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An Adaptive Feature of Some Mangroves of Sundarbans, West Bengal

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Mangrove taxa, apart from their morphological characters, have some unique leaf anatomical features which are very much related to their adaptation as the plants grow in unstable, variable and saline environments with regular tidal influence. Special stomatal structures with extended cuticles render the transpiration rate in many taxa. The presence of glandular and non-glandular hairs on the abaxial and/or adaxial leaf surfaces in some taxa are related to salt secretion of these plants. Comparatively large amounts of water storage tissues occur in the hypodermal or mesophyll tissue of the leaves, reflecting the adaptive nature of mangroves in their stressful habitat. The occurrence of terminal tracheids helps with capillary water storage within the leaf. The coriaceous nature of the leaves in some taxa is due to the presence of sclereids within the mesophyll region. It is noted that *Heritiera* is unsuitable to the highly saline habitat of the Sundarbans forest region because of some anatomical peculiarities.

Key words: Sundarbans, leaf anatomy, mangroves, adaptation

A typical mangrove formation embraces a peculiar assemblage of plant community, including shrubs and trees, dominating on low deltaic islands and sheltered estuaries where regular tidal influence of sea water prevails. These habitats are affected by humidity, precipitation, salinity, substrate, and temperature. Plants are well adapted to the changing biological, chemical and physical traits of this environment through various xeromorphic properties, including morphology, anatomy and physiology (Mullan, 1931a; Atkinson et al., 1967; Waisel, 1972; Zimmermann, 1983). Sundarbans, the largest block of mangrove forest in the world, is located between India and Bangladesh, and is formed by the two most important rivers of the subcontinent, namely the Ganga and the Brahmaputra. In the Indian part (western Sundarbans), the exact forest cover is merely $2300\ km^2$ and is traversed by a dense series of canals, creeks and rivers (Chanda and Dutta, 1986). Differential saline concentration prevails between the western and eastern zones of the Sundarbans as the sweet water influx in the west is much less and thus become more saline than that of the east (Chanda and Dutta, 1986). However, salinity of the water and soil has a direct influence on the leaf architecture of the plants (Chapman, 1976).

Certain aspects of leaf anatomical work have been investigated by several authors (Mullan, 1931a, 1931b; Wehe, 1964; Shah and Sunder Raj, 1965; Rao and Sharma, 1968; Rao, 1971; Chapman, 1976; Fahn and Shimony, 1977; Tomlinson, 1986; Seshavatharam and Srivalli, 1989; Das and Ghose, 1993, 1996). All those works provided mostly detailed descriptions of leaf anatomy but did not relate to the adaptive characteristics of the plants. This work was aimed at studying the adaptive significance of the plants in light of the leaf anatomy of 22 species of true mangroves from the Sundarbans delta of the Indian territory.

MATERIALS AND METHODS

Fresh leaf samples of 22 typical well-identified mangrove taxa belonging to 10 families were collected from different islands of the western part of the Sundarbans forest. Among the collected specimens, 20 belonged to dicotyledons species and the remaining two were monocotyledons. Hand sections were made at a position approximately half-way between the base and apex of a sector from one side of the lamina, stained with Toluidine blue O and mounted in 50% glycerine. Transverse sections 10-16 microns in thickness were prepared by rotary microtome and stained with safranin and fast green (Johansen, 1940; Sass, 1958). Camera lucida drawings (Figs. 1 and 2) and photomicrographs of some representative taxa are provided (Fig. 3). Thickness of leaf, cuticle, epidermal layer, and colorless water storage tissue were also measured The means and standard deviations of measurements were calculated based on an average of 15 transverse sections from each individual.

