NORDIC JOURNAL OF
BOTANY

Research Article

Taxonomic reappraisal of the mangrove genus *Avicennia* (Acanthaceae) in India

Subrata Mondal and Saikat Naskar

Department of Botany, The University of Burdwan, Burdwan, West Bengal, India

Correspondence: Saikat Naskar (saikatnaskar@rediffmail.com)

Nordic Journal of Botany
2026: e05084
doi: 10.1002/njb.05084
Subject Editor: Ranee Prakash
Editor-in-Chief: Jalil Noroozi
Accepted 29 January 2026
Published 7 May 2026

A taxonomic reappraisal of the mangrove genus *Avicennia* in India was undertaken through extensive field surveys and critical examination of herbarium specimens. Three taxa, *Avicennia alba*, *Avicennia marina* subsp. *marina*, and *Avicennia officinalis*, are described in detail. A synonymic list was compiled using the World Checklist of Vascular Plants (WCVP) and assessed through analysis of protologues and original material, with accompanying nomenclatural notes. Accordingly, four lectotypes and one neotype were designated. Leaf forms were investigated using principal component analysis (PCA), as foliar characters have historically served as important criteria for delimiting taxa within the genus. PCA was conducted under four approaches: 1) among *A. alba*, *A. marina*, and *A. officinalis*; 2) among four infraspecific taxa of *A. marina*; 3) across populations from the three major coastal regions of India; and 4) between *A. marina* subsp. *marina* and *A. marina* var. *acutissima*. In all cases, the analysis indicated that leaf form alone could not reliably distinguish taxa. However, PERMANOVA using quantitative variables employed in PCA showed that, in first two cases, the differences among *Avicennia* species and among the infraspecific taxa of *A. marina* were statistically significant. In contrast, the differences among *A. marina* populations from the three major coastal regions of India, as well as between *A. marina* subsp. *marina* and *A. marina* var. *acutissima*, were weak. Phylogenetic analysis using ITS sequences from India and other Indo-West Pacific *Avicennia* accessions showed broad concordance with established multilocus frameworks; however, several GenBank accessions displayed incongruent placements, suggesting probable misidentifications. Similarly, inconsistency in GBIF occurrence records further point to widespread identification errors. The findings also indicate that *A. officinalis* populations from India are morphologically distinct from conspecific populations in Australasia, highlighting taxonomic complexity within the genus. To facilitate identification, a taxonomic key to *Avicennia* taxa in India is provided.

Keyword: *Avicennia*, India, taxonomic reappraisal

NORDIC SOCIETY OIKOS

www.nordicjbotany.org

© 2026 The Author(s). Nordic Journal of Botany published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

The true mangrove genus *Avicennia* (Acanthaceae) is notable for its dominance in mangrove habitats worldwide (Spalding et al. 2010, Tomlinson 2016), playing a crucial role in the blue carbon ecosystem, for which the mangrove forests are widely recognised (Sappal et al. 2016, Choudhary et al. 2024). However, overlapping morphological traits between distantly related species, combined with a high degree of variation in certain traits within this genus, have contributed to considerable taxonomic confusion since their discovery in science.

The genus *Avicennia*, along with several other mangrove genera, was introduced to science (albeit under different names) through the work of three pioneering Asian botanists: Rheede, Rumphius, and Hermann (Baas and Veldkamp 2013, Naskar 2020). The name *Avicennia* was initially used by Linnaeus (1747) based on Paul Hermann's collections from Ceylon (Trimen 1886), now Sri Lanka. Later, Linnaeus (1753) proposed the first species name: *Avicennia officinalis*. In both works, Linnaeus referred to 'Oepata' from *Hortus Malabaricus* of Rheede (1683), indicating that the species was first recorded on the Malabar coast of India. Subsequently, Linnaeus (1763, 1764a, 1764b) himself contributed to the confusion surrounding the correct nomenclature and identity of the species (Bakhuizen van den Brink 1921). Jacquin (1760, 1763) also cited 'Oepata' to the American species *Avicennia tomentosa* Jacq. [*Avicennia germinans*] possibly based on the similarity of the leaves. Since the species composition of the genus *Avicennia* differs in the Indo-West Pacific (IWP) and Atlantic-East Pacific (AEP) biogeographic regions due to allopatric isolation (Duke 1991, Spalding et al. 2010, Tomlinson 2016), Jacquin's citation was inappropriate. Nevertheless, Linnaeus (1763, 1764a, 1764b) and Willdenow (1800) followed Jacquin's concept of the species. Finally, Schauer (1847) distinguished *A. tomentosa* from *A. officinalis*, relying solely on Jacquin's illustration for the former and retaining Rheede's illustration for the latter. However, Schauer included two additional species, *Avicennia alba* Blume and *Sceura marina* Forssk. [*Avicennia marina* (Forssk.) Vierh.], under *A. officinalis*. Bakhuizen van den Brink (1921) recognised four species, namely *A. marina* (Forssk.) Vierh., *A. officinalis*, *Avicennia nitida* Jacq., and *A. tomentosa* Schau. – the first two from the IWP region and the latter two from the AEP region. He further classified *A. marina* into five varieties: var. *typica*, var. *alba*, var. *resinifera*, var. *intermedia*, and var. *rumphiana*. The illustrations of these varieties by Bakhuizen van den Brink (1921) are invaluable for understanding morphological variation and identifying *Avicennia* taxa through comparative analysis. Moldenke (1934, 1938, 1940, 1974, 1975, 1976a, 1976b, 1980) proposed nine new taxa within *Avicennia* – one new species and eight intraspecific categories – based on his examination of herbarium specimens. It highlights the extent of variation within this genus.

Duke's (1991) comprehensive treatment of *Avicennia* from the Australasian region synonymised several previously proposed names under five species: *A. alba* Blume, *Avicennia rumphiana* Hallier f., *Avicennia integra* N.C.Duke, *A. officinalis*, and *A. marina* (Forssk.) Vierh. Furthermore, Duke classified *A. marina* into three varieties: var. *australasica* (Walp.) Moldenke, var. *eucalyptifolia* (Valeton) N.C.Duke, and var. *marina*. The first variety is restricted to temperate and subtropical latitudes along the south-eastern coast of Australia and northern New Zealand. The second variety occurs in tropical latitudes of northern Australia, New Guinea, the southern Solomon Islands, and adjacent regions. In contrast, *A. marina* var. *marina* has a much wider distribution range, extending along the coasts of the Indian Ocean, Bay of Bengal, and Arabian Sea, from western Australia to eastern Africa. Later, Everett (1994) elevated these varieties to subspecies. To date, Duke's treatment remains the only authoritative source for recognising *Avicennia* species in the IWP region, including India.

Indian taxonomists encountered considerable confusion following the treatments of Linnaeus and Willdenow. For many years, *A. officinalis* was considered the sole representative of this genus in India. Roxburgh (1832) reported '*A. tomentosa* Willd. iii. 395' from the 'Soondur-bun' (= Sundarbans). Similarly, Wallich (1832) used the name *A. tomentosa* Linn. for a specimen collected by Hamilton (K001114037!) in the Sundarban. The detailed colour illustration by Wallich (1832), which provides extensive morphological details of *A. officinalis*, confirms the identity of the species. Later, Wight (1850) produced illustrations of '*A. tomentosa* (Linn.)' and '*A. alba* (Blume)'. While the first illustration clearly depicts a typical *A. officinalis*, the second departs from the typical morphology of *A. alba* by showing ovate rather than lanceolate leaves and capitate rather than spicate inflorescences. This latter illustration may correspond to *A. marina*. Griffith (1854) mentioned that 'The species of Avicennia appear to be in a very confused state in botanical works'. The morphological similarities among *Avicennia* species may have contributed to taxonomic uncertainty regarding whether these different forms should be recognised as distinct species. Clarke (1885) considered *A. alba* Blume, characterised by lanceolate, acute leaves and a very short style, to be a variety of *A. officinalis*. However, Prain (1903a) retained *A. alba* as a distinct species and listed it alongside *A. officinalis* from the Sundarbans.

In a subsequent publication, Prain (1903b) noted that woodcutters in the Sundarbans had reported four forms of *A. alba*. According to him, one form, characterised by acute leaves and narrow, sharp-pointed capsules, corresponds to *A. alba*. The other three forms, with blunt leaves and broad capsules, lacked botanically distinguishable characteristics. The latter three forms described by Prain (1903b) appear to correspond to the species *A. marina*, which was later reported from the Sundarbans, India, by Naskar and Guha-Bakshi (1987).

Phylogenetic analyses of *Avicennia* based on multiple loci and broad geographical sampling have shown that the genus diverged into the IWP and AEP lineages approximately six million years ago. Within the IWP lineage, three major subclades were identified: 1) *A. rumphiana* and *A. alba*, 2) *A. officinalis* and *A. integra*, and 3) the *A. marina* complex

(Li et al. 2016). However, this phylogenetic study included no sampling from India. Therefore, retrieving the available GenBank ITS sequences – currently the most widely available molecular data for the genus *Avicennia* from India and other parts of the IWP region – provides an opportunity to assess the phylogenetic placement of Indian *Avicennia* taxa.

Currently, three species – *A. alba* Blume, *A. marina* (Forssk.) Vierh. (subsp. *marina*), and *A. officinalis* – are recognised within Indian Territory (Banerjee et al. 1989, Naskar 2004, Ragavan et al. 2016, Mandal and Bar 2019). In addition to these three species, some infraspecific categories have also been recorded in India. Thus, objective of the present study is to provide a taxonomic enumeration of the genus *Avicennia* in India, based on field investigations conducted in the Sundarbans – the largest and most biodiverse mangrove forest in the country, accounting for approximately 42.5% of India's mangrove area (FSI 2023) – together with herbarium specimens and a comprehensive review of the literature. This study seeks to address the questions: 1) what is the taxonomic and distributional status of *Avicennia* in India? 2) Is the morphological variation in certain traits of *Avicennia* sufficient for infraspecific categorisation? 3) Are the Indian *Avicennia* taxa correctly placed in the phylogeny?

Material and methods

Sampling and morphological characterization of *Avicennia* species

Flowering and fruiting twigs of *A. alba*, *A. marina*, and *A. officinalis* were collected from 13 localities in the Indian part of the Sundarbans to study and document their morphological variation. Herbarium specimens were deposited at the herbarium of Department of Botany, The University of Burdwan (BURD). Based on inflorescence type, flower symmetry, and flower size, the collected plants were classified into the three species. *Avicennia alba* is distinguished by its spicate inflorescences, whereas *A. marina* and *A. officinalis* have capitate inflorescences. Additionally, *A. marina* is characterised by actinomorphic flowers, while *A. officinalis* has zygomorphic flowers, as proposed by Duke (1991), Naskar (2004), and Tomlinson (2016). The flower size of *A. alba* and *A. marina* is more or less the same, whereas *A. officinalis* has larger flowers. Thus, the three species can be easily distinguished in the field based on their reproductive morphology. However, we observed considerable variation in leaf shape, particularly within *A. alba* and *A. marina*, which often leads to misidentification. Therefore, leaf shapes from all collected plants were documented to assess variation and compare them with the infraspecific categories proposed so far. Flowers from at least 15 individuals per species were dissected to document their morphology, and the species were described using standard botanical terminology following Harris and Harris (2006).

Checklist compilation, typification, and assessment of synonymy

A comprehensive checklist of *A. alba*, *A. marina* subsp. *marina*, and *A. officinalis* was compiled using the World Checklist of Vascular Plants (WCVP 2025). Type specimens, original material, and protologues associated with each name were located and critically examined using multiple cybertaxonomic resources, as recommended by Naskar (2025). These included the Biodiversity Heritage Library (www.biodiversitylibrary.org), Tropicos (www.tropicos.org), International Plant Names Index (www.ipni.org), JSTOR Global Plants (plants.jstor.org), TL-2 (https://sil.si.edu/DigitalCollections/tl-2), Plants of the World Online (powo.science.kew.org), and virtual herbaria of relevant institutions.

Typification was carried out where necessary in accordance with the provisions of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2025). Certain synonyms were reassigned to appropriate taxa or excluded to ensure the correct and unambiguous application of names. All examined specimens, including original material and Indian collections, both historical and those newly collected during the present study, were enumerated.

Preparation of distribution map of *Avicennia*

Two maps were prepared within the R environment (www.r-project.org) to illustrate the distribution of the three *Avicennia* species across the Indo-West Pacific (IWP) biogeographic region and within India. Occurrence data for the three species were retrieved from the Global Biodiversity Information Facility (GBIF) database (2025) using the 'rgbif' library. The 'CoordinateCleaner' library was employed to identify and flag potentially erroneous geographic coordinates within the GBIF occurrence dataset. Spatial vector data were read, written, and analysed using the 'sf' library, which follows the Simple Features standard (ISO 19125), widely adopted in geographic information systems (GIS). The 'rnaturalearth' library was used to download and load Natural Earth map data. Maps were generated using the 'ggplot2' library, with cartographic elements added using the 'ggspatial' library. For the map showing the distribution of the three *Avicennia* species in India, geocoordinates derived from collections in the Indian Sundarbans, along with herbarium specimen records from other mangrove zones of India, were utilised.

Acquisition of morphometric variables from leaf and multivariate analysis

Leaf area (LA), leaf length (L), leaf width (W), petiole length (P), distance from the leaf base to the widest point on the midvein (M), leaf tip angle (LT), and leaf base angle (LB) were measured from images of 122 herbarium specimens including our deposition at BURD along with type and other specimens of CAL, HIFP, BSID, L, PBL, K, BM, C, NY, and BISH. Two leaves were measured from each specimen, resulting in a total of 244 leaves from *Avicennia*. The raw data were transformed to achieve normalisation: LA, LT, and LB were $\log_{10}$-transformed, while ratio-transformed variables were calculated as L/W, L/P, and L/M. This yielded six derived variables, which were used for principal component analysis (PCA).

PCA was conducted using four approaches. First, the data were grouped by species: *A. alba*, *A. marina*, and *A. officinalis*. Second, the data were grouped by infraspecific categories

of *A. marina*: subsp. *marina*, subsp. *australasica*, subsp. *eucalyptifolia*, and var. *acutissima*. Third, specimens of *A. marina* from Indian territories were analysed by grouping them into three geographic regions: the Andaman and Nicobar Islands, the east coast, and the west coast. Finally, Indian *A. marina* specimens were categorised into subsp. *marina* and var. *acutissima*. Identification of the taxa was based on the labels or annotations (if available) on the herbarium specimens. PCA and the corresponding two-dimensional plots were generated in R using the 'prcomp', 'ggplot2', 'ggrepel', 'dplyr', and 'tidyr' packages in R (www.r-project.org).

