

An integrative taxonomic reassessment of *Kandelia candel* (Rhizophoraceae), a true mangrove of Thailand

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Abstract. *Ngersaengsaruy C, Uthairatsamee S, Mianmit N, Pravinvongvuthi T, Samart C. 2026. An integrative taxonomic reassessment of *Kandelia candel* (Rhizophoraceae), a true mangrove of Thailand. Biodiversitas 27 (2): d270210. <https://doi.org/10.13057/biodiv/d270210>. *Kandelia candel* (Rhizophoraceae, Rhizophoreae) is revised for Thailand based on an integrative taxonomic reassessment combining morphology, leaf anatomy, pollen morphology, and conservation assessment. This study aims to clarify the taxonomic identity, national distribution, and conservation status of the species through examinations of herbarium specimens and field collections. A detailed morphological description and illustrations are provided, together with notes on distribution, habitat, ecology, phenology, etymology, vernacular names, uses, and specimens examined. Leaf anatomical characters were investigated using light microscopy, pollen morphology was examined following standard palynological methods, and a preliminary conservation assessment was conducted in accordance with the IUCN Red List categories and criteria. In Thailand, *K. candel* occurs as a shrub or small tree and is rare, being confined to the south-eastern and peninsular regions. Leaves are bifacial and composed of five principal tissue layers, exhibiting anatomical adaptations typical of mangrove species, including thick cuticles, sunken stomata restricted to the abaxial surface, large hypodermal cells, and cork warts. Pollen grains are monads, isopolar, tricolporate, suboblate to subprolate or oblate-spheroidal in shape, small to medium in size, and characterized by perforate exine sculpturing. Although the species has a wide global Extent of Occurrence (EOO: 9,344,077.01 km²) and is assessed as Least Concern (LC) at the global level, its distribution in Thailand is highly restricted, with a small national EOO (52,021.25 km²) and Area of Occupancy (AOO: 40 km²). This national rarity has important implications for mangrove management and conservation planning, as locally limited populations may be more sensitive to habitat loss and coastal disturbance. This study represents the first integrative taxonomic revision of *K. candel* for Thailand and provides a baseline dataset for future national conservation assessments and studies on mangrove biodiversity.*

Keywords: Leaf anatomy, palynology, Rhizophoreae, taxonomic revision, true mangrove

Abbreviations: Abe: Abaxial epidermis, Ade: Adaxial epidermis, Cr: Druse crystals, Ct: Cuticle, Cw: Cork wart, EpC: Epidermal cells, Hp: Hypodermis, P: Phloem, Pa: Parenchyma, Pl: Palisade mesophyll, Sp: Spongy mesophyll, St: Stoma, SubC: Subsidiary cells, Vb: Vascular bundle, X: Xylem

INTRODUCTION

Rhizophoraceae is a pantropical family in the order Malpighiales, comprising 15 genera and approximately 148 species, with its highest diversity in the Old World tropics (Schwarzbach 2014; Tomlinson 2016; POWO 2025; WFO 2025). The family is ecologically significant as it includes several lineages of true mangroves—species restricted to intertidal coastal environments and forming the structural foundation of mangrove ecosystems. Within Rhizophoraceae, the tribe Rhizophoreae comprises four strictly mangrove genera (*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*), which share characteristic vegetative and reproductive features such as interpetiolar stipules, cymose inflorescences, baccate fruits, and viviparous germination (Henslow 1878; King 1897; Hou 1958; Tomlinson 1986, 2016; Schwarzbach 2014).

Kandelia is a small genus of true mangrove, small trees or shrubs, widely distributed from India and Myanmar through the South China Sea region to southern China, Taiwan, the Ryukyu Islands, and southern Japan (Hou 1958; Tomlinson 1986, 2016; Sheue et al. 2003b). The genus was long regarded as monotypic, represented solely by *Kandelia candel* (L.) Druce (Hou 1958, 1970; Tomlinson 1986). However, integrative studies based on morphology (Sheue et al. 2003a, 2003b; Tomlinson 2016), leaf anatomy (Naskar and Mandal 1999; Sheue et al. 2003a), chromosome number (Das et al. 1995), ecogeographic and physiological variation (Maxwell 1995), molecular phylogeography (Huang and Chen 2000; Chiang et al. 2001), and genetic variation (Giang et al. 2006) demonstrated the presence of two well-differentiated geographical population groups separated by the South China Sea. Consequently, the genus is now recognized as comprising two distinct species, *K. candel*

and *Kandelia obovata* Sheue, H.Y.Liu & J.W.H.Yong (Sheue et al. 2003a, b; Tomlinson 2016).

In Thailand, *K. candel* was treated in the Flora of Thailand by Hou (1970) with a brief species account that provided only basic morphological information and lacked supporting anatomical, palynological, distributional, and conservation data. Although recent taxonomic revisions of other Rhizophoraceae genera in Thailand—most notably *Rhizophora* (Ngernsaengsaruy et al. 2024; Ngernsaengsaruy et al. 2025) have provided detailed and modern treatments, a comparable revision of *K. candel* has remained absent. Consequently, no integrative national-level taxonomic revision of *Kandelia* has been conducted for Thailand, leaf anatomical and palynological data based on Thai material are lacking, and taxonomic confusion with the closely related *K. obovata* has persisted due to overlapping morphological characters.

As a result, *K. candel* in Thailand has not been systematically studied with respect to its full suite of taxonomic characters, leaf anatomy, pollen morphology, or detailed distribution patterns, and information on its ecology, phenology, and conservation status remains limited. Based on an examination of all available Thai herbarium specimens and recent field collections, no material referable to *K. obovata* was found. All examined specimens conform to the diagnostic morphological and anatomical characters of *K. candel*, thereby excluding the occurrence of *K. obovata* in Thailand under current evidence.

In this paper, we present a comprehensive and integrative taxonomic revision of *K. candel* in Thailand. This study explicitly evaluates whether all *Kandelia* populations occurring in the country correspond exclusively to *K. candel* and can be reliably distinguished from *K. obovata* based on integrated morphological, anatomical, palynological, and distributional characters. To address these gaps, we aim to (i) provide a detailed taxonomic revision of *K. candel* in Thailand, (ii) document and evaluate its leaf anatomical and pollen morphological characters based on Thai material, and (iii) reassess its national distribution and conservation relevance.

MATERIALS AND METHODS

Taxonomic treatment

Field observations and specimen collections were conducted with permission from the Department of Marine and Coastal Resources, DMCR (nr) 0426/2672. The collected specimens were examined with reference to the literature (Hou 1958; Vu 1965; Sheue et al. 2003a, b; Tomlinson 2016; Malabrigo et al. 2021) and by comparison with herbarium specimens housed in BK, BKF, as well as those available through virtual herbarium databases, including A, BR, CAL, E, K, L, SING, and US, and via the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>). All herbarium codes follow Thiers (2025). The taxonomic history of the species was compiled from both published literature and online databases (IPNI 2025; POWO 2025; WFO 2025). Morphological characters, distribution, habitat and ecology, phenology,

and uses were described from historic and newly collected herbarium specimens, as well as from the author's field observations. The distribution map was generated using the R program, based on georeferenced records derived from the specimens examined and selected literature sources (Hou 1958, 1970; Vu 1965; Sheue et al. 2003b; Tomlinson 2016; Malabrigo et al. 2021). Only literature records supported by voucher specimens or clear locality information were included. Coordinates were taken from specimen labels or georeferenced from locality descriptions using standard gazetteers and Google Earth, recorded in decimal degrees, and screened for obvious spatial errors. Records with unclear locality data and duplicate records from the same locality were excluded before map generation. Conservation status was assessed following the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2024), using GeoCAT (Bachman et al. 2011), with Extent of Occurrence (EOO) and Area of Occupancy (AOO) calculated using the standard 2×2 km² grid cell size based on unique georeferenced occurrence records. Although coordinate uncertainty was not formally quantified, potential spatial error was minimized through careful data screening and exclusion of records with uncertain locality information.

Measurements of vegetative and reproductive parts were taken from specimens representing the distribution of the species in Thailand, including the south-eastern region (Chanthaburi and Trat Provinces) and the peninsular region (Ranong Province). The examined material comprised herbarium specimens and recent field collections from multiple localities within these regions, with measurements obtained from multiple individuals across several populations. Sample sizes represent the number of organs measured and were pooled from multiple specimens and individuals across several populations. Multiple organs may have been measured from the same individual; therefore, the reported sample sizes do not correspond to an equal number of independent plants. Accordingly, morphometric data are presented and interpreted using descriptive statistics only, without inferential statistical testing or assumptions of statistical independence among measurements. Vegetative characters were measured from 100 samples. Reproductive characters were measured according to organ availability: sepals, petals, filaments, pedicels, and persistent sepals from 100 samples; inflorescences, number of flowers per inflorescence, fully open flowers, and anthers from 50 samples; mature flower buds, styles, fruits, fruit stalks, hypocotyls, and cotyledonous tubes from 30 samples; and infructescence stalks from 20 samples.

Anatomical study

The leaf anatomical features of *K. candel* were investigated through transverse sectioning using a sliding microtome at a thickness of 15–20 µm. Leaf material was obtained from specimens representing the known distribution of the species in Thailand, comprising three populations, including one population from Trat Province and two populations from Ranong Province. To study the epidermal cells, the leaf epidermis was peeled manually, stained with safranin, and mounted in Permount. Permanent slides were

prepared according to the standard methods described by Johansen (1940) and Kermanee (2008). Stomata, subsidiary cells, and cork warts were examined from 100 samples, whereas leaf thickness, cuticular wax thickness, epidermal cell layer thickness, hypodermal cell layer thickness, presence of crystals, palisade cell layer thickness, and spongy cell layer thickness were measured from 20 samples. All measurements were calibrated using a stage micrometer. Anatomical characteristics were observed and recorded photographically using an Olympus BX53 microscope equipped with an Olympus DP74 digital camera at the Department of Botany, Faculty of Science, Kasetsart University. Anatomical terminology follows the conventions outlined by Metcalfe and Chalk (1957).

Palynological study

Samples of pollen grains were examined and recorded photographically using an Olympus BX53 microscope equipped with an Olympus DP74 digital camera. Pollen material was taken from specimens representing the distribution of the species in Thailand, comprising one population from Trat Province and two populations from Ranong Province. Pollen grains were examined without acetolysis in order to document pollen characters under their natural condition, as preserved in fresh and herbarium material.

For Scanning Electron Microscopy (SEM), pollen grains were mounted on stubs using double-sided adhesive tape, sputter-coated with gold, and examined at the Scientific Equipment Centre, Faculty of Science, Kasetsart University, using an FEI Quanta 450 SEM (Hillsboro, OR, USA) operated at 15.0 kV. The characteristics of pollen grains were examined and measured following Erdtman (1945, 1952) and Simpson (2010), based on 30 samples. Pollen morphological terminology follows Punt et al. (2007).