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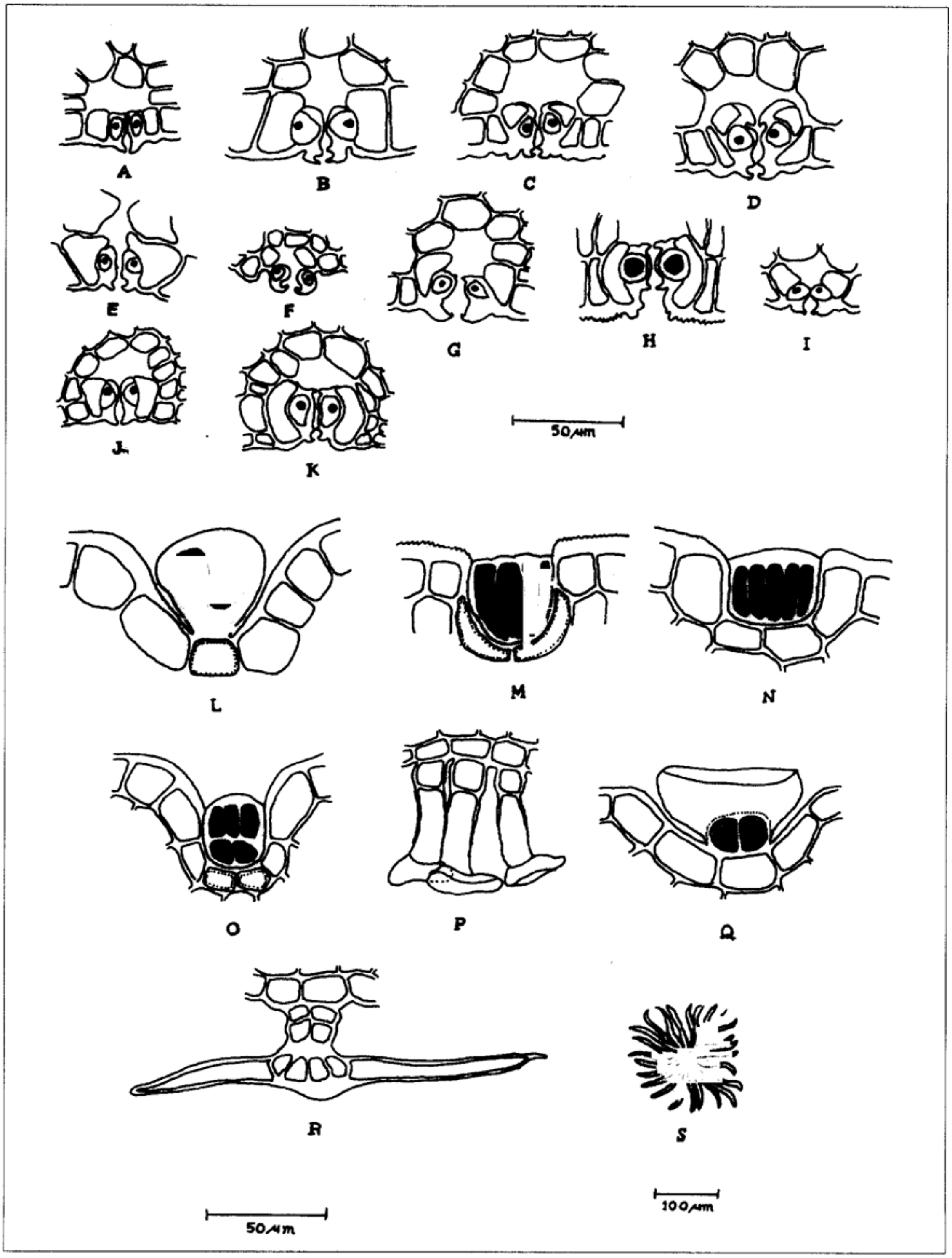

Figure 1. A - K, Sectional views of stomata. A, E, F, I, and J. with one outer ledge. **A.** *Acanthus ilicifolius*, **E.** *Excoecaria agallocha*, **F.** *Heritiera fomes*, **I.** *Xylocarpus granatum*, **J.** *Phoenix paludosa*; **B and C.** with two outer ledges - **B.** *Aegiceras corniculatum*, **C.** *Bruguiera gymnorrhiza*; **D and K.** with one inner and two outer ledges - **D.** *Ceriops decandra*, **K.** *Nypa fruticans*; **G and H** - with one inner and one outer ledge. **G.** *Rhizophora mucronata*, **H.** *Sonneratia apetala*. **L-O. Cross sectional views of glandular hairs. L.** *A.ilicifolius*, **M.** *Aegialitis rotundifolia*, **N.** *A.corniculatum*, **O.** *Avicennia alba*. **P-R. Cross sectional view of non-glandular hairs. P.** *A. alba*, **Q.** *A. ilicifolius*, **R.** *H. fomes*. **S. surface view.** *H. fomes*.

RESULTS

Two types of leaf hairs occur in some species, glandular (salt-secreting glands) and non-glandular. The glandular hairs are present on both the abaxial and adaxial surfaces in *Acanthus ilicifolius, Aegialitis rotundifolia, Aegiceras corniculatum* and *Avicennia* (Fig. 1, L-O) but are totally absent in the rest of the species. The non-glandular hairs develop only on the abaxial surface in *Avicennia* sp., *A. ilicifolius* and *Heritiera* sp. (Fig. 1, P-S).

The glandular hairs have one or two basal collecting cells, one or two stalk cells and a number of radially-arranged secretory cells, which are covered with a thin cuticle layer. Non-glandular hairs have a multicellular sclerotic body which distally produces a shield-like expanse of thin-walled cells or branched star-like cells in *Heritiera* (Fig. 1, R and S) or unbranched filamentous body in *Avicennia* (Fig. 1P and 3C).

