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MORPHOLOGY OF STOMATA AND LEAF HAIRS OF SOME HALOPHYTES FROM SUNDARBANS, WEST BENGAL[1]

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Abstract

Stomatal morphology and their types have some taxonomic interest. The occurrence of glandular and non-glandular leaf hairs reflect a unique adaptive characteristics in the mangrove plants. Out of the twenty nine investigated species, belonging to seventeen families, twenty two are considered as true mangroves and seven are obligate mangroves. Six types of stomata, depending on the arrangement of the guard cells vis-à-vis subsidiary cells, are present. In most, a horn or beak-like cuticular outgrowth is found either on the outer or on both inner and outer side of the stomatal pore. Such structural modification suggests some additional resistance to the stomatal transpiration and perhaps could also be correlated with the ecological habitat. Stomatal frequency, index and size have been recorded. Morphology of different types of glandular and non-glandular leaf hairs has also been studied.

Key Words : Mangrove, stomatal frequency and index, morphology, glandular and non-glandular hair.

Sundarban mangrove forest constitute the largest of all such formations in a single block in the world, which is formed by two important rivers of this subcontinent, the Ganga and the Brahmaputra. This forest extends about 14, 600 sq km; only one-third of this part is included in West Bengal (India) while the remaining two-third extends to Bangladesh (Banarjee 1964). The delta is traversed by a large number of creeks and canals. It is geographically much dynamic and the rate of delta formation is rapid (Morgan & McIntire 1959). Loamy soil surface mixed with clay has good water holding capacity. Varied precipitation, high humidity, moderate rainfall, and saline water and soil create a unique situation for successful propagation of mangrove vegetation. Some typical halophytic characteristics are found in the plants and the vegetation is very much localised within the same genus due to some ecological and physiological factors.

Early works on mangrove vegetation, mainly on ecological and physiological aspects, were those of Prain (1903), Mukherjee (1972), Mukherjee & Chanda (1973), Blasco et al. (1974), Ball & Farquhar (1984), Tomlinson (1986), Naskar & GuhaBakshi (1987).

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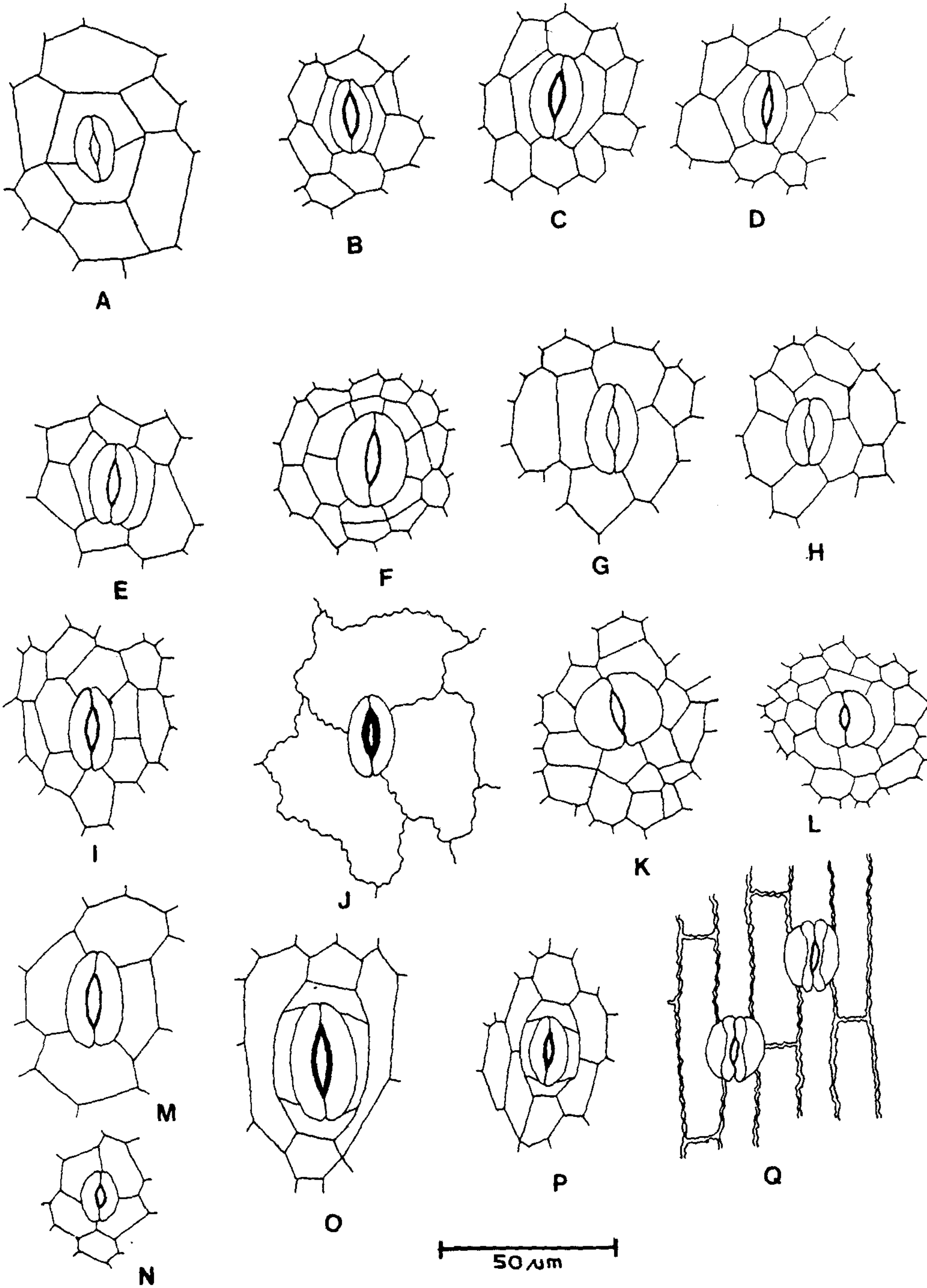