RESULTS AND DISCUSSION

Taxonomic treatment

Kandelia (DC.) Wight & Arn., Prodr. Fl. Ind. Orient. 1: 310. 1834; Kurz, Forest Fl. Burma 1: 448. 1877; G. Hensl. in Hook. f., Fl. Brit. India 2: 437. 1878; King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 66(1): 317. 1897; Guillaumin in Lecomte et al., Fl. Indo-Chine 2(6): 726. 1920; Ridl., Fl. Malay Penins. 1: 694. 1922; Ding Hou in Steenis, Fl. Males., Ser. 1, Spermat. 5(4): 472. 1958 et in Smitinand & K. Larsen, Fl. Thailand 2(1): 12. 1970; V. C. Vu, Fl. Cambodge, Laos, Vietnam 4: 167. 1965; Sheue et al., Taxon 52: 288. 2003; H. Qin & Boufford in C. Y. Wu et al., Fl. China 13: 297. 2007; Schwarzb. in Kubitzki, Fam. & Gen. Vasc. Pl. 11: 293. 2014; Toml., Bot. Mangrove ed. 2: 353. 2016.

Type. *Kandelia rheedei* Wight & Arn., nom. illeg. ≡ *Kandelia candel* (L.) Druce

Description. Habit shrubs or small evergreen trees; buttresses present (observed in *K. candel* populations in Thailand) or absent. Stipules interpetiolar, in opposite pairs, enclosing the young shoot (with terminal bud and

young leaves) and young inflorescences, flattened, with numerous dense colleters at the adaxial base, producing and secreting a sticky exudate. Leaves decussate, margin entire. Inflorescences axillary, pedunculate, dichotomously branched, several- to many-flowered cymes. Bracts 2, connate into a cup-shaped, bilobed, each lobe with colleters at the base. Bracteoles 2, connate into a cup-shaped and adnate to the base of the calyx, bilobed, each lobe with colleters at the base. Flowers bisexual, 5-merous; sepals 5, inserted on the rim of the hypanthium, valvate, narrowly triangular, patent, distal part curved upward after anthesis, glabrous; petals 5, alternisepalous, valvate, bifid, each lobe divided and fringe-like (multifid), glabrous; stamens numerous, unequal in length; anthers dorsifixed, 2-celled, longitudinally dehiscent; filaments distinct; ovary inferior, adnate to the hypanthium, 3-carpellate, unilocular, with 6 ovules; style slender; stigma minutely 3-lobed. Fruits baccate, ovoid (including hypanthium), pedunculate, pendulous (when the hypocotyls protrude from the fruits), with persistent, reflexed sepals. Seeds usually 1, viviparous. Hypocotyls cylindrical-clavate, pendulous, terete.

A genus of two species (*K. candel* and *K. obovata*), distributed from India, the Ganges Delta, Myanmar, through Southeast Asia to south China, the Ryukyu Islands, and south Japan; one species in Thailand.

Kandelia candel (L.) Druce, Bot. Exch. Club Brit. Isles Rep. 3(5): 420. 1914; Merr., Enum. Philipp. Fl. Pl. 3: 148. 1923; Ding Hou in Steenis, Fl. Males., Ser. 1, Spermat. 5(4): 473, fig. 26. 1958 et in Smitinand & K. Larsen, Fl. Thailand 2(1): 12. 1970; V. C. Vu, Fl. Cambodge, Laos, Vietnam 4: 167, t. 3, figs. 6-10. 1965; Sheue et al., Taxon 52: 291, figs. 1A (left), B (left), C (left), D (left), E (top), 2A, C, E (left), F (left). 2003; Toml., Bot. Mangrove ed. 2: 354, fig. B.61. 2016; Malabrigo et al., Philipp. J. Sci. 150(5): 1125-1126, t. 1-4. 2021. (Figures 1-3).

≡ *Rhizophora candel* L., Sp. Pl. 1: 443. 1753; DC., Prodr. 3: 32. 1828.

≡ *Kandelia rheedei* Wight & Arn., Prodr. Fl. Ind. Orient. 1: 311. 1834, nom. illeg.; Miq., Fl. Ned. Ind., Eerste Bijv. [Fl. Ind. Bat.] 1(1): 585. 1855; Kurz, Forest Fl. Burma 1: 449. 1877; G. Hensl. in Hook. f., Fl. Brit. India 2: 437. 1878; King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 66(1): 317. 1897; Guillaumin in Lecomte et al., Fl. Indo-Chine 2(6): 727, fig. 75 (13, 14). 1920; Ridl., Fl. Malay Penins. 1: 694. 1922; Craib, Fl. Siam. 1(4): 594. 1931.

Type. illustration, *Tsjerou-kandel*, Rheede, Hort. Malab. 6: 63, t. 35. (van Rheede 1686) [lectotype, designated by Sheue et al. (2003b: 291)].

Description. Habit shrubs or small trees, 2-8 m tall, 15-35 cm GBH; buttresses present at the base of the stem. Branches and branchlets decussate; branchlets terete, glabrous, with conspicuous annular stipular scars and leaf scars at the nodes. Bark brown to dark brown, rough, shallowly fissured longitudinally or both longitudinally and transversely, with scattered lenticels; inner bark brownish red or red. Stipules pale green, lanceolate, 2-3.7 cm × 3.3-7.5 mm, apex acute, glabrous and caducous, with dense colleters aggregated in a basal band and producing a clear, sticky exudate; colleters pale yellow, finger-like rods with short stalks, 0.25-0.65 mm long (including stalks), 0.1-0.4

mm diam. at the base, apex obtuse. Leaves elliptic, narrowly elliptic, or elliptic-oblong, $9-17 \times 2.8-7$ cm, apex obtuse, base cuneate, margin entire, coriaceous, glossy dark green above, pale green below, glabrous on both surfaces, with scattered 20-30 tiny black cork warts below, midrib pale green (paler than lamina), flattened above, raised below, secondary veins 7-11 on each side, curving towards the margin and connected in distinct loops and united into an intramarginal vein, visible above, obscure below, with intersecondary veins, veinlets reticulate, visible above, obscure below; petioles green, 1-4 cm long, 1-3.5 mm diam., glabrous; fresh leaves brittle when crushed; young leaves glossy pale green; mature leaves turning greenish bright yellow and bright yellow before falling off. Inflorescences axillary, opposite, compound dichasia, dichotomously branched, (2-)4-8-flowered cymes, 3-7 cm long; peduncles pale green, 2.3-4.5 cm long, 2-3 mm diam., glabrous. Bracts 2, pale green, concave, $2-3 \times 3-5.5$ mm, apex rounded. Bracteoles 2, pale green, concave, $1.7-2.8 \times 2.7-4.5$ mm, apex rounded. Flowers 5-merous; flower buds pale green, turning creamy white when mature, narrowly conical, 1.2-2 cm long, 3.7-7.5 mm diam., swollen at the base, apex obtuse; fully open flowers 2-3 cm diam.; pedicels pale green, 3.5-6.5 mm long, 2.4-3.5 mm diam., glabrous; sepals 5, patent, distal part curved upward after anthesis, creamy white outside, apex pale green, white inside, narrowly triangular, $1.2-1.5 \times 2.5-4.5$ mm, apex obtuse, coriaceous, glabrous; petals 5, white, deeply bifid, 1-1.5 cm long, lower part united, 4-5.5 mm long, 0.5-2.2 mm wide, each lobe with 3-6 long sinuate, filiform segments, 0.5-1 cm long; stamens 32-46; anthers pinkish pale brown, turning pale brown when mature, 0.7-1.5 mm long, 0.2-0.5 mm wide; filaments white, slender, 0.9-1.3 cm long; ovary embedded in the hypanthium; style 0.8-1.2 cm long; stigma minutely 3-lobed. Fruits brownish green or greenish brown, ovoid, 1.5-2 cm long (including hypanthium), 6-8 mm diam. at the base, apex obtuse (before seed germination); obpyriform, 3.3-4.3 cm long, 1.2-2.2 cm diam. at the basal part, 0.6-1 cm diam. at the apical part (when the hypocotyls nearly come off); persistent sepals reflexed, narrowly triangular, $1.2-2.3 \times 2.5-5.5$ mm; infructescence stalks 3.5-5 cm long, 3-5 mm diam.; fruit stalks 0.5-1 cm long, 3-6 mm diam. Seeds 1, viviparous. Hypocotyls green, cylindrical-clavate, 35-43.5 cm long, 4-9 mm diam. at the apical part, 0.8-1.3 cm diam. at the widest part, acute at the basal end; cotyledonous cylindrical tubes pale green or yellowish pale green, sometimes tinged with red, 5-8 mm diam. (can be seen when the hypocotyls nearly fall off).

The measurements of the vegetative and reproductive parts of *K. candell* in Thailand are presented in Table 1. Although the diagnostic morphological differences between *K. candell* and *K. obovata* are summarized in Table 2, the Thai specimens examined in this study consistently exhibit the character combination diagnostic of *K. candell*. These include elliptic to elliptic-oblong leaves with a higher number of secondary veins, longer petioles, the presence of basal buttresses, cup-shaped connate bracteoles, narrowly triangular sepals that become patent after anthesis, deeply bifid petals with fewer filiform segments, a

shorter style, and substantially longer hypocotyls. In contrast, none of the examined material shows the suite of characters typical of *K. obovata*. While some individual traits overlap in size ranges, the combined vegetative and reproductive characters clearly support the identification of all Thai material as *K. candell* and the exclusion of *K. obovata* from Thailand under current evidence.

Distribution. India [Sundarbans, Odisha (formerly known as Orissa), Chennai (formerly known as Madras), Karnataka, Andaman Islands], Myanmar (Tenasserim), Peninsular Thailand, Peninsular Malaysia [Terengganu, Pahang, Selangor, Johor (also called Johore)], Singapore, Indonesia [Sumatra, Moluccas (also called Maluku)], Borneo [Malaysia (Sarawak, Sabah), Brunei], Philippines (Aurora) (Figure 4).

Distribution in Thailand. South-Eastern: Chanthaburi, Trat; Peninsular: Ranong, Surat Thani, Phuket (Figure 4).

Habitat and Ecology. This species is restricted to mangrove forests along the river banks.

Phenology. Flowering, fruiting, and viviparous germination are almost year-round, with a peak from November to March.

