of the saline and seaward margin of mangrove swamps; leaves oblong-elliptic or lanceolate, acute or rarely obtuse, acute at base, medium or olive green above, white beneath, 3—16 cm. long, 1.5—5 cm. wide; flowers 10—30 per spike, yellow, paired, spikes 2—3 cm. long; corolla 4—7 mm. long, 5—8 mm. wide; stamens 1.5—2 mm. long; style obsolete; stigma e-

rect; ovary short-puberulent distally; fruit floating". He gives its overall distribution as "Malaysia and adjacent Pacific islands" and comments that in Guam it is "Common in the Apa mangrove areas, apparently absent elsewhere.....associated with Rhizophora and Bruguiera. The corolla is dark yellow — nearly orange. A pioneer species, its seedlings often standing out to sea in suitable locations, but like all mangroves absent on surf-swept rocky or sandy coasts." Gaussen and his associates refer to it as a "colonizer of intertidal zones and estuaries".

Fig. 3. A. alba forest

Navalkar found that in the Indus delta and the Sundribans delta, India-Bangladesh, the mangrove succession is governed by the disintegration of rock, soil salinity, soil humidity, and biotic factors. He recognized the following seven stages in the succession: (1) Avicennia alba Association (Optimum Stage); (2) Avicennia alba and Acanthus ilicifolius Stage. In these two stages the soil is blackish or grayish, composed of clay and salt, is always inundated and swampy, lying between low and high tide marks. (2a) Ceriops candolleana and Acanthus ilicifolius Stage, marked by cutting and burning by man; high level of ground water mingles with creek water; there are areas where sweet water mingles with creek water. (3) Avicennia alba Stage, at a greater distance from shore and weathered rocks; marked by an increase in anthropozoic biotic factors. (4) Sesuvium portulacastrum Stage, at a still greater distance from the shore. (5) Sesuvium portulacastrum and Aeluropus repens Stage, with an increase in height above the sea level and decreasing salinity. (6) Aeluropus repens and Paspalum vagin-

atum Stage, with still greater increase in height above sea level and decreasing salinity. (7) Clerodendrum inerme Stage, with increasing aridity and very little salinity.

Fig. 4. A. alba trees

Puri & Jain (1957) have studied the mangrove vegetation in the Poona region on the west coast of India and have recognized there a number of plant communities that are really edaphic or bio-edaphic in nature. Puri found that in the mangrove associations of the Indus delta there are 279 species of plants in 184 genera and 61 families, while in the Sundribans delta there are 304 species in 230 genera and 72 families.

Richards (1964) affirms that "In Malaya the pioneers [in the mangrove association] are not species of Rhizophora [as they are in the New World], but Avicennia alba and A. intermedia, or sometimes, on deep mud rich in organic matter, Sonneratia griffithii. These pioneer forests establish themselves on shoals or sandbanks out at sea

which are exposed at neap tides, or along the seaward edge of existing forests. Avicennia intermedia grows on a comparatively firm