In most cases, stomata are sunken in *Aegiceras, Bruguiera, Ceriops,* and *Sonneratia* with sub-stomatal chamber (Fig. 1, B-D, and H). Guard cells have cuticular beak-like outgrowths (ledges) on either the outer side or both outer and inner side of the stomatal pore in many species of *A. ilicifolius, A. corniculatum* (Fig. 3B), *Ceriops* sp., *Rhizophora* sp., *Sonneratia apetala* and *Nypa fruticans* (Fig. 1, A, D, G, H, K, and 3H). Stomata are usually restricted to the abaxial surface of dorsiventral leaves and are scattered throughout the lamina. In isolateral leaves, the stomata are equally distributed on both surfaces, and are arranged in longitudinal file along with the epidermal cells in *Kandelia candel*, and *S. apetala*. Though the leaf is isolateral, stomata are restricted to the abaxial surface in *Phoenix paludosa*.

Succulent leaves are a common feature of most mangroves. The highest leaf thicknesses occur in *K. candel* (1.6 mm), *Xylocarpus mekongensis* (0.94 mm) and *S. apetala* (0.9 mm) and lowest in *N. fruticans* (0.28 mm), *A. rotundifolia* (0.3 mm) and *Heritiera fomes* (0.37 mm). In most cases, lamina of mangrove plants are usually dorsiventral, but are isolateral in *K. candel, P. paludosa,* and *S. apetala* (Fig. 2, A-O).

The cuticle is considerably thick in *Bruguiera gymnorrhiza* (0.014 mm), *Avicennia officinalis* (0.009 mm), *Ceriops decandra* (0.009 mm), *K. candel* (0.009 mm) and *S. apetala* (0.009 mm) and thin in *A. corniculatum* (0.001 mm), *Heritiera littoralis, N. fruticans* (0.003 mm) and *P. paludosa* (0.003 mm). The cuticular surface is usually smooth except in *A. rotundifolia* and *S. apetala*, where it is uneven (Fig. 2, C and K). The cuticle layer is interrupted due to the presence of stellate hairs in *Heritiera* sp. and uniseriate capitate hairs on the abaxial epidermis of *Avicennia* sp. (Figs. 2, H, A, and 3C). The epidermis is always cutinized, either wholly in *A. corniculatum, Ceriops* sp. and *Rhizophora* sp. or only the outer tangential walls in *Avicennia* sp., *Bruguiera* sp. and *S. apetala*. The adaxial epidermal cells are often larger than those of the abaxial cells in *Avicennia* sp., *Bruguiera* sp., and *Heritiera* sp..

The hypodermis is composed of one or more layers of colorless cells below the adaxial epidermis. These colorless cells often function as water storage tissue. Four types of hypodermis have been distinguished based upon the number of hypodermal layers:

(i) Hypodermis is totally absent: *K. candel, S. apetala,* and *P. paludosa* (Figs. 2, J, K, N, and 3, F, I).

(ii) Hypodermis is one-layered, below the adaxial epidermis; cells are polygonal, cubical or narrow and sometimes extensively vertically elongated: *A. ilicifolius, Bruguiera* sp., *N. fruticans* and *X. mekongensis* (Figs. 2, D, F, M, O, and 3, A, G, D, L).

(iii) Hypodermis is two-layered, cells are polygonal and larger than the epidermal cells: *Ceriops* sp., *Heritiera* sp. (Figs. 2, E, H, and 3E).

(iv) Hypodermis is more than two-layered, cells are cubical or polygonal in transverse section, larger than epidermal cells: *Avicennia* sp., *A. corniculatum, A. rotundifolia, Excoecaria agallocha, Rhizophora* sp. and *Xylocarpus granatum* (Figs. 2, A - C, G, I, L, and 3, C, J, K).

The mesophyll is composed of thin-walled chlorenchymatous cells and is well differentiated in the dorsiventral leaf into one or more layers of adaxial anticlinally-extended palisade cells and oval- or round-shaped compact or loose abaxial isodiametric cells in *A. ilicifolius, A. corniculatum, Avicennia* sp., *Bruguiera* sp., *Ceriops* sp., *E. agallocha, N. fruticans, Rhizophora* sp. and *Xylocarpus* sp.. One, two, or even three layers of columnar palisade cells occur beneath each surface, and the middle cells are polygonal and colorless as in *K. candel* and *S. apetala*. The adaxial palisade cells in *Heritiera* sp. are very loosely arranged and their intercellular spaces are well developed. These colorless cells seem to function as water storage tissue. Mesophyll tissue often contains dark brown-colored tanniniferous cells in the lower hypodermal region in *Ceriops* sp., and in both upper and lower regions in *K. candel*. Large mucilage cells occur in the adaxial hypodermal region in *Bruguiera* sp. and *Rhizophora* sp., and beneath the epidermis in *S. apetala*. Laticiferous cells are common in the hypodermal region of *E. agallocha*. Crystalliferous cells are common in many species of *Bruguiera* sp., *Ceriops*

