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Micromorphology and Adaptation of leaf epidermal traits in Rhizophoraceae to Coastal Wetland Ecosystem

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ABSTRACT

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The leaf epidermal/cuticular micromorphological feature was studied in four genera *vis-a-vis Rhizophora, Kandelia, Ceriops* and *Bruguiera* of family Rhizophoraceae. While *Rhizophora* has the means to exude excess salt through their stomatal modification (cork-wart-like structure), *Kandelia* shows rupture in the epithelium perhaps for the same reason. No cork-wart-like structure was found in *Kandelia, Ceriops* and *Bruguiera* species. The epidermal cell size, stomatal length and breadth, stomatal index and differentiation in the costal and intercostal cell wall pattern are the identifiable traits in all the species studied. *Rhizophora apiculata* and *Bruguiera caryophylloides* shows increase/ decrease in the epidermal cell size and Stomatal indices with the varying coastal ecology. During salinity related stress the cork-wart-like structure in *Rhizophora apiculata* on the lower epidermis becomes rudimentary and non-functional while it is well developed and of larger size in normal ecological conditions. *Bruguiera cylindrica* differs with all the species in having undulate cell wall pattern in the costal area studded with the stomata and shows closer affinity with *B. gymnorrhiza* (costal cells distinct but with sinuate anticlinal cell wall) and not with its Syn. *B. caryophylloides* in this respect. The stomatal index (SI) in *Rhizophora apiculata* shows similarity with that of *Bruguiera parviflora* and *B. gymnorrhiza*. However, *R. apiculata* growing in stressed environment shows similar SI as in *Bruguiera sexangula* and other species of *Rhizophora, Ceriops* and *Kandelia*. It is understood that perhaps *Rhizophora apiculata* and *C. decandra* (Syn. *C. roxburghiana*) and *B. cylindrica* (Syn. *B. caryophylloides*) have SI as a non-consistent feature that tends to vary with the changing environment. Mangrove species showing similarity in the epidermal traits and their adaptive features may thrive together in a common coastal environment. Leaf epidermal traits of Rhizophoraceae would help in the identification of fossil cuticles at the specific level and their non-consistent features adapting to the changing coastal environment would provide potential proxy data for interpreting palaeoecology.

Key-words—Rhizophoraceae, Leaf micromorphology, Coastal ecosystem.

परिवर्तनशील आर्द्रभूमि तटीय पारिस्थितिकीय तंत्र के परिप्रेक्ष्य में राइज़ोफोरेसी कुल के पर्ण उपचर्म लक्षणपुंजों का सूक्ष्मसंरचनाविज्ञान तथा अनुकूलन

अंजुम फ़ारूक़ी

सारांश

राइज़ोफ़ोरेसी कुल के चार वंशों—*राइज़ोफ़ोरा, कैण्डेलिया, सीरियॉप्स* तथा *ब्रुगुएरा* के पर्ण अधिचर्मीय/सूक्ष्म संरचनात्मक उपचर्मीय अभिलक्षणों का अध्ययन किया गया। *राइज़ोफ़ोरा* अपने स्टोमी (रंध्री) रूपान्तर (कॉर्क-मस्से की भाँति की संरचना) द्वारा अधिक मात्रा में विद्यमान लवण का स्राव करता है, जबकि यह सम्भवतः इसी कारणवश *कैण्डेलिया एपीथीलियम* में दरार प्रदर्शित करता है। *कैण्डेलिया, सीरियॉप्स* तथा *ब्रुगुएरा* प्रजातियों में कोई भी कॉर्क-मस्से के आकार की संरचना नहीं पायी गयी है। अधिचर्मीय कोशिका आमाप, रंध्री लम्बाई तथा चौड़ाई, रंध्री अनुक्रम तथा तटीय एवं अन्तरतटीय कोशिका भित्ति विन्यास में विभेदन सभी अध्ययन की गयी प्रजातियों के अभिनिर्धारणीय लक्षणपुंज हैं। *राइज़ोफ़ोरा एपिक्यूलाटा* तथा *ब्रुगुएरा कैरियोफ़िल्लॉयडीज़* परिवर्ती तटीय पारिस्थितिकी विज्ञान के अनुसार अधिचर्मीय कोशिका आमाप तथा रंध्री अनुक्रमों में वृद्धि/ह्रास प्रदर्शित करते हैं। लवणता सम्बन्धी प्रतिबल के दौरान अधो अधिचर्म पर *राइज़ोफ़ोरा एपिक्यूलाटा* में विद्यमान कॉर्क-मस्से की भाँति की संरचना अल्पवर्धित तथा अक्रियाशील हो जाती है, जबकि यह सुविकसित है तथा सामान्य पारिस्थितिकीय स्थितियों में अपेक्षाकृत बड़े आमाप की है। *ब्रुगुएरा सिलेण्ड्रिका* रंध्री से जड़ित तटीय क्षेत्रों में तरंगित कोशिका भित्ति विन्यास से युक्त सभी प्रजातियों से भिन्न है तथा यह *बी. जिम्नोराइज़ा* (तटीय कोशिकाएँ सुस्पष्ट हैं, किन्तु ये तरंगित अपनतिक कोशिका भित्ति से युक्त हैं) से निकटस्थ बन्धुता प्रदर्शित करता है, जबकि इस सम्बन्ध में यह इसके तुल्य *बी. कैरियोफ़िल्लॉयडीज़* के साथ बन्धुता नहीं प्रदर्शित करता है। *राइज़ोफ़ोरा एपिक्यूलाटा* का रंध्री अनुक्रम *ब्रुगुएरा पार्वीफ़्लोरा* तथा *बी. जिम्नोराइज़ा* के साथ समरूपता प्रदर्शित करता है, जबकि प्रतिबलीय पर्यावरण में उगने वाला *आर. एपिक्यूलाटा, ब्रुगुएरा सेक्सैंग्यूला* तथा *राइज़ोफ़ोरा, सीरियॉप्स* एवं *कैण्डेलिया* की अन्य प्रजातियों के समरूप रंध्री अनुक्रम प्रदर्शित करता है। सम्भव है कि *राइज़ोफ़ोरा एपिक्यूलाटा* एवं *सी. डिकैण्ड्रा* (*सी. रॉक्सबर्गियाना* के तुल्य) तथा *बी. सिलिण्ड्रिका* (*बी. कैरियाफिल्लॉयडीज़* के तुल्य) का रंध्री अनुक्रम एक असंगत अभिलक्षण है, जो परिवर्ती पर्यावरण के अनुसार परिवर्तनशीलता का रुझान रखता है। अधिचर्मीय लक्षणपुंजों तथा उनके अनुकूलित अभिलक्षणों में समरूपता प्रदर्शित करने वाली मैंग्रोव प्रजातियाँ एक उभयनिष्ठ तटीय पर्यावरण में एक साथ फल-फूल सकती हैं। राइज़ोफ़ोरेसी के पर्ण उपचर्मीय लक्षणपुंज एक विशिष्ट स्तर पर अश्मित उपचर्मों के अभिनिर्धारण हेतु सहायक हैं तथा परिवर्ती तटीय पर्यावरण के अनुकूल इनके असंगत अभिलक्षण पुरापारिस्थितिकी के निर्वचन हेतु प्रभावी कूट आंकड़े प्रदान करेंगे।

संकेत शब्द - राइज़ोफ़ोरेसी, पर्णसूक्ष्मसंरचना विज्ञान, तटीय पारिस्थितिकी तंत्र.

INTRODUCTION

IT was in late Silurian- early Devonian Period (400 million yrs ago) that the vascular plants attempted to invade land and acclimatized to the terrestrial environment. Since then plants had to develop features which would help them in adaptation to different ecosystem with special reference to cuticle, stomata and vascular tissue and are considered to have developed simultaneously that led to the emergence and survival of large terrestrial plants (Chaloner, 1970). Such a process is still going on with the number of evidences coming up where the plants adapt to different ecological and edaphic conditions by changing their epidermal traits in order to survive (Stace, 1965a, b; Fahn, 1979; Tukey, 1971; Dilcher, 1974; Farooqui *et al.* 1995, 1997; Farooqui & Bajpai, 1999).