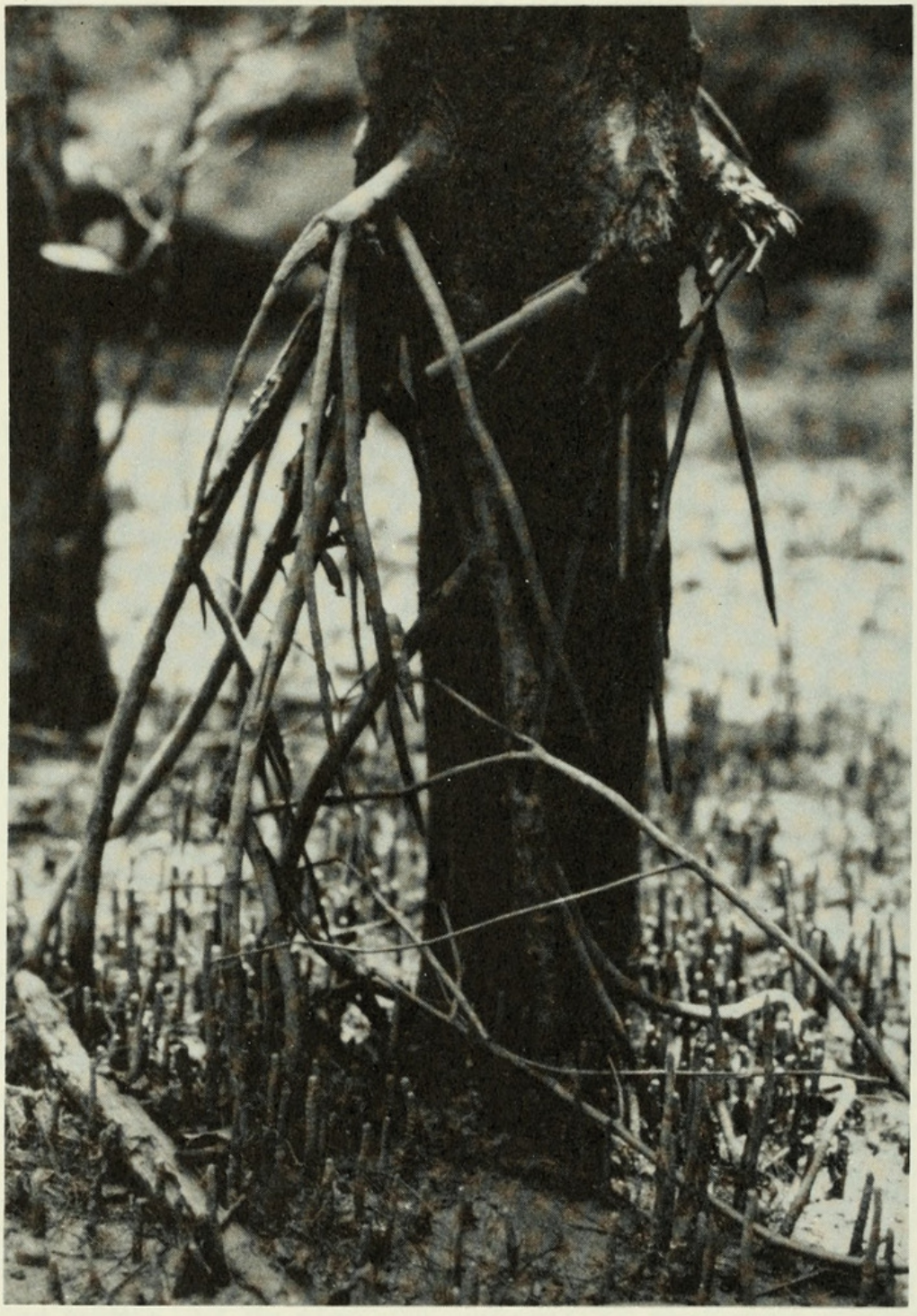

Fig. 5. Avicennia alba, showing stilt-roots. [Fig. 1--5 photographs by Paul Chai, Office of the Conservator of Forests, Sarawak, taken September 14, 1971, June 29, 1973, August 11, 1973, and October 16, 1974]

clayey substratum which is easy to walk on, A. alba and Sonneratia on softer and blacker mud. On the clay soils the Avicennia is normally succeeded by Bruguiera caryophylloides, but where Sonneratia is the pioneer, Rhizophora mucronata usually follows on..... The east coast of Sumatra, according to Troll & Dragendorf (1931), is fringed with an almost unbroken mangrove belt which in places is several kilometers wide. The dominant species in the pioneer zone is Avicennia alba, often associated with Sonneratia alba. Further inland these give way to species of Rhizophora, Bruguiera, Xylocarpus, etc. and at the landward edge of the swamps there is generally a zone of the palm Nipa fruticans with which Sonneratia acida is often associated.....On the Malayan coasts.....[the].... species growing on land flooded by 'medium high tides' [are] Avicennia alba, A. intermedia, Sonneratia griffithii and, on river banks, Rhizophora mucronata."

Chai (1972) reports that in Sarawak Sonneratia alba is "A pioneer species colonising newly formed mud flats along sheltered sea shores and estuaries. Avicennia alba may also come in at the same time or immediately after." Avicennia alba, he says, is a "Small to huge tree —70 ft. tall and 7 ft. girth. Bark dark brown to black. Not buttressed but may develop slender, soft stilt roots. Leaf lanceolate or elliptic-obovate with tapering base; lower leaf surface whitish, salt being excreted from this surface. Fruit glaucous, green, leech-shaped. Occurrence. Another pioneed species colonising newly formed mud flats as Sonneratia alba. Often gregarious along low convex banks of the rivers near the sea but is later replaced by Rhizophora apiculata and Bruguiera parviflora. Rare inland." He says that it grows in Watson's Inundation Class 2 — inundated by medium high tides (flooded 45 to 59 times per month). A. marina normally grows in this same inundation class in Sarawak, but A. officinalis grows only in Class 3, inundated by normal high tides only (flooded 20 to 45 times per month).