Fig. 1A-Q

No detailed anatomical and morphological work on Sundarban mangroves has been published so far though some accounts on mangrove leaves and their morphological sketches were published by Areschoug (1902), Mullan (1931), Walter & Steiner (1936), Biebl & Kinzel (1965), Stace (1965, 1966) and Chapman (1976). Fahn & Shimony (1977) studied development of glandular and non-glandular hairs of *Avicennia marina*.

In this paper an effort has been made to correlate the structural types and frequencies of mature stomata and any special morphological characteristics with the ecological conditions, if any. The morphology of epidermal appendages such as glandular and non-glandular hairs of leaves are also described.

Materials and Methods

Twenty nine species of mangrove taxa (Table 1) belonging to 17 families were collected from different islands of Sundarbans of West Bengal, namely, Sajnakhali, Pirkhali, Sudhanyakhali, Netidhopani, etc. Out of the 29 species, 22 are recognised as true mangroves and seven are "obligate mangroves associates" (Tomlinson 1986).

Epidermal peelings of lamina were prepared from mature leaves of the plants. A portion of the lamina, about 5 mm sq was cut from the mid portion of the leaf excluding the midrib, and finally obtained the peels according to the method described elsewhere (Ghose & Davis 1973). For sectional views of the stomata, and glandular and non-glandular hairs thin hand sections of the lamina were cut and stained with Toluidine blue O and mounted in 50% glycerine. The structural details of glandular and non-glandular hairs, stomatal types and morphology were studied with a binocular Olympus microscope. All the diagrams were made with the help of a camera lucida. The quantitative data on frequency and size of guard cells and other epidermal cells were based on an average of 10 random observations.

Observations

OCCURRENCE OF STOMATAL TYPES — Most of the typical mangroves have stomata on the abaxial surface of lamina, except *Kandelia candel*, *Sonneratia apetala*, *Heliotropium curassavicum*, *Sesuvium portulacastrum*, *Suaeda maritima* and *Porteresia coarctata* which have stomata on both adaxial and abaxial surfaces. The anomocytic type of stomata occurs in most of the plants, and paracytic type in *Aegiceras corniculatum*, *Ceriops decandra*. *B. cylindrica*, and *Suaeda maritima* (Figs. 1B-E, 4D,E). Cyclocytic type occurs only in *Rhizophora mucronata* (Figs 1F, 4G) where the two guard cells are encircled by a ring of 6-8 subsidiary cells and diacytic type occurs in *Acanthus ilicifolius* (Figs 1A, 4A). Monocot type 2 and type 3 (Stebbins & Khush 1961) or tetracytic and paracytic type (Metcalfe 1961)

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Fig. 1A-Q — Stomatal types of the abaxial surface of leaves. A. Diacytic type. *Acanthus ilicifolius*. B-E. Paracytic type. B. *Aegiceras corniculatum*. C. *Ceriops decandra*. D. *Bruguiera gymnorrhiza*. E. *B. cylindrica*. F. Cyclocytic type. *Rhizophora mucronata*. G-N. Anomocytic type. G. *Aegialitis rotundifolia*. H. *Avicennia alba*. I. *Sonneratia apetala*. J. *Excoecaria agallocha*. K. *Heritiera fomes*. L. *H. littoralis*. M. *Kandelia candel*. N. *Xylocarpus granatum*. O,P. Monocot I (tetracytic). O. *Nypa fruticans*. P. *Phoenix paludosa*. Q. Monocot II (paracytic). *Porteresia coarctata*.

