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Morphology on Stipules and Leaves of the Mangrove Genus *Kandelia* (Rhizophoraceae)

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ABSTRACT: The morphology of stipules and leaves of *Kandelia candel* (L.) Druce and *K. obovata* Sheue, Liu & Yong were studied and compared. The discrepancies of anatomical features, including stomata location, stomata type, cuticular ridges of stomata, cork warts and leaf structures, among previous literatures are clarified. Stipules have abaxial collenchyma but without sclereid ideoblast. Colleters, finger-like rod with a stalk, aggregate into a triangular shape inside the base of the stipule. Cork warts may sporadically appear on both leaf surfaces. In addition, obvolute vernation of leaves, the pattern of leaf scar and the difference of vein angles of these two species are reported.

KEY WORDS: ***Kandelia candel, Kandelia obovata,* Leaf, Stipule, Morphology.**

INTRODUCTION

Mangroves are the intertidal plants, mostly trees and shrubs, distributed in regions of estuaries, deltas and riverbanks or along the coastlines of tropical and subtropical areas (Tomlinson, 1986; Saenger, 2002).

The members of mangroves consist of different kinds of plants from different genera and families, many of which are not closely related to one another phylogenetically. Tomlinson (1986) set limits among three groups: major elements of mangal (or known as 'strict mangroves' or 'true mangroves'), minor elements of mangal and mangal associates. Recently, Saenger (2002) provided an updated list of mangroves, consisting of 84 species of plants belonging to 26 families. Lately, a new species *Kandelia obovata* Sheue, Liu & Yong northern to the South China Sea was added (Sheue *et al*., 2003), a total of 85 species of mangroves are therefore found in the world (Sheue, 2003).

As the members of mangroves are quite unique of their occupation in such harsh environment with high salinity, tides, wind, full sun and high temperature, there are several kinds of morphological specialization shared by these plants (Tomlinson, 1986; Saenger, 2002). A great deal of attentions have been devoted to the anatomical works on leaves of mangroves (Areschoug, 1902; Song, 1960; Rao and Sharma, 1968; Rao, 1971; Fahn and Shimony, 1977; Saenger, 1982; Chen, 1984; Chiang, 1984; Hsiao and Chen, 1988; Roth, 1992; Das and Ghose, 1993, 1996; Das, 1999; Naskar and Mandal, 1999; Sheue *et al.*, 2000). Based on these studies, several general adaptive features of leaves of mangroves could be concluded as a range of xeromorphic features, which include thick cuticular wax or a tomentum of hairs on leaf surfaces, sunken stomata, cuticular beak-like ridges of guard cells, succulence presenting as large celled hypodermis or colorless water storage tissue, and enlarged terminal tracheid (Tomlinson, 1986; Saenger, 2002; Sheue *et al.*, 2000).

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Nevertheless, some discrepancies were found from the results of leaf anatomical features of *Kandelia* reported from different regions (Sheue *et al*., 2000; Sheue, 2003). For instance, dorsiventral leaf (Song, 1960; Naskar and Mandal, 1999), semi-isobilateral leaf (Chen, 1984; Chiang, 1984; Hsiao and Chen, 1988) and even isobilateral leaf (Lin, 1997; Das and Ghose, 1996) were reported for the genus. Stomata were reported on abaxial side (Song, 1960; Chen, 1984; Chiang, 1984; Hsiao and Chen, 1988; Naskar and Mandal, 1999; Sheue *et al*., 2000) or on both abaxial and adaxial surfaces (Das and Ghose, 1993). In addition, anomocytic (Das and Ghose, 1993; Naskar and Mandal, 1999) or cyclocytic (Chiang, 1984; Hsiao and Chen, 1988; Keating and Randrianasolo, 1988; Sheue *et al*., 2000) stomata types were reported and the number of stomata ridges of *Kandelia* was inconsistent from different authors (Chiang, 1984; Hsiao and Chen, 1988; Das and Ghose, 1993; Sheue *et al*., 2000). These apparent discrepancies on leaf anatomical features in *Kandelia* raise confusion and need to be clarified. In addition, the previously monotypic genus of *Kandelia* was recognized as two species lately. Thus, a comparative study on leaves of these two species is significantly needed.

