FURTHER CONTRIBUTION TO OUR KNOWLEDGE OF THE ANATOMY OF PTILOPHYLLUM

A. R. RAO & VIMALA ACHUTHAN (Mrs.)

Department of Botany, Lucknow University

ABSTRACT

The epidermal features and the anatomy of the rachis and pinna of a well preserved but fragmentary petrified specimen of Ptilophyllum from the Rajmahal hills are described in detail. The rachis contains a double arc of collateral vascular bundles comparable to those found in the Pteridosperms. Sclerenchymatous patches and sclereids are found in the cortex. The epidermal features agree with those already described for this species by Sahni and Rao and others. It is found that a single bundle coming off from the upper corner of the double arc of the vascular bundles of the rachis, divides into 2 at the base of the pinna and repeatedly dichotomises at different levels to form a more or less parallel venation. The bundles of the pinnae are collateral, exarch with a parenchymatous bundle sheath. Isolated and grouped sclereids occur scattered in the palisade and spongy mesophyll.

INTRODUCTION

ANCROFT (1913) gave the outline of the pinnae and rachis of P. cutchensefrom the Rajmahal Hills without mentioning anything further about its anatomy. Rao (1948) in an unpublished paper described the anatomy of the pinnae of P. cutchense found in a petrified block from Nipania in the Rajmahal Hills. Examination of a few more blocks (K. 15) from the same locality revealed fully the anatomy of the pinnae and the rachis and also the epidermal features, of some well preserved specimens of Ptilophyllum which agree with P. cutchense and to some extent with P. amarjolense (see under Discussion). This forms the subject matter of this paper.

METHOD

Due to the extreme silicification of the tissues, the details of the anatomy could be studied only after staining the sections with safranin and gentian violet. Both the stains gave good results. Apart from the thin sections, ground by hand the peel method (Walton, 1928; Barnes & Duerden, 1930) was also tried for studying the serial sections. But they were not useful. For the stomatal studies 'Duco prints'

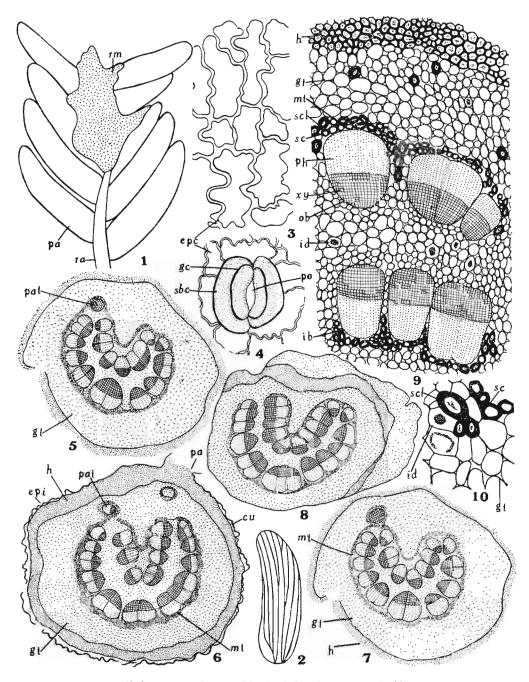
(RAO, 1943) were taken by wetting the surface of the pinnae with absolute alcohol and smearing it with Durofix without any treatment with acid. The peels come off with the impressions of the surface, without any plant bits. This was the only way left, to examine the epidermal features, as no cuticle is preserved and the brittle epidermis does not lend itself for paradermal The details of the structure sectioning. of the stomata were studied from these "Duco prints" and the illustrations also drawn from them. A study of the impressions under strong reflected light was however, helpful in studying the epidermal features. The pinnae and the rachis could however be sectioned satisfactorily.

DESCRIPTION

One fragment of the chert, K. 15, shows 3 pairs of pinnae in the apical part of a leaf (Fig. 1, Рното 1). The individual pinna measures 2 mm. broad and 6 to 7 mm. long with obtuse tip. They are short, sub-opposite, slightly overlapping, obliquely placed and attached to the upper side of the rachis. The base of the pinna is rounded (Fig. 2). The upper surface of the pinna is smooth and the lower surface shows veins which are nearly parallel and branch at all levels (Fig. 2). Two veins can actually be seen to enter the very base of the pinna and they branch and form 4-5 parallel veins within the basal part (Fig. 2). Subsequent branching of the veins leads to 7-9 veins in the middle of the pinna, while at the tip only four or five veins are present.