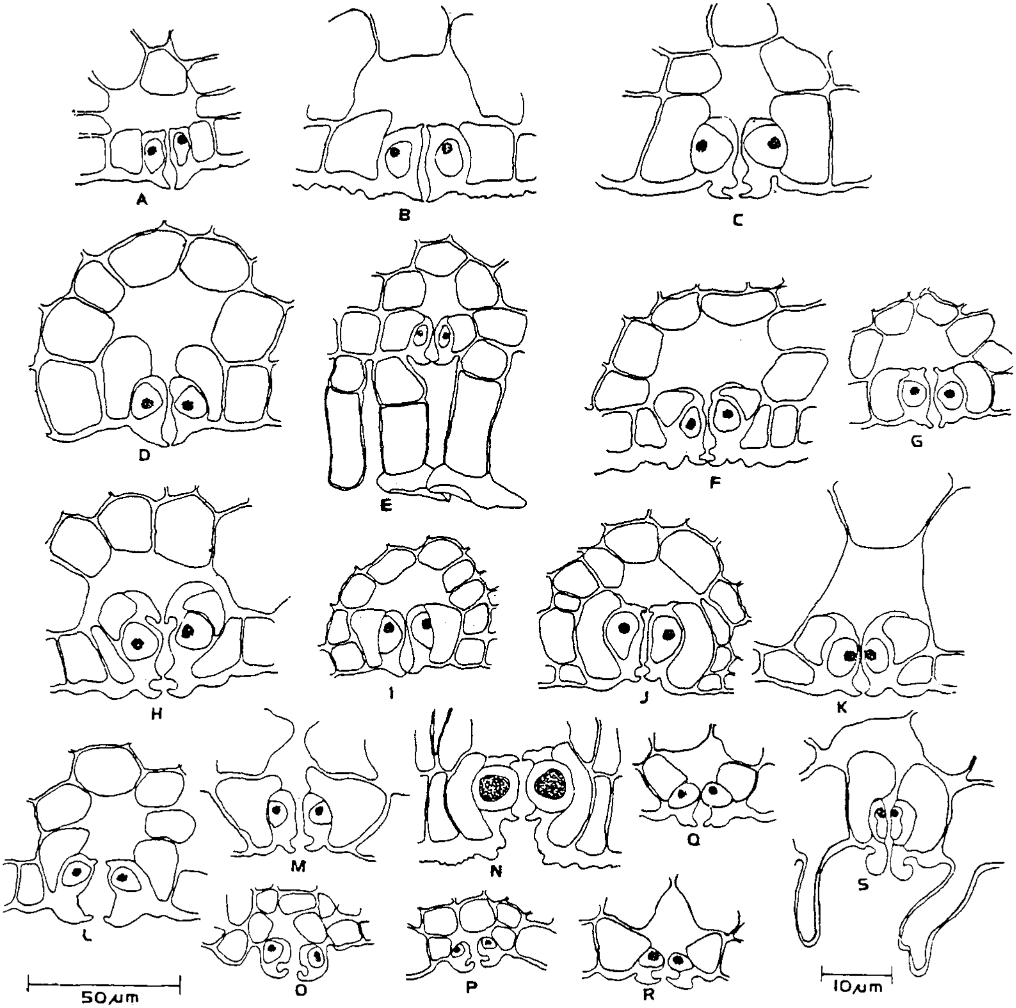

Fig. 2A-S — Sectional views of stomata. **A,D,E,I,K,O-S.** With one outer ledge. **A.** *A. ilicifolius* **D.** *Allamanda cathartica.* **E.** *Avicennia alba.* **I.** *P. paludosa.* **K.** *K. candel.* **M.** *E. agallocha.* **O.** *H. fomes.* **P.** *H. littoralis.* **Q.** *X. granatum.* **R.** *X. mekongensis.* **S.** *P. coarctata.* **B,G,L,N.** With one outer and one inner ledge. **B.** *A. rotundifolia.* **G.** *Derris trifoliata.* **L.** *R. mucronata.* **N.** *S. apetala.* **C.** With two outer ledges. *A. corniculatum.* **F,H,J.** With two outer and one inner ledges. **F.** *B. gymnorrhiza.* **H.** *C. decandra.* **J.** *N. fruticans.*

Fig. 3A-R — Sectional and surface views of glandular and non-glandular leaf hairs. **A-J.** Glandular hairs. **A.** *A. ilicifolius.* Note two basal cells and four radiating terminal cells. **B.** *A. rotundifolia,* showing eight radiating cells arranged in a cup shaped crypt. **C.** *C. inerme* showing two basal and eight terminal cells. **D.** *A corniculatum,* showing eight radiating cells. **E,F.** *A. alba.* **E.** Upper surface. **F.** Lower surface. **G,H.** *A. marina.* **G.** Upper surface. **H.** Lower surface. **K-R.** Non-glandular hairs. **K.** *A. ilicifolius.* **L.** *A. alba.* **M.** *A marina.* **N.** *C. inerme.* **O.** *H. fomes.* **P.** *H. littoralis.* **Q.** *H. fomes,* surface view. **R.** *P. coarctata.*