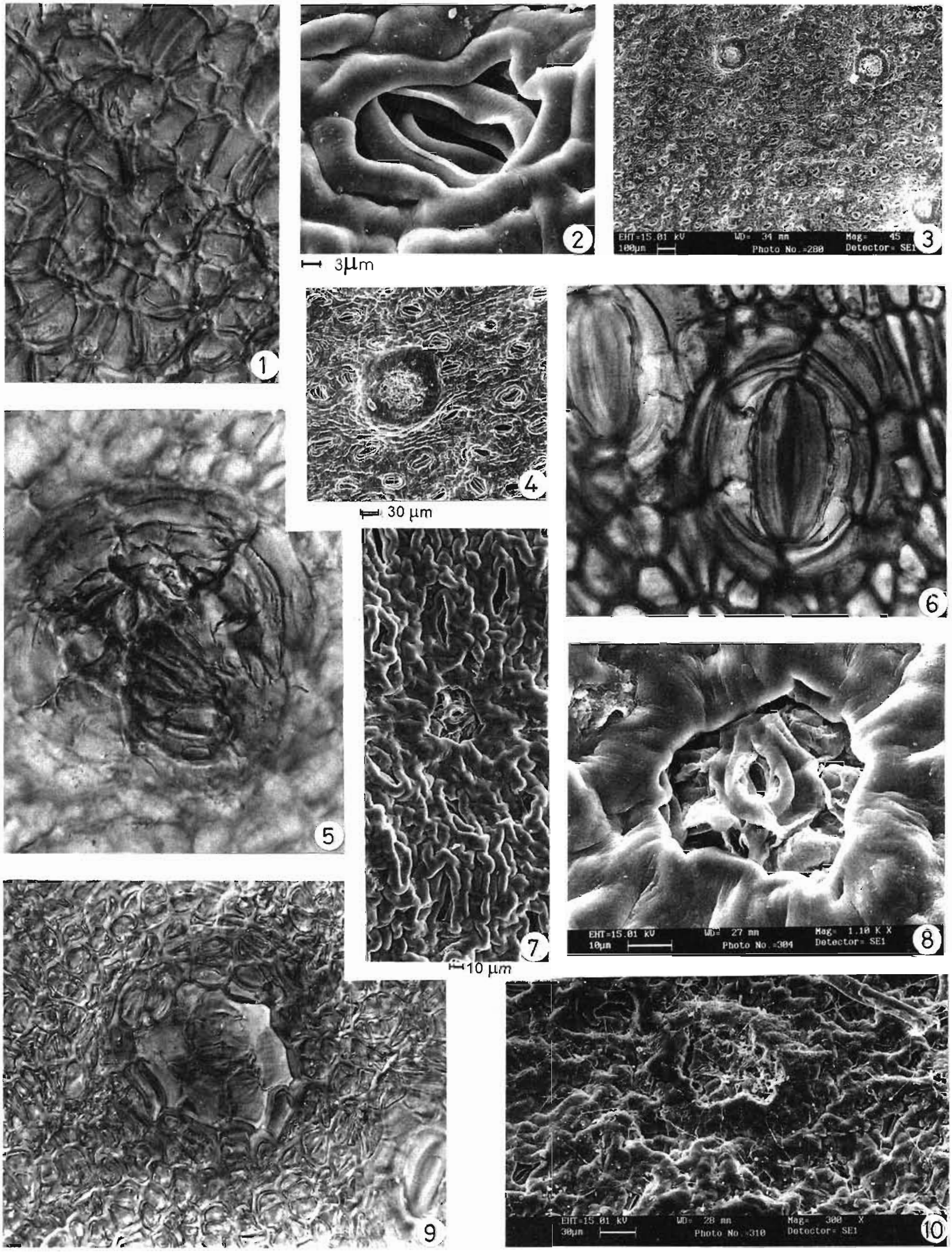
Coastal wetland ecosystems show different ecological zones and each zone is demarcated distinctly by different types of mangrove vegetation (Banerjee, 1994). Any change in the ecology affects the specific zonation of the mangroves depending upon the duration, direction and magnitude of sea-level and climatic fluctuations (Ellison & Stoddart, 1991; Ellison, 1993). It is evident that the distribution of different species is variable along the Indian coastal region and also world wide depending on various factors that also include the geomorphology and geographical distribution (Muller, 1959; Caratini *et al.*, 1973; Blasco, 1975; Chapman, 1977; Tomlinson,

PLATE 1 ⟶

(Scale given below each photoplate is equal to 10 µm unless mentioned otherwise)

Rhizophora apiculata (Specimen Se. No. 1)

1. Upper leaf epidermis showing pentagonal irregular cells with straight- arcuate anticlinal cell walls and underlying hypodermal cells (Light Photomicrographs-LP).
2. Lower leaf epidermis showing sunken stomata, guard cells covered by stomatal legdes (Scanning Electron Microscopic Photomicrographs; SEMP).
3. Lower epidermis (LP) showing compact radially arranged epidermal cells surrounding the reduced stomata that appear highly raised in the surface view called as cork-warts.
4. SEMP of cork-warts in favourable condition.
5. LP of corkwarts.
6. LP of stomata on the lower epidermis.
7. SEMP of cork-warts with reduced stomatal opening in the stress condition (Specimen Se. No. 3).
8. SEMP showing distinct gross features of stomata in the centre of cork-warts.
9. LP of cork-warts in stress condition showing compact and reduced cell size of the stomatal complex.
10. SEMP showing lower epidermis in stress condition with smaller cork-warts and thick epicuticular ornamentation.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10 µm
8
EHT=15.01 kV
10µm
WD= 27 mm
Photo No.=304
Detector= SE1
9
10
EHT=15.01 kV
30µm
WD= 28 mm
Photo No.=310
Mag= 300 X
Detector= SE1

PLATE 1

NO.	TAXA	I	II	III	IV	
						CELL SIZE (μm²) I : A=20-35; B=50-100; C=140-150
1	*Rhizophora apiculata*	C	A	C	B	
2	*R. mucronata*	A	C	C	A	
3	*R. stylosa*	A	B	B	A	STOMATAL LENGTH (μm) II: A=14-15; B=18-21; C=20-21; D=29
4	*Kandelia candel*	B	C	C	A	
5	*Ceriops tagal*	A	C	B	A	
6	*C. roxburghiana*	A	A	A	A	
7	*C. decandra*	A	B	C	A	STOMATAL BREADTH (μm)-III A=8; B=10-12; C=14-17
8	*Bruguiera parviflora*	B	B	C	B	
9	*B. sexangula*	B	B	A	A	
10	*B. caryophylloides*	B	A	A	C	STOMATAL INDEX IV A=7·28-9·9; B= 12·5-13·8; C=21·9-29·2
11	*B. cylindrica*	C	A	B	C	
12	*B. gymnorrhiza*	B	A	A	B	

Fig. 1—Affinity between members of Rhizophoraceae with reference to single parameter.

1986; Naskar & Guha Bakshi, 1987; Ellison, 1989; Dagar *et al.*, 1991; Untawale & Jagtap, 1991; Plaziat,1995; Upchurc, 1995; Naskar & Mandal, 1999). Mangroves have been used as biological sea-level indicators since Tertiary period i.e., 65 million yrs (Ellison, 1989). Besides pollen/spores, the cuticular or epidermal microscopic fragments are also abundant in the sedimentary sequence. Reconstruction of former vegetation, climate and environment through palynology alone cannot hope to answer all our questions about palaeoecology and palaeoenvironment. The leaf epidermal traits play a vital role in the adaptation of plants to different environmental conditions. The gross epidermal features along with the adaptive epidermal traits have great potential for understanding various environmental changes (Ball & Farquhar, 1984; Beerling & Chaloner, 1992). However, it is difficult to evaluate the fossil cuticles unless the modern potential specimens are thoroughly investigated in different environment and the variability in the epidermal features is recorded. In an attempt number of workers have evidently compared the modern analogue with that of fossil specimens (Dilcher, 1974; Mehrotra *et al.*, 1998; Cleal *et al.*, 1999). Previous work related to epidermal features in Rhizophoraceae is limited (Metcalfe & Chalk, 1950; Tomlinson, 1986; Das & Ghose, 1996; Naskar & Mandal, 1999) and the understanding of differences in epidermal traits between the genus and between the species is meagre. So far, the data on modern analogue of mangrove cuticle/ epidermis and its comparison with the fossil specimens is lacking, although mangrove palynological assemblage in India has been reported since Tertiary Period (Ramanujam & Reddy, 1984). With this objective the present paper puts together the studies related to micromorphology of the epidermal characteristics/ traits in the members of Rhizophoraceae and its adapting characters to the changing coastal wetland ecosystem that is directly influenced by sea-level and climatic fluctuations. The study would provide a potential modern analogue for understanding the fossil mangrove cuticle/epidermis *inter alia* dynamics of the coastal palaeovegetation, palaeoecology and palaeoclimate.

MATERIAL AND METHODS

Four genera and ten species belonging to Rhizophoraceae were studied for their leaf epidermal/ cuticular micromorphology. These are: *Rhizophora apiculata* Bl., *R. mucronata* Lamk., *R. stylosa* Griff., *Kandelia candel* (L) Druce, *Ceriops tagal* (Perottet) C.B. Robinson, *C. decandra* (Griff.) Ding Hou (Syn. *C. roxburghiana* Arn.), *Bruguiera parviflora* (Roxb) Wt. & Arn. Ex Griff., *B. sexangula* (Lour.) Poiret, Bl., *B. cylindrica* (L.) Bl. (Syn. *B. caryophylloides* Burm.f.) and *B. gymnorrhiza* (L.) Lamk.