Conservation status. *K. candell* is widely distributed from India to Malesia and has been recorded from numerous localities across its range. At the global level, the species has a large Extent of Occurrence (EOO) of 9,344,077.01 km² and an Area of Occupancy (AOO) of 216 km². These values, together with the presence of numerous populations across multiple regions, support an assessment of Least Concern (LC) under the IUCN Red List criteria, consistent with the global assessment by Duke et al. (2010). In contrast, within Thailand, *K. candell* is relatively rare and restricted to the south-eastern and peninsular regions, with a national EOO of 52,021.25 km² and an AOO of 40 km². These national values are presented solely to illustrate the species' localized rarity and restricted distribution in Thailand, and this study does not propose a formal national Red List category or assessment. Although no evidence currently indicates a rapid population decline at the global scale, the limited distribution and ongoing coastal pressures in Thailand highlight the need for continued monitoring of local populations and provide a baseline for future national-level conservation assessments.

Vernacular names. Rang kathae (รังคะเหาะ) (Ranong, from the specimen *Pipat s.n.*, BKF [049129]); Thua nang choi (ถั่วนางช้อย) (Surat Thani, from the specimen *C. Malakul 99*); Narrow-leaved kandelia (English); Bēras-bēras, Bērus-bērus, Mēm-pisang, Mēmputut, Pisang-pisang laut (Malay Peninsula, Hou 1958); Bēus, Bajau (Borneo, Hou 1958); Lingajong (Brunei, Hou 1958); Pulut-pulut (Malay Peninsula, Brunei, Hou 1958); Vệt dia, Vệt thang (Vietnam, Vu 1965).

Uses. The wood of *K. candell* is used for temporary construction, firewood, and charcoal (Hou 1970; Pattanaik et al. 2008; Manohar 2024). Its bark of *K. candell* yields tannins, which are utilized in the leather industry, in strengthening fishing nets, and in dyeing fabrics in red and brown shades. In addition, the bark is employed as green manure to enhance soil fertility and as fodder for livestock (Pattanaik et al. 2008; Manohar 2024). The bark of *K. candell* also plays an important role in traditional medicine

in India. It has been widely prescribed by local healers, particularly for the treatment of diabetes (Pattanaik et al. 2008; Manohar 2024). The bark is reported to be used, together with dried ginger or long pepper and rosewater, in the treatment of diabetes (Kirtikar and Basu 1935).

Taxonomic notes. van Rheede (1686) named this species “*Tsjerou-kandel*”, and this name was cited in the protologue of *R. candel* (Linnaeus 1753). van Rheede’s description and illustration of this species from the sole basis for Linnaeus’ name; therefore, van Rheede’s illustration was selected by Sheue et al. (2003b) as the lectotype. The generic name and specific epithet of *K. candel* are Latin and are derived from the name “*Tsjerou-kandel*” in the protologue of *R. candel* (van Rheede 1686; Linnaeus 1753).

Kandelia is distinguished from related genera in the Rhizophoraceae by its narrowly triangular sepals; numerous stamens with slender filaments; multifid, glabrous petals; unilocular ovaries; and the absence of specialized roots (aerial roots or pneumatophores). The hypocotyl of the seedling is typically slender and tapered at each end.

Specimens examined. THAILAND. South-Eastern. Chanthaburi [Khlung District, s.d., *A. F. G. Kerr* 17953, (K [K005699984]); Mangrove forest along the Welu River, Bo Sub-district, Khlung District, opposite Ban Tha Chot, Saen Tung Sub-district, Khao Saming District, Trat Province, observation by *C. Ngernsaengsaruy, N. Mianmit, S. Uthairatsamee & A. Jaikuea*, with photos, 20 Nov 2025]; Trat [Mangrove forest along the Welu River, Ban Tha Chot, Saen Tung Sub-district, Khao Saming District, fl., fr. & vivipary, 20 Nov 2025, *C. Ngernsaengsaruy, N. Mianmit, S. Uthairatsamee & A. Jaikuea* Kc05-20112025, Kc06-20112025]; Peninsular. Ranong [La-un District, fl. & vivipary, 2 Nov 1981, *Pipat s.n.* (BKF [049129, 049133]); La-un District, fl., 13 Jan 1982, *Pipat s.n.* (BKF [049131]); La-un District, fl. & vivipary, 26 Mar 1982, *Unknown s.n.* (BKF [103128, 103129]); La-un District, fl., 10 Nov 1983, *Pipat s.n.* (BKF [049132]); La-un Mangrove Station, La-un District, fl. & fr., 27 Mar 1987, *D. D. Soejarto et al.* 5821 (BKF [102545], L [L2496209]); Kapoe District, vivipary, 15 Jan 1929, *A. F. G. Kerr* 16675 (E [E01058305], K [K005699986]); Locality unspecified, fl., 23 Dec 1983, *N. Fukuoka & M. Ito* T-35519 (BKF [049130], L [L4198579]); Mangrove forest at Pak Khlung Si Kim (Si Kim Estuary), along the Kra Buri River, Sai dang Subdistrict, Mueang Ranong District, fl. & vivipary, 10 Aug 2024, *C. Ngernsaengsaruy, N. Mianmit, S. Punpon & T. Longting* Kc01-10082024, Kc02-10082024, Kc03-10082024; Mangrove forest at Tham Phra Khayang (Phra Khayang Cave), Lam Liang Sub-district, Kra Buri District, fl., 16 Aug 2025, *C. Ngernsaengsaruy & N. Mianmit* Kc04-16082025]; Surat Thani [Tha Chang estuary, Tha Chang District, fl., 16 Sep 1934, *C. Malakul* 99 (BKF [049134, 199625]); Ban Don, vivipary, July 1927, *A. F. G. Kerr* 13032 (E [E01058304], K005699985)]; Phuket [reported by Hou (1970); based on literature only and not supported by examined specimens in the present study].

Table 1. Measurements of the vegetative and reproductive parts of *Kandelia candel* in Thailand

Measurements of vegetative and reproductive parts (units)	Sample sizes	Ranges	Mean ± SD
Stipule length (cm)	100	2.00-3.70	2.85 ± 0.51
Stipule diameter at the base (mm)	100	3.30-7.50	5.31 ± 1.23
Colleter length (mm)	100	0.25-0.65	0.46 ± 0.11
Colleter diameter at the base (mm)	100	0.10-0.40	0.23 ± 0.09
Leaf length (cm)	100	9.20-17.30	12.14 ± 2.35
Leaf width (cm)	100	2.80-7.00	4.61 ± 0.98
Leaf length/width ratio	100	1.54-3.47	2.67 ± 0.40
Number of secondary veins on each side	100	7-11	8.05 ± 0.88
Petiole length (cm)	100	1.00-4.00	2.21 ± 0.75
Petiole diameter at the middle (mm)	100	1.00-3.50	2.19 ± 0.62
Inflorescence length (cm)	50	3.00-7.00	5.20 ± 1.21
Peduncle length (cm)	50	2.30-4.50	3.55 ± 0.65
Peduncle diameter at the middle (mm)	50	2.00-3.00	2.68 ± 0.24
Number of flowers per inflorescence	50	2-8	5.92 ± 1.19
Mature flower bud length (cm)	30	1.20-2.00	1.57 ± 0.23
Mature flower bud diameter at the basal part (mm)	30	3.70-7.50	5.69 ± 1.18
Mature flower bud length/diameter ratio	30	1.60-4.70	2.89 ± 0.77
Fully open flower diameter (cm)	50	2.00-3.00	2.66 ± 0.31
Sepal length (cm)	100	1.20-1.50	1.35 ± 0.12
Sepal width at the base (mm)	100	2.50-4.50	3.51 ± 0.44
Sepal length/width ratio	100	3.08-4.74	3.89 ± 0.46
Petal length (cm)	100	1.00-1.50	1.32 ± 0.17
Petal width at the middle (mm)	100	0.50-2.00	1.42 ± 0.47
Anther length (mm)	50	0.70-1.50	1.08 ± 0.21
Anther width at the middle (mm)	50	0.20-0.50	0.37 ± 0.07
Filament length (cm)	100	0.90-1.30	1.15 ± 0.11
Style length (cm)	30	0.80-1.20	0.97 ± 0.11
Pedicel length (mm)	100	3.50-6.50	5.00 ± 0.81
Pedicel diameter (mm)	100	2.40-3.50	3.00 ± 0.30
Fruit length (cm) (hypocotyls nearly come off)	30	3.30-4.30	3.80 ± 0.35
Fruit diameter at the basal part (cm)	30	1.20-2.20	1.80 ± 0.28
Fruit diameter at the apical part (cm)	30	0.60-1.00	0.79 ± 0.10
Persistent sepal length (cm)	100	1.20-2.20	1.75 ± 0.26
Persistent sepal width at the base (mm)	100	2.50-5.50	4.20 ± 0.74
Infructescence stalk length (cm)	20	3.50-5.00	4.48 ± 0.59
Infructescence stalk diameter (mm)	20	3.00-5.00	3.99 ± 0.59
Fruit stalk length (cm)	30	0.50-1.00	0.71 ± 0.12
Fruit stalk diameter (mm)	30	3.00-6.00	4.50 ± 0.74
Hypocotyl length (cm)	30	35.00-43.50	37.96 ± 2.17
Hypocotyl diameter at the apical part (mm)	30	4.00-9.00	6.50 ± 1.50
Hypocotyl diameter at the widest part (cm)	30	0.80-1.30	1.03 ± 0.14
Cotyledonous tube diameter (cm)	30	5.00-8.00	6.72 ± 0.90

Table 2. Comparison of the morphological characteristics between *Kandelia candel* and *Kandelia obovata*. The morphological characteristics of *K. obovata* are based on Sheue (2003), Sheue et al. (2003a, b), and Sheue et al. (2012)