To determine whether the groups identified in these PCA analyses differed significantly, PERMANOVA was performed on the corresponding quantitative variables. The test used Euclidean distance and 999 permutations, with the relevant taxonomic or geographic grouping treated as the fixed factor. Analyses were run using the 'vegan' package in R (www.r-project.org).

Phylogenetic analysis of IWP *Avicennia* species by complete ITS sequence

A complete ITS sequence of *A. marina* from the Indian Sundarbans was used to perform a BLAST search in the NCBI database (www.ncbi.nlm.nih.gov). ITS sequences showing 98–99% similarity, representing *A. alba*, *A. marina*, *A. officinalis*, *A. integra*, and *A. rumphiana*, and approximately 650 bp in length, were selected to construct a FASTA file. *Avicennia germinans* (AEP lineage) and *Thunbergia alata* were included as outgroups, as the genus *Thunbergia* is considered the sister to *Avicennia* (McDade et al. 2008). The sequences were aligned using the MUSCLE algorithm in MEGA11 (Tamura et al. 2021). The aligned dataset was tested to determine the best-fit substitution model, and a maximum likelihood tree was inferred using the T92+G model, with bootstrap support values calculated based on 100 replicates.

Results

Avicennia alba Blume (Blume 1826, p. 821) (Fig. 1)

Type: Indonesia, Java, s.d., Blume, s.n., L341/5 (lectotype, designated here: L2758406).

[Note: Duke (1991) referred to 'Blume 1700 (L, lecto)' as the lectotype. Moldenke (1960) also examined three specimens, which he referred to as 'Blume 1700 (Le Le Le)'. We traced three specimens (L341/No. 1, 5, and 11) that can be regarded as original material, as they represent Blume's collections preserved at Herbarium L and were gathered from 'Nusae Kambangae' in Java – the locality cited in the protologue. All three specimens were annotated by Moldenke in 1936 as *A. alba*. However, none of these three sheets (examined on both sides) bear the number '1700', and no other *Blume* specimens of this species are preserved at L (pers. comm. S. A. Guerrero, L), resulting in ambiguity regarding the precise application of the name. Since Duke's lectotypification is ambiguous, specimen L341/No. 5 is designated here as the lectotype, in accordance with Art. 9.3 of Turland et al. (2025), as it is morphologically consistent with *A. alba*.]

Based on the same type: *A. marina* var. *alba* (Blume) Bakh. (Bakhuizen van den Brink 1921, p. 103), *A. officinalis* var. *alba* (Blume) C. B. Clarke (Clarke 1885, p. 604).

Taxonomic synonym

Avicennia alba var. *latifolia* Moldenke (Moldenke 1940, p. 410)

Type: Indonesia, Archipel. Ind. Celebes Kpi Wadjo, Leg. Noerkas Exp. Vuuren no. 58, L341/15 (holotype: L0003640).

[Note: Moldenke cited Noerkas's specimen (no. 58), which does not represent a typical form of *A. alba*. The leaves are considerably broader. This form of *A. alba* has not yet been reported from India. Unfortunately, only a single specimen is currently known. Further investigation is needed to determine whether it represents a variety of *A. alba*.]

Avicennia spicata Kuntze (Kuntze 1891, p. 502).

Type: Myanmar, *A. spicata* ... Otto Kuntze (lectotype, designated here: K000885468; other original material: K000885459, K000885461, K000885469, NY00337288, and P03593044).

[Note: In the protologue, four collections were cited, namely: 'Birma (Griffith 6071)', 'Malaya (Maingay 1209)', 'Java (Horsfield 31)', and 'Borneo (Beccari 1770)'. We were able to locate three of these specimens. The first, third, and fourth collections correspond to the specimen barcode numbers K000885468!, K000885459!, and P03593044!, respectively. However, Moldenke labelled an uncited specimen collected by Kuntze (NY00337288!) as the holotype. As the original author did not explicitly designate any specimen as the holotype, it is inappropriate to treat NY00337288 as such. Moreover, although Kuntze was the author of the name, he did not cite any of his own specimens in the protologue. There is no clear evidence that Kuntze examined specimen NY00337288 during, or prior to, the preparation of the species description; consequently, it cannot be regarded as original material under Art. 9.4 of Turland et al. (2025). In accordance with Art. 9.6 of Turland et al. (2025), all the cited specimens must therefore be regarded as syntypes. We designate the specimen bearing the barcode number K000885468 as the lectotype according to Art. 9.3 of Turland et al. (2025), as it best matches the description provided in the protologue. Moreover, all the specimens were annotated by Moldenke as *A. alba*, and we concur with this identification, given the elongated capsule and spicate inflorescence of the specimen, both of which are consistent with *A. alba*].

Description

Tree, height ca 3.8–10.3 m; canopy spread 2.1–6.1 m; perennial, woody, arborescent, intertidal, tropical, inhabiting swampy, muddy substrates; obligate halophyte. Phenology:

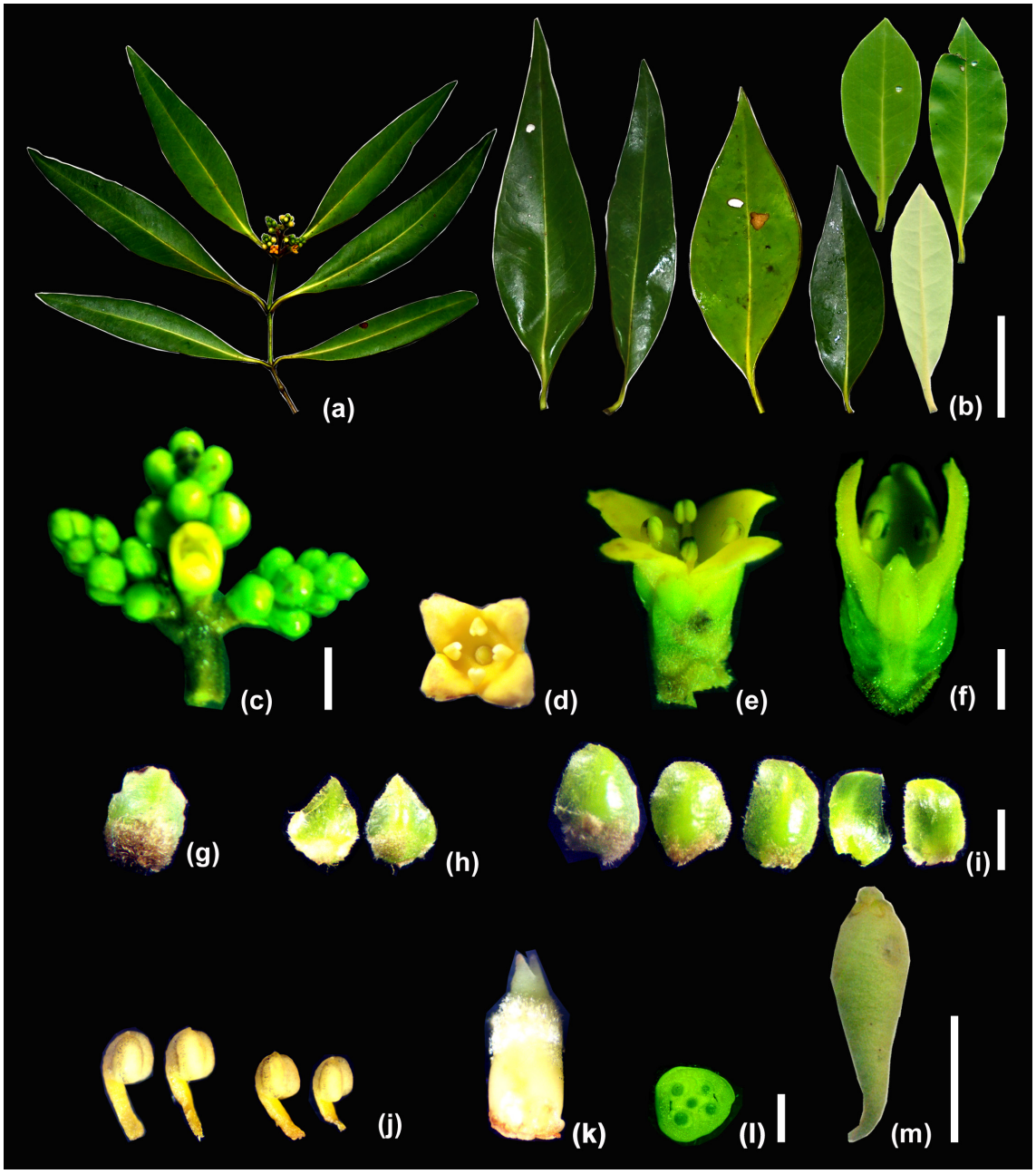


Figure 1. *Avicennia alba.* (a) Flowering twig; (b) leaves (showing variation); (c) portion of the inflorescence; (d) flower in top view showing actinomorphic corolla; (e) flower in side view; (f) longitudinal section of a flower; (g) bract; (h) bracteoles; (i) sepals; (j) slightly didynamous condition of the four stamens; (k) pistil; (l) transverse section of the ovary showing axile placentation; and (m) fruit. Scale bars: (a), (m) = 3 cm; (c) = 4 mm; (d)–(i) = 2 mm; (k), (j–l) = 1 mm.

flowering from April to May (rarely extending to September); fruiting from July to September (rarely until November). Root system a woody taproot with numerous lateral cable, anchoring, and absorbing roots; pneumatophores pencil-like, greyish brown, 10.0–32.0 × 0.6–1.5 cm, with numerous lenticels, 0.3–0.8 × 0.3–0.5 mm; occasionally, still (peg) roots present, cylindrical, greyish brown, 60.0–152.0 × 1.5–3.2 cm, lenticels numerous, 0.4–0.8 × 0.3–0.7 mm. Stem caulescent, indeterminate, sympodial, square in cross-section when young, greenish with whitish capitate hairs; becoming blackish-brown, rounded, smooth, and lenticular in mature stages. Bark smooth to slightly rough, greyish, greyish-green, greyish-black, or brownish; minutely furrowed; lenticels vertically elliptic, 0.6–2.2 × 0.5–2.0 mm. Twigs terete, woody, bearing 8–16 leaves. Pith solid, circular in outline. Leaf scars slightly raised, orbicular with a truncate apex. Buds axillary,

small, 1–2 mm long; terminal buds lance-ovate, elongated, 2–3 cm long. Leaves simple, evergreen, petiolate, exstipulate, opposite and decussate; lamina narrowly elliptic to elliptic, 7.8–17.0 × 1.6–8.4 cm, entire, coriaceous, reticulate with pinnate, camptodromous venation; upper (adaxial) surface whitish, bearing capitate hairs; lower (abaxial) surface shiny with numerous salt glands; stomata sunken. Apex acute (angle 19.2°–78.7°), base acute (29.5°–74.9°). Petiole green, terete to canaliculate, 0.5–2.5 × 0.2–0.6 cm. Inflorescence compound spike (racemose), 5.5–12.5 × 3.5–6.5 cm. Flowers bisexual, actinomorphic, aromatic, yellowish turning saffron at maturity, semi-pedicellate (pedicel 0.1–0.2 mm), with nectariferous tissues. Bract solitary, subtending each floral unit, ovate, boat-shaped, greenish, 1.7–2.3 × 1.8–2.6 mm, apex acute to rounded, base cuneate to broadly obtuse; margin ciliate (0.2–0.3 mm); dorsal surface hairy, ventral surface glabrous, often with basal hairs. Bracteoles two, subbasal, subtending lateral flowers, ovate, greenish, 1.2–2.0 × 1.4–2.1 mm; apex broadly acute to rounded, base cuneate to broadly obtuse; margin ciliate (0.2–0.4 mm); dorsal surface villous, ventral surface glabrous, hairs frequent at base. Calyx polysepalous, persistent, imbricate, actinomorphic, green to greenish-brown, outer surface hairy, inner surface with long hairs; sepals 5, ovate, margin spiny, apex obtuse to broadly acute, 1.8–2.6 × 1.7–2.8 mm; dorsal surface hairy, ventral glabrous. Corolla gamopetalous, rotate, valvate, yellowish turning saffron, thick, 2.8–5.0 × 1.9–4.3 mm; petals 4 (rarely 5), apex acute, 2.6–5.0 × 1.8–2.6 mm; dorsal surface villous. Androecium of 4 stamens, epipetalous, yellowish turning blackish; filaments short, reddish, 0.1–0.2 × 0.3–0.8 mm; anthers divaricate, rounded, dorsifixed, 0.7–0.9 × 0.6–0.8 mm, dehiscing longitudinally. Gynoecium syncarpous, hairy, cream-white, 1.6–3.2 × 0.3–2.1 mm; ovary superior, bilocular, elongated, upper half pubescent, 1.2–3.2 × 0.2–1.9 mm; style short, glabrous, 0.2–0.3 × 0.3–0.6 mm; stigma bifid, equal or subequal, hyaline, 0.1–0.3 × 0.2–0.4 mm; placentation axile; ovules 4 per ovary, 0.05–0.08 × 0.03–0.06 mm. Fruit a drupe, greenish, ellipsoidal, 3.0–5.5 × 0.5–1.5 cm, apex acuminate; dorsal surface with capitate hairs; calyx persistent. Seed dicotyledonous, germination cryptoviviparous, 2.5–5.2 × 0.3–1.3 cm; hypocotyl with numerous hyaline hairs, apical cell hook-like, 0.2–1.5 cm long.