Navalkar (1961) asserts that "From the point of exchangeable bases, which are far more important in determining associations than the pH, $CaCO_3$, humus etc., three different types of soils have been distinguished so far as the mangroves of the Western coast of India are concerned, particularly for Bombay and Salsette Islands and the surrounding area. Each type of soil is characterised by its own peculiar flora as : (a) Ca-Mg soil with Avicennia alba as the dominant plant to the extend of excluding competitors; (b) Ca-Na soil characterised by Acanthus ilicifolius vegetation is almost in pure stage; (c) Ca-K soil characterised by Suaeda fruticosa vegetation and a few associated plants. The high osmotic pressure in the cell sap of the leaves of Avicennia alba Bl. due to higher chloride content than in any other mangrove species, may account for the dominance of Avicennia alba near the foreshores of Bombay and Salsette Islands."

Navalkar (1940) has found that osmotic pressure of this man-

grove's cell sap varies directly with tide and temperature and inversely with humidity and rainfall. Its physiological anatomy has been studied and reported on by Mullan (1932).

Puri (1960) reports that Navalkar found an osmotic pressure in Avicennia alba of 38.607 atmospheres, while Sen Gupta found it to be 41.29 atmospheres. He found the species' geographic distribution in India to be confined to the East Coast (like A. marina), in contradistinction to A. officinalis which he found on both the West and East Coasts, the Indus delta, the Sundribans, Chittagong, Burma, and the Andaman Islands. In the "Low mangrove forest" it grows in association with Ceriops roxburghiana, Aegialitis rotundifolia, and Excoecaria agallocha, while in the "Tree mangrove forest" on the river deltas of the East Coast it grows with Rhizophora conjugata, Kandelia rheedii, Bruguiera gymnorhiza, Carapa moluccensis, Ceriops candolleana, etc.

Ten & Keng (1969) assert that "A. intermedia was suggested to be a natural hybrid of A. alba and A. officinalis, by Griffith (cf. Ridley, 1923). However, seedlings of this species are uniform, and do not reveal any hybrid nature. Although the pollen grains exhibit intermediate characters between A. alba and A. officinalis, they are mostly well-filled, rather than empty, thus suggesting that it is a distinct species." I regard it as A. marina (Forsk.) Vierh., although perhaps a small-leaved form worthy of varietal or form rank.

Backer & Bakhuizen van den Brink (1965) differentiate A. alba from A. marina as follows: A. alba — "Flowers in 10--3-flowered spikes; flower-pairs, at least in the lower part of the spike, conspicuously distant; adult spikes 1 1/2 -- 3 cm long; style absent or very short (1/4 -- 1 1/2 mm); stigmas erect during anthesis. Leaves oblong or lanceolate, rarely elliptic, from an acute, rarely broadly cuneate base, with an acute, rarely obtuse tip, white beneath, 3—16 cm by 1 1/2 -- 5 cm." A. marina — "Flowers in 2--12-flowered heads; lowermost flower pair sometimes distant from the other ones, but nevertheless the inflorescence not spiciform; adult heads 1/2 -- 1 1/2 cm long; style robust, c. 1 1/2 mm long; stigmas recurved. Leaves elliptic-oblong or oblong-obovate, from an acute base, with an obtuse or rounded tip, greenish white beneath, 3--9 cm by 1 1/4 -- 4 1/2 cm."

Both of these species are distinguished by having the "Expanded flowers 5--8 mm across; corolla from the base of the tube up to the tops of the segments measuring 4--7 mm; segments subequal; stamens (inclusive of anthers) 1 1/2 -- 2 mm long; ovary glabrous in the lower half, in the upper half or apically densely covered with upcurved, appressed, short hairs; style short (at most 1 1/2 mm) or nearly absent; stigmatic lobes equal."