Morphological characters	<i>Kandelia candel</i>	<i>Kandelia obovata</i>
Habit	Shrubs or small trees, 2-8 m tall	Small trees, up to 3 m tall
Buttresses	Present at the base of the stem	Absent
Stipules	2-3.7 cm long	(2-)2.5-3.2 cm long
Leaves	Elliptic, narrowly elliptic or elliptic-oblong, 9-17 × 2.8-7 cm	Obovate to obovate-elliptic, very rarely obovate-oblong, (5-)6-12 × 2.5-5 cm
Secondary veins (Lateral veins)	7-11 on each side	5-8 on each side
Petioles	1-4 cm long	(0.5-)1-1.8 cm long
Inflorescences	Dichotomously branched, (2-)4-8-flowered; peduncles 2.3-4.5 cm long	Dichotomously branched, (4-)6-8(-13)-flowered; peduncles 1-3 cm long
Pedicels	3.5-6.5 mm long	(3-)5-6 mm long
Bracteoles	Connate into a cup-shaped, 1.7-2.8 mm long, bilobed	U-shaped in outline, (2.5-)3 mm long, bilobed
Sepals	Creamy white outside, apex pale green, white inside, narrowly triangular, 1.2-1.5 cm × 2.5-4.5 mm, patent, distal part curved upward after anthesis	White on both sides when blooming, linear, 1.5-1.9 cm × 2.5-3 mm, reflexed after anthesis
Petals	Deeply bifid, 1-1.5 cm long, lower part united, 4-5.5 mm long, 0.5-2.2 mm wide, each lobe with 3-6 long, sinuate, filiform segments, 0.5-1 cm long	Partially bifid, with or without a long seta in the sinus, each half 1-1.2 mm wide, with (6-)8-12(-14) uneven long slightly curved threads, the lower united part 2.2-2.5 mm long
Stamens	32-46; anthers brown, 0.7-1.5 mm long; filaments white, slender, 0.9-1.3 cm long	(35-)40(-45); anthers deep pink before splitting, 1.2-1.8 mm long; filaments 0.7-1.3 cm long
Pistils	Style 0.8-1.2 cm long	Style 1.4-1.6 cm long
Fruits (before seed germination)	Ovoid, 1.5-2 cm long (including hypanthium), 6-8 mm diam. at the base	Ovoid, 1-1.5 cm long, with calyx tube 6-8 mm long
Fruits (hypocotyls nearly come off)	Obpyriform, 3.3-4.3 cm long, 1.2-2.2 cm diam. at the basal part, 0.6-1 cm diam. at the apical part	-
Hypocotyls	35-43.5 cm long, 4-9 mm diam. at the apical part, 0.8-1.3 cm diam. at the widest part	15-20(-23) cm long, 0.9-1.4 cm wide at the broadest part

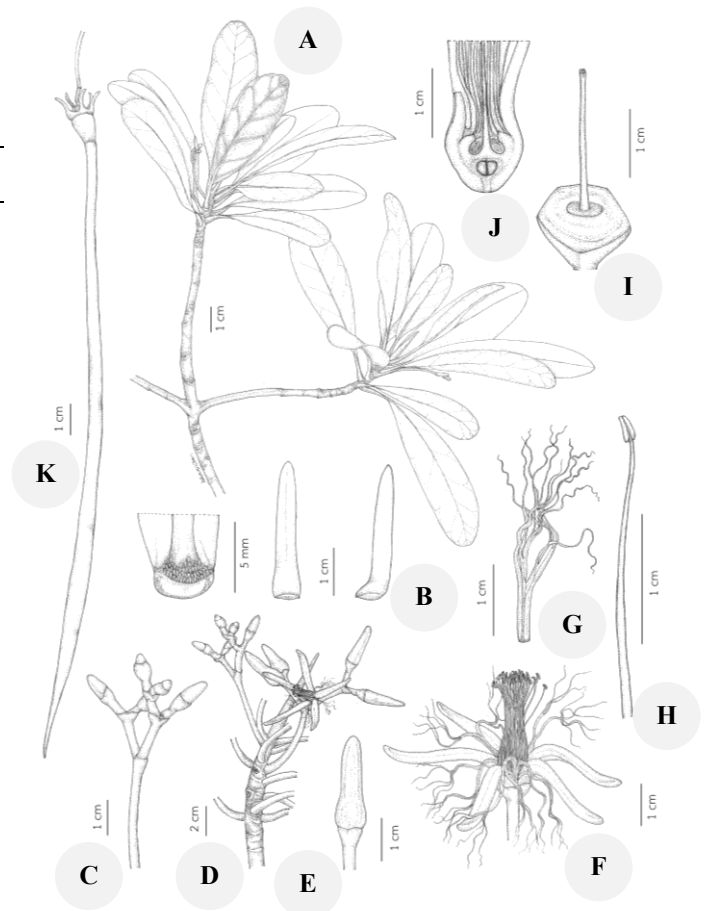


Figure 1. *Kandelia candel*. A. Flowering branchlets, terminal interpetiolar stipule, leaves, and inflorescences with flower buds; B. Interpetiolar stipules in an opposite pair with densely aggregated colleters at the adaxial base; C. Inflorescences with flower buds; D. Flowering branchlet, inflorescences with flower buds and fully open flower; E. Flower bud; F. Fully open flower; G. Petal; H. stamen; I. Pistil; J. Flower in longitudinal section showing pistil; K. Fruit with persistent sepals and viviparous seed (seedling) with a cylindrical-clavate hypocotyl. Photo: Drawn by Wanwisa Bhuchaisri

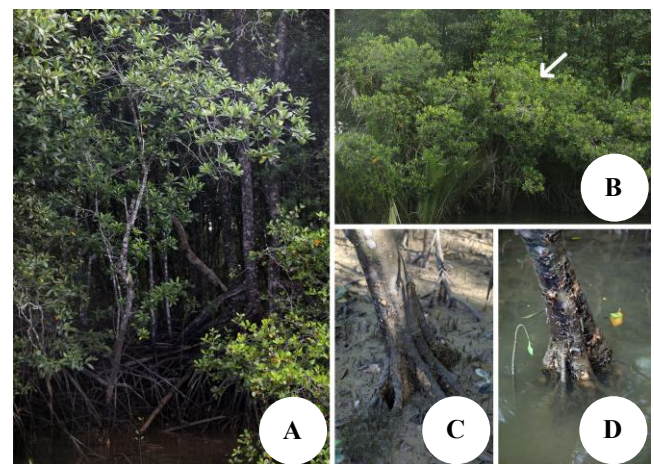


Figure 2. *Kandelia candel*. A, B. Habitats and habit; C, D. Buttresses at the base of the stem

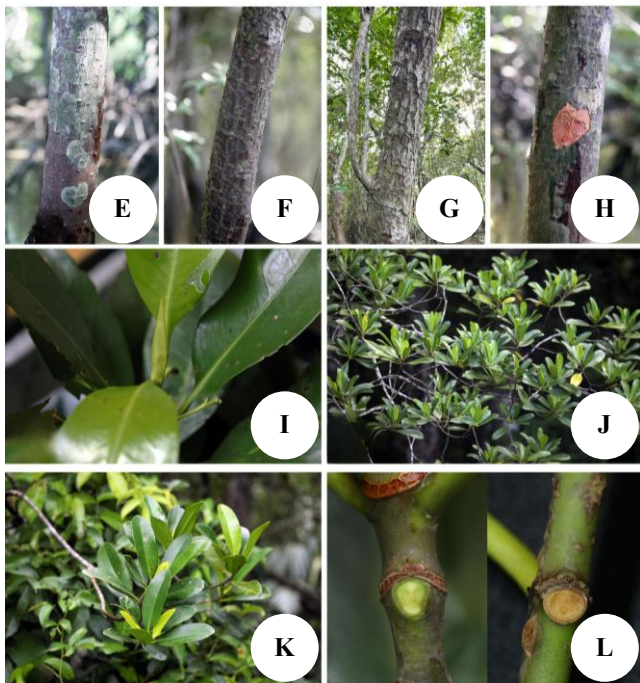


Figure 2. (Continued) *Kandelia candel*. E-G. Stems and outer bark; H. Stem, outer bark, and inner bark; I. Terminal interpetiolar stipule; J, K. Branchlets and leaves; L. Leaf scars, three major vascular bundle strands, two upper curved strands distinctly larger than the lower one. Photos: Chatchai Ngernsaengsaruy

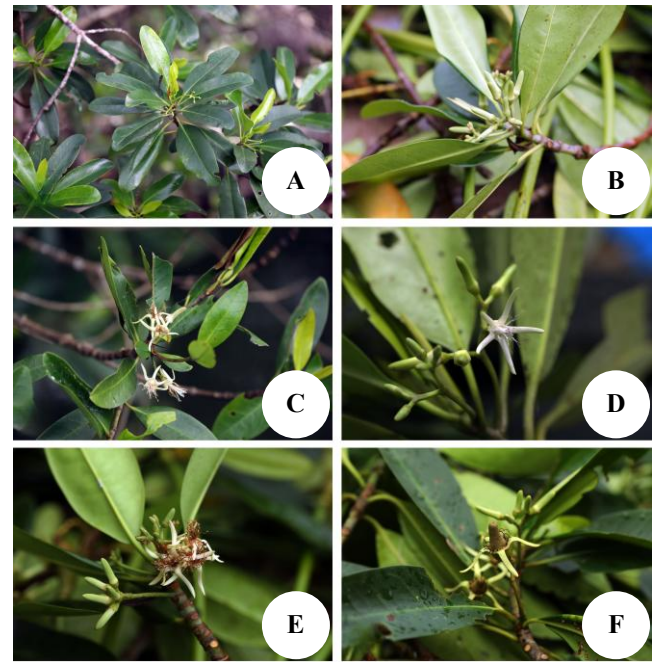


Figure 3. *Kandelia candel*. A, B. Flowering branchlets and inflorescences with flower buds; C-E. Flowering branchlets, inflorescences with flower buds and fully open flowers; F. Flowering and fruiting branchlets, flower buds, and fruits with persistent sepals before seed germination