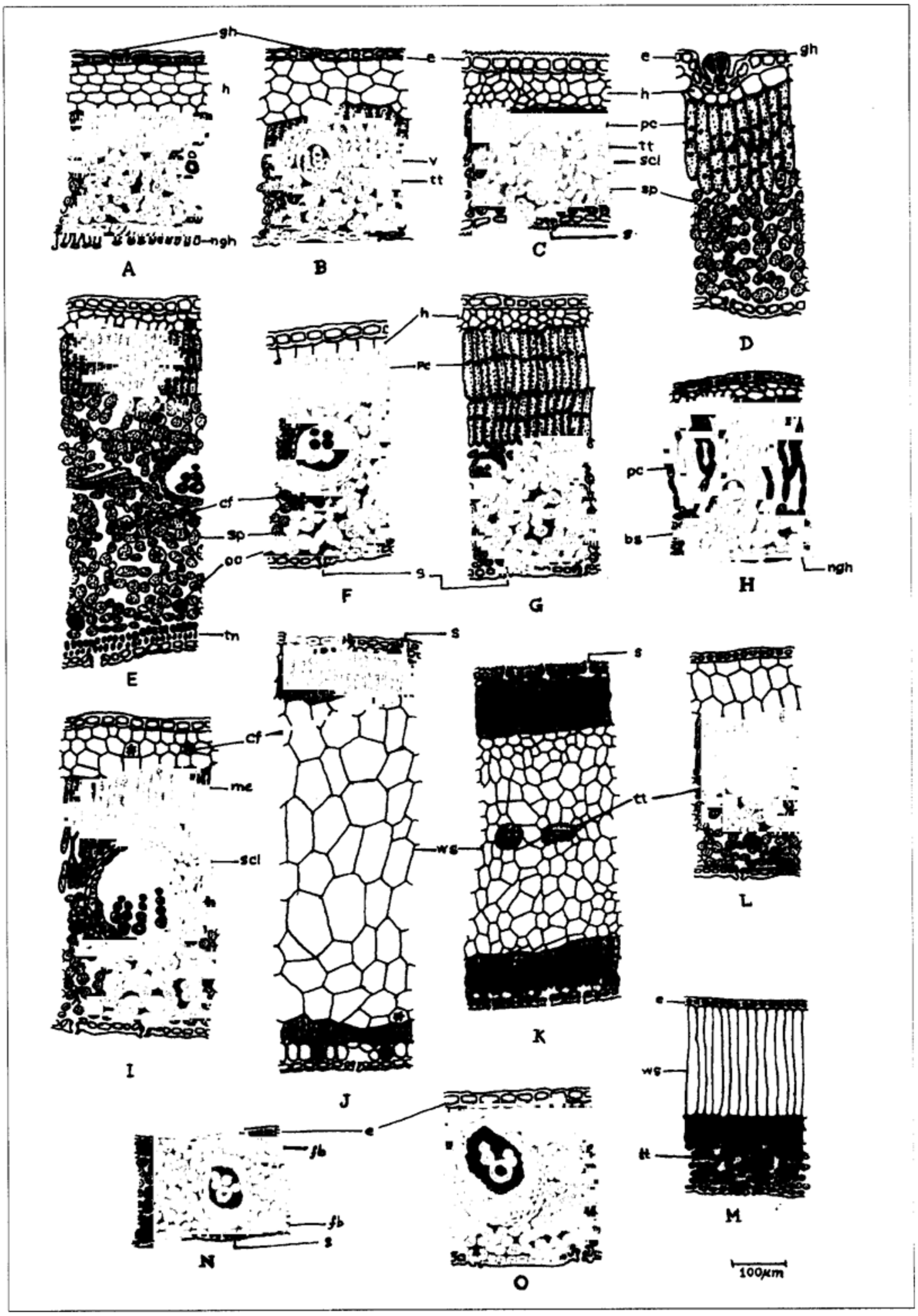

Figure 2. A-O. Camera lucida drawings of transverse sections of leaves showing typical anatomical features (**bs,** bundle sheeth; **cf,** crystalliferous cells; **e,** epidermal cells; **fb,** fibre bundle; **gh,** glandular hairs; **h,** hypodermis; **mc,** mucilagenous cell; **ngh,** non-glandular hairs; **oc,** oil cells; **pc,** palisade cells; **s,** stomata; **scl,** sclereids; **sp,** spongy parenchyma; **tn,** tannin cells; **tt,** terminal tracheids; **v,** vascular bundle; **ws,** water storage tissue). **A.** *A. alba*. **B.** *A. corniculatum*. **C.** *A. rotundifolia*. **D.** *A. ilicifolius*. **E.** *C. decandra*. **F.** *Bruguiera gymnorrhiza*. **G.** *E. agallocha*. **H.