In contradistinction, A. officinalis is characterized by the "Expanded flowers 10—15 mm across; corolla from the base of the tube up to the tops of the segments measuring 7--10 mm; posterior segment broadest, shallowly bilobed; stamens (inclusive of the an-

thers) 3 1/2 -- 4 1/2 mm long; ovary densely appressed-pubescent throughout; style subulate, pubescent throughout or at least at base, 3--4 mm long; stigmatic lobes much shorter than the rest of the style, often unequal." It might also have been mentioned that in A. officinalis there are 5 fibrovascular bundles leading into the corolla, while the other two species have only 4.

Burk (1966) asserts that he feels Bakhuizen van den Brink was in error in reducing A. alba to varietal rank under A. marina (Forsk.) Vierh. because of the "dissimilarity of the habitat of the Red Sea plant, which is the original A. marina, on the shore of a very saline sea", while A. alba "is found away from the salt water, up creeks into which an abundance of fresh water descends.....it seems best to regard it as a species." Watson (1928) asserts that its flowers are the smallest of all the Malayan species, but the dimensions for A. marina and A. lanata Ridl. are only a trifle larger.

Shah & Patel (1970) reduce A. alba to synonymy under A. marina var. acutissima Stapf & Moldenke, but by this they doubtless mean the "A. alba" of Jafri (1966) and Stewart (1972), not of Blume.

Kuntze (1891), in proposing his new species, A. spicata Kuntze, says: "Inflorescentiae distiche spicatae, novellae longe conicae demum dissitiflorae axi villoso vix foveato. Fructus longus (1: 1 1/2 -- 2) e basi ovodea acuminatus. Singapur. Hierzu A. officinalis 'S. Kurz' Fl. Burma non L., ferner A. alba Miq. p. p. und A. officinalis var. alba Clarke p. p.; non Avic. alba Blume. Weder Blume noch Clarke geben die oben beschriebenen Merkmale an und Miquel hat die 2 scharf und leicht zu unterscheidenen Arten confundirt. Im Kew Herbar fand ich diese Art von Birma (Griffith 6071), Malaya (Maingay 1209), Java (Horsfield 31), Borneo (Beccari 1770). Diese Art ist nur mit lanzettlichen unterseits weisslich schwach behaarten Blättern und entsprechenden schwach behaarten Blüthen bekannt; die Inflorenzaxis ist aussergewöhnlich behaart, rostfilzig. Ich fand die Art als Baum und Strauch, mit gelblichen Corollen; die in der Frucht entwickelten Keimblätter sind dunkelgrün mit braunbehaarter hypocotyler Axe." I have seen 3 of the 5 collections, including the type, which he cites and find them to be typical A. alba Blume.

Nakanishi (1965) has found that the flowers of Avicennia alba contain "sterols, phenolics and no alkaloids. $LD_{50}$ was greater than 1000 mg/kg" and that the flowers exhibited activity against Bacillus subtilis and Staphylococcus aureus, but no activity against Proteus vulgaris or Escherischia coli. They showed no antitumor activity against the Yoshida sarcoma. The stems gave a positive alkaloid test and equivocal stereols and phenolic tests; they exhibited the same toxicity as the flowers and the same negative results against Yoshida sarcoma, and had the same antimicrobial activity as the flowers. The leaves gave equivocal alkaloid and sterol tests and positive tests for phenolics, showed the same toxicity as the flowers and stems and no activity against

the Yoshida sarcoma and the same antimicrobial results as the stems and flowers. Willamen & Li (1970) report the presence of an unnamed alkaloid in the leaves and stems.

Cuadra reports that wood of this species is used for firewood in Sabah. Shah (1962) and Santapau & Shah (1969) record it from Salsette Island, Santapau (1967) from Saurashtra, and Rao, Aggarwal, & Mukherjee (1963) from Ramaswaram Island, India. Prain (1908) reports finding it on riverbanks in the Sundribuns, describing it as "A shrub; leaves acute; capsules narrow". Navalkar (1956) records it from Bombay and Salsette Islands, where, he affirms, it grows in association with Ceriops candolleana and Acanthus ilicifolius. Brunig (1969) records it from Sarawak.