Additional specimens examined

India, S. Mondal & S. Naskar, SM/DCHA/AA09, Dakshin Chandanpiri, South 24 pgs, W.B. [21°38′56.50″N, 88°17′25.81″E,], 21 Apr. 2019 (BURD12292/2025); S. Mondal & S. Naskar, SM/DCHA/AA11, DakshinChandanpiri, South 24 pgs, W.B. [21°38′57.90″N, 88°17′28.86″E], 21 Apr. 2019 (BURD12294/2025); S. Mondal & S. Naskar, SM/LOTH/AA12, Lothian, South 24 pgs, W.B. [21°38′7.77″N, 88°18′32.09″ E], 22 Apr. 2019 (BURD12296/2025); S. Mondal & S. Naskar, SM/LOTH/AA82, Lothian, South 24 pgs, W.B. [21°38′3.75″N, 88°18′30.93″E], 1 June 2019 (BURD12360/2025); S. Mondal & S. Naskar, SM/MAIP/AA74, Maipith, South 24 pgs, W.B. [21°53′58.53″N, 88°33′53.31″E], 21 May 2019 (BURD12345/2025); S. Mondal & S. Naskar, SM/JHAS/AA67, Jharkhali Somobay more, South 24 pgs, W.B. [22°1′48.81″N, 88°41′12.79″E], 24 May 2019 (BURD12327/2025); S. Mondal & S. Naskar, SM/GADK/AA107, Gadkhali, South 24 pgs, W.B. [22°10′0.49″N, 88°47′11.17″E], 16.05.2021 (BURD12402/2025); S. Mondal & S. Naskar, SM/PAKH/AA178, Pakhiraloy, Gosaba, South 24 pgs, W.B. [22°8′14.23″N, 88°50′5.04″E], 23 May 2021 (BURD12440/2025); S. Mondal & S. Naskar, SM/JATI/AA130, Jotirampur, Gosaba, South 24 pgs, W.B. [22°8′47.43″N, 88°50′50.04″E], 17 May 2021 (BURD12408/2025); S. Mondal & S. Naskar, SM/SAMS/AA273, Samsernagar, North 24 pgs, W.B. [22°8′35.79″N, 88°51′40.59″E], 29 June 2022 (BURD12534/2025); S. Mondal & S. Naskar, SM/HEMN/AA311, Heamnagar, North 24 pgs, W.B. [22°12′23.46″N, 88°58′55.41″E], 7 July 2022 (BURD12572/2025); S. Mondal & S. Naskar, SM/HEMN/AA319, Heamnagar, North 24 pgs, W.B. [22°12′30.85″N, 88°58′33.79″E], 7 July 2022 (BURD12576/2025); S. Mondal & S. Naskar, SM/JOGE/AA282, Jogesgange Bazar, North 24 pgs, W.B. [22°14′26.06″N, 88°57′47.38″E], 30 June 2022 (BURD12543/2025); S. Mondal & S. Naskar, SM/CANN/AA239, Canning, South 24 pgs, W.B. [22°18′16.93″N, 88°40′38.96″E], 16 June 2022 (BURD12498/2025); S. Mondal & S. Naskar, SM/CANN/AA141, Canning, South 24 pgs, W.B. [22°18′15.64″N, 88°40′39.15″E], 22 May 2021 (BURD12418/2025); L. K. Banerjee, Col. No: 10264, Kansardaian, Odisha, 21 July 1973, (BSID0005606); L. K. Banerjee, Col. No: 10264, Kansardaian, Odisha, 21 July 1973, (BSID0005607); L. K. Banerjee, Col. No: 10254, Balighar, Odisha, 18 July 1973, (BSID0005609); L. K. Banerjee, Col. No: 8561, Hetamundi, Odisha, 16 Oct. 1971, (BSID0005612); L. K. Banerjee, Col. No: 10244, Thakurdian, Odisha, 26 Feb. 1973, (BSID0005620); A. R. K. Sastry, Col. No: 7382, Martlapalem series-Patayerucoringa Estuarine complex, Andrapradesh, 6 Jan. 1970, (BSID0005622); G. Thanikaimoni, Yelatturdibba, Krishna Delta, Andrapradesh, 27 Mar. 1974 (HIFP_002967); B.R. Ramesh, Coringa Mangrove Reserve Forest, Kakinada, Andrapradesh, 13 Sept. 2001(HIFP_002975).

Avicennia marina (Forssk.) Vierh. (Vierhapper 1907, p. 435) subsp. *marina* (Fig. 2)

Type: Yemen, '125/59, TYPE' (lectotype, designated by Moldenke 1960, p. 215: BM000950260; other original material**:** C10003011 and C10003012).

Based on the same type

Sceura marina Forssk. (Forsskål 1775, p. 37), *A. tomentosa* var. *arabica* Walp. (Walpers 1845, p. 133).

[Note: W.G. Walpers (1845) cited '*Sceura marina* Forsk. *Fl. Aeg. Arab.* 37' under *A. tomentosa* var. *arabica*, indicating that the two names are homotypic. No specimen attributed to Walpers could be traced.]

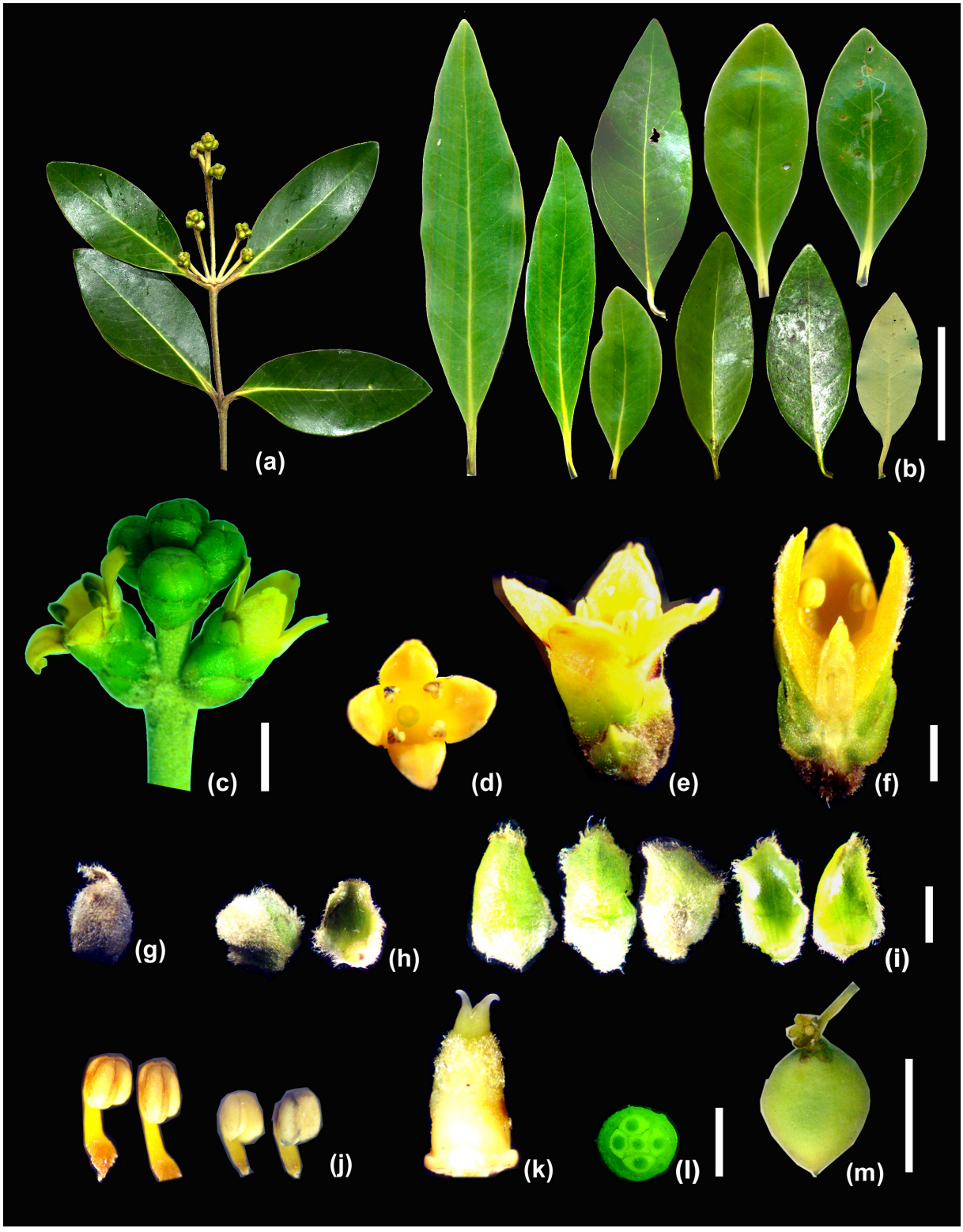


Figure 2. *Avicennia marina.* (a) Flowering twig; (b) leaves (showing variation); (c) portion of the inflorescence; (d) flower in top view showing actinomorphic corolla; (e) flower in side view; (f) longitudinal section of a flower; (g) bract; (h) bracteoles; (i) sepals; (j) slightly didynamous condition of the four stamens; (k) pistil; (l) transverse section of the ovary showing axile placentation; and (m) fruit. Scale bars: (a), (m) = 3 cm; (c) = 4 mm; (d)–(i) = 2 mm; (k), (j–l) = 1 mm.

Taxonomic synonym

Avicennia mindanaensis **Elmer (Elmer 1915, p. 2868)**

Type: Philippines, Philippine Islands Plants, 11 990, *A. alba* Blume (lectotype**,** designated here: NY00337291; Isolectotype: The Field Museum (F) – 11 990).

[Note: Elmer (1915) cited specimen number 11 990 as the type. We traced two specimens bearing this number, namely NY00337291 and F–11 990. Thus, these two specimens constitute syntypes in accordance with Art. 9.6 of Turland et al. (2025). The NY00337291 specimen has been selected here as the lectotype, in accordance with Art. 9.3 of Turland et al. (2025). Moldenke annotated both specimens as *A. marina*, and this identification is supported by diagnostic leaf and fruit characters.]

Avicennia sphaerocarpa **Stapf ex Ridl. (Ridley 1920, p. 151)**

Type: Malaysia: '*A. sphaerocarpa*, Stapf, *A. officinalis* … Sungie Pinang … Aug. 1900 … C. Curtis' (lectotype, designated here: K000885463; Isolectotype: K000885462).

[Note: Ridley (1920) cited specimens collected by Curtis for this species. We traced two such specimens at K (K000885462! and K000885463!), which constitute syntypes. The specimen K000885463 is designated here as the lectotype, in accordance with the provisions of Turland et al. (2025). Moldenke annotated the specimen as *A. marina*.]

Avicennia marina **var. *acutissima* Stapf & Moldenke (Moldenke 1940, p. 411)**

Type: India, (holotype: K000885470; holotype fragment**:** NY00337284).

[Note: Moldenke (1940) established this variety based on a specimen collected by R.K. Bhide from the Salsette Islands, Mumbai, India, primarily on the basis of its sharply acute or acuminate leaf apex and the presence of a beaked fruit. However, Mondal and Naskar (2025) also observed similar leaf morphology in *A. marina* from the Sundarbans and concluded that leaf shape is insufficient to distinguish among *A. alba*, *A. marina*, and *A. officinalis*. Furthermore, Moldenke (1960) noted that the fruits of *A. marina* are distinctly beaked when young but are mostly unbeaked at maturity.]

Avicennia marina **f. *angustata* Moldenke (Moldenke 1976b, p. 18)**

Type: Malaysia, [MALAYSIA], Buntal village, Buntal River, First Division, Sarawak, June 18, 1971 (holotype: Paul Chai S.29949).

[Note: Moldenke described a forma of *A. marina* based on its dwarf habit. However, dwarfism is commonly observed in this species when it grows in landward sites where tidal water rarely reaches (Naidoo 2025). We also recorded individuals of *A. marina* measuring only 1.0–1.5 m in height that had initiated flowering, which may be comparable to the dwarf form described by Moldenke.]

Avicennia marina **var. *acutissima* f. *pumila* S. Dutta, Chakral & H. Rodrigues (Dutta et al. 2019, p. 32)**

Type: India, Suchandra Dutta & Farhan Suraliwala 002, Maharashtra, Mumbai, Kandivli West, Charkop, Tarzan Lake: 1 Mar. 2019 (holotype: BLAT; Isotypes: CAL and RDNCP).

[Note: The authors relied solely on the dwarf habit of *A. marina* var. *acutissima* to establish this forma. However, as noted earlier, dwarfism in *A. marina* is often a consequence of soil desiccation resulting from infrequent tidal inundation.]

Halodendrum thouarsii **Roem. & Schult. (Roemer and Schultes 1818, p. 485)**

Type: 'halodendrum ... Aubert' (neotype, designated here: P00657609).

[Note: The authors cited 'H. Thouarsi' (Herbarium of Du Petit-Thouars) as the collector and 'Ad littoral maris in Madagascar' as the locality in the protologue. Moldenke (1960) noted the existence of a *Haleodendron* specimen housed at the P. We traced a single specimen labelled as *Haleodendron* at P, which was annotated by Moldenke as *A. marina*; we concur with this identification. However, the attribution of this specimen to Du Petit-Thouars cannot be confirmed, a fact also noted in TL-2. To reduce ambiguity and ensure the precise application of the name, specimen P00657609 is designated here as the neotype, in accordance with the Art. 9.8 of Turland et al. (2025).]

Avicennia officinalis **f. *flaviflora* Kuntze (Kuntze 1898, p. 249)**

Type: Tanzania, Kuntze s.n. (B), Zanzibar.

[Note: Both Moldenke (1960) and Duke (1991) informally designated a specimen collected by Kuntze from Zanzibar as the type. However, we were unable to locate this specimen at B. As the taxon represents an African element, the forma should be placed under *A. marina* rather than *A. officinalis*.]

Avicennia officinalis **f. *tomentosa* Kuntze (Kuntze 1898, p. 249)**

Type: Tanzania, '*A. officinalis* γ *ovalifolia* OK f. *tomentosa* OK …Zanzibar 1/IV 94, Otto Kuntze', 694897 (holotype: US00119377).

[Note: As this taxon was collected from Zanzibar, Tanzania, it is referable to *A. marina*. Moldenke annotated the specimen as *A. marina*, and we concur with this determination.]