The aim of this study, therefore, is to compare the morphology on the stipules and leaves of *Kandelia*, especially the stipule characters which were generally ignored by most of the previous workers. The results will not only elucidate the discrepancies mentioned above, but also find additional features of *Kandelia* for taxonomic distinction of the two species and the mangrove Rhizophoraceae genera including *Bruguiera*, *Ceriops*, *Kandelia* and *Rhizophora*.

MATERIALS AND METHODS

For anatomical studies, *Kandelia candel* were collected from riverbank of Benut (103°6' E 1°7' N) of Malay Peninsula in May of 2002 and Sundarbans (89°0' E 22°0' N) of West Bengal of India in the late April of 2003. *K. obovata* were collected from riverbank at Tongshi (120°09' E 23°27'N), Chiayi County in Taiwan during 1999 to 2003. The voucher specimens were deposited in the Herbarium of Department of Biological Sciences (SYSU), National Sun Yat-sen University, Kaohsiung, Taiwan.

Two or three individuals of *Kandelia* were collected from each population. One leaf of the third pair from the shoot apex was collected from one branchlet, and three branchlets were chosen from each individual. Therefore, a total of three leaves and 5-6 stipules at the incipiency of extension of the young leaves were sampled from each individual. Fresh leaves and stipules were observed, measured and pictured with Zeiss Stemi SV 11 Stereoscope. The base of each stipule and the middle part of each leaf were cut into 3 small pieces, c. 3 mm × 3 mm, smeared with triton on its surface for decreasing surface tension, and then put into 1.25-1.5% glutaraldehyde in 0.1 M phosphate buffer with 5% sucrose for fixation in the fields. The materials collected overseas were stored in this fixative for 5-7 days, and those collected from Taiwan were in the same fixative for 1-2 days. They were subsequently transferred to 1% OsO_4 in 0.1 M phosphate buffer for about 4 hours for the second fixation. After dehydration through an ethanol series, they were infiltrated for 3 days and embedded within Spurr's-resin. The embedded materials were polymerlized in an oven at 70˚C for 12 hours. Semi-thin (90 nm) sections were made by Ultracut E or MTX Microtome, and stained with 0.1% Toluidine blue. After staining, semi-thin sections were observed and pictured by Olympus BH-2 Light Microscope. For SEM study, the materials was fixed and dehydrated as above, and then treated with critical point drying and coated with gold. These samples were examined and taken photos with Hitach S-2400 Scanning Electron Microscope.

Some leaf materials were cleared for investigation of leaf veins, sclereids, cork warts and crystals. Samples were first immersed within 90% ethanol and boiled, then put into 2- 4% NaOH at 40 °C in an oven for 5-14 days, stained with 1% Safranin O, and observed with an Olympus BH-2 Light Microscope.

Dried specimens from herbaria of SING, TAI and TAIF were used for morphometric study, including stipule, leaf shape and size, petiole length, lateral vein, vein angle (the angle at which the vein departs from the midrib, named as vein angle for convenient) and feature of leaf scar.

RESULTS

Stipule

Kandelia has distinct stipules paired outside the young leaves. The stipule vernation of *Kandelia* is clasping, of which one margin is free (Fig. 1A). In addition, the stipules of *Kandelia* have the abaxial side thickening in the middle region and gradually thin out towards its edge from the base to slightly upper part (Fig. 1A). Therefore, the morphology of their stipule appears flattened and forms a triangular space within the adaxial base of the stipule, where colleters aggregate (Figs. 1B; 2A).

Kandelia candel has longer stipules than *K. obovata* (Table 1). The two species have no sclereid ideoblasts in the stipules. However, collenchyma tissue near the abaxial side is commonly found. Drused calcium oxalate crystals, as well as tannins are very abundant.

Colleters

Colleters are finger-like protruding gland structures, which can produce sticky milky excudate. Six to nine series of aggregated colleters appear as a triangular shape inside the base of the flattened stipules (Figs. 1B; 2A; Table 1).

Due to the tightly overlapping margins of the stipules, it is difficult to observe the colleters if the stipule was not cut into two halves. The series and number of the colleters per stipule are greater in *K. obovata* (Table 1). Nevertheless, the individual shape of a colleter is very similar in these two species, i.e. finger-like rod with a short stalk (Figs. 1B; 2A). The lengths of colleters vary, with a range of 275-680 μm and an average of 500 ± 129 μm measured from *K. obovata* (stalk included, n=10).