Sebastine & Ellis (1967) cite Sebastine 10646 from Madras, India. Bakhuizen van den Brink gives its overall distribution as from Sind to Malacca, the Malayan Archipelago, the Philippines, New Guinea, Polynesia, and China [the "Sind" record is erroneous, being based on specimens which prove to be A. marina var. acutissima]. He cites the following: INDIA: Falconer 2415. GREATER SUNDA ISLANDS: Borneo: Boschwezen 1974; Labohm 1964. Celebes: Rachmad 357; Teijsmann 13766; Van Vuuren 58. Java: Backer 1172, 1191, 1719, 1720, 1721, 1722, 2112, 2699, 7293, 21443; Hallier f. 163; Koorders 9694, 9695, 9696, 13478, 22009, 22022, 24112, & 25613; Scheffer 11. Sumatra: Gusdorf 8; Koorders 10591 & 10592; Lörzing 6029 & 7285. LESSER SUNDA ISLANDS: Bali: Becking 39. PHILIPPINE ISLANDS: Mindanao: Hutchinson 3947.

Cooke (1958) records the species from Salsette Island and from Konkan, India, citing Bhide s.n., Ganime s.n., Ryan s.n., and Stocks s.n. He gives its overall distribution, as known to him, as "India in tidal creeks; Malaya, S. E. Asia, N. Australia". Stewart (1972) records it from tidal mangrove swamps of Sind and Baluchistan, citing Jafri s.n., Stearn 19, and HB.20683, but the plant here referred to is actually A. marina var. acutissima.

On the other hand, it seems likely that the "Avicennia tomentosa Roxb." of Mukherjee & Chanda (1973) from the Sundribuns of Bengal is actually A. alba Blume.

Material of A. alba has been misidentified and distributed in some herbaria as A. marina (Forsk.) Vierh. On the other hand, the Backer 15324 and Gill 24, distributed as A. alba, are actually A. marina (Forsk.) Vierh. and Stearn 19 is A. marina var. acutissima Stapf & Moldenke.

Additional citations: INDIA: Andhra Pradesh: Thanikaimoni s.n. [Yanam, 15.3.74] (Ld). West Bengal: Prain s.n. [August 5, 1902] (Pd). BURMA: Tenasserim: Falconer 241 (Pd, Pd). THAILAND: R. M. King 5588 (W--2435842), 5601 (W--2435928). MALAYA: Malacca: W. Griffith 59 (Pd). GREATER SUNDA ISLANDS: Java: Koorders 9696 β (Pd), 22009 β (Pd). Sabah: Cuadra A.1232 (W--2187104); Orolfo 690 (W--1674491). Sarawak: Chai & al. S.26764 (Ld), S.27535 (Ac),

S.29936 (Ld), S.29944 (Ld, Z), S.30626 (Ft, Ld), S.30667 (Ld). NEW GUINEA: Papua: Gill s.n. [Port Moresby, 6 April 1970] (E--2035070).

AVICENNIA ALBA var. LATIFOLIA Moldenke

Additional bibliography: Moldenke, Phytologia 15: 71. 1967.

Recent collectors describe this plant as a shrubby tree, 20--25 feet tall, with a short bole about 5 feet tall and 6 inches in diameter at breast height, 18 inches in girth, branching low, the crown spreading, the bark greenish-gray-brown, smooth, or black and pinkish-mottled with the basal part blackish throughout, the under bark green, the inner bark cream-colored, lenticels many, small, leaves subcoriaceous, with gray matted hairs beneath, peduncles and petioles of younger leaves brown-tomentose, corollas orange-yellow, pistil greenish, fruit light-green, with a velvety surface. They have encountered it at sealevel on the edges of the mangrove association inundated only by high tides, flowering in June.

Paul Chai writes me, in a letter dated September 14, 1971, that his no. S.29946, cited below, "was collected recently. It has much broader leaves than S.27535, S.29936, S.29944 and S.30626 [=A. alba Blume]. It has lenticillate bark surface throughout the main trunk, another feature which is not found in the other four numbers. It is possible that the tree is still at a relatively younger stage. The leaf size puts it quite nicely with A. alba Bl. var. latifolia."

Material of this variety has been misidentified and distributed in some herbaria as A. marina (Forsk.) Vierh.