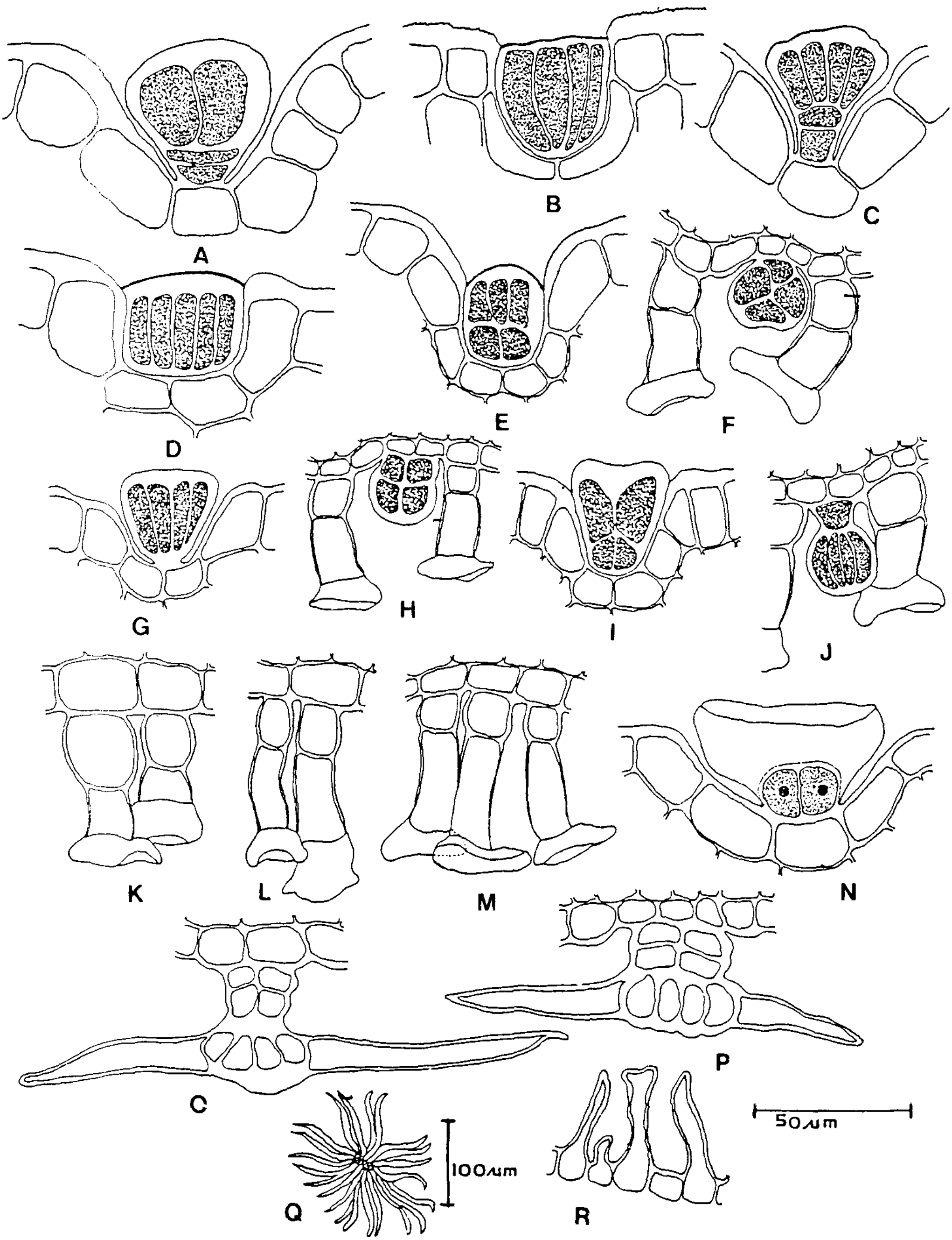

Fig. 3A-R

of stomata occur in the Palmae (*Phoenix paludosa* and *Nypa fruticans*) and Poaceae (*Porteresia coarctata*) respectively (Figs 1O-Q, 4C,F). The anomocytic stomata are surrounded by 4-6 epidermal cells without any definite orientation with respect to guard cells (Figs 1G-N, 4B). In paracytic type, the two subsidiary cells border the guard cells in parallel with the long axis of the pore e.g. *A. corniculatum, C. decandra*. In *Nypa* and *Phoenix* (Palmae), (type-2, monocot), the guard cells are surrounded by four subsidiary cells of which the two square-shaped polar cells slightly overarch the guard cells, and lateral two cells are comparatively longer lying parallel to the guard cells. The guard cells of all the taxa, except *Porteresia*, are kidney-shaped with thinner dorsal wall. In *Porteresia* (Figs 1Q, 4F) the guard cells are dumb-bell shaped (type-3, monocot); the polar ends are swollen and thin-walled but middle portion is narrow and thick-walled. In *Nypa, Phoenix* and *Porteresia* the stomata are arranged in the longitudinal files along the long axis of the lamina, but in other mangroves the stomata are scattered.