Vernation, leaf morphology and leaf scar

The young leaves of *Kandelia* ensheathed within stipules appear as obvolute vernation (Bell and Bryan, 1991) while viewing from the transverse section of leaf buds (Fig. 1A). It has two V-shaped young leaves opposite each other obliquely. The successive leaf pairs forming an angle of 69-70° (measured from *K. obovata*) showed the bijugate phyllotaxy (Tomlinson & Wheat, 1979), a kind of modified decussate arrangement (Fig. 1A; Table 1).

Kandelia candel has oblong to elliptic and long leaves contrasting to *K. obovata* of mostly obovate and short leaves (Figs. 1D; 1E; Table 1). According to observation in the field, the leaves of *K. obovata* are usually upward and reflexed at margins, but the leaves of *K. candel* generally keep horizontal to slightly upward and less reflexed.

Kandelia obovata has 5-8 lateral veins; *K. candel* has 8-11 lateral veins. The vein angle can be relatively constant feature and useful for specific distinction. As the results showed (Table 1), the vein angle can be applied to distinguish the two species. *K. candel* constantly has the vein angle 55.5° ± 3.0; whereas *K. obovata* has narrower vein angle about 39.8° ± 6.1. The lengths of petioles of these two species are close, about 1-1.8 cm (Table 1).