Additional citations: GREATER SUNDA ISLANDS: Sarawak: Chai S. 29946 (Ld, Z). NEW GUINEA: Papua: Gill s.n. [Port Moresby, 6 April 1970] (E--2034437); Havel NGF.17393 (W--2484749).

AVICENNIA BALANOPHORA Stapf & Moldenke

Additional bibliography: Moldenke, Phytologia 7: 159--160. 1960; R. Good, Geogr. Flow. Pl. 241. 1964; V. J. Chapm., Trop. Ecol. 11: 5, fig. 3. 1970.

AVICENNIA BICOLOR Standl.

Additional bibliography: Fedde & Schust. in Just, Bot. Jahresber. 53 (1): 1068. 1932; I. M. Johnst., Sargentia 8: 260. 1949; Bascope, Bernardi, Jorgensen, Hueck, Lamprecht, & Martinez E., Mangl. Am. [Inst. Forest. Latinoam. Invest. Capac. Descrip. Arb. Forest. 5:], imp. 1, 16. 1959; Moldenke, Phytologia 14: 310. 1967; Moldenke, Résumé Suppl. 16: 3. 1968; Bascope, Bernardi, Jorgensen, Hueck, Lamprecht, & Martinez E., Mangl. Am. [Inst. Forest. Latinoam. Invest. Capac. Descrip. Forest. 5:], imp. 2, 16. 1970; V. J. Chapm., Trop. Evol. 11: 5, fig. 3. 1970; Gibson, Fieldiana Bot. 24 (9): 176--177. 1970; Moldenke in Woodson, Schery, & al., Ann. Mo. Bot. Gard. 60: 150 & 154. 1973; "H. R.", Biol. Abstr. 57: 1904. 1974; Molina R., Ceiba 19: 95. 1975.

Duke says of the Avicennia population in Panama: "Holdridge and

I believe there are two species in Darién, this is a larger tree with larger leaves and more pronounced white beneath". He reports this tree to 75 feet tall, the diameter of the trunk at breast height to 14 inches, "often hollow and often with projections similar to the pencil roots", the pencil roots (pneumatophores) ranging from 2 to 5 inches in height. Other collectors refer to it as a tree, 3--13 m. tall or more, the trunk 10--30 inches in diameter, with somewhat rough brown bark, and have encountered it in mangrove swamps and along the outskirts of the tidal belt, in flower in April, August, and November to January.

Additional citations: HONDURAS: Valle: Molina R. 21457 (N). PANAMA: Darién: Duke 5488 (Ac). Casaya Island: Duke 10372 (Oh, W--1908630). PEARL ISLANDS: San José: I. M. Johnston 1259 (E--1591147, W--2024284).

AVICENNIA ELLIPTICA Holm in Thunb., Pl. Bras. Dec. 3: 37. 1821.

Synonymy: Avicennia elliptica Thunb. ex Schau. in A. DC., Prodr. 11: 700, in syn. 1847.

Bibliography: Thunb., Pl. Bras. Dec. 3: 37. 1821; Jacks. in Hook. f. & Jacks., Ind. Kew., imp. 1, 1: 254. 1893; Moldenke, Prelim. Alph. List Invalid Names 5. 1940; Moldenke, Alph. List Invalid Names 5. 1942; Jacks. in Hook. f. & Jacks., Ind. Kew., imp. 2, 1: 254. 1946; Moldenke, Résumé 235. 1959; Jacks. in Hook. f. & Jacks., Ind. Kew., imp. 3, 1: 254. 1960; Moldenke, Phytologia 7: 166 & 206 (1960) and 14: 328. 1967; Moldenke, Fifth Summ. 1: 392. 1971; Moldenke, Phytologia 30: 15 (1975) and 31: 383, 384, & 393. 1975.

In my publications previous to 1975 I regarded A. elliptica as a synonym of A. germinans (L.) L., as was done by some previous authors, and specimens were so annotated by me in various herbaria. It seems to me now, however, that the very long-, narrow-, and smooth-leaved population in northeastern Brazil is sufficiently distinct to warrant the resurrection of Holm's specific name for it. According to Gardner the species is "a large tree" and according to Curran it lives "in fresh water". Vasconcales Sobrinho found it in flower in July and reports the vernacular name, "mangle", for it. His photograph no. 135 shows the tree in situ. Jackson (1893) regarded it, curiously, as a synonym of the Asiatic A. officinalis L., a completely untenable disposition.