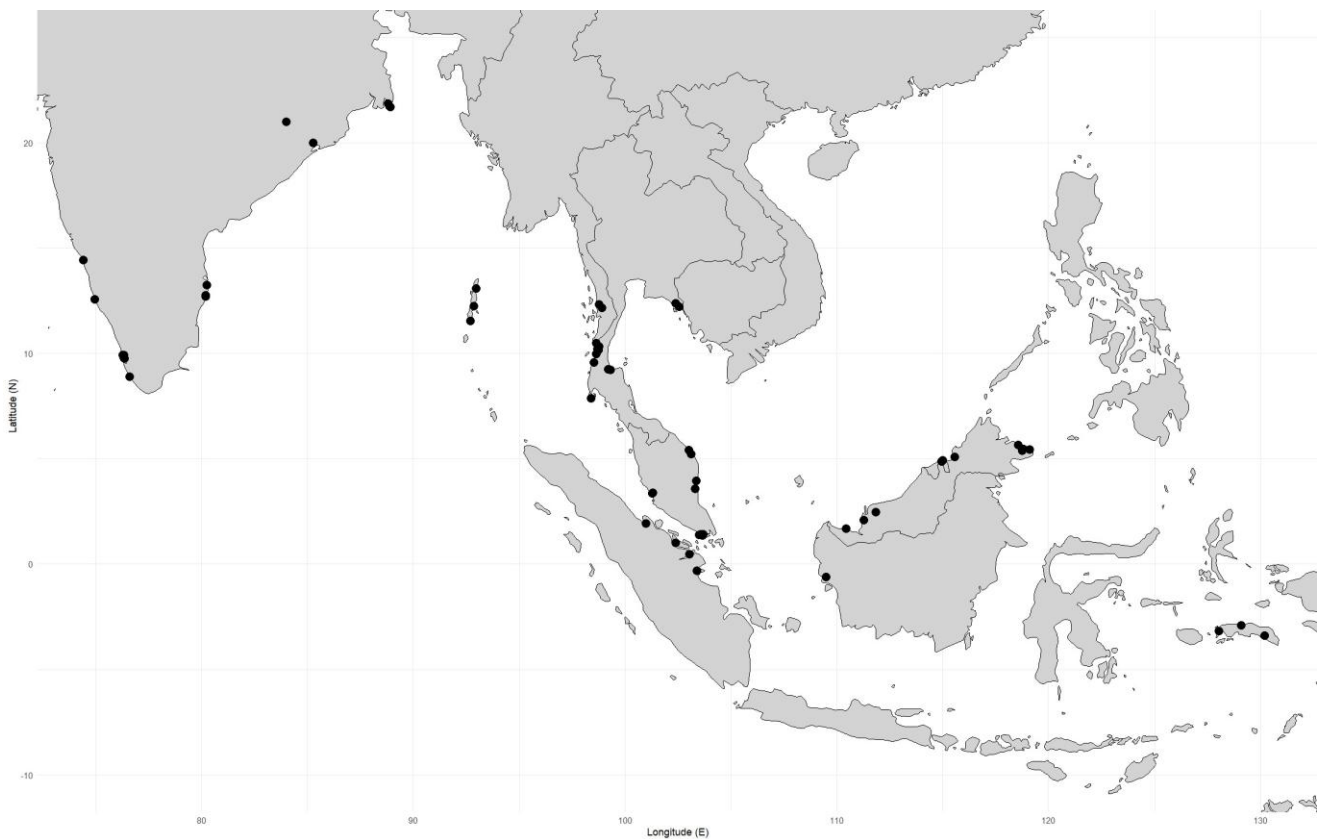


Figure 4. Distribution of *Kandelia candel*. Occurring from India to Malesia, and in Thailand confined to the south-eastern and peninsular regions. Map: Pichet Chanton and Chatchai Ngernsaengsaruy



Figure 3. (Continued) *Kandelia candel*. G, H. Fruiting branchlets, leaves, infructescences, fruit with persistent sepals, and viviparous seed (seedling) with a cylindrical-clavate hypocotyl; I. Fruiting branchlet and fruit, after the hypocotyl falls off. Photos: Chatchai Ngernsaengsaruy

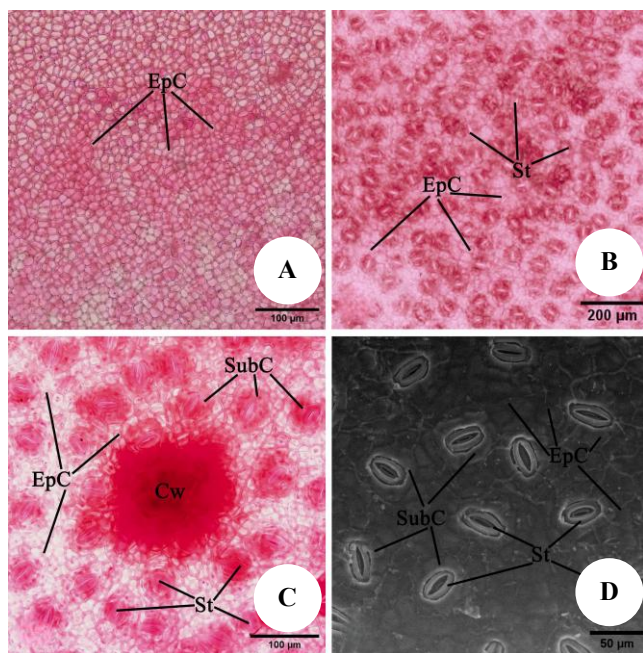


Figure 5. Leaf anatomy of *Kandelia candel*. A. Adaxial epidermis (under LM); B, C. Abaxial epidermis (under LM); D. Abaxial epidermis (under SEM) (Cw: Cork wart, EpC: Epidermal cells, St: Stoma, SubC: Subsidiary cells). Photos: Pichet Chanton and Chatchai Ngernsaengsaruy

Anatomical study

Leaf anatomy of Kandelia candel in Thailand

The leaf anatomical structure of *K. candel*, based on material collected from three populations in Thailand (one population from Trat Province and two populations from Ranong Province), is composed of five principal tissue

layers: adaxial epidermis, hypodermis, palisade mesophyll, spongy mesophyll, and abaxial epidermis. Leaf thickness in these populations ranges from 443.03 to 555.92 μm . A thick cuticular wax layer (cuticle) covers both epidermal surfaces, with the adaxial surface bearing a slightly thicker cuticle than the abaxial surface (Figure 6).

Epidermal cells are distinctly polygonal, with straight anticlinal walls, and were observed to be arranged in a single layer on both adaxial and abaxial surfaces. The thickness of the adaxial epidermis is comparable to that of the abaxial epidermis (Figure 5).

The stomata of *K. candel* are confined to the abaxial leaf surface, and the leaves are hypostomatic. The stomata are of the sunken cyclocytic type, surrounded by 4-6 subsidiary cells arranged in a concentric ring around each stoma (Figure 5). Stomatal size ranges from 26.65-49.32 \times 18.24-36.45 μm , with a density of 176-394 stomata/ mm^2 .

Cork warts are present on the abaxial surface, with 20-30 cork warts per leaf, each with a diameter of 51.02-67.87 μm (Figure 5).

The hypodermis was composed of relatively large cells arranged in two to three layers beneath the epidermis. These cells are often filled with tannins, which cause them to appear darkly stained. The adaxial surface (49.68-83.44 μm) exhibits a greater average hypodermal thickness compared to the abaxial surface (37.18-54.04 μm). Hypodermal cells on the adaxial side are typically elliptic, broadly elliptic, circular, or rounded polygonal in shape, while those on the abaxial side tend to be broadly elliptic, circular, or rounded polygonal. The average cell size of the hypodermis is also larger on the adaxial surface (38.24-71.09 \times 15.54-48.62 μm) than on the abaxial surface (13.92-35.68 \times 17.56-36.65 μm) (Figure 6).

Druse crystals are present in the hypodermal cells on both the adaxial and abaxial surfaces, as well as in the spongy mesophyll. Their diameters range from 8.91-17.74 μm (Figure 6).

The palisade parenchyma consists of two to four layers of tightly packed, elongated cells located directly beneath the hypodermis. The spongy parenchyma is composed of 10-14 layers of loosely arranged, irregularly shaped cells situated below the palisade parenchyma and above the abaxial epidermis. This tissue exhibits prominent intercellular spaces, forming a characteristic net-like structure (Figure 6).

Observations of the vascular bundle arrangement in the midrib of *K. candel* reveal a complex structure, divided into three distinct regions: adaxial, medullary (central), and abaxial. Each vascular bundle comprises phloem located on the outer side and xylem on the inner side. These vascular bundles are incompletely enclosed by a layer of sclerenchyma cells (Figure 6).

A comparison of the leaf anatomical characteristics of *K. candel* from three populations in Thailand (one population from Trat Province and two populations from Ranong Province) with data from previous studies on this species and *K. obovata* outside Thailand is presented in Table 3.

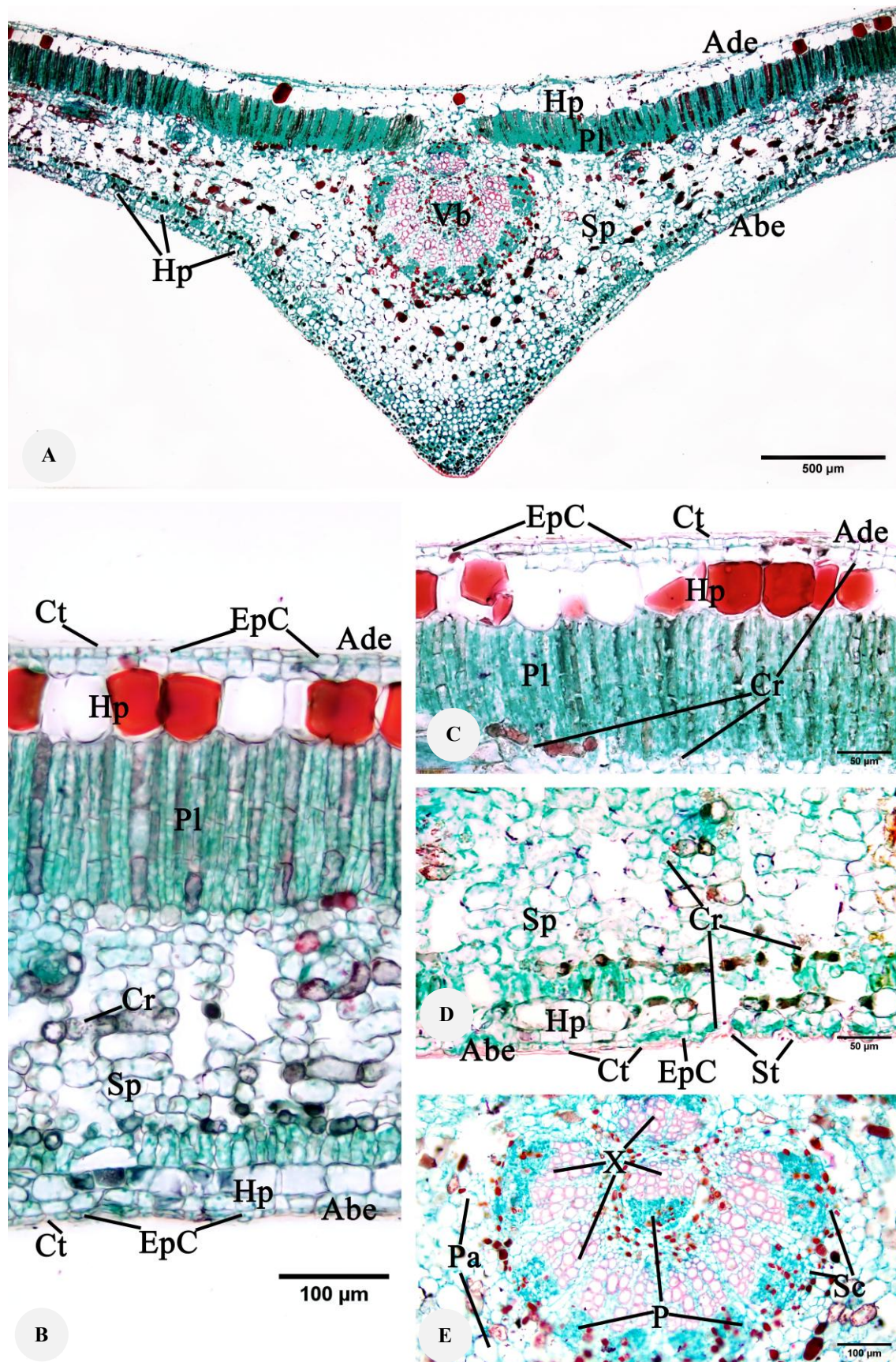


Figure 6. Leaf anatomy of *Kandelia candel*. A-E. Transverse section (Abe: Abaxial epidermis, Ade: Adaxial epidermis, Cr: Druse crystals, Ct: Cuticle, EpC: Epidermal cells, Hp: Hypodermis, P: Phloem, Pa: Parenchyma, Pl: Palisade mesophyll, Sp: Spongy mesophyll, St: Stoma, Vb: Vascular bundle, X: Xylem). Photos: Pichet Chanton and Chatchai Ngernsaengsaruy