Most of the true mangroves have sunken stomata with substomatal chamber, but non-sunken stomata are observed in *Acanthus, Aegialitis, Aegiceras*, and *Xylocarpus* (Fig. 2A-C,O-R). The mangrove associates such as *Allamanda cathartica, Clerodendrum inerme, Derris trifoliata, Heliotropium curassavicum, Sesuvium portulacastrum*, and *Suaeda maritima* also show non-sunken stomata (Fig. 2D, G). Most of the taxa, specially true mangroves, have a beak-like cuticular outgrowth (ledge) either on the outer side or both outer and inner side of the stomatal pore (Fig. 2F, H-P). In the members of the family Rhizophoraceae, these ledges are observed on both sides of the stomatal pore. *Ceriops* spp. and *Bruguiera gymnorrhiza* (not *B. cylindrica* and *B. parviflora*), show two distinct ledges above the stomatal pore, and thus a clear upper chamber is formed (Fig. 2 F,H). Sunken stomata with prominent horn-like ledges on both sides are present in *Sonneratia apetala* (Fig. 2M). Dense hair covering found on the stomata of *Avicennia, Heritiera* and *Porteresia* make observations very difficult. In *Phoenix* and *Nypa* (Arecaceae), the two lateral subsidiary cells are comparatively longer than the polar ones (Fig. 2'I,J). The cuticular ledges in *Phoenix* are found only at the outer face of the stomatal pore, but in *Nypa*, they are present both on outer and inner side of the pore, and also in between the outer and inner ledges. The guard cells of *Porteresia coarctata* (Figs 1Q, 2R) are dumb-bell shaped from surface view, and in sectional view the two guard cells and the two subsidiary cells are crowned with a pair of pillate-shaped ledges on the outer side of the stomatal pore. The stomatal complex is hidden within the epidermal hairs.

QUANTITATIVE OBSERVATION OF THE STOMATAL COMPLEX — The maximum number of stomata (Table 1) per sq mm area occurs in the genus *Heritiera* (176.86 and 168.28) and *Xylocarpus mekongensis* (167.71), and minimum in *Heliotropium curassavicum* (16.0) and *Suaeda maritima* (11.71). The highest stomatal index is found in *Heritiera littoralis* (38.0) followed by *Acanthus ilicifolius* (27. 59) but the lowest in *Sonneratia apetala* (2.7) and *Rhizophora mucronata* (3.13). The width of the guard cell is higher than the length in *Heritiera*. Longest guard cells occur in *Nypa* (57.11 μm). The maximum number of epidermal cells per sq mm occurs in *Xylocarpus granatum* (1350.57) and *Rhizophora apiculata* (1168.28) and minimum in *Sesuvium* (45.43) and *Suaeda* (46.0), (Table 2). The smallest and the largest size of epidermal cells occur in *Xylocarpus mekongensis* (12.44 μm x 8.65 μm) and *Sesuvium portulacastrum* (111.83 μm x 82.18 μm), respectively.