It is very probable that many of th 41 other collections cited by me in Phytologia 7: 206 (1960) and the 5 cited in Phytologia 14: 328 (1967) as A. germinans from Brazil will prove on re-examination to be A. elliptica Holm, A. elliptica var. martii Moldenke, or A. germinans var. guayaquilensis (H.B.K.) Moldenke. It is not now feasible for me to borrow back these specimens for re-examination.

Citations: BRAZIL: Bahia: Blanchet s.n. [Bahia 1832] (M). Pará: H. M. Curran 16 (F--740465, S, W--1617777). Pernambuco: G. Gardner 1101 (Bm, Cb, Cb, Ed, Ed, K, K, N, P, P, S, V, V, V, V, W--1066491), s.n. [Pernambuco, III.1837] (N); Vasconcales So-

brinho 287 [photo 135] (N, N, N--photo). State undetermined: Westin s.n. (N--photo of type, Th--type, Z--photo of type).

AVICENNIA ELLIPTICA var. MARTII Moldenke, Phytologia 30: 15. 1975.

Bibliography: Moldenke, Phytologia 7: 204--206 (1960), 14: 328 (1967), 30: 15 (1975), and 31: 383 & 384. 1975.

This variety differs from the typical form of the species in having leaves whose blades are more broadly elliptic, 7--13 cm. long (including the petiole), 2--3.5 cm. wide, and very sharply and conspicuously acute or acuminate at box the apex and base.

Lanjouw & Lindeman describe this plant as a tree or shrub with pale-yellow flowers, called "parwa" in Surinam, and found it growing on mud banks, flowering in September. Drouet refers to it as a tree to 10 m. tall, bordering tidal flats. Martius found it growing in river forests at the mouths of maritime streams, flowering in March, August, and September.

In my publications previous to 1975 I regarded this plant as merely an anomalous form of A. germinans (L.) L. and herbarium specimens are so annotated by me in various herbaria. I feel now that it is, rather, a variety of the northeastern South American A. elliptica Holm and it is very probable that some other of the many collections cited by me in Phytologia 7: 204--206 (1960) and 14: 328 (1967) as A. germinans may prove, on re-examination, to be A. elliptica var. martii instead.

Citations: SURINAM: Lanjouw & Lindeman 301 (N, Ut--17661b). BRAZIL: Ceará: Drouet 2442 (E--1110546, F--857471, F--949342, N, N, S, Sp--37514, W--1594848). Pará: Ducke 9818 [Herb. Rio Jan. 5407] (N); Martius 2644 (Mu--1070), s.n. [Mart. 1820] (Mu--1072), s.n. [Rio Toncatins, Aug.] (Mu--1071), s.n. [sylvis ripariis ad ostia fluv. maritimorum, Sept.; N. Y. Bot. Gard. Type Photo. Coll. Neg., new ser. 8922] (Mu--1069--type, N--photo of type, Z--isotype, Z--photo of type).

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Additional bibliography: Lamotte, Geol. Soc. Am. Mem. 51: [Cat. Cenoz. Pl. N. Am.] 80. 1952; Moldenke, Phytologia 7: 161--162. 1960; Moldenke, Fifth Summ. 1: 375 (1971) and 2: 839. 1971; Moldenke, Phytologia 32: 365. 1975.

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Additional synonymy: Avicennia marina var. resimifera Perry ex Moldenke, Phytologia 26: 370, in syn. 1973 [not A. marina var. resinifera (Forst.) Bakh., 1921].

Additional bibliography: Prain, Ind. Kew. Suppl. 4, imp. 1, 21. 1913; Fedde & Schust. in Just, Bot. Jahresber. 56 (2): 285. 1937; Prain, Ind. Kew. Suppl. 4, imp. 2, 21. 1958; R. Good, Geogr. Flow. Pl. 241. 1964; Moldenke, Phytologia 15: 71. 1967; V. J. Chapm., Trop. Ecol. 11: 5, fig. 3. 1970; Moldenke, Fifth Summ. 1: 314, 329, 331, 333, 334, 338, 340, 344, 349, 391, & 393 (1971) and 2: 839. 1971; Mukherjee, Journ. Palynol. 9: 178, 180, & 181, fig. 5—