** *H. fomes*. **I.** *Rhizophora mucronata*. **J.** *K. candel*. **K.** *S. apetala*. **L.** *X. granatum*. **M.** *X. mekongensis*. **N.** *P. paludosa*. **O.** *N. fruticans*.

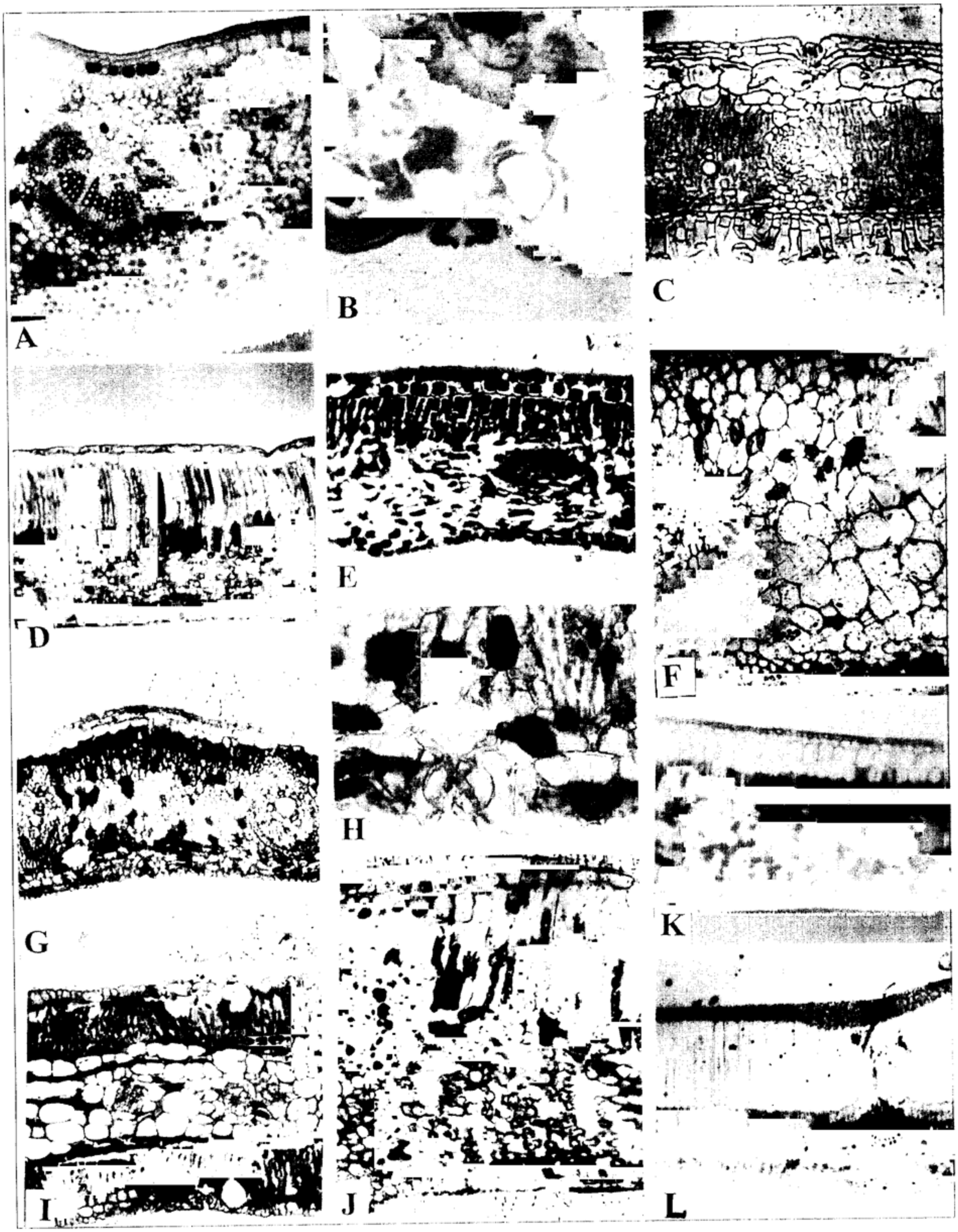

Figure 3. A-L. Photomicrographs of transverse sections of leaves and stomata. **A.** *Acanthus ilicifolius* (x65). **B.** *Aegiceras corniculatum*-sectional view of stomata (x450). **C.** *Avicennia marina* (x60) **D.** *B. gymnorrhiza* (x45). **E.** *C. decandra* (x32). **F.** *K. candel* (x30). **G and H.** *N. fruticans*. **G.** Leaf section (x75), **H.** Sectional view of stomata (x450). **I.** *S. apetala* (x33). **J.** *Rhizophora apiculata* (x68). **K.** *R. mucronata* (x42). **L.** *X. mekongensis* (x25).