The middle portion from margin to the midrib part of the leaf blade was selected for epidermal micromorphological studies in order to minimize variability (Poole *et al.*, 1996). The samples were soaked in 50 per cent (v:v) glycerine overnight

PLATE 2 ⟶

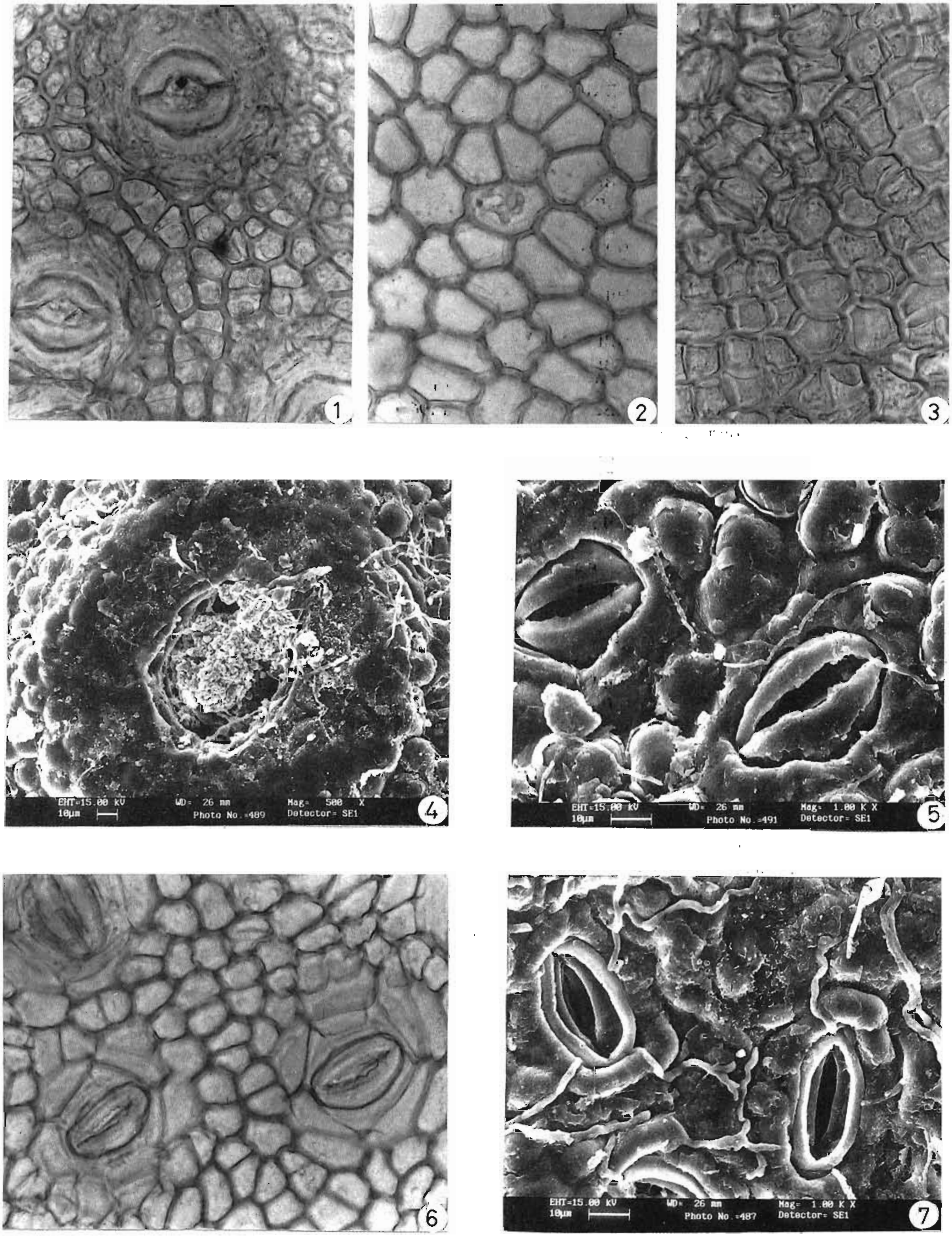
(Scale given below each photoplate is equal to 10 μm unless mentioned otherwise)

R. mucronata (Specimen Se. No. 7)

1. LP of lower leaf epidermis.
2. LP of upper leaf epidermis.
4. SEMP of cork-wart filled with particulate encrustations in the stomatal cavity similar to in *R. apiculata*.
5. SEMP showing stomatal ledges and flaky to granular epicuticular wax.

R. stylosa (Specimen Se. No. 8).

3. LP of upper leaf epidermis.
6. LP of lower leaf epidermis.
7. SEMP of the lower leaf epidermis.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2
3
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10µm Photo No.=489 Detector= SE1
4
EHT=15.00 kV WD= 26 mm Mag= 1.00 K X
10µm Photo No.=491 Detector= SE1
5
6
EHT=15.00 kV WD= 26 mm Mag= 1.00 K X
10µm Photo No.=487 Detector= SE1
7

PLATE 2

Se No	Taxa	Herbarium Specimen No., Name (Collector), Year & Area of Collection
1.	*Rhizophora apiculata* Blume.	HIFP 311, Pascal 1974, Pichavaram
2.	*R. apiculata*	NBRI 88395, Saran & Party 1961, Long Island, Andaman
3.	*R. apiculata*	BSIP 11940, Farooqui 1998, Pichavaram
4.	*R. mucronata* Lamk.	HIFP 312, Pascal 1974, Pichavaram
5.	*R. mucronata* Pichavaram	HIFP 904, Thanikaimoni 1982
6.	*R. mucronata* Pichavaram	NBRI 2652, Ramalingam 1945
7.	*R. mucronata*	BSIP 11941, Farooqui 1998, Pichavaram
8.	*R. stylosa* Griff. Marakkanam	HIFP 494, Thanikaimoni 1979
9.	*Kandelia candel* (L.) Druce	HIFP UT 1154, Thanikaimoni 1979, Mahanadi estuary
10.	*Ceriops decandra* (Griff.) Ding Hou (Syn. *C. roxburghiana* Arn.)	HIFP 1002, Thanikaimoni 1973, Pichavaram
11.	*Ceriops roxburghiana*	NBRI 67212, Srivastava 1960, Sunderbans
12.	*C. roxburghiana*	NBRI 79622, Saran and Party 1961, Long Island, Andaman
13.	*C. roxburghiana*	NBRI 67212, Srivastava 1960, Mahanadi estuary
14.	*C. decandra*	BSIP 4527, Takhtajan & Lakhanpal 1966, Sunderbans
15.	*C. tagal* (Perottet) C.B. Robinson	NBRI 38895, Srivastava 1960, Sunderbans
16.	*Bruguiera caryophylloides* (Burm. F.) Bl. (growing in fish pond)	NBRI 38, Backer 1913, Java
17.	*B. caryophylloides*	NBRI 2653, Swaminathan 1945, Pichavaram
18.	*B. caryophylloides*	NBRI 79463, Saran & Party 1961, Long Island Andaman
19.	*B. gymnorrhiza* (L.) Lamk.	HIFP 493, Ramesh 1984, Pichavaram
20.	*B. gymnorrhiza*	NBRI 86721, Kaul & Party 1965, Cuttack, Orissa
21.	*B. gymnorrhiza*	BSIP 4549, Lakhanpal & Takhtajan 1966, Sunderbans
22.	*B. parviflora* (Roxb.) Wt. & Arn. Ex Griff.	HIFP VKB 12, Legris 1957, Mahanadi estuary
23.	*B. sexangula* (Lour.) Poir	HIFP 1769, Blasco & Thanikaimoni 1974, Sunderbans
24.	*B. sexangula*	BSIP 3224, Lakhanpal 1966, Ceylon
25.	*B. cylindrica* (L.) Blume.	HIFP VKB 1, Legris 1957, Pichavaram
26.	*B. cylindrica*	HIFP 314, Pascal 1974, Pichavaram
27.	*B. cylindrica*	BSIP 4540, Takhtajan & Lakhanpal 1966, Sunderbans

Fig. 2—List of Herbarium specimens studied (HIFP—Herbarium French Institute, Pondicherry; NBRI—National Botanical Research Institute and BSIP—Birbal Sahni Institute of Palaeobotany, Lucknow).

and the leaf epidermis was separated following Ahmad (1974) and Dilcher (1974). The micromorphological description of epidermal features has been followed after Dilcher (1974). The percentage of stomatal index (SI)= Number of stomata (per sq mm leaf area)/ Number of stomata+ No. of non-stomatal epidermal cells per sq mm leaf area x 100 was calculated following Salisbury (1927). The Scanning Electron Microscopic study was carried out after processing the samples through ethanol series and gold-palladium alloy coating before examining in LEO – 430 Scanning Electron Microscope (SEM).