Table 3. Comparison of the leaf anatomical characteristics of *Kandelia candel* in Thailand with those of *K. candel* and *K. obovata* from previous studies (Sheue 2003; Sheue et al. 2003a; Surya and Hari 2017)

Anatomical characters	From the author's observations	Previous studies	
	<i>Kandelia candel</i>	<i>Kandelia candel</i>	<i>Kandelia obovata</i>
Leaf thickness (µm)	443.03-555.92 (448.28 ± 32.07, n = 20)	396.30 ± 19.00 (Malaysia) (Sheue 2003); 80.64 (Surya and Hari 2017)	480.20 ± 114.00 (Taiwan) (Sheue 2003)
Leaf structure type	Bifacial leaves	Dorsiventral leaves (= bifacial leaves) (Sheue 2003; Sheue et al. 2003a); isobitateral leaves (Surya and Hari 2017)	Semi-isobitateral leaves (Sheue 2003; Sheue et al. 2003a)
Cuticular wax thickness on the adaxial leaf surface (µm)	4.39-10.56 (6.73 ± 1.66, n = 20)	5.60 ± 1.20 (Sheue 2003); 0.74 (Surya and Hari 2017)	8.80 ± 1.20 (Sheue 2003)
Cuticular wax thickness on the abaxial leaf surface (µm)	2.77-8.26 (5.57 ± 1.47, n=20)	4.10 ± 0.50 (Sheue 2003); 0.42 (Surya and Hari 2017)	5.30 ± 1.00 (Sheue 2003)
Number of epidermal cell layers on the adaxial leaf surface	1-layered	2-layered (Sheue 2003; Sheue et al. 2003a; Surya and Hari 2017)	2-layered (Sheue 2003; Sheue et al. 2003a)
Number of epidermal cell layers on the abaxial leaf surface	1-layered	2-layered (Sheue 2003; Sheue et al. 2003a; Surya and Hari 2017)	2-layered (Sheue 2003; Sheue et al. 2003a)
Epidermal layer thickness on the adaxial leaf surface (µm)	6.47-15.65 (10.21 ± 2.42, n = 20)	1.87 (Surya and Hari 2017)	-
Epidermal layer thickness on the abaxial leaf surface (µm)	4.57-15.20 (8.91 ± 3.17, n = 20)	1.87 (Surya and Hari 2017)	-
Epidermal cell shapes on the adaxial leaf surface	Polygonal	Polygonal (Surya and Hari 2017)	-
Epidermal cell shapes on the abaxial leaf surface	Polygonal	Polygonal (Surya and Hari 2017)	-
Stomatal types	Sunken cyclocytic	Sunken cyclocytic (Sheue 2003; Sheue et al. 2003a; Surya and Hari 2017)	Sunken cyclocytic (Sheue 2003; Sheue et al. 2003a)
Stomatal density per mm ²	176-394 (304.70 ± 69.54, n = 100)	-	-
Stomatal length (µm)	26.65-49.32 (27.45 ± 5.68, n = 100)	Guard cell length 35.20 ± 1.39 (Sheue 2003); 15.20 (Surya and Hari 2017)	Guard cell length 33.73 ± 2.27 (Sheue 2003)
Stomatal width (µm)	18.24-36.45 (27.45 ± 4.59, n = 100)	Guard cell width 31.90 ± 1.20 (Sheue 2003); 2.86 (Surya and Hari 2017)	Guard cell width 31.17 ± 1.66 (Sheue 2003)
Stomatal length/width ratio	0.78-2.28 (1.38 ± 0.31, n = 100)	Guard cell length/width ratio 1.10 (Sheue 2003)	Guard cell length/width ratio 1.08 (Sheue 2003)
Number of subsidiary cells	4-6 (5.04 ± 0.72, n = 100)	5-6 (Sheue 2003; Sheue et al. 2003a); 4 or more (Surya and Hari 2017)	5-6 (Sheue 2003; Sheue et al. 2003a)
Number of cork warts per leaf	20-30 (23.55 ± 2.03, n = 100)	Sporadically occurring on both leaf surfaces (Sheue et al. 2003a)	Sporadically occurring on both leaf surfaces (Sheue et al. 2003a)
Cork wart diameter (µm)	51.02-67.87 (59.91 ± 4.82, n = 100)	-	-
Hypodermal layer thickness on the adaxial leaf surface (µm)	49.68-83.44 (72.93 ± 7.73, n = 20)	-	-

Hypodermal layer thickness on the abaxial leaf surface (μm)	37.18-54.04 (41.95 ± 4.62 , n = 20)	-	-
Number of hypodermal cell layers on the adaxial leaf surface	2-3-layered (2.40 ± 0.50 , n = 20)	1-layered (large-sized) (Sheue 2003; Sheue et al. 2003a; Surya and Hari 2017)	1-layered (Sheue 2003; Sheue et al. 2003a)
Number of hypodermal cell layers on the abaxial leaf surface	2-3-layered (2.55 ± 0.51 , n = 20)	1-layered (small-sized) (Sheue 2003); 1-layered (Sheue et al. 2003a; Surya and Hari 2017)	1-layered (Sheue 2003; Sheue et al. 2003a)
Hypodermal cell shapes on the adaxial leaf surface	Elliptic, broadly elliptic, circular, or rounded polygonal	-	-
Hypodermal cell length on the adaxial leaf surface (μm)	38.24-71.09 (52.34 ± 12.32 , n = 20)	12.84 in size (Surya and Hari 2017)	-
Hypodermal cell width on the adaxial leaf surface (μm)	15.54-48.62 (34.92 ± 10.86 , n = 20)	-	-
Hypodermal cell shapes on the abaxial leaf surface	Broadly elliptic, circular, or rounded polygonal	-	-
Hypodermal cell length on the abaxial leaf surface (μm)	13.92-35.68 (25.87 ± 6.07 , n = 20)	11.29 in size (Surya and Hari 2017)	-
Hypodermal cell width on the abaxial leaf surface (μm)	17.56-36.65 (25.42 ± 4.80 , n = 20)	-	-
Crystal location, type, and diameter (μm)	Druse (in hypodermal cells and spongy mesophyll) 8.91-17.74 (12.94 ± 2.70 , n=20)	Druse	Druse
Number of palisade cell layers	2-4-layered (3.10 ± 0.85 , n = 20)	3-layered (adaxial) and 0(1-2)-layered (abaxial) (Sheue 2003); 2-3-layered (adaxial) and 0(-1)-layered (abaxial) (Sheue et al. 2003a); 2-layered (abaxial) (Surya and Hari 2017)	4-layered (adaxial) and 2(3)-layered (abaxial) (Sheue 2003); 3-4-layered (adaxial) and 1-2-layered (abaxial) (Sheue et al. 2003a)
Number of spongy cell layers	10-14-layered (11.95 ± 1.36 , n = 20)	9-10-layered (Sheue 2003); 9-14 series (Sheue et al. 2003a)	11-13(-15)-layered (Sheue 2003); 10-13 series (Sheue et al. 2003a)

Palynological study

Pollen morphology of Kandelia candel in Thailand

The pollen grains of *K. candel* from three populations in Thailand (Trat and Ranong Provinces) are monads, isopolar, radially symmetrical, and tricolporate. They exhibit a suboblate, subprolate, or oblate spheroidal shape, with a P/E ratio ranging from 0.75 to 1.31. In polar view (amb), the outline is a rounded triangular. The pollen grains are classified mainly as small, and occasionally medium in size. The polar axis measures between 15.22 and 27.73 μm , and the equatorial axis ranges from 19.33 to 24.15 μm . The ectocolpus length varies from 10.60 to 14.99 μm , and the ectocolpus width is between 1.18 and 7.40 μm . The endoaperture diameter ranges from 1.10 to 6.08 μm . The exine thickness ranges from 1.01 to 1.32 μm , and the exine sculpturing is perforate (Figure 7). Pollen size categories follow the classification of Erdtman (1945, 1952): very small (< 10 μm), small (10-25 μm), medium (25-50 μm), large (50-100 μm), very large (100-200 μm), and gigantic (> 200 μm). A comparison of pollen morphology with previous studies on *K. candel* and *K. obovata* is presented in Table 4.

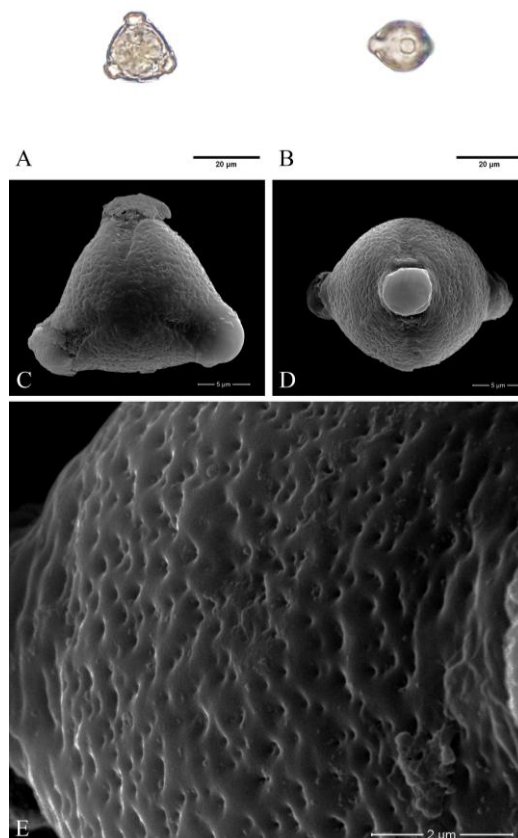


Figure 7. LM and SEM micrographs of pollen grains of *Kandelia candel*. A. Tricolporate aperture and rounded-triangular shape in polar view; B. Colporate aperture in equatorial view; C. Tricolporate aperture and rounded-triangular shape in polar view; D. Colporate aperture in equatorial view; E. Exine sculpturing, perforate, observed under LM (A, B) and SEM (C-E). Photos: Pichet Chanton and Chatchai Ngernsaengsaruy