sp., *E. agallocha, K. candel, Rhizophora* sp. and *Xylocarpus* sp..

Branched fibre-sclereids occur in a few species and are scattered in the mesophyll cells of *A. rotundifolia* and *R. mucronata* (Fig. 2, C and I). Fibre bundles are frequent in the hypodermal tissue of *P. paludosa* (Fig. 2N). Enlarged terminal tracheids are common in the mesophyll tissue of many species investigated, including *Avicennia* sp., *A. corniculatum, Bruguiera* sp., *Ceriops* sp. and *E. agallocha* (Fig. 2, A-B, and E-G).

DISCUSSION

The anatomical observations showed four common features in mangrove plants: (i) colorless water storage tissue, (ii) short terminal tracheids at vein endings, (iii) absence of sclerotic bundle sheaths, and (iv) sclereids of various shapes. Considerably thick cuticles are present on the epidermal layer of mangrove taxa, which also restricts non-stomatal water loss. This adaptive feature in mangrove plants was also supported by Waisel (1972). Due to the presence of colorless water storage tissue at different levels of mesophyll and hypodermal layers, mangrove leaves become thick and succulent, which can be correlated with the extra water storage capacity. Comparatively succulent leaves occur in those plants which usually grow in the slope region, where the tidal influence of sea water is maximal (twice a day), such as in *B. gymnorrhiza, C. decandra, Kandelia* and *Sonneratia*. Wehe (1964) has experimentally proven that the leaf succulence of mangroves increases with the increase of substrate salinity.

The glandular (salt-secreting) and non-glandular leaf hairs present in some taxa were investigated. In *Avicennia*, glandular hairs occur in both abaxial and adaxial surfaces of the leaf; on the adaxial side, the glandular hairs are sunken in densely-distributed crypts, whereas on the abaxial side they occur on the leaf surface and are distributed along with non-glandular hairs. Glandular hairs on both surfaces of the leaf occur in *Aegialitis*, but in *Aegiceras* it is restricted to the abaxial surface. The glandular hairs show some structural similarities in all of the above cases, such as having a basal cell, one or two cutinized stalk cells and a capitate group of terminal-radiating cells. Fahn and Shimony (1977) commented that in *Avicennia*, all glandular and non-glandular hairs are formed similarly up to the three-celled primordium stage, but after this two types of hairs start to appear. Osmand et al. (1969) experimentally showed that salt is secreted by the cytoplasm of the secretary cells into the large vacuole and that secretary cells dry out with the aging of the leaf and salt remains on the leaf surface as a white, powdery layer. Atkinson et al. (1967) provided experimental evidence that glandular hairs are responsible for secretary function in *Avicennia* and *Aegialitis*. Non-glandular hairs are only present on the abaxial surface of the leaf in *Avicennia* and *Heritiera*.

Table 1. Leaf anatomical characters of some mangrove taxa.