The herbarium samples were obtained from Institut Francais, Pondicherry, National Botanical Research Institute and Birbal Sahni Institute of Palaeobotany, Lucknow. The names of the species with their Synonyms documented in the respective herbarium sheets have been retained in order to

PLATE 3

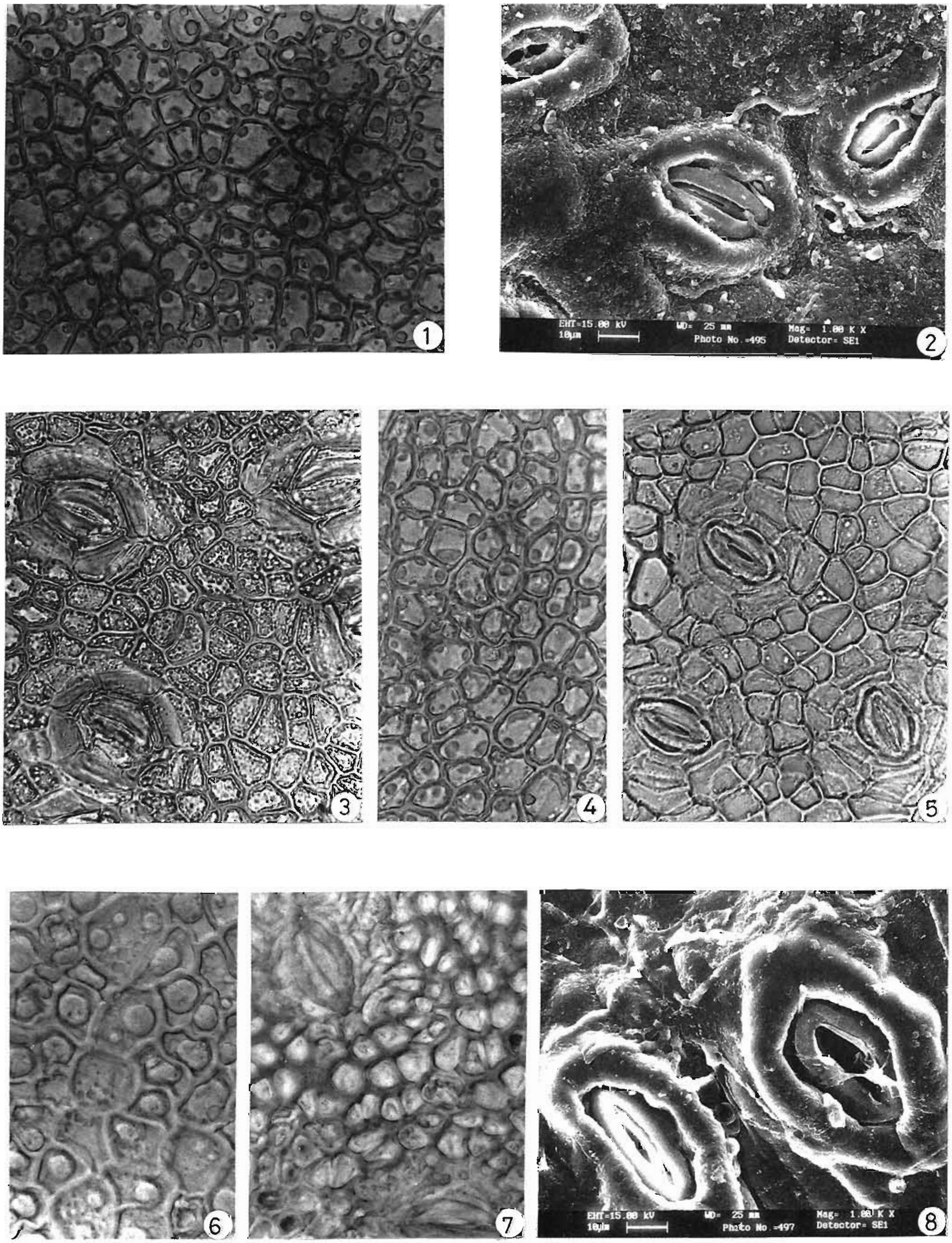
(Scale given below each photoplate is equal to 10 µm unless mentioned otherwise) ⟶

Ceriops decandra (Specimen Se. No. 14)

1. LP of upper leaf epidermis; lower leaf surface.
2. SEMP showing finely lamellated to granular epicuticular ornamentation.
3. As seen under light microscope

C. roxburghiana (Specimen Se. No. 13)

4. LP of upper leaf surface.
5. LP of lower leaf surface; *C. tagal* (Specimen Se. No. 15).
6. LP of upper leaf surface.
7. LP of lower leaf surface.
8. SEMP showing lower leaf surface with typical rhomboid stomatal complex. Finely striated–granular cuticular ornamentation.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7
EHT=15.00 kV
10µm
WD= 25 mm
Photo No.=497
Mag= 1.00 K X
Detector= SE1
8

PLATE 3

study the variation. The list of herbarium specimens is given in Fig. 2.

RESULT AND DISCUSSION

As a barrier to excessive and uncontrollable water loss, the leaf epidermal cells are the most numerous and usually they show considerable variation in size and shape along with number of consistent and non-consistent characteristics (Willmer & Fricker, 1996; Mc Elwain & Chaloner, 1996; Farooqui *et al.*, 1995, 1997; Chaloner & Mc Elwain, 1997; Farooqui & Bajpai,1999).

Rhizophoraceae (Dahlgren, 1980; Tomlinson, 1986; Naskar & Guha Bakshi, 1987), a pantropical family consists of 16 genera and 120 species. It is in a separate order Rhizophorales; Tribe Rhizophoreae and comprises of four true mangrove genera i.e., *Rhizophora* L., *Ceriops* Arn., *Kandelia* Wt. & Arn. and *Bruguiera* Lamk. These are generally confined to the intertidal zone. Although these thrive well in fresh water ecology but sooner its growth is overpowered by fresh water plant taxa (Camilleri & Ribi, 1983).

The number of plant species growing in mangal is small. But, the nomenclature is still a confusing chapter. Most early systematic work was done entirely on the basis of herbarium specimens, so number of descriptions of the same species under different names came into being. Elementary synonymy has been extensively used in the literature (Rollet, 1981; Tomlinson, 1986). During the present study the synonyms of *Ceriops decandra* i.e., *C. roxburghiana* and *Bruguiera cylindrica* i.e., *B. caryophylloides* have been dealt in separately for their significant identifiable difference in leaf micromorphological features in different specimens.

In all the species studied the leaves are dorsiventral and stomata are present on the lower leaf surface. The sunken stomata described by Metcalfe and Chalk (1950) is a mixture of ranunculaceous, cruciferous and rubiaceous type. It consists of guard cells covered by stomatal ledges which are plain and conspicuous. There is no specific subsidiary cell and the epidermal cells surrounding the stomata are arranged radially to form stomatal complex. These are elongated and distinct from other epidermal cells. The size, number, position, its obscurity or distinction from other areas are the identifiable features which vary from species to species.

The upper leaf surface in members of Rhizophoraceae show irregular epidermal cells with insignificant difference in cell wall thickness. The anticlinal cell wall pattern is straight to arcuate in all the species. The costal and intercostal area is well differentiated in *B. cylindrica* (Syn. *Bruguiera caryophylloides*). Other species do not show well defined costal or intercostal areas. The cell size shows a wide range (54-145 mm^2) of variability within species. Larger cell size (80-145 mm^2) was found in *Rhizophora* (Pl. 1.1; pl. 2.2-3) closely related with *Kandelia* (Pl. 4.1-3). However, *Bruguiera* spp. (Pl. 5.1, 5; Pl. 6.2, 4; Pl. 7.1) differs in having well demarcated costal and intercostal cells that have sinuate anticlinal cell walls. The smallest cell size (50-60 mm^2) was found in *Ceriops* spp. (Pl. 3.1, 4, 7) with a slight thickened anticlinal cell wall. The multilayered epidermis is prominent in the surface view only in *Rhizophora apiculata* and *Kandelia candel*.

Fig. 1 shows the characteristic features of the lower leaf surface. The cell size in Group A (20-35 µm^2) comprises *Rhizophora mucronata, R. stylosa, Ceriops tagal* and *Ceriops decandra* (*C. roxburghiana*). The Group B (50-100 µm^2) includes *Kandelia candel, Bruguiera parviflora, B. sexangula, B. caryophylloides* and *Bruguiera gymnorrhiza*. The largest cell size (140-150 µm^2) was found in *Rhizophora apiculata* and *Bruguiera cylindrica*. The cell size in *Bruguiera caryophylloides* growing in the coastal waters (77±2.5 µm^2) and in the fresh water fish pond (48 ±1.3 µm^2) show significant variation with 50 % reduction in the latter. Thus, the cell size varies in different ecology. However, the cell size in *B. cylindrica* was found to be 140±4.9 µm^2. As *B. caryophylloides* is Synonym of *B. cylindrica* it may be that either the cell size is the non-consistent epidermal trait or it should be kept separately while identifying the micromorphological features. Similar feature has also been recorded in *R. apiculata* (Farooqui, 2000) where the cell size reduces in salinity related stress. Thus, *Bruguiera caryophylloides* shows affinity with the *Rhizophora apiculata*. Previously, *B. caryophylloides* Blume was also named as *Rhizophora caryophylloides* Jack Mal. or *R. cylindrica* Linn. (Hooker, 1879).

Affinity between different species with respect to stomatal length and breadth and stomatal index is shown in Fig. 1. It was found that *Rhizophora apiculata* has the longest stomatal length followed by *R. mucronata, Kandelia candel* and *Ceriops tagal* (20-21 mm). However, stomatal length in *Rhizophora stylosa, Ceriops decandra, Bruguiera parviflora,* and *Bruguiera sexangula* is 18-21 mm. *Bruguiera cylindrica* (Syn. *B. caryophylloides*) and *B. gymnorrhiza* show only 14-15 mm stomatal length. With respect to stomatal length and breadth *Ceriops decandra* (Specimen No. 10 & 14) and its Syn. *C. roxburghiana* (Specimen No. 11-13) show considerable

PLATE 4

(Scale given below each photoplate is equal to 10 µm unless mentioned otherwise) →

Kandelia candel (Specimen Se. No. 9)

1-3. LP of upper leaf epidermis showing dark patches of thickened epidermal cells distinct from the surrounding cells; Lower leaf epidermis.