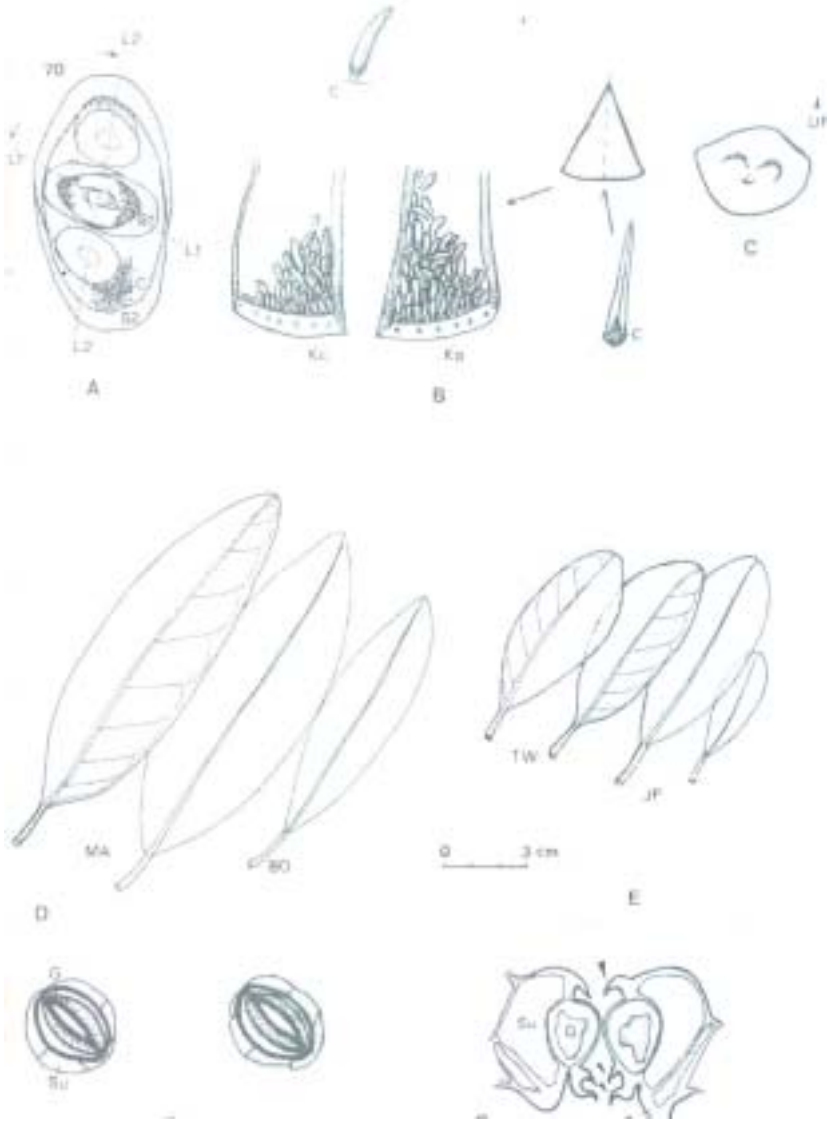

Fig. 1. Morphological characters of stipules and leaves of *Kandelia*. A. A cross section of a shoot of *K. obovata*, showing the clasping stipules, colleters and obvolute vernation of young leaves. The successive leaf pairs (L1 and L2, L2 is the position of petiole) with bijugate phyllotaxy forming an angle of 70°. B. The stipule and the aggregated colleters of triangular shape inside the base of it, half of the tissue removed in Kc (*K. candel*) and Ko (*K. obovata*). C. Leaf scar of *K. obovata*, with two upper curved vascular strands and a lower small one. D. Leaf shapes of *K. candel* from different regions. E. Leaf shapes of *K. obovata* from different regions. F. The cyclocytic stomata type of *Kandelia*, with 5-6 subsidiary cells. G. The cuticular ridges of stomata in *Kandelia*, with two pairs of outer ridges (small arrowheads, abaxial side) and one pair of inner ridge (large arrowhead, adaxial side). BO: Boneo; Co: colleters; Cu: cuticular wax; G: guard cell; JP: Japan; L: Leaf; Kc: *K. candel*; Ko: *K. obovata*; MA: Malay Peninsula; S: stipule; Su: subsidiary cell; TW: Taiwan.

The helical arrangement of the leaf scars (petiole scars) resulting from the bijugate phyllotaxy at the shoots is distinctive in *Kandelia*. Leaf scar of *Kandelia* looks like a “tricky face” which has two upper curved strands of vascular bundles distinctly larger than the lower one (Fig. 1C; Table 1). There is no difference of the vascular pattern in the leaf scar between the two species.