Sl no.	Name of the investigated taxa	Family	Leaf symmetry	Leaf	Thickness^1 and ± sd^2 of		
					Cuticle	Epidermis	Colorless zone^3
1	*Acanthus ilicifolius* L.	Acanthaceae	Dorsiventral	0.61±0.22	0.004±0.01	0.026±0.05	0.065±0.03
2	*Aegilitis rotundifolia* Roxb.	Plumbaginaceae	Dorsiventral	0.30±0.01	0.007±0.01	0.017±0.03	0.043±0.09
3	*Aegiceras corniculatum* (L.) Blanco	Myrsenaceae	Dorsiventral	0.37±0.13	0.001±0.04	0.072±0.03	0.082±0.07
4	*Avicennia alba* Blume.	Avicenniaceae	Dorsiventral	0.44±0.21	0.006±0.02	0.001±0.01	0.12 ±0.04
5	*Avicennia marina* (frosk.) Vierh.	Avicenniaceae	Dorsiventral	0.48±0.17	0.004±0.02	0.011±0.06	0.085±0.03
6	*Avicennia officinalis* L.	Avicenniaceae	Dorsiventral	0.41±0.11	0.009±0.05	0.019±0.08	0.10 ±0.03
7	*Bruguiera cylindrica* (L.) Bl.	Rhizophoraceae	Dorsiventral	0.39±0.23	0.006±0.05	0.015±0.05	0.12 ±0.04
8	*Bruguiera gymnorrhiza* (L.) Lamak.	Rhizophoraceae	Dorsiventral	0.54±0.42	0.014±0.07	0.018±0.02	0.027±0.03
9	*Bruguiera parviflora* W. & A.	Rhizophoraceae	Dorsiventral	0.55±0.56	0.006±0.06	0.01 ±0.03	0.037±0.03
10	*Ceriops decandra* (Griff.) Ding Hou.	Rhizophoraceae	Dorsiventral	0.70±0.63	0.009±0.03	0.017±0.02	0.097±0.02
11	*Ceriops tagal* (Pierr.) Robins	Rhizophoraceae	Dorsiventral	0.61±0.73	0.004±0.03	0.014±0.03	0.084±0.02
12	*Excoecaria agallocha* L.	Euphorbiaceae	Dorsiventral	0.50±0.49	0.006±0.07	0.014±0.04	0.045±0.04
13	*Heritiera fomes* Buch. Ham.	Sterculiaceae	Dorsiventral	0.37±0.62	0.005±0.05	0.019±0.03	0.037±0.02
14	*Heritiera littoralis* Dry.	Sterculiaceae	Dorsiventral	0.41±0.71	0.003±0.06	0.016±0.03	0.036±0.03
15	*Kandelia candel* (L.) Druce.	Rhizophoraceae	Isolateral	1.60±0.84	0.009±0.04	0.016±0.03	1.35 ±0.03
16	**Nypa fruticans* (Thunb.) Wurmb.	Arecaceae	Dorsiventral	0.28±0.42	0.003±0.03	0.006±0.02	0.14 ±0.05
17	**Phoenix pludosa* Roxb.	Arecaceae	Isolateral	0.22±0.38	0.003±0.02	0.006±0.02	–
18	*Rhizophora apiculata* Bl.	Rhizophoraceae	Dorsiventral	0.48±0.59	0.004±0.04	0.013±0.02	0.068±0.02
19	*Rhizophora mucronata* Lam.	Rhizophoraceae	Dorsiventral	0.54±0.47	0.006±0.03	0.015±0.05	0.074±0.02
20	*Sonneratia apetala* Buch. Ham.	Sonneratiaceae	Isolateral	0.90±0.68	0.009±0.03	0.015±0.04	0.54 ±0.02
21	*Xylocarpus granatum* Koning.	Meliaceae	Dorsiventral	0.49±0.51	0.006±0.02	0.015±0.03	0.10 ±0.03
22	*Xylocarpus mekongensis* Pierre.	Meliaceae	Dorsiventral	0.94±0.83	0.004±0.06	0.016±0.04	0.59 ±0.04

*monocot; 1-thickness measured in mm; 2-calculated on 15 random observations of each sample; 3-considering the colorless non-assimilatory zone.

In *Avicennia*, it the hair is a three-celled structure in which the basal cell is heavily cutinized like the adjacent epidermal cells and the terminal cell has a thin cuticle. Stellate, multicellular hairs densely occur in *Heritiera*. Metcalfe and Chalk (1950) suggested the adaptive significance of glandular and non-glandular hairs in *Avicennia*. The salt-secreting mechanism of the above taxa and the occurrence of epidermal hairs are very much important in relation to their adaptive nature.

In the dorsiventral leaf, stomata occur only on the abaxial surface, but in the isolateral leaf, stomata are on both surfaces in *K. candel* and *S. apetala* but not in *P. paludosa*. Most of the mangroves have sunken stomata, but not *A. ilicifolius*, *A. rotundifolia*, *A. corniculatum* or *Xylocarpus* sp. (Das and Ghose, 1993). The depth to which stomata are sunken may depend on the leaf age (Chapman, 1976). Mullan (1931a) observed that the stomata are not depressed in young leaves of *S. apetala*.

Sclereids of different shape occur in *Rhizophora* sp. and *A. rotundifolia* and terminal tracheids are common in *Avicennia* sp., *A. corniculatum*, *Bruguiera* sp., *Ceriops* sp. and *E. agallocha*. These features can be interpreted as adaptive characters of the mangroves since the terminal tracheids provide mechanical support to the leaves and capillary water storage function (Zimmermann, 1983). Tomlinson (1986) has suggested that in addition to water storage, sclereids might also provide mechanical support to leaves with diminished turgor, or discourage herbivores. The coriaceous nature of many mangrove leaves is probably due to presence of these sclereids.