Description

Tree, 1.8–8.8 m tall; canopy spread 1.9–5.9 m; perennial, woody, intertidal, tropical, inhabiting swampy, muddy

substrates; obligate halophyte. Phenology: Flowering from May to July (rarely up to September); fruiting from July to August (rarely up to November). Root system a woody taproot with numerous lateral (cable and absorbing) roots; pneumatophores pencil-like, greyish, 10.0–30.0 × 0.5–1.2 cm, bearing numerous lenticels, 0.3–0.8 × 0.3–0.5 mm; still roots (peg roots) occasionally present, cylindrical, greyish brown, 30.0–122.0 × 1.5–3.2 cm, lenticels numerous, 0.2–0.7 × 0.2–0.8 mm. Stem caulescent, arborescent, indeterminate, sympodial; young stems greenish, quadrangular, with whitish capitate hairs; mature stems rounded, blackish-brown, smooth, lenticular. Bark smooth or exfoliating in small flakes or patches; colour greyish, whitish-brown to brownish; surface smooth to finely furrowed; lenticels vertically elliptic, 0.5–1.8 × 0.3–1.5 mm. Twigs terete, woody, bearing 6–12 leaves; pith solid, circular; leaf scars slightly raised, orbicular with a truncate apex. Buds axillary, small, 1–2 mm long; terminal buds lance-ovate, elongate, 2–3 cm long. Leaves simple, evergreen, opposite, decussate, exstipulate, petiolate; lamina narrowly elliptic to elliptic, 7.8–17.0 × 1.6–8.4 cm, entire, coriaceous; apex acute (34.2°–84.8°), base acute (44.2°–101.9°); venation pinnate, camptodromous, reticulate; adaxial surface whitish, with capitate hairs; abaxial surface shiny, with numerous salt glands; stomata sunken. Petiole green, terete to canaliculate, 0.5–2.0 × 0.2–0.5 cm. Inflorescence a capitate, compound spike (racemose), 4.5–18.5 × 3.5–15.5 cm. Flowers bisexual, actinomorphic, yellowish turning saffron, aromatic, with nectary; semi-pedicellate, 3.4–6.5 × 2.1–6.1 mm; pedicel 0.1–0.2 mm. Bract solitary, subtending each floral unit, ovate, greenish, boat-shaped, hairy; 1.45–2.06 × 1.64–2.42 mm; margin ciliate (0.10–0.25 mm); apex acute, broadly acute or rounded; base cuneate to broadly obtuse; dorsal surface hairy, ventral glabrous, frequently hairy at base. Bracteoles two, sub-basal, subtending lateral flowers, ovate, greenish, 1.12–1.77 × 1.25–1.84 mm; margin ciliate (0.2–0.3 mm); apex broadly acute to rounded; base cuneate to broadly obtuse; dorsal surface villous, ventral glabrous, hairs frequently at base. Calyx polysepalous, persistent, imbricate, actinomorphic, green to greenish-brown; sepals 5, ovate, 1.67–2.43 × 1.72–2.58 mm; outer surface with smooth hairs, inner surface with long hairs; margin spiny; apex obtuse to broadly acute; dorsal surface hairy, ventral smooth, hairs frequently at base. Corolla gamopetalous, rotate, valvate, actinomorphic, yellowish turning saffron, thick; 2.52–4.78 × 2.34–4.24 mm; petals 4 (rarely 5), apex acute, 2.45–4.75 × 1.85–2.75 mm; dorsal surface villous. Androecium of 4 stamens, epipetalous, inserted; filaments short, reddish, 0.21–0.32 × 0.15–0.25 mm; anthers divaricate, rounded, dorsifixed, 0.63–1.10 × 0.54–0.73 mm; anther dehiscence longitudinal. Gynoecium syncarpous, hairy, cream-white, 1.34–2.84 × 0.36–2.22 mm; ovary superior, bilocular, elongate, upper half pubescent, 1.23–2.26 × 0.24–1.24 mm; style short, glabrous, 0.2–0.3 × 0.3–0.6 mm; stigma bifid, equal or subequal, 0.11–0.62 × 0.14–0.36 mm; placentation axile; ovules 4, 0.05–0.06 × 0.03–0.05 mm. Fruit a drupe, flattened ovoid, greenish, 1.8–3.0 × 2.0–3.5 cm; apex acuminate; dorsal surface smooth, with capitate hairs; calyx persistent. Seed dicotyledonous; germination crypto-viviparous; 1.6–2.8 × 1.8–2.5 cm; hypocotyl with numerous hyaline hairs, terminal cell straight to slightly curved, 0.2–1.5 cm long.

Additional specimens examined

INDIA: S. Mondal & S. Naskar, SM/DCHA/AM101, DakshinChandanpiri, South 24 pgs, W.B. [21°38′59.35″N, 88°17′47.23″E], 30 June 2019 (BURD12375/2025); S. Mondal & S. Naskar, SM/PAKH/AM160, Pakhiraloy, Gosaba, South 24 pgs, W.B. [22°8′14.24″N, 88°50′6.94″E], 30 May 2021 (BURD12444/2025); S. Mondal & S. Naskar, SM/PAKH/AM163, Pakhiraloy, Gosaba, South 24 pgs, W.B. [22°8′14.31″N, 88°50′7.13″E], 30 May 2021 (BURD12446/2025). S. Mondal & S. Naskar, SM/RAMC/AM265, Ramchandrakhali, South 24 pgs, W.B. [22°11′50.33″N, 88°44′4.47″E], 2 July 2022 (BURD12561/2025); K. Ramamurthy, Col. No: 88840, Near Port, Andrapradesh, 11 Sept. 1988, (BSID0005623); sn. Col., Col. No: 22576, Lankevanidibba, Andrapradesh, 16 Jan. 1991, (BSID0005624); D. Ghosh & L. K. Banerjee, Col. No: 17006, Raj kawla, Andrapradesh, 5 Aug. 1989, (BSID0005627); D. Ghosh & L. K. Banerjee, Col. No: 17006, Raj kawla, Andrapradesh, 5 Aug. 1989, (BSID0005628); sn. Col., Col. No: 22511, Nuch, Andrapradesh, 16 Jan. 1991, (BSID0005629); L. K. Banerjee, D. Ghosh & A. K. Sen, Krishna & Godabori delta, Andrapradesh, Col. No: 17075, sn. Date., (BSID0005630); L. K. Banerjee, D. Ghosh & A. K. Sen, Krishna & Godabori delta, Andrapradesh, Col. No: 17075, sn. Date., (BSID0005631); L. K. Banerjee, Col. No: 10305, Talcher, Odisha, 10 Aug. 1973, (BSID0005632); L. K. Banerjee, Col. No: 9467, Thakurdian, Odisha, 6 Nov. 1972, (BSID0005636); L. K. Banerjee, Col. No: 10263, Kansardaian, Odisha, 21 July 1973, (BSID0005640); L. K. Banerjee, Col. No: 10118, Mahisamara, Odisha, 16 Feb. 1972, (BSID0005643); L. K. Banerjee, Col. No: 10243, Thakurdian, Odisha, 26 Feb. 1973, (BSID0005644); N. Parthasarathy & K. Ravikumar, Col. No: 85388, Tuticorin; near thermal power station, Tamil Nadu, 24 Feb. 1987, (BSID0011871); K. Karthigeyan, Col. No: 21408, Boat Island, South Andamans, Andaman and Nicobar Islands, 15 May 2004, (PBL0000015794); S. K. Jain & N. P. Balakrishnan, Col. No: 6085, Carbyn's Cove, South Andamans, Andaman and Nicobar Islands, 24 Aug. 1977, (PBL0000015796); L. Rasingam, Col. No: 17592, Dugong Creek, Little Andaman, Andaman and Nicobar Islands, 16 Aug. 2004, (PBL0000015798); N. G. Nair, Col. No: 1582, Kimus, Car Nicobar, North Nicobars, Andaman and Nicobar Islands, 10 June 1974, (PBL0000015800); J.C. Sen Gupta, Digha, West Bengal, 20 Mar. 1960 (HIFP_002959); A.K. Mukherjee, Ganga sagar, West Bengal, 29 Apr. 1967 (HIFP_002982); G. Thanikaimoni, Yanam, Bairavapale, Puducherry, 15 Mar. 1974 (HIFP_002988); F. Blasco, Chikmagalur, Linkadahalli-Chickmagalur, Karnataka, 1 Jan. 1976 (HIFP_002994); G. Thanikaimoni, Muthupet, Thiruthiraipoondi, Tamil Nadu, 16 Jan. 1977 (HIFP_003004); G. Thanikaimoni, Ramanathapuram, Kurusadi Island, Gulf of Mannar south

of Pamban Island, Rameshwaram, Tamil Nadu, 18 Jan. 1977 (HIFP_003006); S. Aravajy, Ariyankuppam, Puducherry, 28 Sept. 1988 (HIFP_003022); N. Barot, Ahmadabad, Dholera Village, Ahmedabad, Gujarat, sn. Date (HIFP_003068); S. Aravajy, Cuddalore, Pichavaram Mangrove Forest, Tamil Nadu, 14 May 1991 (HIFP_003110); G. Thanikaimoni, Ahmadabad, Gujarat, 31 Mar. 1975 (HIFP_003025); G. Thanikaimoni, Gogha Port, Bhavnagar, Gujarat, 21 Mar. 1975 (HIFP_003026); G. Thanikaimoni, Karumbar Island, Jamnagar, Gujarat, 24 Mar. 1975 (HIFP_003032); G. Thanikaimoni, Navlakhi, Rajkot, Gujarat, 25 Mar. 1975 (HIFP_003035); G. Thanikaimoni, Rann of Kutch, Gujarat, 25 Mar. 1975 (HIFP_003037); G. Thanikaimoni, Thane, Konkan, Maharastra, 30 Mar. 1975 (HIFP_003040); G. Thanikaimoni, Cortalim, Panjim, North Goa, Gujarat, 5 Apr. 1975 (HIFP_003056); Kurian. Thomas, Bhav Nagar Port, Gujarat, Gujarat, 2 Aug. 1979 (HIFP_003061); G. Thanikaimoni, Konkan, Malavan Mangrove, Sindhudurg, Maharastra, 14 May 1986 (HIFP_003062); Anupama C., Col. No: 81240, Kallai, Kozhikode, Kerala, 12 Apr. 2002 (CALI123082), Anupama C., Col. No: 81267, Mankavu, Kozhikode, Kerala, 16 June 2002 (CALI123094).

Avicennia officinalis (Linnaeus 1753, p. 110) (Fig. 3)

Type: [icon] *Oepata* in Rheede, *Hortus Malabaricus* 4: 95, t. 45. 1683 (lectotype, designated by Stearn 1958)

Based on the same type

Avicennia oepata F. Buch.-Ham. (Buchanan-Hamilton 1835, p. 221)

[Note: In the protologue, Buchanan-Hamilton cited 'Oepata' of Rheede, thereby rendering this name homotypic with *A. officinalis*]

The synonymic and typification status of the three taxa of *Avicennia* have been summarized in Table 1.

Description

Habit: tree, 0.839–11.020 m tall; canopy spreading, 3.24–10.42 m across; perennial, obligate halophyte of tropical intertidal swampy mudflats. Phenology: flowering from June to July; fruiting from July to August. Root system: taproot woody, with numerous lateral roots. Pneumatophores pencil-like, greyish brown, 8.0–36.0 × 0.4–1.6 cm, with numerous lenticels 0.3–0.7 × 0.3–0.6 mm. Stilt roots frequently present, greyish brown, terete, 35.0–184.0 × 1.2–4.2 cm, with lenticels 0.3–0.8 × 0.2–0.8 mm. Stem: Caulescent, arborescent, indeterminate, sympodial. Bark: fissured to finely fissured; greyish to greyish brown; lenticels vertically elliptic, 0.6–2.0 × 0.2–1.8 mm. Twigs: terete, woody, bearing 6–10 leaves per node. Pith solid, circular in outline. Leaf scars orbicular, slightly raised, with truncate apex. Buds axillary, small, 1–2 mm long; terminal buds lance-ovate, elongate, 2–3 cm long. Leaves: opposite, decussate, simple, evergreen, coriaceous, petiolate, exstipulate, broadly elliptic, 8.42–16.75 × 8.29–14.75 cm. Lamina entire, divergent to inclined, planar to recurved, 7.42–13.25 × 8.29–14.75 cm; venation pinnate, reticulate, camptodromous. Adaxial surface whitish, with capitate hairs; abaxial surface shiny, with numerous salt glands; stomata sunken. Leaf apex obtuse (81.59°–128.05°), base rounded (64.31°–160.05°). Petiole terete to canaliculate, green, 1.0–3.5.0 × 0.6–1.2 cm. Inflorescence: racemose, capitate, 6.5–14.5 × 5.5–8.5 cm. Flowers: bisexual, zygomorphic, actinomorphic at calyx level, yellowish to orange-yellow turning saffron, aromatic, semi-pedicellate; pedicel 0.1–0.3 mm. Nectary present. Flower size 9.56–13.36 × 6.02–9.66 mm. Bract: single, subtending each flower; greenish with brown spot at apex, ovate, boat-shaped, hairy, 2.48–3.76 × 2.65–3.45 mm; margin ciliate (0.1–0.3 mm), apex acute to rounded, base cuneate to broadly obtuse; dorsal surface hairy, ventral glabrous; hairs often present at base. Bracteoles: two, sub-basal, ovate, hairy, greenish with brown spot at apex, 2.13–2.82 × 2.45–3.05 mm; margin ciliate (0.25–0.35 mm); apex broadly acute or rounded; base cuneate to broadly obtuse; dorsal surface villous, ventral surface smooth; hairs frequently present at base. Calyx: polysepalous, persistent, imbricate, actinomorphic; sepals 5, ovate, green to greenish brown with brown spot at apex, margin spiny, apex obtuse to broadly acute, 2.75–4.05 × 2.65–3.55 mm; outer surface hairy, inner surface with long hairs, hairs frequent at base. Corolla: gamopetalous, rotate, valvate, zygomorphic; petals 4 (rarely 5), unequal in size, yellowish to saffron, thick, 3.77–9.06 × 4.15–10.02 mm; apex acute; dorsal surface villous. Androecium: stamens 4, epipetalous, exserted, yellowish turning black; filament reddish, 1.20–2.64 × 0.25–0.5 mm; anthers divaricate, rounded, dorsifixed, 1.38–1.62 × 0.85–1.25 mm; dehiscence longitudinal. Gynoecium: syncarpous, cream-white, hairy, 5.51–6.97 × 3.25–5.46 mm; ovary superior, bilocular, rounded to elliptic, fully pubescent, 5.29–6.05 × 3.25–5.46 mm; style hairy, long, 2.35–3.23 × 1.32–2.62 mm; stigma bifid, unequal, 0.22–0.92 × 0.08–0.16 mm; placentation axile; ovules 4, 0.08–0.12 × 0.05–0.08 mm. Fruit: drupe, calyx persistent, greenish; surface smooth with capitate hairs dorsally; shape flattened ovoid; apex acuminate; size 2.5–4.0 × 2.8–4.2 cm. Seed: dicotyledonous, crypto-viviparous germination; seed 2.2–3.8 × 2.5–3.8 cm; hypocotyl hairy, hyaline, with conversely hooked apical cell, 0.2–2.5 cm.