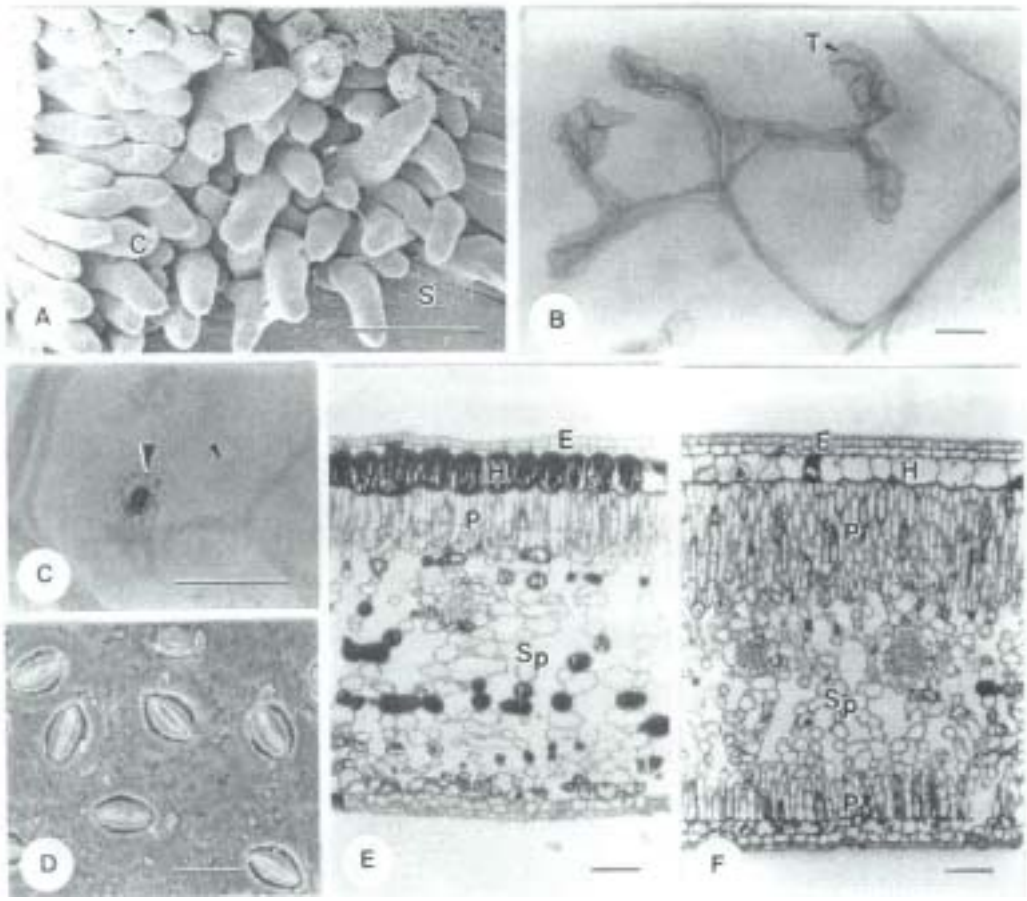

Fig. 2. Leaf anatomical features of *Kandelia*. A. SEM view of the aggregated colleters of *K. obovata*. B. Leaf vein and the enlarged terminal tracheid of *K. obovata*. C. The abaxial leaf surface of *K. candel*, with one cork wart (the large arrow head) and stomata (the small arrow head). D. SEM view of stomata of *K. obovata*. E. Leaf transverse section of *K. candel*, showing the dorsiventral structure. F. Leaf transverse section of *K. obovata*, showing the semi-isobilateral structure. Co: colleters; E: epidermis; H: hypodermis; L: Leaf; P: palisade tissue; S: stipule; Sp: spongy tissue; T: terminal tracheid. A: Bar=500 μm; B: Bar=100 μm; C: Bar=250 μm; D-F: Bar=50 μm.

Anatomical feature of leaf

The stomata are confined on the lower leaf surface in *Kandelia* (Figs. 2C; 2D). The stomatal type is cyclocytic (Fig. 1F; Table 1). However, the extremely thin cell walls of the subsidiary cells lead difficulty to recognize the stomata type and to count the number of subsidiary cells per stomatal complex. Herein, the authors used the peels of lower epidermis, the cuticular layer and the cleared leaves for the observation of stomata complex.

The number of subsidiary cells of each stomata complex of *Kandelia* ranges from 5 to 6 (Table 1; Fig. 1F). The guard cells have one inner cuticular ridge and two outer ridges, as beak-like shape by lateral view (Fig. 1G; Table 1). The sizes of the guard cells in surface view of the two species are similar, with a measurement of about 33-35 μm by 31 μm.

It was noteworthy that cork warts may occasionally occur on both surfaces of leaves in *Kandelia* (Fig. 2C; Table 1). Cork warts always originate from the stoma of the abaxial surface, but they originate from the normal epidermis of the adaxial surface. The cork warts in different sizes and stages could be observed from the same leaf.

Table 1. Comparison of morphological features on stipules and leaves in *Kandelia candel* (L.) Druce and *K. obovata* Sheue, Liu & Yong.

Characters	*K. candel*	*K. obovata*
Stipule	Flattened, clasping, 3-4 cm long before dropping	Flattened, clasping, 2.5-3.2 cm long before dropping
Colleters	Aggregated as triangular, 6-7 series, 75-96 colleters, finger-like rod with a stalk	Aggregated as triangular, 8-9 series, 95-110 colleters, finger-like rod with a stalk
Vernation	Obvolute	Same as *K. candel*
Leaf orientation	Horizontally to slightly upward, margins usually not reflexed	Distinctly upward, margins usually reflexed
Leaf shape	Elliptic-oblong to oblong-lanceolate	Obovate to obovate-elliptic
	6-16 cm × 3-6 cm	6-12 cm × 2.5-5 cm
Leaf vein	8-11(-13)	5-8
Vein angle	55.5° ± 3.0	39.8° ± 6.1
Petiole length	1-1.5 cm	(0.5-)1-1.8 cm
Leaf scar	Two upper curved strands and a small lower one	Same as *K. candel*
Stoma	Cyclocytic, 5-6 subsidiary cells, with 2 outer ridges & 1 inner ridge	Same as *K. candel*
Cork warts	Sporadically occurring on both surfaces	Same as *K. candel*
Leaf structure	Dorsiventral, thickness 396 ± 19 μm; with two layered eipdermis, one layered hypodermis, adaxial palisade 2-3-layered and abaxial palisade 0(-1)-layered, spongy tissue 9-14 series	Semi-isobilateral, thickness 480 ± 114 μm; with two layered eipdermis, one layered hypodermis, adaxial palisade 3-4-layered and abaxial palisade 1-2-layered, spongy tissue 10-13 series
Vein ending	Enlarged terminal tracheid	Same as *K. candel*
Crystal type	Druse	Same as *K. candel*

It was interesting that the two species have different anatomical structure in leaves (Figs. 2E; 2F; Table 1). In *K. obovata* the leaf has two groups of palisade tissues neighboring to both adaxial (upper) and abaxial (lower) hypodermis, although the abaxial palisade tissue usually is half in layers (1-2 layered) of the adaxial (3-4 layered) (Fig. 2F). Therefore, the leaf of *K. obovata* is called as "semi-isobilateral". However, the leaf of *K. candel* does not have such lower palisade tissue and is typically dorsiventral (Fig. 2E). Only one leaf of *K. candel* from Benut in Malaysia was found to have 1-2 layers of extremely short and negligible abaxial palisade tissue during the study.