It is interesting to note that *Heritiera* sp. possesses some anatomical features which do not help with adaptation to its habitat, for example, the presence of the highest number of stomata per unit area (Das and Ghose, 1993), a thin cuticle interrupted by stellate hairs, an almost absence of water storage tissue, loosely-arranged mesophyll tissue, extensive bundle sheath extension up to both hypodermal tissue layers, and poor presence of chlorenchyma cells. All these features indicate that *Heritiera* sp. is unsuitable to the highly saline habitat of the Sundarbans. A somewhat similar situation is also noticed in *N. fruticans* and *P. paludosa*.

The saline conditions of water and soil have direct impact on the succession of vegetation as evident in mangrove swamps. Troup (1926) explained that edaphic forest formations are well represented in India with instances of mangroves and tidal forests of littoral regions in which water happens to be the controlling factor. The eastern part of Sundarbans receives comparatively huge amounts of fresh water from the Ganga-Brahmaputra system and its tributaries, but the western Sundarbans receives much less fresh water because of the river Hooghly (Ganga) which serves the purpose of local drainage, heavy silt deposition in the river bed and the southern extremities which act as arms of the sea. Consequently, the western part is more saline and does not accumulate silt to the same extent as the eastern Sundarbans. Chanda and Dutta (1986) have opined that the impact of the changed circumstances has proved disastrous for the two major species, *N. fruticans* and *H. fomes*, which have become very rare in the western part of the delta but are still found growing well along the water course in Bangladesh. The leaf anatomical features can also explain why these two species are not in equilibrium with the present environment of the western Sundarbans .

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LITERATURE CITED

Atkinson MR, Findlay GP, Hope AB, Pitman MG, Saddler HDW, West KR (1967) Salt regulation in the mangrove *Rhizophora mucronata* Lam. and *Aegialitis annulata* R. Br Aust J Biol Sci 20: 589-599

Chanda S, Datta SC (1986) Prospects and problems of a mangrove ecosystem in western Sundarbans (India). Trans Bose Res Inst 49: 47-57

Chapman VJ (1976) Mangrove vegetation. J Cramer, Valduz, Germany

Das S, Ghose M (1993) Morphology of stomata and leaf hairs of some halophytes from Sundarbans, West Bengal. Phytomorphology 43: 59-70

Das S, Ghose M (1996) Anatomy of leaves of some mangroves and their associates from Sundarbans (West Bengal). Phytomorphology 46: 139-150

Fahn A, Shimony C (1977) Development of the glandular and non-glandular leaf hairs of *Avicennia marina* (Forssk.) Vierh Bot J Linn Soc 74: 37-46

Johansen DA (1940) Plant microtechnique. McGraw Hill Book Company, New York, p 523

Metcalfe CR, Chalk L (1950) Anatomy of the dicotyledons, Vols.1 and 2, Oxford Univ Press

Mullan DP (1931a) Observations on the water storing device in the leaves of some Indian halophytes. J Ind Bot Soc 10: 126-132

Mullan DP (1931b) On the occurrence of glandular hairs (salt glands) on the leaves of some Indian halophytes. J Ind Bot Soc 10: 184-209

Osmand CB, Luttge U, West KR, Pallaghy CK, Shacher-Hill B (1969) Ion absorption in *Artiplex* leaf tissue: II, secretion of ions to epidermal bladders. Aust J Biol Sci 22: 797-814

Rao AN (1971) Morphology and morphogenesis of foliar sclereids in *Aegiceras corniculatum*. Isr J Bot 20: 124-132

Rao AR, Sharma M (1968) The terminal sclereids and tracheids of *Bruguiera gymnorrhiza* Blume. and the cauline sclereids of *Ceriops roxburghiana* Arn. Proc Natl Sci India 34B No. 6: 267-275

Sass JE (1958) Botanical microtechnique. The Iowa State College Press, Ames, Iowa, USA, p 228

Shah JJ, Sunder Raj KP (1965) Stipular sclereids in *Rhizophora mucronata*. Curr Sci 5: 155

Seshavatharan V, Srivalli M (1989) Systematic leaf anatomy of some Indian mangroves. Proc Ind Acad Sci (Plant Sci) 99: 557-565

Tomlinson PB (1986) The botany of mangroves. Cambridge University Press, Cambridge, New York, p 413

Troup RS (1926) Problems of forest ecology in India. *In* Aims and methods in the study of vegetation (Tansley, AG, Chipp TF eds.), London

Waisel Y (1972) Biology of Halophytes. Academic Press, New York

Wehe V (1964) Beitrage zur Okologie der mittle und west-europaischen Salzgetation (Gezeitenkusten). I Biet Biol Pflanzen 39: 189-237

Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer-Verlag, Berlin