Additional specimens examined

India, S. Mondal & S. Naskar, SM/LOTH/AO44, Lothian, South 24 pgs, W.B. [21°38′3.86″N, 88°18′30.76″E], 30. June 2019 (BURD12376/2025); S. Mondal & S. Naskar, SM/JATI/AO92, Jotirampur, Gosaba, South 24 pgs, W.B. [22°9′8.62″N, 88°50′44.89″E], 17 May 2021 (BURD12414/2025); S. Mondal & S. Naskar, SM/SATJ/AO124, Satjelia, South 24 pgs, W.B. [22°9′32.11″N, 88°51′16.08″E], 5 June 2021 (BURD12491/2025); S. Mondal & S. Naskar, SM/SATJ/AO121, Satjelia, South 24 pgs, W.B. [22°8′35.53″N, 88°51′40.05″E], 5 June 2021 (BURD12488/2025); L. K. Banerjee, Col. No: 8562, Hetamundi, Odisha, 16 Oct. 1971, (BSID0005615); M. K. Ghosh, Col. No: 311, Jambu Island, Odisha, 31 May 1967 (BSID0005619); Ramamurthy,Col. No: 88836,

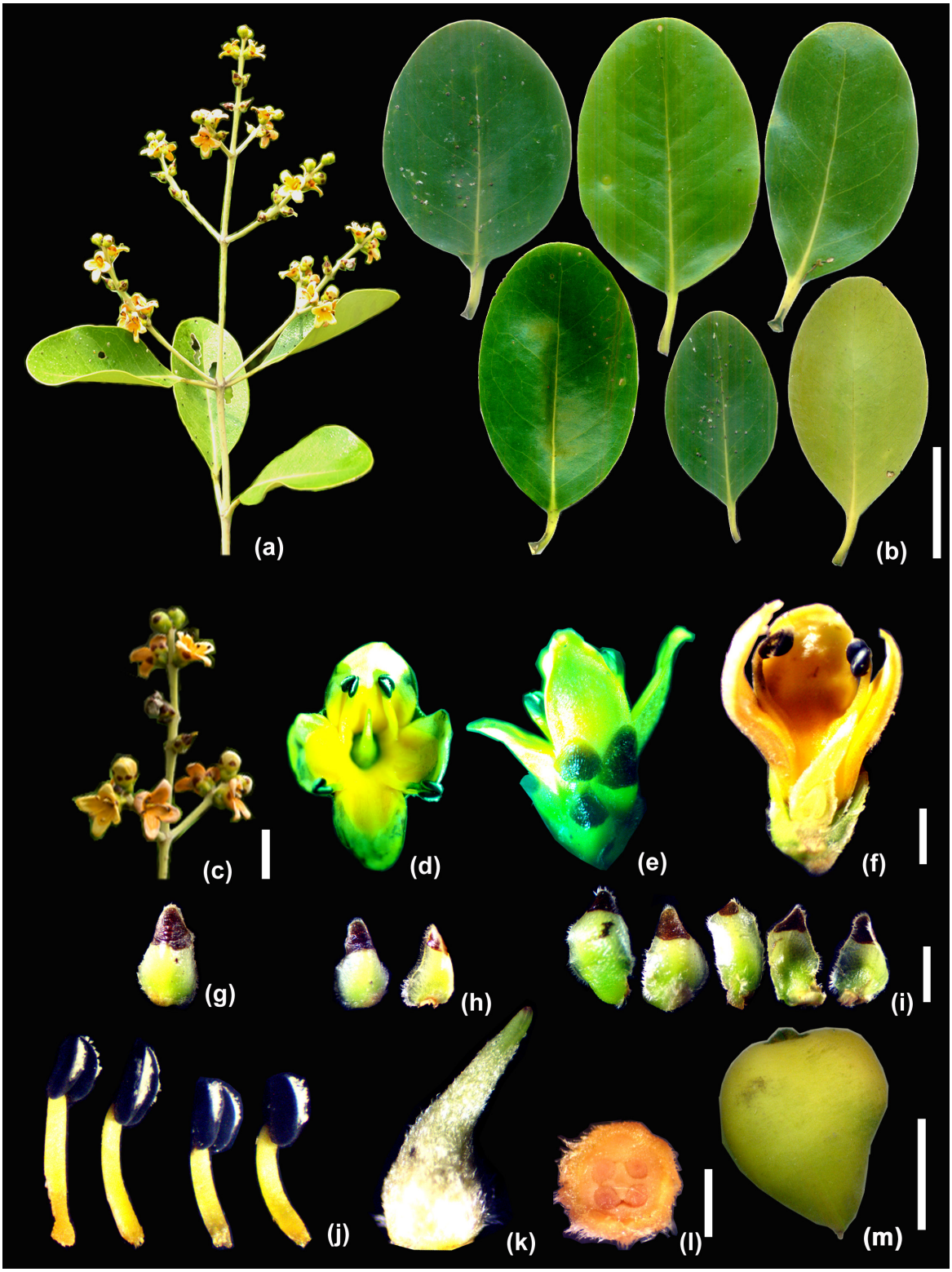


Figure 3. *Avicennia officinalis*. (a) Flowering twig; (b) leaves (showing variation); (c) portion of the inflorescence; (d) flower in top view showing actinomorphic corolla; (e) flower in side view; (f) longitudinal section of a flower; (g) bract; (h) bracteoles; (i) sepals; (j) slightly didynamous condition of the four stamens; (k) pistil; (l) transverse section of the ovary showing axile placentation; and (m) fruit. Scale bars: (a), (m) = 3 cm; (c) = 1 cm; (d)–(i) = 2 mm; (j)–(l) = 1 mm.

Table 1. Synonymic list of three *Avicennia* taxa retrieved from the World Checklist of Vascular Plants (WCVP) (2025), with their correct nomenclatural placement and type information. [1] *A. marina* var. *anomala* Moldenke (1940, p. 411), cannot be treated as a synonym of *A. marina* subsp. *marina*, as its occurrence was mentioned in the protologue from Tasmania, Australia (a southern state of the country). According to Duke (1991), *A. marina* var. *marina* is restricted to Western Australia, whereas in the higher latitudes of southern and eastern Australia, *A. marina* var. *australasica* is found. Therefore, *A. marina* var. *anomala* is likely referable to *A. marina* var. *australasica*. However, we were unable to trace the type specimen. [2]In WCVP, the name appears as *A. marina* f. *pumila* S. Dutta, Chakraborty & H.Rodrigues. [3]Gmelin's herbarium and type material are unknown (TL-2). Moldenke (1960) treated this name as a synonym of *A. marina* rather than *A. officinalis*. In the absence of a type specimen and given the inadequacy of the original description, the acceptability of this name is untenable within the highly variable *Avicennia* species. [4]The authors indicated its occurrence in 'Arabia, Abyssinia, [and] Nubia'; however, *A. officinalis* is not known to occur in these regions (Duke 1991). As noted by Moldenke (1960), most authors of African and Arabian Peninsula floras misapplied the name *A. officinalis* to specimens that are, in fact, referable to *A. marina*. This suggests that the taxon in question was likely *A. marina*. Furthermore, we were unable to locate any corresponding specimen. [5]Moldenke (1960) noted that this species is entirely distinct from *A. officinalis*. [6]The geographical origin (Queensland, Russell River, Australia) of the taxon indicates that it belongs to *A. marina* subsp. *eucalyptifolia* (Valeton) J.Everett.

Avicennia taxa in India	Synonyms	Correct placement	Type
A. alba Blume	≡ *A. officinalis* var. *alba* (Blume) C.B.Clarke	*A. alba*	L2758406 (**Lectotype, designated here**)
	≡ *A. marina* var. *alba* (Blume) Bakh.	*A. alba*	
	A. alba var. *latifolia* Moldenke	A variety or a distinct species	L0003640 (Holotype)
A. marina (Forssk.) Vierh. subsp. *marina*	≡ *Sceura marina* Forssk.	*A. marina* subsp. *marina*	BM000950260 [Lectotype, designated by Moldenke (1960)]
	≡ *A. tomentosa* var. *arabica* Walp.	*A. marina* subsp. *marina*	
	A. intermedia Griff. ≡ *A. marina* var. *intermedia* (Griff.) Bakh.? ≡ *A. marina* f. *intermedia* (Griff.) Moldenke	*A. officinalis*	K004570766 (Holotype)
	= *A. spicata* Kuntze	*A. alba*	K000885468 (**Lectotype, designated here**)
	= *A. mindanaensis* Elmer	*A. marina* subsp. *marina*	NY00337291 (**Lectotype, designated here**)
	= *A. sphaerocarpa* Stapf ex Ridl.	*A. marina* subsp. *marina*	K000885463 (**Lectotype, designated here**)
	= *A. marina* var. *acutissima* Moldenke	*A. marina* subsp. *marina*	K000885470 (Holotype)
	A. marina var. *anomala* Moldenke[1]	*A. marina* subsp. *australasica* (Walp.) J.Everett	D. Henne and C. Wilhelmi s.n. (Holotype at B and Isotype at NY)
	= *A. marina* f. *angustata* Moldenke	*A. marina* subsp. *marina*	Paul Chai (no. S.29949) (Holotype)
	= *A. marina var. acutissima* f. *pumila S.Dutta, Chakral & H.Rodrigues*[2]	*A. marina* subsp. *marina*	Suchandra Dutta & Farhan Suraliwala 002', 'BLAT' (Holotype); Isotypes at CAL and RDNCP
A. officinalis	≡ *A. oepata* Buch.-Ham.	*A. officinalis*	'Oepata' in Rheede Hort. Malab. 4: 95, t. 45. 1683
	Racka torrida J.F.Gmel.[3]	*A. marina* subsp. *marina*?	Unable to locate
	Halodendrum thouarsii Roem. & Schult.	*A. marina* subsp. *marina*	P00657609 (**Neotype, designated here**)
	R. ovata Roem. & Schult.[4]	*A. marina* subsp. *marina*?	Unable to locate
	A. obovata Griff.[5]	*A. officinalis*?	Unable to locate
	A. officinalis f. *flaviflora* Kuntze	*A. marina* subsp. *marina*	Unable to locate
	A. officinalis f. *tomentosa* Kuntze	*A. marina* subsp. *marina*	US00119377 (Holotype)
	A. officinalis var. *acuminata* Domin[6]	*A. marina* subsp. *eucalyptifolia* (Valeton) J. Everett.?	Unable to locate

Alt: sea lavel Near port, Kakinada, Andrapradesh, 11 Sept. 1988, (BSID0005647); K. Ramamurthy, Col. No: 17066, Nachgunta, Andrapradesh, 11 Aug. 1989, (BSID0005649); sn. Col., Col. No: 22572, Nizapattanam, Andrapradesh, 22 Jan. 1991, (BSID0005650); L. K. Banerjee, D. Ghosh & A. K. Sen, Col. No: 17001, Raj kawla, Andrapradesh, 5 Aug. 1989, (BSID0005652); L. K. Banerjee, D. Ghosh & A. K. Sen, Col. No: 17074, Repalle, Gundukhal, Andrapradesh, 13 Aug. 1989, (BSID0005653); L. K. Banerjee & D. Ghosh, Col. No: 22572, Nizapattanam, Andrapradesh, 22 Jan. 1991, (BSID0005657); L. K. Banerjee, Col. No: 10300, BhitarKanika, Odisha, 16 June 1972, (BSID0005662); K. Thothathri & N. G. Nair, Col. No: 1089, Chiriatapu, South Andamans, Andaman & Nicobar Islands, 30 May 1974, (PBL0000015790); N. P. Balakrishnan, Col. No:172, Guptapara, South Andamans, Andaman and Nicobar Islands, 27 May 1973, (PBL0000015792); M. Y. Kamble, Col. No: 30652, Paget Island Wildlife Sanctuary, North Andamans, Andaman and Nicobar Islands, 15 Mar. 2012, (PBL0000029613); M.K. Ghosh, Kendrapara, False point Island, mangrove, Odisha, 23 May 1966 (HIFP_003072); G. Thanikaimoni, Yanam, Bairavapale, Puducherry, 5 Mar. 1974

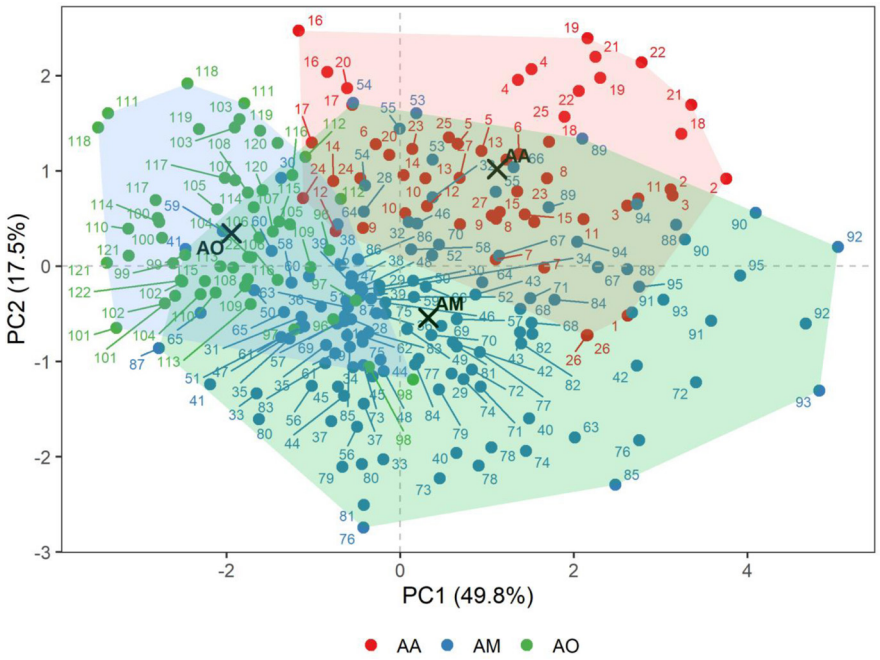


Figure 4. Two-dimensional plot of 122 individuals of *Avicennia alba* (AA), *A. marina* (AM), and *A. officinalis* (AO) based on scores of their morphometric variables along PC1 and PC2. The morphometric data were derived from herbarium specimen images, including both original collections and images retrieved from herbarium databases. Centroid values for each species are indicated by '×' symbols in the plot. Numbers in the plot indicate specimen IDs: AA (1–27), AM (28–95), and AO (96–122).

(HIFP_003077); G. Thanikaimoni, South Goa, Ribandar, Goa, 4 Apr. 1975 (HIFP_003086); G. Thanikaimoni, Uttar Kannada, Kalinadi Geek, Karwar, Karnataka, 6 Apr. 1975 (HIFP_003087); G. Thanikaimoni, Uttar Kannada, Kalinadi Geek, Karwar, Karnataka, 6 Apr. 1975 (HIFP_003088); G. Thanikaimoni, Udupi, Kundapur, Karnataka, 7 Apr. 1975 (HIFP_003090); RozennKerrest, Cuddalore, Pichavaram Mangrove Forest, 11 June 1976 (HIFP_003095); G. Thanikaimoni, Konkan Division, Shirgaon Mangrove, Ratnagiri, Maharastra, 13 May 1986 (HIFP_003106); G. Thanikaimoni, South Goa, 15 May 1986 (HIFP_003108); P.C. Devasya, Col. No: 2126, Kadalundi, Kerala, 5 May 1972 (CALI126804); K.H.AmithaBachan, Col. No: 117732, Elanthikkara, Kerala, 7 Dec. 2009 (CALI114896); Anupama C., Col. No: 81251, Kolavipalam, Kozhikode, Kerala, 29 Apr. 2002 (CALI123088); Sunil C.N., Col. No: 1596, Aroor, Kerala, 7 May 1993 (CALI117861).