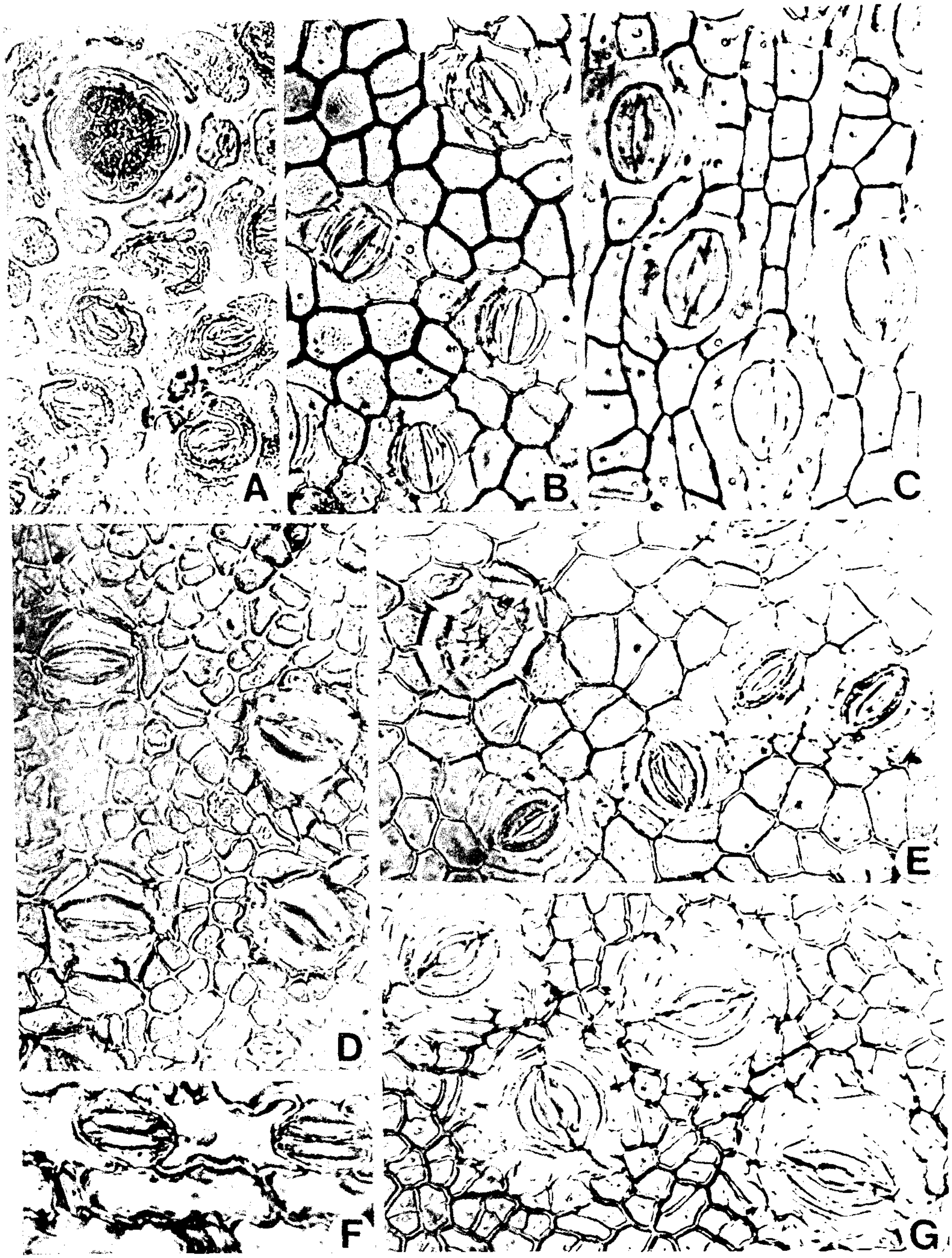

Fig. 4A-G — Photomicrographs of stomata and trichomes in surface views. **A.** *A. ilicifolius*. Diacytic type. x 310. **B.** *B. gymnorrhiza*. Anomocytic type. x 250. **C.** *N. fruticans*. Monocot type I or tetracytic type. x 230. **D.** *C. decandra*. Paracytic type. x 310. **E.** *A. corniculatum*. Paracytic type. x 230, **F.** *P. coarctata*. Monocot type II or paracytic type. x 425. **G.** *R. mucronata*. Cyclocytic type. x 310.

TABLE 1 — STOMATAL INDEX, FREQUENCY AND SIZE OF THE STOMATA

SL. No.	NAME OF THE TAXA	STOMATAL INDEX	FREQUENCY/ mm^2 ± S E	Size (μm) LENGTH ± S E	WIDTH ± S E
	MONOCOTYLEDON				
1.	*Nypa fruticans* (Thunb.) Wurmb.	6.35	37.14±0.73	57.11±0.21	33.07±0.34
2.	*Phoenix paludosa* Roxb.	6.82	78.26±1.06	35.57±0.24	22.57±0.16
3.	*Porteresia coarctata* (Roxb.), Takeoka	8.84	22.00±0.74	30.44±0.27	21.89±0.16
	DICOTYLEDON: Herb/ Twiner				
4.	*Allamanda cathartica* L.	10.28	38.28±0.82	47.19±0.35	32.14±0.30
5.	*Clerodendrum inerme* (L.) Gaertn.	12.69	16.00±0.63	30.78±0.21	24.28±0.23
6.	*Derris trifoliata* Lour.	10.74	77.42±1.48	36.92±0.29	18.12±0.20
7.	*Heliotropium curassavicum* L.	19.85	22.26±0.68	32.18±0.68	20.86±0.26
8.	*Sesuvium portulacastrum* L.	26.73	16.57±0.71	47.20±0.25	35.91±0.34
9.	*Suaeda maritima* Dumort.	20.80	11.71±0.66	43.78±0.25	27.70±0.28
	Shrub/Tree				
10.	*Acanthus ilicifolius* L.	27.59	58.85±1.35	25.90±0.20	17.10±0.21
11.	*Aegialitis rotundifolia* Roxb.	6.54	37.71±1.26	40.26±0.25	25.91±0.16
12.	*Aegiceras corniculatum (L.)* Blanco	6.88	40.60±1.06	47.80±0.26	21.35±0.21
13.	*Avicennia alba* Bl.	6.05	34.85±0.67	35.57±0.16	24.62±0.25
14.	*A. marina* (Forsk.) Vierh.	10.46	63.14±0.75	28.73±0.16	21.20±0.13
15.	*A. officinalis* L.	12.10	72.06±1.02	30.10±0.02	22.57±0.29
16.	*Bruguiera cylindrica* (L.) Bl.	5.99	36.28±0.71	32.83±0.16	23.25±0.20
17.	*B. gymnorrhiza* (L.) Lam.	7.91	30.86±0.93	39.00±0.37	19.15±0.22
18.	*B. parviflora* W. & A.	9.89	32.89±0.95	37.65±0.36	17.14±0.24
19.	*Ceriops decandra* (Griff.) Ding Hou	5.01	38.28±0.83	43.78±0.25	23.26±0.30
20.	*C. tagal* (Perr.) Robins.	4.71	34.75±0.93	37.62±0.27	22.91±0.23
21.	*Excoecaria agallocha* L.	17.66	54.00±1.56	31.12±0.18	16.07±0.21