4-5. LP showing dark areas of thickened cells.

6. LP showing the dark areas with epidermal rupture in the centre.

7. SEMP showing fine granular ornamentation with flakes of epicuticular wax.

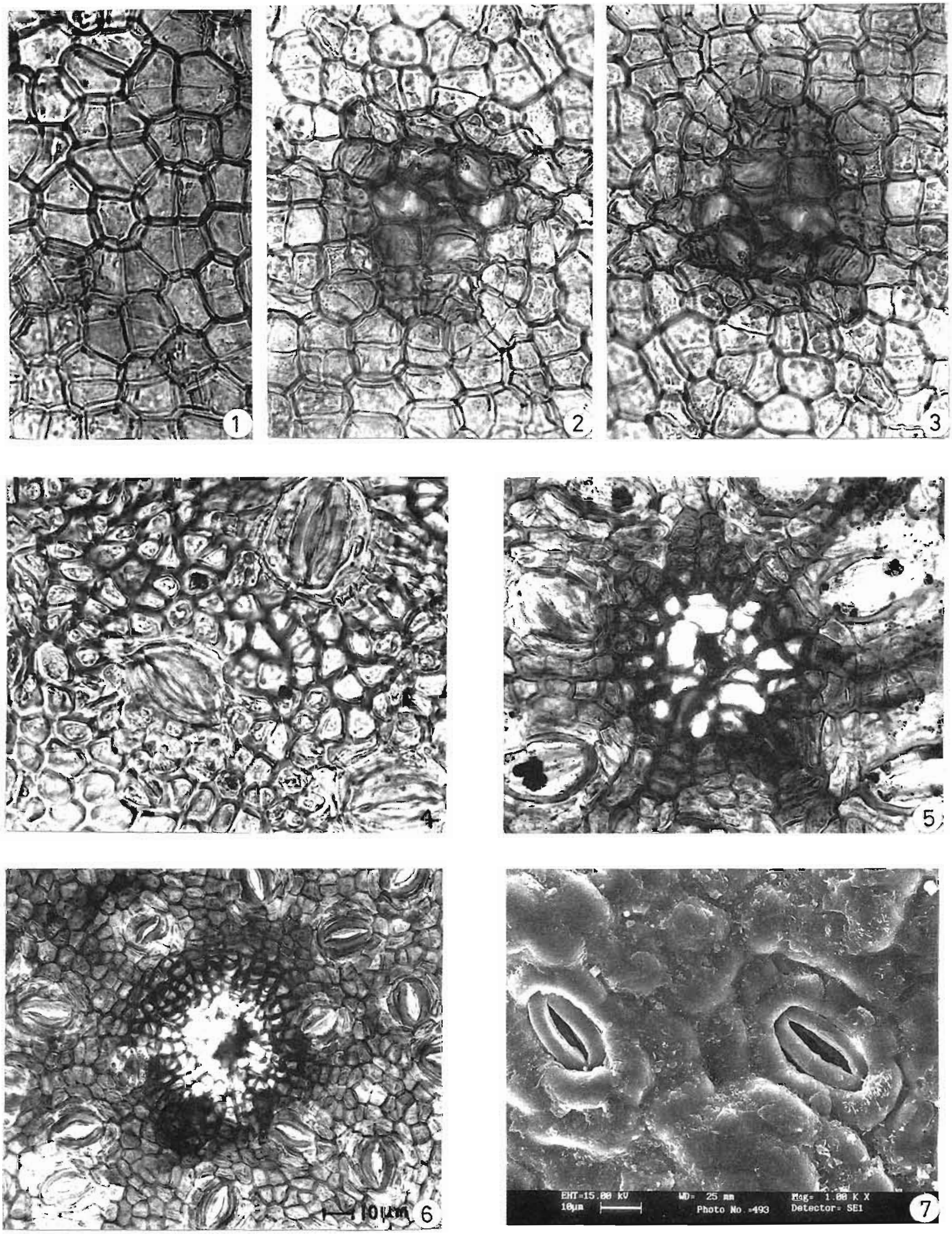
1
2
3
4
5
6
10μm
7
EHT=15.00 kV
10μm
WD= 25 mm
Photo No.=493
Mag= 1.00 K X
Detector= SE1

PLATE 4

variation with significant smaller stomatal length and breadth and larger cell size at 5 per cent error probability in the latter case. This trend is similar to as in *B. cylindrica* (Specimen Se. No. 25-27) and its Syn *B. caryophylloides* (Specimen Se. No. 17 & 18). Therefore, both the species differ with their synonyms with respect to leaf epidermal micromorphological features. Number of stomata increased in *B. caryophylloides* (Specimen. Se. No. 16) while growing in fresh water fish pond than in coastal water (Pl. 5.2-4).

In all the species stomata are sunken covered by the plain and conspicuous stomatal ledges as in *Rhizophora apiculata* (Pl. 1.2), that indicates the xerohalophytic nature of the plants to avoid excess transpiration when the available water becomes physiologically inactive in highly saline ecosystem. There are no salt glands in Rhizophoraceae. Being the salt excluders (Scholander, 1968) they have high sodium and chloride in the xylem sap (Dagar *et. al*, 1991). The excess salt that enters into the plant system has to be excreted by the plants. As studied earlier in *Rhizophora mucronata* by Tomlinson (1986) and Metcalfe and Chalk (1950) *Rhizophora* has cork-wart-like structure to function as hydathodes and help in salt excretion through the leaves. However, the present leaf epidermal studies in *R. apiculata* shows that the cork warts (Pl. 1.3, 4) are the modifications in the stomatal complex (Farooqui & Bajpai, 1999) and these shed off the excess salts excreted by plants during rainy season (Farooqui, 2000). Earlier it was reported (Mullan, 1931) that the excreted salts through cork-warts being hygroscopic absorbs moisture from the atmosphere and supplements the water need of the plant during stress condition. As previously recorded by Stace (1965b) and Fahn (1979) these are either an enlarged stoma or the epidermal rupture. However, our study shows that these are the modifications in the stomatal complex where the stoma reduces to a pore like structure (Pl 1.6, 7, 8) with a stomatal cavity filled with particulate/salty encrustations surrounded by compact, smaller, elongated and radially arranged epidermal cells around the stomata. These appear as circular, distinct structures placed haphazardly on the lower leaf surface which are highly raised when observed in the surface view (Pl. 1.5). It was also observed that in the exponential phase of the leaf growth, the size and frequency of these cork-warts varies even within a single leaf and different stages of the development in cork-warts is evident (Farooqui & Bajpai, 1999). In *Rhizophora apiculata* these are more active during normal ecological system (strong tidal and fresh water influx) and becomes rudimentary type with small size and low frequency in hypersaline conditions (Pl. 1.9, 10) which in the case of *R. mucronata* was functional. This is perhaps that the Na : K ratio in *R. apiculata* is low and high in *R. mucronata*. According to Kinraide (1999) low levels of K relieved Na toxicity in plants, but low levels of Na enhanced K toxicity. My observations show a high Na:K ratio (4 to 8) in *R. mucronata* which would have probably lowered the toxic effects of high Na in leaves (Farooqui, 2000) and thus tolerant to a wide range of saline coastal ecology.

The stomatal index (SI) recorded (Fig. 1) remains same in *Rhizophora* species except in *R. apiculata* (12.5) showing higher values comparable to *B. parviflora* and *B. gymnorrhiza* (13.8). *Rhizophora apiculata* (Specimen Se. No. 3) growing in the stress condition has similar SI i.e., 8.27 as compared to *R. mucronata* (8.03) and *R. stylosa* (8.97). *Ceriops tagal, Kandelia candel* and *Ceriops decandra* have lowest values as 7.28, 7.30 and 7.69, respectively. However, in *Ceriops roxburghiana* the SI was found to be 10.66 which is quite high as in other specimens of *C. decandra* (Syn. *C . roxburghiana*). It may be that the SI is the non-consistent feature of this species and should be considered while identifying the species through the leaf epidermal micromorphology. Of all the species, SI in *Bruguiera cylindrica* (Specimen Se. No. 25–27) and its Syn. *B. caryophylloides* (Specimen Se. No. 17 & 18) was highest i.e., 29.2 and 21.9, respectively. However, in *B. caryophylloides* (Specimen Se. No.16) growing in the fish pond the SI was found to be 26.6. *Rhizophora, Ceriops* and *Kandelia* have closer affinity with respect to stomatal indices that also shows affinity with *B. sexangula*. But, only *R. apiculata* shows affinity with *B. parviflora* and *B. gymnorrhiza*. However, *R. apiculata* growing in stressed environment shows SI similar to as in other species of *Rhizophora, Ceriops* and *Kandelia.*

Earlier the SI has served as proxy data for the analysis of past atmospheric changes (Chaloner & McElwain, 1997; Beerling & Woodward, 1997). Palaeoecological interpretations through fossil and modern epidermis has been successfully explained earlier (Palmer, 1976; Upchurch *et al.*, 1985; Upchurch, 1995). Both the atmospheric and palaeoecological changes are generally controlled by modified epidermal cells which surround the stomata (Willmer & Fricker, 1996) with the result plants show varying Stomatal indices (Spackman *et al.*, 1966; Ball & Farquhar, 1984; McElwain & Chaloner, 1996; Poole *et al.*, 1996;). The comparison of past

PLATE 5

(Scale given below each photoplate is equal to 10 µm unless mentioned otherwise) ⟶

Bruguiera caryophylloides (Specimen No. 17)

1. LP of upper leaf epidermis showing sinuate anticlinal cell wall in the costal area and straight –arcuate in inter costal areas. Lower leaf epidermis.
2. LP showing 4-5 epidermal cells out of which those with 4 surrounding cells 2 are lateral to the guard cells and the other 2 on the poles of the guard cells.