Principal component analysis based on morphometric data of leaves in *Avicennia* species

The first PCA approach, conducted for *A. alba*, *A. marina*, and *A. officinalis* from the IWP region based on leaf morphometric data, reveals considerable overlap among the species (Fig. 4), indicating that leaf morphology is unreliable for species discrimination. The greatest variation in leaf morphometric traits is observed in *A. marina*, which may support its further sub-specific classification. However, PERMANOVA showed significant separation among species ($R^2 = 0.3368$, $F = 61.207$, $p = 0.001$), demonstrating that species accounted for 33.7% of the total multivariate variation.

In the second PCA approach, the three subspecies and one variety – *A. marina* subsp. *marina*, subsp. *australasica*, subsp. *eucalyptifolia*, and var. *acutissima* – again exhibit a high degree of overlap, particularly between var. *acutissima* and subsp. *marina* (Fig. 5). By contrast, the two Australian subspecies are clearly separated on the PCA plot, suggesting that leaf morphology can be useful for their discrimination. The considerable variation observed in subsp. *marina*, likely attributable to its broad geographic distribution relative to the other two subspecies, may lead to misinterpretation and the superfluous proposal of new taxa. The PCA biplot further indicates that leaf tip (LT) and the leaf length-to-width ratio (L:W) are inversely correlated, potentially reflecting two distinct evolutionary trajectories towards subsp. *australasica* and subsp. *eucalyptifolia*. Nevertheless, the PCA biplot does not support a clear distinction between subsp. *marina* and var. *acutissima*. In this analysis, PERMANOVA likewise indicated significant differences among the infraspecific categories of *A. marina* ($R^2 = 0.45145$, $F = 36.212$, $p = 0.001$), with group identity explaining 45.14% of the total multivariate variation.

In the third PCA approach, no distinct separation was detected among *A. marina* populations from the three geographic regions of India (Fig. 6A). Although PERMANOVA identified a statistical significant effect of geographic location ($R^2 = 0.14865$, $F = 8.9919$, $p = 0.001$), the factor explains only 14.86% of total multivariate variation, indicating that the differentiation attributes to geography is weak. This suggests that, as documented in Australian populations, geographic separation within India does not contribute meaningfully to morphological divergence in *A. marina*.

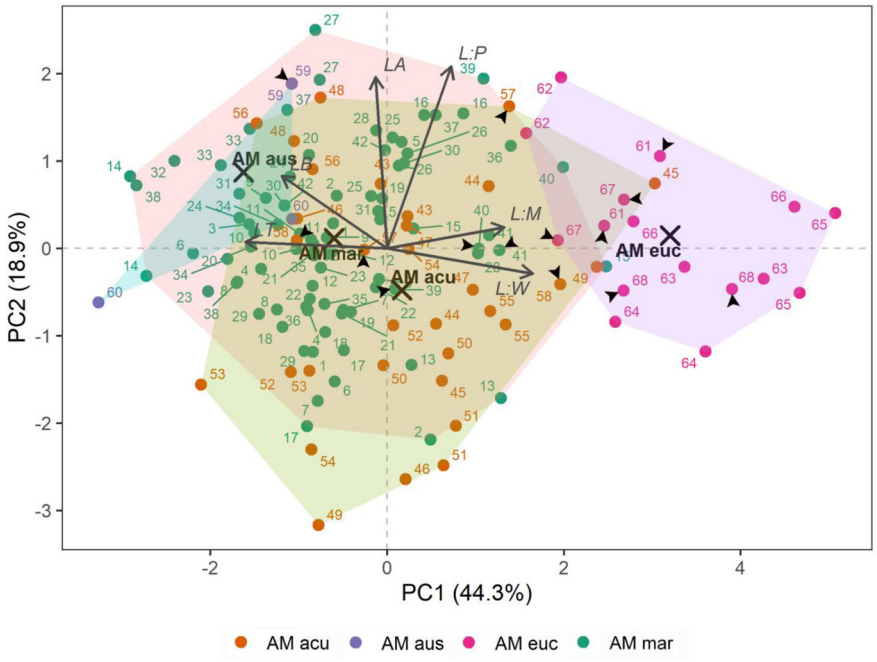


Figure 5. Two-dimensional PCA plot of 68 individuals of *Avicennia marina*, including four infraspecific categories – subsp. *australasica* (AM aus), subsp. *eucalyptifolia* (AM euc), subsp. *marina* (AM mar), and var. *acutissima* (AM acu) – based on morphometric data derived from herbarium specimen images. The morphometric data failed to distinguish among all the varieties, indicating substantial overlap. Centroid values for each subspecies are represented by '×' symbols in the plot. Numbers in the plot indicate specimen IDs: AM mar (1–42), AM acu (43–58), AM aus (59–60), and AM euc (61–68).

Likewise, the PCA comparing subsp. *marina* and var. *acutissima* from India did not reveal separation between the two taxa (Fig. 6B). PERMANOVA also returned a significant result ($R^2 = 0.07002$, $F = 7.8305$, $p = 0.001$), but the grouping accounted for only 7.00% of total variation, further indicating minimal morphological differentiation between these infraspecific categories.

Phylogenetic analysis based on ITS sequences

Phylogenetic analysis of *A. alba*, *A. marina*, and *A. officinalis* based on ITS sequences retrieved from the NCBI GenBank database yielded some notable findings. The *A. germinans* lineage, used as the outgroup, is strongly supported by a high bootstrap value (99%). Three major subclades are formed, each with strong bootstrap support. The first subclade (97%

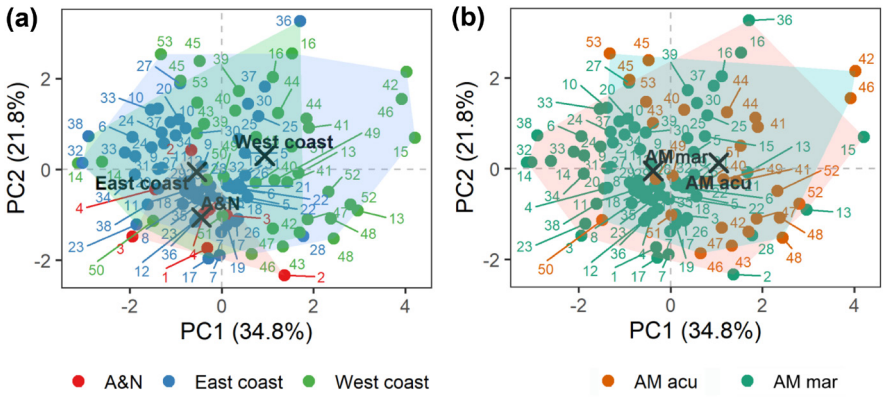


Figure 6. PCA based on morphometric variables of *Avicennia marina*, employing two modes of data categorisation: (a) categorisation based on geographic origin of herbarium specimens into three major zones – coasts of the Andaman and Nicobar Islands (A & N), the Bay of Bengal (east coast), and the Arabian Sea (west coast) of India; (b) categorisation into *A. marina* subsp. *marina* (AM mar) and *A. marina* var. *acutissima* (AM acu) of India. Centroid values for each category are indicated by '×' symbols in the plot. Numbers in the plot denote specimen IDs. In (a): A & N (1–4), east coast (5–12 and 17–38), and west coast (13–16 and 39–53). In (b): AM mar (1–39) and AM acu (40–53).

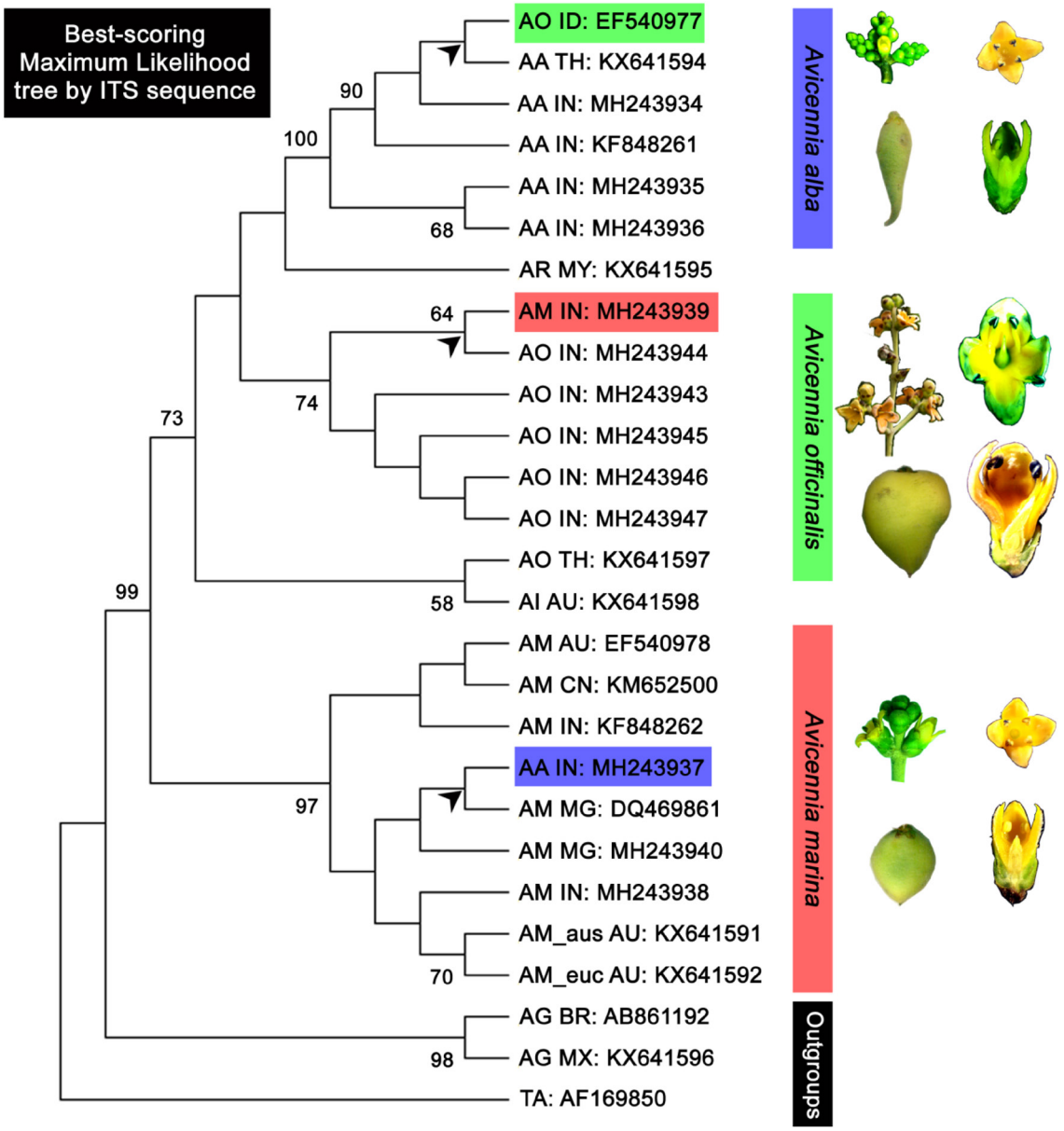


Figure 7. Maximum Likelihood tree based on ITS sequences of Indo-West Pacific *Avicennia* species, inferred using the T92+G model, with bootstrap support values based on 100 replicates. *Avicennia germinans* (AG) and *Thunbergia alata* (TA) were used as outgroups. Entity names in the tree are coded to indicate taxon, country of origin, and NCBI GenBank accession number. Bootstrap support values greater than 50 are shown on the branches. The ambiguous placement of certain entities – *A. officinalis* (AO ID: EF540977), *A. marina* (AM IN: MH243939), and *A. alba* (AA IN: MH243937) – may be due to misidentification, as these accessions are nested within clades of other species (indicated by arrowheads), forming part of larger clades corresponding to those species. Abbreviations used: AA: *A. alba*; AM: *A. marina*; AO: *A. officinalis*; AR: *A. rumphiana*; AI: *A. integra*; AM_aus: *A. marina* var. *australasica*; AM_euc: *A. marina* var. *eucalyptifolia*; IN: India; ID: Indonesia; TH: Thailand; MY: Malaysia; AU: Australia; CN: China; MG: Madagascar; BR: Brazil; MX: Mexico. The right panel shows inflorescence (top left), flower in top view (top right), longitudinal section of flower (bottom right), and fruit (bottom left) characteristics of *Avicennia* species.

bootstrap support), comprising *A. marina*, is phylogenetically closer to AEP *A. germinans*. Further diversification of the IWP *Avicennia* species occurs within two distinct subclades, corresponding to the *A. alba–A. rumphiana* group and the *A. officinalis–A. integra* group (Fig. 7).

However, notable incongruence in species placement was observed. Specifically, *A. alba* (AA IN: MH243937) clustered within the *A. marina* subclade, *A. marina* (AM IN: MH243939) grouped with the *A. officinalis* subclade, and *A. officinalis* (AO ID: EF540977) appeared within the *A. alba*

subclade (Fig. 7). Such discrepancies are likely stem from species misidentification. Moreover, these misplaced species show very low bootstrap support, further indicating probable misidentification.

Discussion

Confusing identity and status of the taxa under *Avicennia* in India

Confusion regarding the naming and identification of *Avicennia* species in India can be traced back to Roxburgh (1832), Wallich (1932), Wight (1850), Clarke (1885), and Prain (1903a, 1903b), and was perpetuated by Moldenke (1940). Moldenke described a new variety, *A. marina* var. *acutisima*, based on a collection by R.K. Bhide from Salsette Island, Bombay (now Mumbai). This variety was distinguished from the typical *A. marina* subsp. *marina* by its sharply acute or acuminate leaf apex, extremely short petiole, and the absence of a fruit beak. However, morphometric analyses based on leaf variables which include leaf tip angle and petiole length fail to reliably distinguish the *Avicennia* taxa found in India. Mondal and Naskar (2025) noted that the same leaf form described for *A. marina* also occurs in the Sundarbans. Notably, leaf shape variables offer limited taxonomic resolution and cannot accurately discriminate among *Avicennia* taxa, except in the case of *A. marina* subsp. *australasica* and *A. marina* subsp. *eucalyptifolia*, which are geographically isolated (Duke 1991). Furthermore, the beak on the fruit tends to disappear upon maturity (Moldenke 1960).