Table 4. Comparison of the pollen morphology of *Kandelia candel* in Thailand with those of *K. candel* and *Kandelia obovata* from previous studies (Sheue et al. 2003b; Mao et al. 2012; Surya and Hari 2017; Dalimunthe et al. 2023)

Pollen characters	From the author's observations	Previous studies	
		<i>Kandelia candel</i>	<i>Kandelia obovata</i>
Polar axis [P] length (μm)	15.22-27.73 (21.74 \pm 4.35, n = 30)	13.12-16.16 (14.64 \pm 0.20) (Dalimunthe et al. 2023); 2.97-3.81 (Surya and Hari 2017)	17.20-25.30 (21.50) (Mao et al. 2012)
Equatorial axis [E] length (μm)	19.33-24.15 (21.61 \pm 1.34, n = 30)	27.42-27.82 (27.62 \pm 0.20) (Dalimunthe et al. 2023); 3.03-3.38 (Surya and Hari 2017); 21.20 \pm 1.60 (Sheue et al. 2003b)	16.70-21.50 (18.20) (Mao et al. 2012) 26.50 \pm 1.30 (Sheue et al. 2003b)
P/E ratio	0.75-1.31 (1.01 \pm 0.19, n = 30)	0.53 (Dalimunthe et al. 2023); 2.94-2.58 (Surya and Hari 2017)	-
Pollen size classes	Small, sometimes medium	Medium (Dalimunthe et al. 2023)	-
Pollen shapes (equatorial view)	Suboblate, subprolate, or oblate spheroidal	Prolate (Dalimunthe et al. 2023); oblate-spheroidal (Surya and Hari 2017)	Subprolate to spheroidal (Mao et al. 2012)
Pollen shapes (polar view)	Rounded triangular	Circular (Dalimunthe et al. 2023)	Subcircular (Mao et al. 2012)
Pollen aperture	Tricolporate	Tricolporate (Dalimunthe et al. 2023); 3zonocolporate (Surya and Hari 2017)	Tricolporate (Mao et al. 2012)
Ectocolpus length (μm)	10.60-14.99 (12.48 \pm 1.36, n = 30)	-	ca. 14.10 (Mao et al. 2012)
Ectocolpus width (μm)	1.18-7.40 (3.51 \pm 1.49, n = 30)	-	-
Endoaperture diameter (μm)	1.10-6.08 (3.36 \pm 1.47, n = 30)	-	-
Exine thickness (μm)	1.01-1.32 (1.17 \pm 0.10, n = 30)	-	ca. 1 μm (Mao et al. 2012)
Exine sculpturing	Perforate	Perforate (Dalimunthe et al. 2023); punctate (Surya and Hari 2017)	Rugulate to irregularly foveolate (Mao et al. 2012)
Tectum perforation diameter (μm)	0.10-0.18 (0.13 \pm 0.03, n = 30)	-	-

Discussion

Taxonomic treatment

Earlier records of *Kandelia* from Thailand were published under a monotypic species concept and before the recognition of *K. obovata*, increasing the potential for historical misidentification. However, re-examination of all available Thai material in the present study confirms that these records correspond exclusively to *K. candel*.

According to Schwarzbach (2014) and Tomlinson (2016), buttresses are absent in *Kandelia*. However, buttresses were present at the basal stem of *K. candel* in the populations examined in Thailand. This finding is based on field material from a limited number of localities, and buttress development may reflect environmental plasticity or site-specific conditions. Further observations across the species' geographic range are needed to determine whether this character is consistently expressed in *K. candel*.

In this study, the stipules of *K. candel* are flattened, with the colleters aggregated into a triangular form and appearing as finger-like rods with short stalks. These results are consistent with those reported by Sheue (2003), Sheue et al. (2003a), and Sheue et al. (2012), who noted that the stipule shape (as seen in transverse section), the shape of aggregated colleters, and the form of individual colleters in *Ceriops* and *Kandelia* are similar.

Leaf scars of *K. candel* have three major vascular bundle strands, with the two upper curved vascular bundle strands distinctly larger than the lower one. These observations are in agreement with Sheue (2003) and Sheue et al. (2003a), who reported that the patterns of leaf scars are very similar within the same genus, but differ among genera (*Rhizophora*, *Bruguiera*, and *Ceriops*) in the tribe Rhizophoreae.

According to previous studies (Hou 1958, 1970; Sheue 2003, et al. 2003b; Schwarzbach 2014), the sepals of *Kandelia* have been described as united at the base, forming a calyx tube with five lobes above. However, our observations indicate that the five sepals are not united but are instead free and basally adnate to the rim of the hypanthium. This suggests that the calyx of *Kandelia* is more appropriately described as consisting of five free sepals basally adnate to the hypanthium, rather than as a 5-lobed calyx. This interpretation more closely reflects the floral morphology observed in the present study and may provide a clearer structural understanding than previous descriptions.

Taken together, the combined evidence from macromorphology, leaf anatomy, and palynology provides integrative taxonomic confirmation that the Thai populations examined in this study belong unequivocally to *K. candel*. The congruence of multiple independent character systems supports the distinct species status of *K. candel* in Thailand and helps to clarify historical ambiguity arising from earlier monotypic treatments of the genus. This integrative approach strengthens species delimitation within *Kandelia* and contributes to a more robust taxonomic framework for mangrove systematics in the Indo-West Pacific region.

From a conservation perspective, this taxonomic clarification is important because accurate species

delimitation underpins effective biodiversity assessment and management. Although *K. candel* is globally assessed as Least Concern, its distribution in Thailand is geographically restricted, and local populations may therefore be more vulnerable to habitat loss and coastal disturbance than suggested by the global status. The integrative taxonomic framework presented here provides a reliable baseline for future ecological studies, population monitoring, and national-level conservation planning for mangrove ecosystems in Thailand.

Anatomical study

Several anatomical traits documented here differ from earlier descriptions of *K. candel* and are discussed below in the context of methodological and environmental variation. Previous studies have reported a two-layered epidermis in *K. candel*, whereas the present study consistently observed a single-layered epidermis on both adaxial and abaxial surfaces. This discrepancy may reflect differences in sectioning plane, developmental stage of the sampled leaves, or the criteria used to distinguish epidermal from hypodermal layers. Similar interpretational variation has been noted in anatomical studies of mangrove leaves, where thick-walled hypodermal cells may be interpreted as part of the epidermis depending on preparation and observation methods. Therefore, the single-layered epidermis observed here is interpreted as more likely reflecting methodological or developmental differences, rather than representing a taxonomically diagnostic character.

In contrast to earlier reports describing a single-layered hypodermis in *K. candel*, the present study documents a hypodermis composed of two to three cell layers. This difference may reflect environmental plasticity associated with habitat conditions, particularly variation in water availability and salinity regime, or differences in sampling strategy and anatomical interpretation among studies. Mangrove species are known to exhibit substantial intraspecific variation in hypodermal development, and multilayered hypodermis has been widely reported as a common feature in halophytic plants. Accordingly, the increased hypodermal layering observed in Thai populations of *K. candel* is interpreted as environmentally influenced anatomical variation, rather than as evidence of taxonomic inconsistency.

Based on the classification proposed by Juairiah (2014), stomatal density in *K. candel* is categorized as low to medium. It should be noted, however, that this classification system is not universally applied and is used here solely as a comparative reference. Low stomatal density and sunken stomata have been broadly interpreted as adaptive features in mangrove species, potentially contributing to reduced transpiration under saline and high-light conditions. In the present study, these features are discussed in a correlational context and are not interpreted as direct evidence of functional adaptation.

Clear differences in hypodermal thickness and cell layering were observed between *K. candel* and *Rhizophora stylosa* Griffith. In the present study, *K. candel* was recorded exclusively from riverbank mangrove forests, particularly along the Welu River in Trat and Chanthaburi

Provinces and the Kra Buri River in Ranong Province. These habitats are seasonally influenced by freshwater input during the rainy season and are characterized by brackish to occasionally freshwater conditions. In association with these environments, *K. candell* exhibits a relatively thin hypodermal layer on the adaxial leaf surface (49.68-83.44 μm), consisting of 2-3 cell layers. In contrast, *R. stylosa* typically occupies exposed coastal environments at the seaward edge of mangrove forests, growing on muddy-sandy to sandy-rocky substrates where seawater salinity remains consistently high (Ngernsaengsaruy et al. 2025). Correspondingly, *R. stylosa* shows substantially thicker and more developed hypodermal layers on the adaxial leaf surface (206.41-361.11 μm) with 4-6 cell layers. This pattern is consistent with anatomical trends reported for mangrove species distributed along salinity gradients. However, because salinity levels and plant water status were not measured directly in the present study, these differences are interpreted as habitat-associated structural variation rather than as direct causal responses to salinity.

Hypodermal tissues in mangrove leaves have been interpreted as contributing to water storage, protection of photosynthetic tissues, and, in some taxa, salt sequestration. Previous studies have suggested that hypodermal cell size and layering may influence water retention efficiency in saline environments. The hypodermal characteristics observed in *K. candell* are therefore consistent with general functional interpretations reported for mangrove species, while remaining within a conservative, correlational framework.

Leaf thickness values recorded in the present study substantially exceed those reported by Surya and Hari (2017). Given the magnitude of this discrepancy, it is unlikely to reflect biological variation alone and may instead result from differences in measurement methodology, sectioning technique, or reporting units. As these methodological details could not be independently verified, this discrepancy is treated with caution and is not interpreted as evidence of anatomical divergence.

It should be noted that the anatomical observations in this study were based on material from only three populations in south-eastern and peninsular Thailand. Although the characters documented were consistent among the examined samples, broader population sampling would be required to fully capture intraspecific anatomical variation across the species' range in Thailand.

Palynological study

The polar axis and equatorial axis measurements of pollen grains observed in the present study fall within the range reported by several previous studies on *K. candell* and *K. obovata*, supporting general consistency in pollen size and morphology within the genus. In contrast, Surya and Hari (2017) reported markedly smaller pollen dimensions, with polar and equatorial axes several times lower than those documented here and elsewhere. Given the magnitude of this difference, it is difficult to attribute the discrepancy solely to intraspecific variation. Instead, it may reflect differences in measurement approach, sample preparation, imaging technique, or reporting units, none of

which could be independently assessed from the published data. Accordingly, the values reported by Surya and Hari (2017) are treated with caution in the present study and are not interpreted as evidence of biological, anatomical, or taxonomic divergence.

This study provides the first comprehensive taxonomic revision of *K. candell* in Thailand, incorporating morphological, anatomical, palynological, and distributional evidence. All examined herbarium specimens and recent field collections confirm *K. candell* as the sole species in the country, with no evidence of *K. obovata* occurring in Thailand. The morphological descriptions and quantitative measurements provide clarity on intraspecific variation and enable accurate identification of *K. candell* in both field and herbarium contexts.