B. caryophylloides (Specimen Se. No.16).

3. LP growing in fresh water fish pond showing increase in stomatal frequency.
4. SEMP showing smooth cuticular ornamentation.

B. parviflora (Specimen Se. No. 22)

5. LP of upper leaf surface.
6. LP of lower leaf surface.

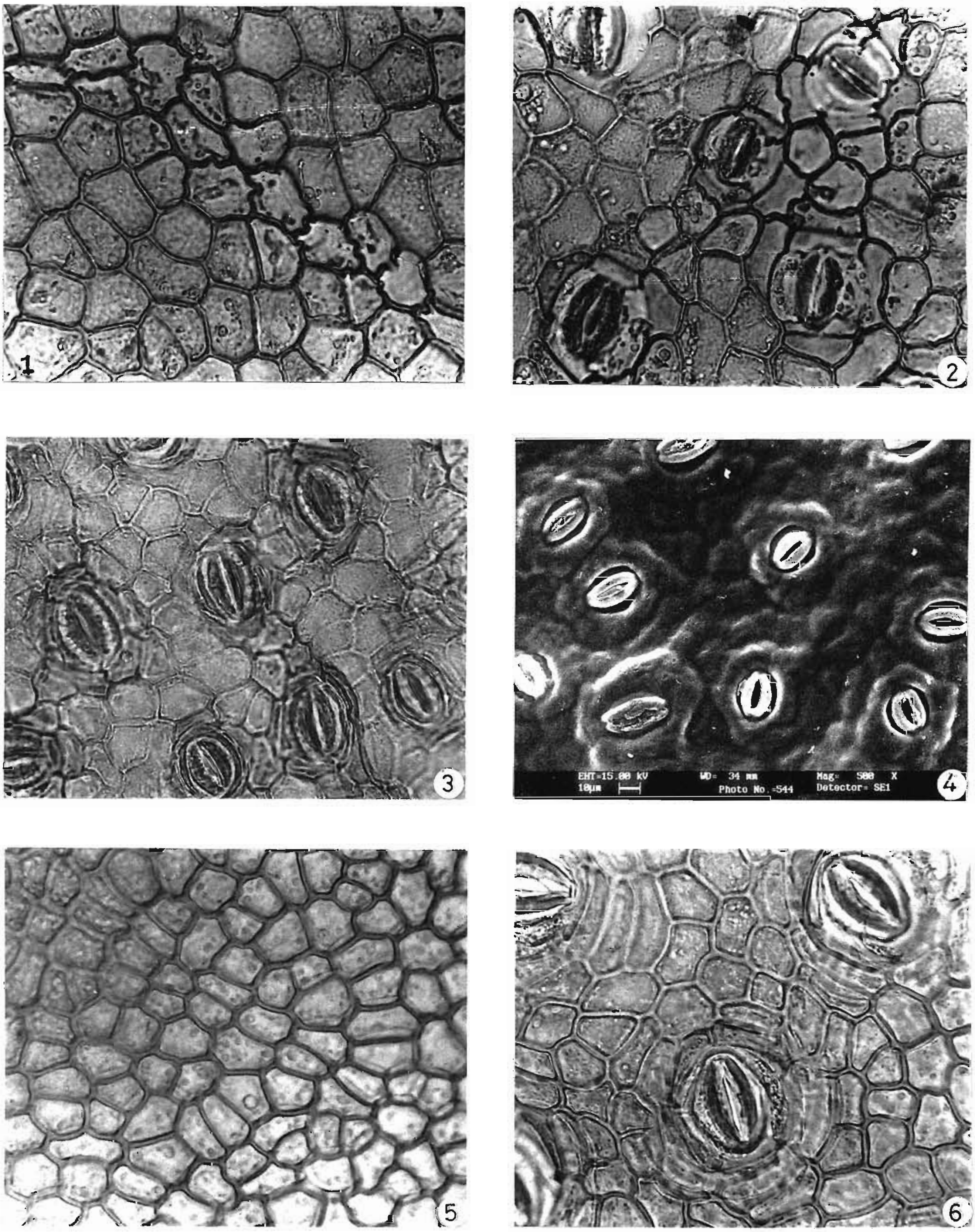
1
2
3
EHT=15.00 kV
10µm
WD= 34 mm
Photo No.=544
Mag= 500 X
Detector= SE1
4
5
6

PLATE 5

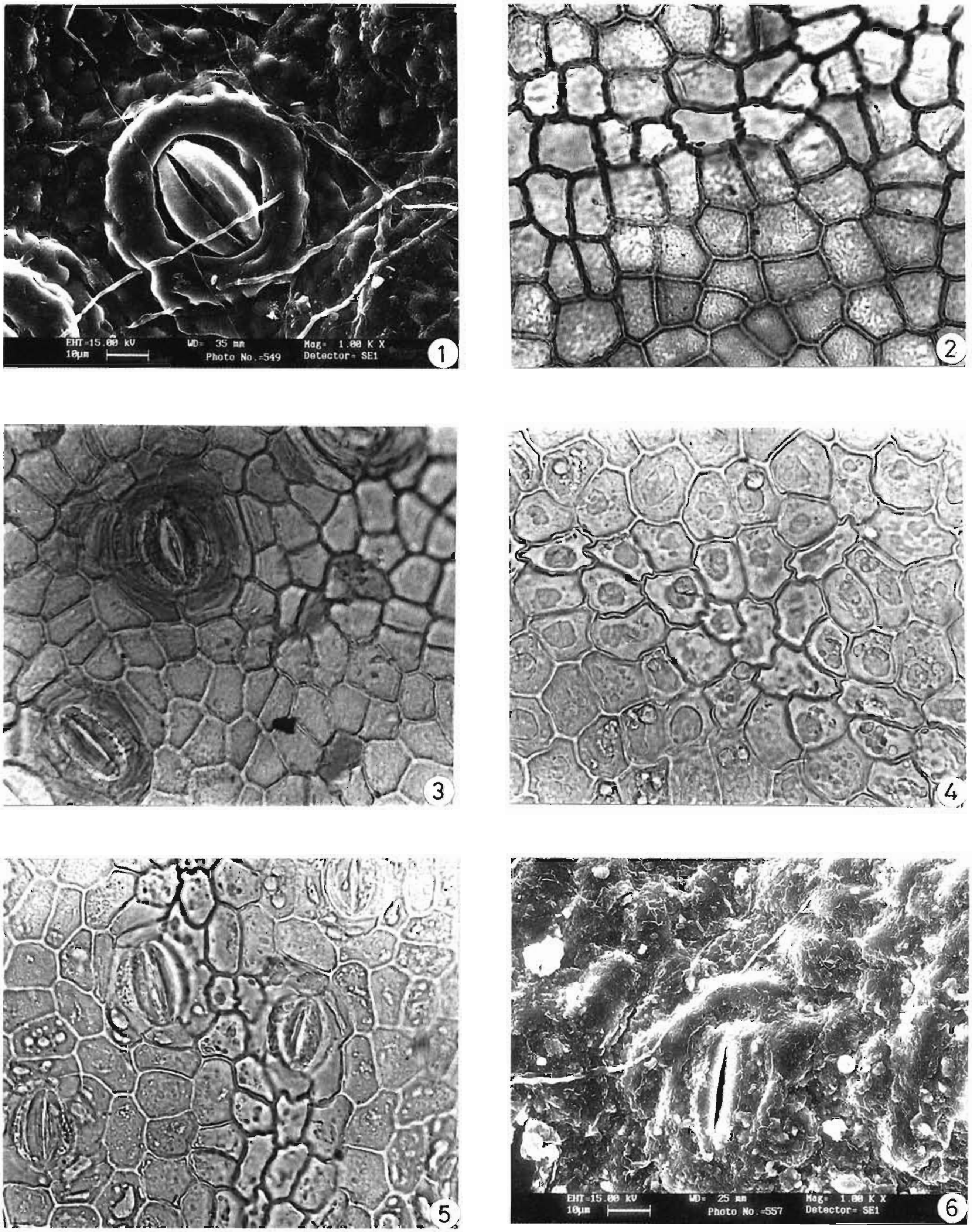
EHT=15.00 kV
10µm
WD= 35 mm
Photo No.=549
Mag= 1.00 K X
Detector= SE1
1
2
3
4
5
EHT=15.00 kV
10µm
WD= 25 mm
Photo No.=557
Mag= 1.00 K X
Detector= SE1
6