In India, mangrove vegetation is distributed patchily along the east coast (Bay of Bengal), west coast (Arabian Sea), and in the Andaman and Nicobar Islands. Despite their geographic separation, no discernible differences in leaf shape of *A. marina* have been observed among these coastal regions. To date, all records of *A. marina* var. *acutisima* originate exclusively from the west coast of India, suggesting that subsequent taxonomic identifications may have been influenced by Moldenke's original proposal of this variety. Dutta et al. (2019) went further and proposed a new forma, *A. marina* var. *acutisima* f. *pumila* [recorded as *A. marina* f. *pumila* S. Dutta, Chakral & H. Rodrigues in IPNI (2025)], based on the dwarf habit of this variety. However, Moldenke (1940), who worked primarily with herbarium material (Duke 1991, Mondal and Naskar 2025), did not describe the habit of Bhide's specimen, leaving it unclear whether the original plant was indeed a dwarf form. Dwarfism in mangroves is a well-documented physiological response to environmental stress, particularly in inland locations with limited tidal influence, where plants face severe soil desiccation (Naidoo 2025). Such forms are not genetically distinct, and therefore dwarfism is taxonomically insignificant. Mondal and Naskar (2025) recorded reproductively mature dwarf *Avicennia* from the Sundarbans.

Moldenke (1980) later mentioned four taxa of *Avicennia*, namely *A. alba*, *A. marina*, *A. marina* var. *acutissima*, and *A. officinalis*, from India. Moldenke's variety was recognised from India by Banerjee et al. (1989) and Paul et al. (2019); and along with this variety, *A. marina* var. *resinifera* (G. Forst.) Bakh. was also recognised by Singh et al. (2001) in India. None of these works mentioned the position of the stigma relative to the stamens, an important morphological characteristic for distinguishing varieties according to Duke (1991). The geographically isolated distribution of these two varieties in India was never reported by any Indian taxonomists, while Duke's varieties are geographically isolated in Australasia. Therefore, it is doubtful to consider these two taxa as varieties. Shaikh and Chavan (2011) argued that these varieties do not have enough characteristics to be called a variety. Duke (1991) had synonymized *A. marina* var. *acutissima* under *A. marina* var. *marina* and *A. marina* var. *resinifera* under *A. marina* var. *australasica*, an endemic taxon of the southeast coast of Australia and northern New Zealand. The morphological characters used to designate varieties of *A. marina* from India are not unique.

Although *A. officinalis* is common across all mangrove zones of India (Mandal and Bar 2019), *A. alba* is restricted to the east coast. Its occurrence on the west coast was long erroneously reported (Talbot 1911, Cooke 1967) due to taxonomic confusion. Finally, Shaikh and Chavan (2011) resolved the misidentification of *A. marina* as *A. alba* on the west coast of India through field and herbarium surveys. Goutham-Bharathi (2014) confirmed that *A. alba* is absent from the Andaman and Nicobar Islands, the second-largest mangrove area in India. It can thus be concluded that only three taxa of the genus *Avicennia* occur in India, among which *A. alba* has the most restricted distribution, while *A. marina* subsp. *marina* exhibits the highest morphological variability.

Distribution record of *Avicennia* species cues misidentification

The GBIF database is the world's largest provider of species distribution data (Barve 2023). Its data sources include digitized specimen records, georeferenced observational data often validated by experts and the community, open-access research datasets, biodiversity assessment data from NGOs and institutions, digitized species checklists, and georeferenced GenBank data (Robertson et al. 2014, GBIF 2025). The distribution of IWP species, *A. alba*, *A. marina*, and *A. officinalis* (Fig. 8), based on GBIF data, shows ambiguity even after applying the 'CoordinateCleaner' package in R, a tool designed to improve the quality of gridded datasets with low spatial resolution during map generation (Waller 2019). The distribution of *A. alba* in the west coast of India and distribution of *A. officinalis* on the coast of East Africa has certainly arisen due to wrong identification, highlighting the need for proper identification of the species. The distribution of *Avicennia* taxa in India (Fig. 9) is based on scrutiny of herbarium specimens and consultation of relevant literature.

Confusing morphology of *A. officinalis* described from Australasia

The plants of *A. officinalis* collected from Sundarban have curved and entirely pubescent pistils. Wallich (1932) also

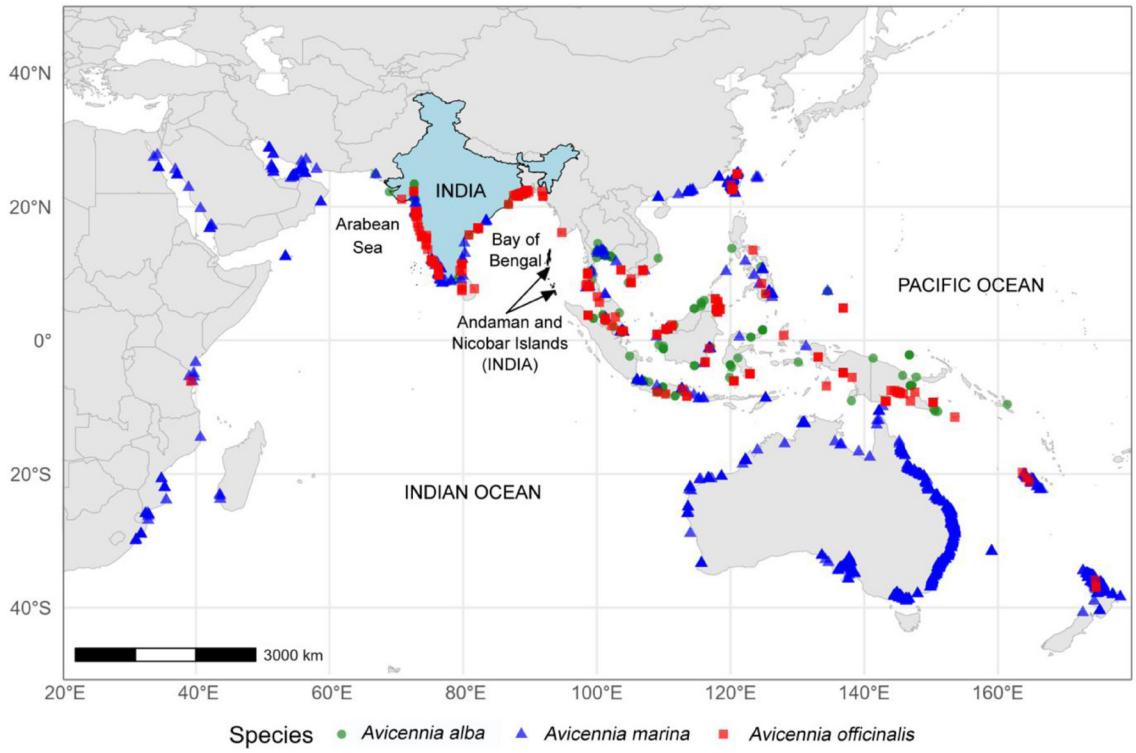


Figure 8. Distribution of *Avicennia alba*, *A. marina*, and *A. officinalis* in the Indo-West Pacific (IWP) biogeographic region, based on locality records retrieved from GBIF.org. To enhance data quality and minimise errors, species distribution data were cleaned and validated using the 'CoordinateCleaner' package. Taxonomic names were resolved and verified using multiple databases via the 'taxize' package. The 'flora' package was used to filter out cultivated records and resolve synonyms. The map was generated in R.

showed the curved pistil in an illustration of *A. officinalis* (Fig. 10). It fully corroborates with our examined specimens of the species from Sundarbans. However, Wallich erroneously used the name *A. tomentosa* for this illustration (details in the Introduction). On the other hand, Duke (1991) described the pistil of *A. officinalis* as 'style elongate, about 2 mm long, glabrous, ovary ampulla-shaped, about 4 mm long, densely tomentose'. Duke's drawing of the pistil also shows an elongated, straight, and glabrous style (Fig. 10A and B), and bifurcated stigma where the two forks are of equal size (Fig. 10B). In contrast, our specimens show a linear stigma with two unequal closed forks [Fig. 3(k) and 10B]. Furthermore, we found contrasting difference between *A. officinalis* of Sundarban and Australasia in calyx character. Duke (1991) described the calyx of *A. officinalis* as 'calyx lobes ovate, 5–7 mm long, 4–5 mm wide, edges ciliate or hairy, outer surface shiny, mostly glabrous'. Albeit this detailing of calyx lobes mostly agrees with the calyx lobes of *A. officinalis* from Sundarban, we noticed an additional feature. We observed the apical portion of calyx lobes is blackish-brown [Fig. 3(i)]. It seems that *A. officinalis* of Australasia as described by Duke (1991) is not the same as the species found in India. Since the name *A. officinalis* was based on material from the Indian subcontinent and Wallich's illustration matches with our specimens, we can assume that our specimens represent a true *A. officinalis*. Li et al. (2016) showed the immediate common ancestry of *A. integra* and *A. officinalis*. Furthermore, Duke (1991) mentioned that both species are morphologically similar, but their occurrence is allopatric. This may suggest that the *A. officinalis* described by Duke is actually a subspecies of *A. integra*. The common ancestry of *A. integra* and *A. officinalis* (Li et al. 2016) could have a double meaning: either they are two species or two subspecies. It is also unusual to see that *A. integra* is confined to a limited area of the Australian Northern Territory, unlike other *Avicennia* species having wider distribution but alike the Australian varieties/subspecies of *A. marina* having limited distribution. Therefore, a re-evaluation taking into account specimens of *A. officinalis* from Australasia and the Indian subcontinents is required to resolve this troublesome systematics.

Identity crisis of *Avicennia* species revealed through phylogenetic analysis

Approximately 10.6 million years ago in the Miocene, the closure of the Tethys Seaway led to the establishment of two distinct mangrove biogeographic zones: the AEP and the IWP (Takayama et al. 2021). Phylogenetic analyses support the position of *A. marina* as the sister taxon to the AEP species *A. germinans*. The exclusive presence of *A. marina* among *Avicennia* species along the Red Sea coast suggests that *A. marina* served as the ancestral lineage for the diversification of IWP *Avicennia* following the closure of the Tethys Seaway.

The results of our ITS-based phylogenetic analysis corroborate this hypothesis and further delineate three major

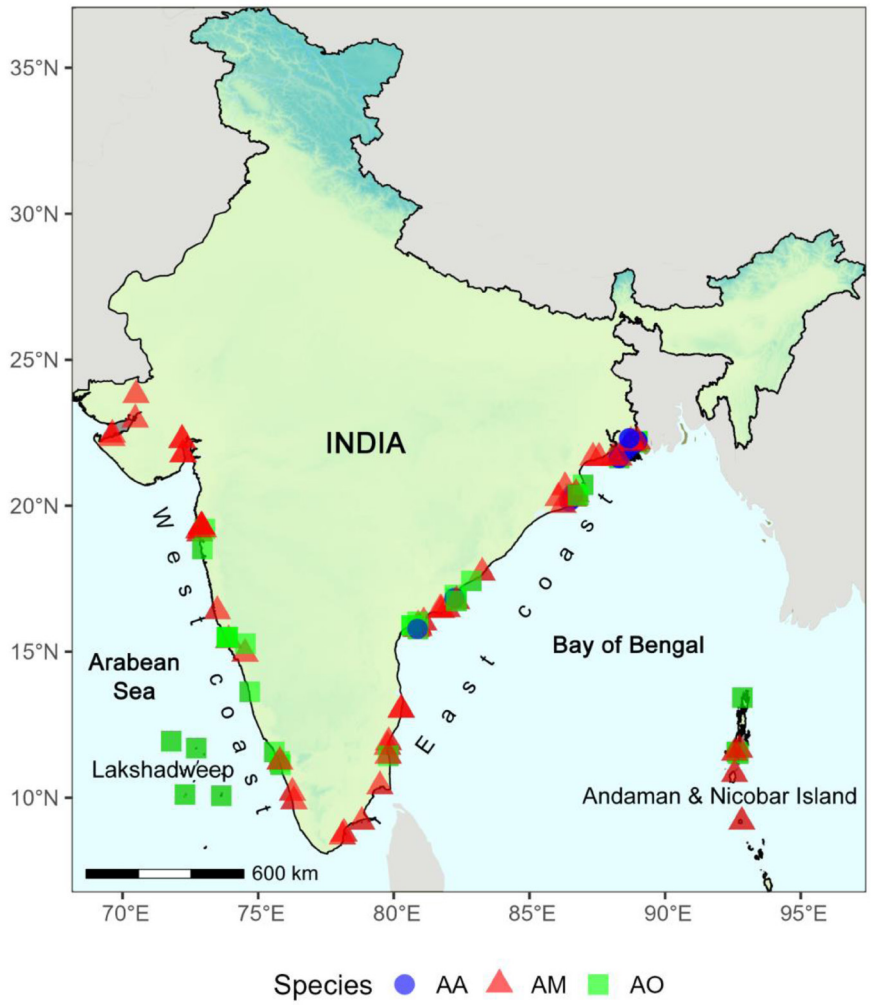


Figure 9. Distribution of *Avicennia alba* (AA), *A. marina* (AM), and *A. officinalis* (AO) in India, based on collection records from herbarium specimens and field collections conducted during the present study.

lineages within IWP *Avicennia*, consistent with the findings of Li et al. (2016) based on multilocus nucleotide data. However, the ambiguous placement of certain GenBank accessions such as *A. alba* appearing within the *A. marina* clade, *A. marina* within the *A. officinalis* clade, and *A. officinalis* within the *A. alba* clade likely results from species misidentification rather than reflecting actual phylogenetic relationships. While the possibility of hybridization cannot be entirely dismissed, natural hybridization among *Avicennia* species has not been conclusively reported, even in regions where species occur sympatrically. In this regard, *Avicennia* appears to differ from other widely distributed mangrove genera such as *Lumnitzera*, *Rhizophora*, and *Sonneratia* (Duke 1998, Mondal and Naskar 2025).

Overall, these findings highlight the critical importance of accurate species identification in molecular phylogenetic studies of *Avicennia*.