The thickness of leaves of the two species is somewhat different. *K. candel* has leaves with a thickness 396 ± 19 μm; but, *K. obovata* may have thicker leaves with 480 ± 114 μm.

Kandelia has two-layered epidermis. The iso-diametric epidermis cells arrange tightly, viewed from the transverse section. The first and the second layered epidermis are very similar in shape, but the inner ones are larger in size than the outer ones (Figs. 2E; 2F). Although the leaves of *Kandelia* have only one layered hypodermis in both adaxial and abaxial sides, the abaxial side has smaller hypodermis cells. On the other hand, the layers of spongy tissue were rather variable, with 9-13 layers.

The distinct enlarged terminal tracheids were found in the two species of *Kandelia* (Fig. 2B; Table 1). The tanniferous cells may appear in hypodermis, palisade and spongy tissue, especially abundant in hypodermis. Drused calcium oxalate crystals were commonly observed

in the leaves of *Kandelia*. They may occur in any tissue in leaves, including epidermis and hypodermis, with high frequency and abundance in vein sheath and hypodermis tissue.

DISCUSSION

The large and distinctive stipules of *Kandelia* are clasping together, as the other genera of the Rhizophoraceae (Hou, 1958; Tomlinson, 1986). The morphology of stipules of the mangrove Rhizophoraceae is flattened with abaxial thickening in both *Kandelia* and *Ceriops* (Sheue, 2003). Compared to the abaxial thickening of the stipules of *Ceriops*, *Kandelia* has less distinctive thickening. Due to the gradual abaxial thickening of stipule from the upper part, a triangular space is formed within the adaxial base where colleters aggregated, as the genus of *Ceriops*.

Colleters of the mangrove Rhizophoraceae were reported (Hou, 1958; Tomlinson, 1986) and anatomically described in *Rhizophora mangle* L. (Lersten and Curtis, 1974) previously. Tomlinson (1986) suggested that the color and the consistency of the exudate from colleters are variable and somewhat diagnostic for different species, such as milky fluid in *Rhizophora* and more resinous in *Ceriops*. However, the application of series or number of colleters in the taxonomic value for the mangrove Rhizophoraceae was firstly noted lately (Sheue, 2003; Sheue *et al*., 2003). The aggregated forms, series number, colleter number and individual morphology of colleters of the stipules are characteristic generically or specifically, and could be an aid for taxonomic identification (Sheue, 2003). However, the works relevant to the exudate and the function of the colleters need reinforced.

Vernation of the mangrove Rhizophoraceae except the genus of *Kandelia* was described by Hou in 1958. He mentioned that the vernation is convolute in *Bruguiera* and *Rhizophora*, and involute in *Ceriops* (Hou, 1958). We are the first to indicate that *Kandelia* has unique obvolute vernation in the mangrove Rhizophoraceae. This character implies the particular taxonomic position of *Kandelia* in this tribe. The bijugate phyllotaxy of *Kandelia* is a kind of modified decussate arrangement as the other genera of this tribe, with successive leaf pairs offsetting by angles of 70° (measured from *K. obovata*). The result agrees with the conclusion of Tomlinson and Wheat (1979) in the mangrove Rhizophoraceae. Tomlinson (1986) stated that the bijugate arrangement reduces shading and produces branch systems with a greater diversity of orientation compared with a decussate arrangement.

Culter (1978) stated that vein angle is quite stable specifically and could be an aid for identification. We found his statement was supported by the results of the two species, *K. candel* with wider angle (55°) than that of *K. obovata* (40°).

The diagnostic differences of the leaf scars between *Rhizophora* and *Bruguiera* of the family based on the arrangements of the vascular bundles were pointed out by Hou in 1958. However, the vascular arrangements of the leaf scars in *Kandelia* were firstly described. It is expected that the leaf scars have the diagnostic value to differentiate the genera of the tribe Rhizophoreae (Sheue, 2003). Tomlinson (1986) pointed out that these differences are the results of the different time lag of dispersion of the traces because the nodal anatomy is similar in all members of the Rhizophoraceae.