PLATE 6

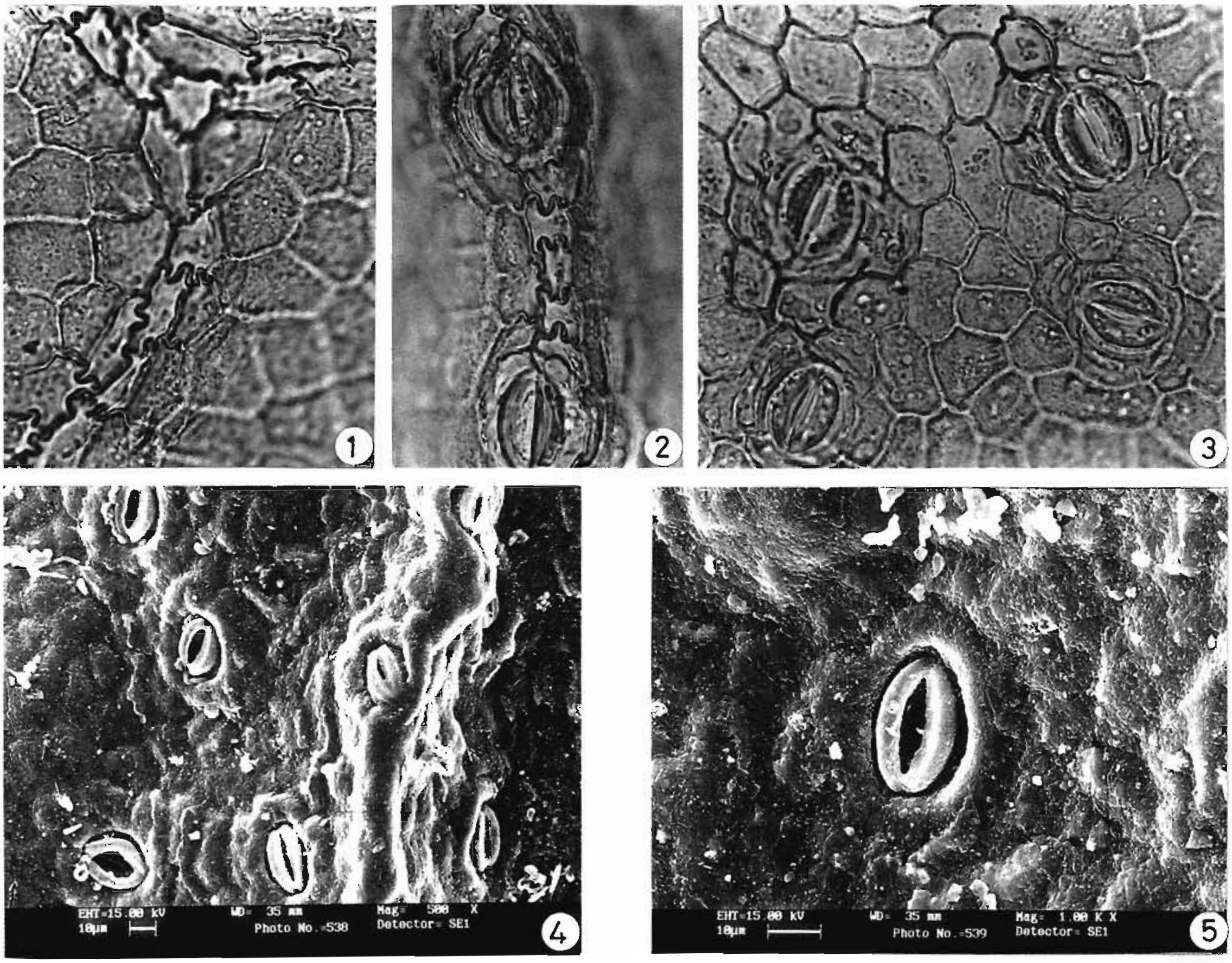

PLATE7

(Scale given below each photoplate is equal to 10 µm unless mentioned otherwise)

B. cylindrica (Specimen Se. No. 25)

1 LP of upper leaf epidermis showing costal area (sinuate) and intercostal (straight) areas. Lower leaf epidermis.
2. LP showing costal (undulate anticlinal cell wall studded with stomata).
3. LP showing the intercostal areas with the stomata.
4. SEMP upper leaf epidermis showing costal and intercostal cuticular ornamentation.
5. SEMP of lower leaf surface showing stomata and finely striated ornamentation and flaky epicuticular wax.

and present cuticles/epidermis have been studied from Tertiary (Burgh *et al.*, 1993; Kurschner *et al.*, 1996, Mehrotra *et al.*, 1998), Mesozoic (McElwain & Chaloner, 1996; Cleal *et al.*, 1999) Palaeozoic (McElwain & Chaloner, 1995 etc.). The present study shows identifiable variation in the SI of Rhizophoraceae species that would help in the identification of fossil cuticles at the specific level. Adaptive epidermal traits in species would help in the interpretation of palaeoecology.

PLATE6

← (Scale given below each photoplate is equal to 10 µm unless mentioned otherwise)

1 SEMP of lower leaf surface in *B. parviflora* showing granulated cuticular ornamentation.

B. sexangula (Specimen Se. No. 24)

2. LP of upper leaf surface with costal (sinuate) and inter costal straight to arcuate anticlinal cell wall.
3. LP showing lower leaf surface

B. gymnorrhiza (Specimen Se. No. 21)

4. LP of lower leaf surface with costal (sinuate–arcuate) and intercostal straight to arcuate anticlinal cell walls.
5. LP of lower leaf surface showing distinct costal (sinuate) and inter costal (straight-arcuate) anticlinal cell walls.
6. SEMP of lower leaf surface showing finely striated ornamentation and flaky epicuticular wax.

The size of the stomatal complex is the largest in *Rhizophora apiculata* while it is comparatively smaller and equal in *R. mucronata* and *R. stylosa*. The anticlinal cell walls of the surrounding epidermal cells are arcuate and elongate, quite distinguishable from rest of the epidermal cells lined parallel to the guard cells with 3 cells each on either side (Pl. 1.6). The poles of the guard cells are slightly occluded (Pl. 1.2) which is not in *R. mucronata* and *R. stylosa* (Pl. 2.1, 6). The surrounding epidermal cells radial to the stomata are 5 in number in *R. stylosa*. The anticlinal cell walls adjacent to the guard cells are straight and not arcuate as in *R. apiculata*. Therefore, 2 cells lie parallel on either sides of the guard cells and one cell covers one of the poles to form a pentagon, which is a distinct identifiable feature (Pl. 2.6).

In *C. decandra* (Pl. 3.3) the stomatal complex resembles *R. stylosa*. The surrounding epidermal cells radial to stomata are not distinguishable in *Rhizophora stylosa, Ceriops tagal* and *Kandelia candel* (Pl. 4.4). In *Kandelia candel* the patches of thickened small epidermal cells are observed on both the leaf surfaces that appear ruptured in the later stages (Pl. 4.1, 2, 3, 5). Initially a single cell wall is thickened which is gradually surrounded by number of radially arranged cells to appear as a dark patch of small-thickened cells (Pl. 4.6). Although, this is the normal feature of the plant, these become much more active during the stress condition and probably behave like hydathodes through which the salts are exuded. The present study shows that while in *Kandelia* this feature is an epithelium rupture, it is the stomatal modification in *Rhizophora* through which the excess salts are shed off.

The stomatal complex in *Bruguiera caryophylloides* show only 4-5 surrounding cells. Out of which 2 lie parallel and 2 on either side of the poles of the guard cells (Pl. 5.2) in case of 4 cells surrounding the stomata. The anticlinal cell walls are straight to arcuate. Similarly as in Pl. 5.3 *B. caryophylloides* growing in fresh water pond show increase in stomatal frequency. The costal and intercostal cells are not well distinguishable with only few cells showing slightly sinuate anticlinal cell walls. These features resemble to that in *B. parviflora* (Pl. 5.6) and *B. sexangula* (Pl. 6.3). However, in *B. gymnorrhiza* (Pl. 6.5) the costal cells are well demarcated by sinuate anticlinal cell walls on the lower leaf surface. The stomata are lined along on either sides of the costal area. However, the stomata in *B. cylindrica* are lined in the costal area (Pl. 7.2) and also in the intercostal areas (Pl. 7.3). The cells in the costal area show undulate anticlinal cell wall pattern and appears distinct and quite raised in the surface view (Pl. 7.4) which is completely different micromorphological feature when compared with its synonym *B. caryophylloides* (Pl. 5.2-3) or other species in Rhizophoraceae. Fine cuticular striations on the lower leaf epidermis are observed in *B. gymnorrhiza* and *B. cylindrica*. Therefore, with respect to leaf epidermal micromorphological features these two species are closely related and perhaps may show similar pattern of leaf adaptivity to changing coastal ecosystem.