Table 1 Continued →

22.	*Heritiera fomes* Buch. Ham.	22.26	168.28±1.84	22.57±0.20	30.40±0.23
23.	*H. littoralis* Dry.	30.00	176.86±1.04	19.83±0.20	23.94±0.40
24.	*Kandelia candel* (L.) Druce.	8.84	37.14±1.23	30.78±0.30	18.46±0.16
25.	*Rhizophora apiculata* Bl.	6.00	23.14±0.79	27.71±0.26	15.73±0.15
26.	*R. mucronata* Lam.	3.13	24.28±0.93	49.60±0.17	30.78±0.20
27.	*Sonneratia apetala* Buch. Ham.	2.70	22.28±0.71	31.12±0.18	21.55±0.15
28.	*Xylocarpus granatum* König.	7.57	62.00±1.65	35.91±0.17	25.65±0.29
29.	*X. mekongensis* Pierre	12.07	167.71±1.52	23.60±0.23	17.40±0.29

S E - Standard error

OCCURRENCE OF GLANDULAR AND NON-GLANDULAR HAIRS — Leaf epidermal hairs occur in *Avicennia, Aegialitis, Aegiceras, Clerodendrum, Heritiera* and *Porteresia* (Fig. 3A-R). Glandular hairs (salt secreting glands) are present both on adaxial and abaxial leaf surfaces in all the taxa except *Aegiceras* where it is found only on abaxail surface (Fig. 3D). Non-glandular hairs are present in *Avicennia* and *Heritiera* on abaxial surface only (Fig. 3K-R). Densely distributed stellate multicellular hairs with a basal stalk have been observed in *Heritiera* (Fig. 3P-R). Salt-secreting glandular hairs are met with in *Aegialitis, Aegiceras, Acanthus* and *Clerodendrum*; they are always sunk in well distributed crypts (Fig. 3A-D). Both glandular and non-glandular hairs are observed in the leaves of *Avicennia* and *Clerodendrum*. In *Avicennia* the glandular hairs are sunk in the crypts on adaxial surface (Fig. 3E-J), but on abaxial side they occur above the leaf surface and are distributed among the non-glandular hairs. In *Avicennia marina* and *A. alba*, pear-shaped glandular hairs with 8-12 radially arranged secretory cells are present (Fig. 3E-H), but in *A. officinalis*, a prominent stalk cell and 6-12 radiating secretory cells are present (Fig. 3I,J). The glandular hair of *Acanthus* has 2 short basal cells and 4 large radially arranged cells which are enclosed in a large vacuole (Fig. 3A). *Clerodendrum inerme* shows the glandular hair having linearly arranged 2 stalked cells and 8-12 radially arranged secretory cells enclosed by the cuticular layer (Fig. 3C) whereas non-glandular hair comprises 2 basal cells and a large cup-shaped vacuolated cell (Fig. 3N). Non-glandular hairs in *Avicennia* are present only on the abaxial surface. These are 3-celled structures with a terminal axe-shaped cell and the basal cell is strongly cutinized like the other adjacent epidermal cells (Fig. 3K-M). Simple unicellular non-glandular hair is observed in *Porteresia* (Fig. 3R). The cuticle is very thin in terminal cells of the non-glandular hairs, but it is heavily cutinized in glandular hairs.

Discussion

The above observations reveal that six types of mature stomata occur in the mangroves of Sundarbans. Anomocytic type is very frequent, though paracytic, diacytic, cyclocytic, monocot type 2 (tetracytic) and type 3 (paracytic) are also present. Tomlinson (1986)