Kandelia was reported having cork warts on leaves (Areschoug, 1902; Song, 1960). Our result agreed with the report and found cork warts sporadically on both adaxial and abaxial leaf surfaces of *Kandelia*. The possible function of the cork warts is still an open question; only a few studies had been carried out and hinted at the possible function of salt physiology

(Areschoug, 1902; Baijnath and Charles, 1980; Garcia, 1979; Roth, 1992; Sheue and Sarafis, unpublished). Thus, the presence of cork warts in all members of the mangrove Rhizophoraceae (Sheue, 2003) actually encourages us to elucidate the physiological function of this structure.

Cyclocytic stomata with five to six subsidiary cells were found in the two species. The cell walls of subsidiary cells are very thin, which results in the difficulty to examine the stomata type. The anomocytic type of this genus, which were reported by Das and Ghose (1993) and Naskar and Mandal (1999), may attribute to such difficulty. Additionally, it was noted that all members of the mangrove Rhizophoraceae have cyclocytic stomata (Hsiao and Chen, 1988; Keating and Randrianasolo, 1988; Sheue *et al*., 2000), but the inland species of the Rhizophoraceae have different types of stomata (Keating and Randrianasolo, 1988; Sheue, 2003).

In *Kandelia*, each guard cell has two outer cuticular ridges and one inner ridge, which was reported by Areschoug (1902), Chiang (1984) and was confirmed by the authors (Sheue *et al*., 2000). The sunken stomata and the prominent cuticle ridges of guard cells in the mangrove Rhizophoraceae were thought to be an adaptation to the mangrove environment as the xerophytes (Areschoug, 1902; Saenger, 1982; Tomlinson, 1986; Das, 1999). Harberlandt (1965) described this feature and proposed that the external and internal air-chamber formed by the cuticle ridges and each stoma thus opens into a cavity, the atmosphere of which remains undisturbed, and hence highly charged with water-vapor, however the surface of the leaf may be swept by air-currents.

The discrepancy of the reports on leaf anatomy of *Kandelia* was clarified in present study. The results showed that *K. candel* has dorsiventral leaves (Naskar and Mandal, 1999) whereas *K. obovata* has semi-isobilateral leaves (Chen, 1984; Chiang, 1984; Hsiao and Chen, 1988; Sheue *et al*., 2000). The dorsiventral leaf of *K. obovata* reported by Song (1960) from Taiwan was due to ignore the short lower palisade tissue, which is not distinct. *K. candel* from India reported having isobilateral leaves (Das and Ghose, 1996) is possibly resulted from misidentification of species. It might be owing to such misidentification, the stomata features (location, stomata type and stomata ridge) were also reported incorrectly (Das & Ghose, 1993).

As our field investigation, the leaves of *K. obovata* are mostly upward and reflexed, but the leaves of *K. candel* generally keep horizontal and less reflexed. In addition, *K. obovata* has semi-isobilateral leaves in natural habitat, while the abaxial palisade tissue reduced from 1-2 layered to 1-0 layered (almost dorsiventral leaves) in the leaves of plant cultivated in fresh water (Chiang, 1984). Furthermore, one of the examined leaves of *K. candel* was observed to have one-layered abaxial palisade cells. Therefore, the plasticity in the leaves of *Kandelia* is adaptively significant and worthy of a further study through the eyes of the plant physiologist and ecologist.

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紅樹林水筆仔屬 (*Kandelia*) 的托葉和葉片之形態

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摘　　要

本研究針對水筆仔屬 (*Kandelia*) 的印度水筆仔 (*K. candel*) 和水筆仔 (*K. obovata*) 之托葉及葉部形態和構造進行觀察及比較。本文釐清了前人研究結果中若干解剖特徵的分歧與矛盾處，包括氣孔分布、氣孔型、氣孔角質層突起、木痂疣和葉片結構。本屬的指狀腺體 (colleter) 具一小柄，於托葉向軸面基部聚集成三角形，托葉具遠軸面加厚，且無厚壁異形細胞。木痂疣偶爾零星地散布於葉上、下表面。水筆仔屬跨褶式 (obvolute) 的幼葉捲疊型 (vernation)、葉跡的形式和側脈夾角於兩種間的差異也被報導。

關鍵詞: 印度水筆仔、水筆仔、葉、托葉、形態。

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