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REFERENCES

Ahmad KJ 1974. Cuticular studies in some Nelsoniodeae (Acanthaceae). Botanical Journal of Linnaen Society 68 : 73-80.

Ball MC & Farquhar GD 1984. Photosynthetic and stomatal responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long term salinity and humidity conditions. Plant Physiology 74 : 1-6

Banerjee LK 1994. Conservation of coastal plant communities in India. Bulletin of Survey of India 36 : 160-165.

Beerling DJ & Chaloner WG 1992. Stomatal density as an indicator of atmospheric CO_2 concentration. The Holocene 2 : 74-75.

Beerling DJ & Woodward FI 1997. Changes in land plant functions over the Phanerozoic Reconstructions based on the fossil record. Botanical Journal of the Linnean Society 124 : 124-137.

Blasco F 1975. The mangroves of India. Institut. Francais Pondicherry, Travaux De la Scientifique et Technique, No.15.

Burgh J, vander Visscher H, Dilcher DL & Kurschner WM 1993. Palaeoatmospheric signatures in Neogene fossil leaves. Science 206 : 1788-1790.

Camilleri JC & Ribi G 1983. Leaf thickness of mangroves (*Rhizophora mangle*) growing in different salinities. Biotropica 15 : 139-141.

Caratini C, Blasco F & Thanikaimoni G 1973. Relations between the pollen spectra and vegetation of a South Indian Mangrove. Pollen et Spores 15 : 281-292.

Chaloner WG 1970. The rise of the first land plants. Biological Review of Cambridge Philosophical Society 45 : 353-377.

Chaloner WG & Mc Elwain J 1997. The fossil plant record and global climatic change. Review of Palaeobotany and Palynology 95 : 73-82.

Chapman VJ 1977. Ecosystems of the World 1 Wet Coastal Ecosystem. Elsevier Publication, New York. 428pp.

Cleal CJ, James RM & Zodrow E 1999. Variation in stomatal density in the late Carboniferous Gymnosperm Frond *Neuropteris ovata*. PALAIOS, An International Journal of SEPM (Society for Sedimentary Geology) 14 : 180-185.

Dagar JC, Mongia AD & Bandhopadhyay AK 1991. *Mangroves of Andaman and Nicobar Islands*. Oxford and IBH Publishing Co. Pvt. Ltd. 160 p.

Dahlgren RMT 1980. A revised system of classification of the angiosperms. Botanical Journal of Linnean Society 80 : 91-124.

Das S & Ghose M 1996. Anatomy of leaves of some mangroves and their associates of Sunderbans, West Bengal. Phytomorphology 46 : 139-150.

Dilcher DL 1974. Approaches to the Identification of Angiosperm leaf remains. The Botanical Review 40 : 1-157.

Ellison JC 1989. Pollen analysis of mangrove sediments as a sea-level indicator: Assessment from Tongatapu, Tonga. Palaeogeography, Palaeoclimatology, Palaeoecology 74 : 327-341.

Ellison JC 1993. Mangrove retreat with rising sea level, Bermuda. Estuarine Coastal & Marine Sciences 37 : 5-87.

Ellison JC & Stoddart DR 1991. Mangrove ecosystem collapse during predicted sea level rise: Holocene analogues and implications. Journal of Coastal Research 7 : 151-165.

Fahn A 1979. Secretory tissues in plants, Academic Press, London : 277.

Farooqui A 2000. Leaf cuticular/ epidermal traits in *Rhizophora* species adapting to the nutrients in the coastal wetland ecosystem, Pichavaram, Tamil Nadu. Phytomorphology 50 : 317-325.

Farooqui A & Bajpai U 1999. Stomatal modifications for salt exudation in *Rhizophora apiculata* Bl. Proceedings of National Conference on Electron Microscopy. DMSRDE, Kanpur : 121-123.

Farooqui A, Kulshreshtha K, Srivastava K, Singh SN, Pandey V & Ahmad KJ 1995. Photosynthesis, stomatal response and metal accumulation in *Cineraria maritima* L. and *Centauria moschata* L. grown in metal rich soil. The Science of the Total Environment (STOTEN) 164 : 203-207.

Farooqui A, Kulshreshtha K, Singh SN, Farooqui SA, Yunus M & Ahmad KJ 1997. Foliar content and changes in epidermal traits of *Lagerstroemia parviflora* (L) ROXB. Environmental Monitoring and Assessment 48 : 107-115.

Hooker JD 1879. Flora of British India, L. Reeve and Co. Ltd. England Vol. II, 792 p.

Kinraide TB 1999. Interactions among Ca^{+2}, Na^{+} and K^{+} in salinity toxicity, quantitative resolution of multiple toxic and amelioration effects. Journal of Experimental Botany 50 : 1495-1505.

Kurschner WM, Burgh J, vander Visscher H & Dilcher DL 1996. Oak leaves as biosensors of late Neogene and early Pleistocene atmospheric CO_2 concentrations: Marine Micropalaeontology 27 : 299-312.

McElwain J & Chaloner WG 1995. Stomatal density and index of fossil plants track atmospheric CO_2 in the Palaeozoic. Annals of Botany 76 : 389-395.

McElwain J & Chaloner WG 1996. The fossil cuticle as a skeletal record of environmental change: PALAIOS. An International Journal of SEPM (Society for sedimentary Geology 5 : 376-388.

Mehrotra RC, Dilcher DL & Awasthi N 1998. A Palaeocene Mangifera-like leaf fossil from India. Phytomorphology 48 : 91-100.

Metcalfe CR & Chalk L 1950. Anatomy of Dicotyledons, Vol I Claredon Press, London. Vol. I, 724 p.

Mullan DP 1931. On the occurrence of glandular hairs (salt glands) on the leaves of some Indian Halophytes. Journal of Indian Botanical Society 10 : 184-189.

Muller J 1959. Palynology of Recent Orinoco delta and shelf sediments; Micropalaeontology 5 : 11-32.

Naskar KR & Guha Bakshi DN 1987. Different Phytoecological zones in the 24-Paraganas District of West Bengal with special reference to its land utilization patterns. Journal of Indian Society of Coastal Agricultural Research. 5 : 183-187.

Naskar KR & Mandal R 1999. Ecology & Biodiversity of Indian mangroves. Vol II DAYA Publishing House. 574pp. & 164 Pl.

Palmer PG 1976. Grass cuticles: a new palaeoecological tool for East African lake sediments. Canadian Journal of Botany : 54 : 1725-1734.

Plaziat JC 1995. Modern and fossil mangroves and mangals, their climatic and biogeographic variability. *In* : Bosence DWJ & Allison PA (Editors)—Marine Palaeoenvironmental Analysis from fossils : 73-96. Geological Society Special Publication No. 83.

Poole I, Weyers JDB, Lawson T & Raven JA 1996. Variations in stomatal density & index: Implications for palaeoclimatic reconstructions. Plant, Cell & Environment 19 : 705-712.

Ramanujam CGK & Reddy PR 1984. Palynoflora of Neyvelli lignite-floristic and palaeoenvironmental analysis. Journal of Palynology 20 : 58- 74.

Rollet B 1981. Bibliography on mangrove research, 1600-1975 Paris, UNESCO.

Salisbury EJ 1927. On the causes and ecological significance of stomatal frequency with special reference to woodland flora. Philosophical Transactions Society, London Series, B 216 : 1-65.

Scholander PF 1968. How mangroves desalinate water. Plant Physiology 21 : 251-261.

Spackman W, Dolsen CD & Riegel W 1966. Phytogenic organic sediments and sedimentary environments in the Everglade mangrove complex. Palaeontographica (B) 117 : 135-152.

Stace CA 1965a. The significance of the leaf epidermis in the taxonomy of the Combretaceae I. A general review of tribal generic and specific characters. Botanical Journal of Linnaen Society 59 : 229-252.

Stace CA 1965b. Cuticular studies as an aid to plant taxonomy. Bulletin of British Museum of Natural History 4 : 3-78.

Tomlinson PB 1986. The Botany of mangroves. Cambridge University Press, Cambridge. 413 p.

Tukey H Jr. 1971. Leaching of substances from Plants. *In:* Preece TF & Dickinson CH (Editors)—Ecology of leaf surface Microorganisms : 56-57. Academic Press.

Untawale AG & Jagtap TG 1991. Floristic composition of the Deltaic regions of India. Journal of Geological Society of India, Special Vol. 22 : 243-263.

Upchurch Jr. GR 1995. Dispersed angiosperm cuticles: Their history, preparation & application to the rise of angiosperms in Cretaceous & Palaeocene coals, southern western interior of N. America. Indian Journal of Coal Geology 28 : 161-227.

Upchurch Jr. GR, Nichols DJ, Flemming RF, Tschudy RH & Pillmore CI 1985. Cuticular & palynological analysis of vegetational change across the Cretaceous-Tertiary boundary at Sagarite, Raton Basin New Mexico. American Journal of Botany 72 : 904.

Willmer C & Fricker M 1996. Stomata 2nd : Topics in Plant functional Biology, 2: Chapman & Hall, London, 375 pp.