Taxonomic key

1. Bark fissured to finely fissured, greyish or greyish brown; Leaves broadly elliptic, tip obtuse, base rounded, length/width ratio 1.01–1.13; Flower zygomorphic, large, 9.56–13.36 mm; brown spot present at apex of sepal; Stamen exserted, long, 2.52–4.12 mm; Ovary throughout hairy, style long, 2.35–3.23 mm, hairy, curved ……..…… *Avicennia officinalis*
– Bark smooth to rough postural, small flakes or flaky patches, Greyish or greyish green or greyish black or brownish, smooth to minutely turrowed; Leaves narrowly elliptic to elliptic, tip and base acute, length/width ratio 4.77–1.72; Flower actinomorphic, small, 3.36–7.04 mm; brown spot absent at apex of sepal; Stamen inserted, short, 0.8–1.32 mm; Ovary partially hairy, style short, 0.2–0.3 mm, glabrous, straight ……..…… (2)
2. Bark smooth to rough postural, Greyish or greyish green or greyish black or brownish; Inflorescence spitcate, short, 5.5–12.5 cm; Fruit elongated ellipsoidal drupe, 3.0–5.5 × 0.5–1.5 cm ……..…… *A. alba*
– Bark smooth postural or small flakes or flaky patches, greyish or whitish brown or brownish; Inflorescence capitate, long, 4.5–18.5 cm; Fruit flattened ovoid drupe, 1.8–3.0 × 2.0–3.5 cm ……..…… *A. marina*



Figure 10. Illustration of *Avicennia tomentosa* (= *A. officinalis*), drawn by Wallich (1832) after a specimen from Sundarbans. The illustration clearly shows a zygomorphic flower with a curved stigma, which agrees with our photos (left photos of Fig. 10 **A** and **B**), but differs from the illustrations (right illustrations of Fig. 10 **A** and **B**) of Australasian specimens drawn by Duke (1991).

Conclusion

Nomenclatural stability and accurate identification remain unresolved within *Avicennia*, the most diverse genus of mangroves. In India, taxonomic recognition of the genus has largely relied on historical literature without critical verification. For instance, the variety of *A. marina* described by Moldenke from India, based solely on herbarium specimens, has not yet been thoroughly examined or validated by most Indian taxonomists. Additionally, there is a considerable gap in molecular studies on this genus in the Indian context. Several synonyms have been incorrectly applied, and species distribution records are sometimes inaccurate. Misidentifications are also evident in several GenBank accessions. The present study contributes toward clarifying the identity of *Avicennia* taxa in India. However, comprehensive molecular analyses based on samples collected from across the Indian coastline are essential. Such efforts will enhance scientific understanding and support more effective conservation strategies for this ecologically important blue carbon genus.

Funding – State Funded Fellowship from the Government of West Bengal, India [grant no. FC(Sc.)/RS/SF/BOT/ 2018-19/77].
Conflict of interest – The authors declare no conflict of interest.

Author contributions

Subrata Mondal: Data curation (lead); Funding acquisition (lead); Investigation (lead); Methodology (equal); Writing – original draft (lead). **Saikat Naskar**: Conceptualization (lead); Formal analysis (lead); Methodology (equal); Software (lead); Supervision (lead); Validation (lead); Visualization (equal); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.fqz612k62 (Mondal and Naskar 2026).

References

Baas, P. and Veldkamp, J. F. 2013. Dutch pre-colonial botany and Rumphius's Ambonese Herbal. – Allertonia 13: 9–19.
Bakhuizen van den Brink, R. C. 1921. Revisio generis Avicenniae (cum annotationibus diversis). – Bull. Jard. Bot. 3: 199–223.
Banerjee, L. K., Shastry, A. R. K. and Nayar, M. P. 1989. Mangroves in India: identification manual. – Botanical Survey of India.
Barve, V. 2023. Elevating the fitness of use of GBIF occurrence datasets: a proposal for peer review. – Bio. Inf. Sci. Sta. 7: e112237.
Blume, C. L. 1826. Bijdragen tot de flora van Nederlandsch Indie. 14. – Thr Lands Drukker Ij, p. 821.
Buchanan-Hamilton, F. 1835. A commentary on the fourth part of the Hortus Malabaricus. – Trans. Linn. Soc. 17: 221.
Choudhary, B., Dhar, V. and Pawase, A. S. 2024. Blue carbon and the role of mangroves in carbon sequestration: its mechanisms, estimation, human impacts and conservation strategies for economic incentives. – Flora 199: 102504.
Clarke, C. B. 1885. *Avicennia*. – In: Hooker, J. D. (ed.), Flora of British India, Vol. 4. – Reeve and Co., p. 604.
Cooke, T. 1967. Flora of the Presidency of Bombay, Vol. I–III. – Botanical Survey of India.
Duke, N. C. 1991. A systematic revision of the mangrove genus *Avicennia* (Avicenniaceae) in Australasia. – Aust. Syst. Bot. 4: 299–324.
Duke, N. C., Benzie, J. A. H., Goodall, J. A. and Ballment, E. R. 1998. Genetic structure and evolution of species in the mangrove genus *Avicennia* (Avicenniaceae) in the Indo-west Pacific. – Evolution 52: 1612–1626.
Dutta, S., Rodrigues, H., Chakral, K., and Suraliwala, F. 2019. Comments on the identity of mangrove and mangrove associates from Mumbai, India. – J. Econ. Taxon. Bot. 42: 31–36.
Elmer, A. D. D. 1915. Leaflets of Philippine botany. – Phillippine Island, Manila 8: 2868.
Everett, J. 1994. New combinations in the genus *Avicennia* (Avicenniaceae). Telopea 5: 627–629.
Forsskål, P. 1775. Flora Aegyptiaco-Arabica. – Ex officina Mőlleri. Aule typographi, Hauniae.
FSI 2023. Forest Survey of India: state of forest report 2023. – https://fsi.nic.in/forest-report-2023.
GBIF 2025. Global Biodiversity Information Facility. – https://www.gbif.org/.
Goutham-Bharathi, M. P., Roy, S. D., Krishnan, P., Kaliyamoorthy, M. and Immanuel, T. 2014. Species diversity and distribution of mangroves in Andaman and Nicobar Islands, India. – Bot. Mari 57: 421–432.
Griffith, W. 1854. Notulae ad plantas Asiaticas, Part IV. – Charles A. Serrao.
Harris, J. G. and Harris, M. W. 2006. Plant identification terminology: an illustrated glossary, 2nd edn. – Spring Lake Publishing.
IPNI 2025. The International Plant Names Index. – https://www.ipni.org/.
Jacquin, N. J. 1760. Systematica plantarum. – Lugduni Batavorum.
Jacquin, N. J. 1763. Selectarum stirpium Americanarum historia, Vol. I & II. – Ex officina Krausiana, Vindobonae.
Kuntze, O. 1891. Revisio generum plantarum, Vol. 2. – Klincksieck, p. 502.
Kuntze, O. 1898. Revisio generum plantarum, Vol. 3. – Klincksieck, p. 249.
Li, X., Duke, N. C., Yang, Y., Huang, L., Zhu, Y., Zhang, Z., Zhou, R., Zhong, C., Huang, Y. and Shi, S. 2016. Re-evaluation of phylogenetic relationships among species of the mangrove genus *Avicennia* from Indo-west Pacific based on multilocus analyses. – PLoS One 11: e0164453.
Linnaeus, C. 1747. Flora Zeylanica: sistens plantas Indicas Zeylo nae Insulae. – Sumtu and Literis Laurentii Salvii.
Linnaeus, C. 1753. Species plantarum, tomus I. – Impensis Laurentii Salvii.
Linnaeus, C. 1763. Species plantarum, tomus II, editio Secunda. – Impensis direct Laurentii Salvii.
Linnaeus, C. 1764a. Genera plantarum, editio sextra. – Impensis Direct Laurentii Salvii.
Linnaeus, C. 1764b. Species plantarum, tomus II, editio tertia. – Trattner's Typis Joannis Thomae.
Mandal, R. N. and Bar, R. 2019. Mangroves for building resilience to climate change: a field manual. – Apple Academic Press and Waretown.
McDade, L. A., Daniel, T. F. and Kiel, C. A. 2008. Toward a comprehensive understanding of phylogenetic relationships among lineages of Acanthaceae s.l. (Lamiales). – Am. J. Bot. 95: 1136–1152.
Moldenke, H. N. 1934. Studies of new and noteworthy tropical American plants – III. – Phytologia 1: 273–284.
Moldenke, H. N. 1938. Studies of new and noteworthy tropical American plants – II. – Phytologia 1: 95–105.
Moldenke, H. N. 1940. Novelties in the Avicenniaceae and Verbenaceae. – Phytologia 1: 410–411.
Moldenke, H. N. 1960. Materials toward a monograph of the genus *Avicennia* – I, II and III. – Phytologia 7: 123–168, 179–232, 259–293.
Moldenke, H. N. 1974. A fifth summary of the Verbenaceae, Avicenniaceae, Stilbaceae, Dicrastylidaceae, Symphoremaceae, Nyctanthaceae, and Ericaulaceae of the world as to valid taxa, geographic distribution, and synonymy, Supplement 4. – Phytologia 28: 432–507.
Moldenke, H. N. 1975. Additional notes on the genus *Avicennia* – V and VI. – Phytologia 32: 343–370, 436–457.
Moldenke, H. N. 1976a. New combinations in the Rocky Mountain flora. – Phytologia 33: 238–270.
Moldenke, H. N. 1976b. Additional notes on the genus *Avicennia*. VIII and IX. – Phytologia 34: 70–94, 167–303.

Moldenke, H. N. 1980. Additional notes on the genus Avicennia. XIII, XIV and XV. – Phytologia 46: 193–199, 226–228, 308–317.
Mondal, S. and Naskar, S. 2025. Harnessing morphological traits and adaptive strategies of three *Avicennia* species in the Indian Sundarbans for species delimitation. – Flora 330: 152783.
Mondal, S. and Naskar, S. 2026. Data from: Taxonomic reappraisal of the mangrove genus *Avicennia* (Acanthaceae) in India. – Dryad Digital Repository, https://doi.org/10.5061/dryad.fqz612k62.
Naidoo, G. 2025. Salt secretion in the mangrove *Avicennia marina*: effects of hypersalinity. – Phy. Plant. 177: e70105.
Naskar, K. 2004. Manual of Indian mangroves. – Daya Publishing House.
Naskar, K. and Guha-Bakshi, D. N. 1987. Mangrove swamps of the Sundarban: an ecological perspective. – Naya Prokash.
Naskar, S. 2020. Nomenclatural notes and typification of names in the mangrove tribe Rhizophoreae (Rhizophoraceae) of India. – Nord. J. Bot. 2020: e02624.
Naskar, S. 2025. Cybertaxonomy to overcome taxonomic impediments: a discussion in the context of plants of India. – Natl. Acad. Sci. Lett. 48: 503–507.
Paul, T. K., Lakshminarasimhan, P., Dash, S. S., Singh, P. and Chowdhery, H. J. 2019. Flora of West Bengal, Volume IV (Convolvulaceae–Ceratophyllaceae). – Botanical Survey of India.
Prain, D. 1903a. Bengal plants. – Botanical Survey of India.
Prain, D. 1903b. Flora of the Sundaribuns. – Botanical Survey of India.
Ragavan, P., Saxena, A., Jayaraj, R. S. C., Mohan, P. M., Ravichandran, K., Saravanan, S. and Vijayaraghavan, A. 2016. A review of the mangrove floristics of India. – Taiwania 61: 224–242.
Rheede, H. V. 1683. Hortus Malabaricus, Vol. 4. – Amstelodami.
Ridley, H. N. 1920. New and rare Malayan plants. – J. F. M. S Mus. 10: 151.
Robertson, T., Döring, M., Guralnick, R., Bloom, D., Wieczorek, J., Braak, K., Otegui, J., Russell, L. and Desmet, P. 2014. The GBIF integrated publishing toolkit: facilitating the efficient publishing of biodiversity data on the Internet. – PLoS One 9: e102623.
Roemer, J. J. and Schultes, J. A. 1818. Caroli a Linné ... Systema vegetabilium: secundum classes, ordines, genera, species. Cum characteribus differentiis et synonymis. Editio nova, speciebus inde ab editione XV. Detectis aucta et locupletata. Stuttgardtiae. – Sumtibus J. G. Cottae, Stuttgarriae, pp. 485.
Roxburgh, W. 1832. Flora Indica, Vol. III. – Thacker and Co. Calcutta & Parbury, Allen and Co.
Sappal, S. M., Ranjan, P. and Ramanathan, A. 2016. Blue carbon ecosystems and their role in climate change mitigation – an overview. – J. Cli. Cha 2: 1–13.
Schauer, J. C. 1847. Verbenaceae. – In: De Candolle, A. (ed.), Prodromus systematis naturalis regni vegetabilis, pars undecima. Sumptibus Victoris Masson, Parisiis, pp. 522–716.
Shaikh, S. S. and Chavan, N. S. 2011. Critical observations of the family Avicenniaceae from Maharashtra and Goa, India. – J. Bombay Natl Hist. Soc. 108: 2–7.
Singh, N. P., Lakshminarasimhan, P., Karthikeyan, S. and Prasanna, P. V. 2001. Flora of Maharashtra state, Vol. 2. – Botanical Survey of India.
Spalding, M., Kainuma, M. and Collins, L. 2010. World atlas of mangroves. – Earthscan Publications.
Stearn, W. T. 1958. A key to West Indian mangroves. – Kew Bull. 13: 33–37.
Takayama, K., Tateishi, Y. and Kajita, T. 2021. Global phylogeography of a pantropical mangrove genus *Rhizophora*. – Sci. Rep. 11: 7228.
Talbot, W. A. 1911. Forest flora of the Bombay Presidency and Sind, Vol. II. – Government Photozincographic Department.
Tamura, K., Stecher, G. and Kumar, S. 2021. MEGA11: molecular evolutionary genetics analysis version 11. – Mol. Biol. Evol. 38: 3022–3027.
Tomlinson, P. B. 2016. The botany of mangroves, 2nd edn. – Cambridge Univ. Press.
Trimen, H. 1886. Hermann's Ceylon herbarium and Linnaeus's 'Flora Zeylanica'. – J. Linn. Soc. Bot. 24: 129–155.
Turland, N. J. et al. (eds) 2025. International Code of Nomenclature for algae, fungi and plants (Madrid Code) adopted by the Twentieth International Botanical Congress Madrid, Spain, July 2024. Regnum Veg. 162. – Univ. Chicago Press.
Vierhapper, F. 1907. Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-Naturwissenschaftliche Klasse. – Vienna 71, p. 435.
Waller, J. 2019. Data location quality at GBIF. – Biodivers. Inf. Sci. Stand. 3: e35829.
Wallich, N. 1932. Plantae Asiaticae rariores, Vol. III. – Treuttel and Wurtz.
Walpers, W. G. 1845. Repertorium botanices systematicae – Sumtibus Friderici Hofmeister. – Lipsiae 4: 133.
WCVP 2025. World Checklist of Vascular Plants. – https://checklistbuilder.science.kew.org/.
Wight, R. 1850. Icones plantarum Indiae orientalis, Vol. IV. – Messrs Franck and Co.
Willdenow, C. L. 1800. Species plantarum, tomus III, editio quarta. – Impensis GC Nauk.