Leaf anatomical analysis reveals typical mangrove adaptations in *K. candell*, including bifacial leaves, sunken cyclocytic stomata, a multilayered hypodermis with druse crystals, and a developed mesophyll system. These anatomical features reflect adaptation to riverine and brackish environments. While *K. candell* is globally widespread and classified as Least Concern, its distribution in Thailand is limited to the southeastern and peninsular regions, with an Extent of Occurrence of 52,021.25 km² and an Area of Occupancy of 40 km². These figures emphasize its localized rarity in the country and the need for ongoing monitoring, particularly with respect to habitat modifications in coastal and riverine ecosystems.

In conclusion, this taxonomic revision establishes a solid anatomical and palynological foundation for *K. candell* in Thailand, offering valuable reference data to inform future ecological, conservation, and systematic studies on mangrove biodiversity at national and regional levels.

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REFERENCES

- Bachman S, Moat J, Hill AW, de Torre J, Scott B. 2011. Supporting red list threat assessments with GeoCAT: Geospatial conservation assessment tool. *Zookeys* 150: 117-126. <https://doi.org/10.3897/zookeys.150.2109>.

- Chiang TY, Chiang YC, Chen YJ, Chou CH, Havanond S, Hong TN, Huang S. 2001. Phylogeography of *Kandelia candel* in East Asiatic mangroves based on nucleotide variation of chloroplast and mitochondrial DNAs. *Mol Ecol* 10 (11): 2697-2710. <https://doi.org/10.1046/j.0962-1083.2001.01399.x>.
- Dalimunthe SH, Damayanto IGP, Martiansyah I, Tihurua EF, Rahmawati K, Fastanti FS, Muhaimin M. 2023. Pollen micromorphology of mangrove species in South Sumatera coastal area, Indonesia. *Sains Malays* 52 (9): 2499-2511. <http://doi.org/10.17576/jsm-2023-5209-03>.
- Das AB, Basak UC, Das P. 1995. Karyotype diversity and genomic variability in some Indian tree mangroves. *Caryologia* 48 (3-4): 319-328. <http://doi.org/10.1080/00087114.1995.10797341>.
- Duke N, Kathiresan K, Salmo III SG, Fernando ES, Peras JR, Sukardjo S, Miyagi T. 2010. *Kandelia candel*. The IUCN Red List of Threatened Species 2010. <https://www.iucnredlist.org/species/178857/7629021> (accessed on 23 October 2025).
- Erdtman G. 1945. Pollen Morphology and Plant Taxonomy V. on the Occurrence of Tetrads and Dyads. *Svensk Botanisk Tidskrift Utgifven af Svenska Botaniska Foreningen* 39: 286-297.
- Erdtman G. 1952. Pollen Morphology and Plant Taxonomy: Angiosperms V. 1. Almquist and Wiksell, Stockholm, Sweden. <https://doi.org/10.1080/11035895209453507>.
- Giang LH, Geada GL, Hong PN, Tuan MS, Lien NTH, Ikeda S, Harada K. 2006. Genetic variation of two mangrove species in *Kandelia* (Rhizophoraceae) in Vietnam and surrounding area revealed by microsatellite markers. *Intl J Plant Sci* 167 (2): 291-298. <https://doi.org/10.1086/499611>.
- Henslow G. 1878. Rhizophoreae. In: Hooker JD (eds). The Flora of British India V. 2. L. Reeve & Co., London.
- Hou D. 1958. Rhizophoraceae. In: van Steenis CGGJ (eds). Flora Malesiana Series 1, V. 5. Noordhoff-Kolff N. V., Jakarta.
- Hou D. 1970. Rhizophoraceae. In: Smitinand T, Larsen K (eds). Flora of Thailand V. 2. The Forest Herbarium, Bangkok.
- Huang S, Chen YC. 2000. Patterns of genetic variation of *Kandelia candel* among populations around the South China Sea. In: Chiang TY, Hsu TW (eds). Wetland Biodiversity: Proceedings of Symposium of Biodiversity in Wetlands. Taiwan Endemic Species Research Institute, Nantou, Taiwan.
- International Plant Names Index (IPNI). 2025. International Plant Names Index. The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries, and Australian National Herbarium. <https://www.ipni.org/> (accessed on 23 October 2025).
- IUCN Standards and Petitions Committee. 2024. Guidelines for Using the IUCN Red List Categories and Criteria Version 16. Standards and Petitions Committee. <https://www.iucnredlist.org/resources/redlistguidelines> (accessed on 23 October 2025).
- Johansen DA. 1940. Plant Microtechnique. McGraw-Hill, New York.
- Juairiah L. 2014. Stomatal characteristics study on some revegetation plants of the post tin-mining land in Bangka. *Widyaset* 17 (2): 213-218. [Indonesian]
- Kermanee P. 2008. Techniques of Plant Tissue. Kasetsart University, Bangkok. [Thai]
- King G. 1897. Materials for A Flora of The Malayan Peninsula (Rhizophoreae). *J Asia Soc Bengal* 2 (1): 311-326.
- Kirtikar KR, Basu BD. 1935. Indian Medicinal Plants V. 2. Lalit Mohan Basu, India.
- Linnaeus C. 1753. Species Plantarum V. 1. Impensis Laurentii Salvii, Holmiae.
- Malabrigo Jr PL, Eduarte GT, Malabrigo LD, Coracero EE. 2021. *Kandelia candel* (L.) Druce, a true native species in the Philippines. *Philipp J Sci* 150 (5): 1121-1129. <https://doi.org/10.56899/150.05.24>.
- Manohar SM. 2024. Botanical, phytochemical, and pharmacological profile of the mangrove plant *Kandelia candel* (L.) Druce. *J Med Pharm Allied Sci* 13 (5) 6633: 6770-6779. <https://doi.org/10.55522/jmpas.V13I5.6633>.
- Mao L, Batten DJ, Fujiki T, Li Z, Dai L, Weng C. 2012. Key to mangrove pollen and spores of southern China: An aid to palynological interpretation of Quaternary deposits in the South China Sea. *Rev Palaeobot Palynol* 176-177: 41-67. <https://doi.org/10.1016/j.revpalbo.2012.03.004>.
- Maxwell GS. 1995. Ecogeographic Variation in *Kandelia candel* from Brunei, Hong Kong, and Thailand. In: Wong YS, Tam NFY (eds). Asia-Pacific Symposium on Mangrove Ecosystems. Developments in Hydrobiology, vol 106. Springer, Dordrecht. https://doi.org/10.1007/978-94-011-0289-6_8.
- Metcalfe CR, Chalk L. 1957. Anatomy of the Dicotyledons: Leaves, Stem, and Wood in Relation to Taxonomy, with Notes on Economic Uses V. 1. Oxford University Press, Oxford.
- Naskar K, Mandal R. 1999. Ecology and Biodiversity of Indian Mangroves. Daya Publishing House, Delhi.
- Ngernsaengsaruy C, Chanton P, Leksungnoen N, Uthairatsamee S, Mianmit N. 2024. A taxonomic revision of *Rhizophora* L. (Rhizophoraceae) in Thailand. *PeerJ* 12: e17460. <https://doi.org/10.7717/peerj.17460>.
- Ngernsaengsaruy C, Mianmit N, Kamsanor S, Pothitan R, Jintana V, Jintana N, Chanton P, Sukantatul A, Khade J. 2025. *Rhizophora stylosa* (Rhizophoraceae) newly recorded from Thailand: lectotypification, leaf anatomy, and pollen morphology. *PhytoKeys* 259: 1-25. <https://doi.org/10.3897/phytokeys.259.157847>.
- Pattanaik C, Reddy CS, Dhal NK, Das R. 2008. Utilisation of mangrove forests in Bhitarkanika wildlife sanctuary, Orissa. *Indian J Tradit Knowl* 7 (4): 59-603.
- Plants of the World Online (POWO). 2025. Plants of the World Online. The Royal Botanical Gardens, Kew. <http://www.plantsoftheworldonline.org/> (accessed on 23 October 2025).
- Punt W, Hoen PP, Blackmore S, Nilsson S, Thomas AL. 2007. Glossary of pollen and spore terminology. *Rev Palaeobot Palynol* 143 (1-2): 1-81. <https://doi.org/10.1016/j.revpalbo.2006.06.008>.
- Schwarzbach AE. 2014. Rhizophoraceae. In: Kubitzki K (eds). The Families and Genera of Vascular Plants V. 11. Springer-Verlag, Berlin/Heidelberg, 283-295. https://doi.org/10.1007/978-3-642-39417-1_23.
- Sheue CR, Chen YJ, Yang YP. 2012. Stipules and colleters of the mangrove Rhizophoraceae: Morphology, structure, and comparative significance. *Bot Stud* 53 (2): 243-254.
- Sheue CR, Liu HY, Yang YP. 2003a. Morphology on stipules and leaves of the mangrove genus *Kandelia* (Rhizophoraceae). *Taiwania* 48 (4): 248-258. [https://doi.org/10.6165/tai.2003.48\(4\).248](https://doi.org/10.6165/tai.2003.48(4).248).
- Sheue CR, Liu HY, Yong JWH. 2003b. *Kandelia obovata* (Rhizophoraceae), a new mangrove species from Eastern Asia. *TAXON* 52 (2): 287-294. <https://doi.org/10.2307/3647398>.
- Sheue CR. 2003. The Comparative Morphology and Anatomy of the Eastern Mangrove Rhizophoraceae. [Ph.D. Dissertation]. National Sun Yat-sen University, Kaohsiung, Taiwan.
- Simpson MG. 2010. Plant Systematics 2nd edn. Elsevier Academic Press, Burlington/San Diego. <https://doi.org/10.1016/B978-0-12-374380-0.50001-4>.
- Surya S, Hari N. 2017. Pollen morphology of selected true mangrove species in Kerala. *Intl J Res Pharm Pharm Sci* 2 (3): 11-14.
- Thiers B (2025) [continuously updated] Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. <https://sweetgum.nybg.org/science/ih/>
- Tomlinson PB. 1986. The Botany of Mangroves. 1st edn. Cambridge University Press, Cambridge.
- Tomlinson PB. 2016. The Botany of Mangroves. 2nd edn. Cambridge University Press, Cambridge.
- van Rheede HA. 1686. Hortus Indicus Malabaricus V. 6. Henrici & Viduae Theodori Boom, Amsterdam [Amstelaedami].
- Vu VC. 1965. Rhizophoraceae. Flore du Cambodge, du Laos et du Vietnam Fasc. 4. Muséum National D'histoire Naturelle, Paris. [French]
- World Flora Online (WFO). 2025. World Flora Online. <https://www.worldfloraonline.org/> (accessed on 23 October 2025).