TABLE 2 — FREQUENCY AND SIZE OF THE EPIDERMAL CELLS

SL. NO.	NAME OF THE TAXA	FREQUENCY/ mm^2 ± S E	Size (µm)	
			LENGTH ± S E	WIDTH ± S E
1.	*Acanthus ilicifolius L.*	213.71±0.85	43.09±0.25	23.94±0.25
2.	*Aegialitis rotundifolia* Roxb.	322.57±0.90	35.11±0.40	22.91±0.25
3.	*Aegiceras corniculatum* (L.) Blanco	544.71±1.75	30.78±0.78	19.38±0.18
4.	*Allamanda cathartica* L.	344.00±0.80	28.04±0.35	21.54±0.39
5.	*Avicennia alba* Bl.	541.14±0.82	29.70±0.15	20.52±0.24
6.	*A. marina* (Forsk.) Vierh.	513.14±0.75	31.80±0.20	25.90±0.15
7.	*A. officinalis L.*	527.43±0.97	19.83±0.18	15.39±0.15
8.	*Bruguiera cylindrica* (L.) Bl.	529.28±1.07	25.65±0.21	17.44±0.33
9.	*B. gymnorrhiza* (L.) Lam.	523.14±1.27	27.70±0.26	20.86±0.22
10.	*B. parviflora* W. & A.	532.13±1.28	24.68±0.30	21.80±0.18
11.	*Ceriops decandra* (Griff.) Ding Hou	725.71±1.95	25.99±0.23	18.46±0.20
12.	*C. tagal* (Perr.) Robins.	779.43±1.69	16.24±0.25	11.63±0.16
13.	*Clerodendrum inerme* (L.) Gaertn.	90.00±0.75	51.30±0.49	38.65±0.30
14.	*Derris trifoliata* Lour.	642.86±0.98	33.85±0.58	15.39±0.26
15.	*Excoecaria agallocha* L.	251.76±1.06	34.88±0.23	24.96±0.20
16.	*Heliotropium curassavicum* L.	130.57±0.57	78.66±0.14	40.69±0.22
17.	*Heritiera fomes* Buch. Ham.	511.71±1.15	14.97±0.30	12.83±0.20
18.	*H. littoralis* Dry.	288.57±0.86	11.46±0.24	10.06±0.18
19.	*Kandelia candel* (L.) Druce.	382.86±1.10	33.17±0.53	23.59±0.64
20.	*Nypa fruticans (Thunb.) Wurmb.*	335.71±0.98	35.51±0.53	15.39±0.21
21.	*Phoenix paludosa* Roxb.	806.28±1.39	19.15±0.15	9.32±0.20
22.	*Porteresia coarctata* (Roxb.) Takeoka.	324.28±0.82	57.11±0.34	9.91±0.17
23.	*Rhizophora apiculata* Bl.	1168.28±1.01	18.12±0.20	11.62±0.15
24.	*R. mucronata* Lam.	840.00±2.00	15.0±0.79	9.87±0.43
25.	*Sesuvium portulacastrum* L.	45.43±0.74	111.83±0.92	82.18±0.15

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Table 2 Continued

26.	*Sonneratia apetala* Buch. Ham.	804.57±1.16	22.23±0.33	15.39±0.25
27.	*Suaeda maritima* Dumort.	46.00±0.31	101.89±0.56	69.95±0.58
28.	*Xylocarpus granatum* Köenig.	1350.57±1.54	17.65±0.20	10.55±0.21
29.	*X. mekongensis* Pierre	956.86±0.81	12.44±0.22	8.65±0.14

S E - Standard error

suggested that there is no high degree of specialization of stomatal types among the mangrove taxa. Areschoug (1902) pointed out that only the thick cuticle, and, the sunken and chambered stomata were related to water conservation as the plants suffer from physiological draught. Most of the true mangrove species have sunken stomata, but exceptions also exist in case of *Avicennia, Acanthus, Xylocarpus, Phoenix* and *Nypa*.

All the true mangroves and some mangrove associates show some cuticular protuberances on the guard cells present above or both above and below the stomatal aperture. In cross-sections these protuberances appear as horn-shaped ledges. These prominent or even elaborated ledges seem to act as increased resistance to stomatal transpiration and might be correlated with the adaptive characteristics of the typical mangrove vegetation.

A large variety of glandular and non-glandular hairs occur in most of the mangrove taxa. According to Fahn & Shimony (1977), in *Avicennia*, all glandular and non-glandular hairs are formed similarly up to the stage of 3-celled primordium, after this two types of hairs start to appear. Most of the non-glandular hairs are covered by a very thin cuticle, but the peripheral wall of the cell corresponding to the stalk cell in glandular hair is heavily cutinized. According to Osmand et al. (1969) the salt is secreted by the cytoplasm of the secretory cells of the glandular hair into the large vacuole and the secretory cell dries out with ageing of the leaf, and the salt content remain on the leaf surface as a white powdery layer. The suggestion made by Metcalfe & Chalk (1950) regarding the structural differences of glandular and non-glandular hairs of *Avicennia* are probably as a result of adaptive evolution, and the evolution of a mangrove plant being in favour of the salt secreting glands. The glandular hairs occur on both surfaces of leaf in contrast to the non-glandular hairs which are present only on the abaxial leaf surface. It is interesting to note that, the salt glands in all salt-secreting mangroves show some structural similarities in having a basal or collecting cell, one or two cutinized stalk cells and a capitate group of terminal radiating cells. These are probably good evidences of evolutionary convergence among the taxa. A comparable experimental evidence of the ultrastructure of glands responsible for secretory function was found in *Avicennia* and *Aegialitis* (Atkinson et al. 1967). Though in the other mangroves where the salt gland is absent, the salt secreting mechanism is less clearly established, but the taxonomic use of epidermal hairs with relation to their adaptive nature is very much important.

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