STRUCTURE AND DISTRIBUTION OF THE STOMATA

The upper surface is smooth, devoid of stomata and has, elongated sinuous walled epidermal cells. The lower surface (Рното 2) shows the veins, stomata and the epidermal cells with sinuous walls (Fig. 3). Between any two veins occur generally 2-3



All figures are drawn with the help of a camera lucida.

TEXT-FIGS. 1-10.

rows of stomata with a more or less regular orientation (Photo 2 & 3). The stomata are roughly oval in outline and measure 43-58 μ long by 36-57 μ broad, slightly sunken, with two subsidiary cells enclosing the entire stoma (Fig. 4). Often a subsidiary cell may be divided into two. The frequency of the stomata is 100-110 per sq. mm. The veins are generally composed of 4 rows (Photo 3) of elongated almost straight walled cells which increase to 6 at the forking of the vein. The margin of the pinna is composed of 4 rows of slightly elongated and sinuous walled cells devoid of papillae and stomata.

ANATOMY OF THE RACHIS

The rachis in cross sections (Figs. 5-8, Pното 4 & 5) shows a thick layer of cuticle (Fig. 6) overlying the epidermis which is not well preserved. The hypodermis is made up of small thick walled cells with some contents inside (Fig. 9). The ground tissue consists of thin walled, round or oval to elongated (due to compression) compact cells with small intercellular spaces (Fig. 9). A few thick walled isolated or grouped cells with lamellated walls, are scattered in the ground tissue (Figs. 9 & 10, Рното 6 & 7). They occur in a discontinuous ring outside as well as in between, the fibrovascular bundles (Figs. 9, 11 & 12, Photo 4). They are the sclereids (MENON, MALAVIYA & RAO, 1965) referred to as stone-cells in Williamsonia sewardiana flower peduncle by Sahni (1932). The vascular bundles are arranged in a double arc (Figs. 5-8, Photo 4 & 5), the concavity facing upwards and the bundles vary from 25-32 in number. Many of the bundles are in a state of incomplete division (Figs. 5-8). The bundles of the arc are at places so much united as

to suggest a continuous C-shaped strand as in some Pteridosperms. This evidently becomes split up into a number of bundles, which are collateral, endarch with more or less equally well developed phloem, and compact xylem with scalariform thickenings. The xylem in the outer and inner arcs face in opposite directions. The well preserved phloem cells are polyhedral and compact without any intercellular spaces (Fig. 12). Apart from the sclereids, a discontinuous layer of sclerenchyma cells is also present outside, as well as in between, the vascular bundles (Figs. 9, 11 & 12, Рното 6). Both these are joined together and form a more or less continuous ring of mechanical tissue outside the vascular bundles (Figs. 5-9, 11 & 12, Рното 4 & 5).

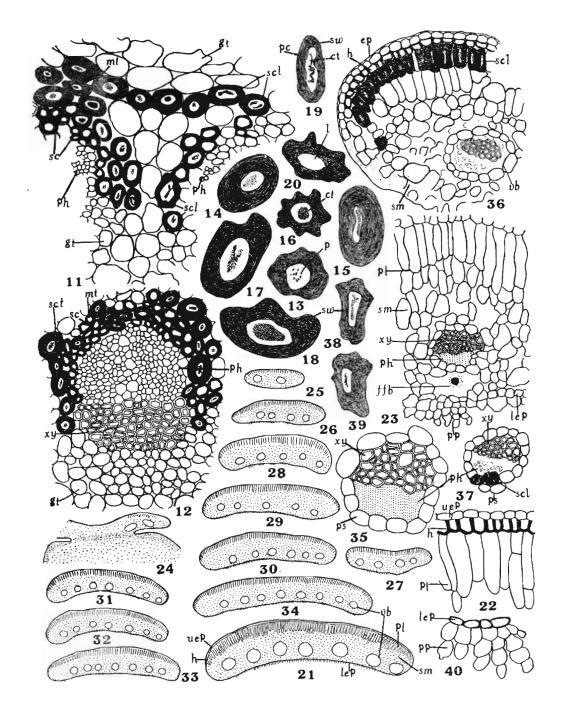
The sclereids found in the rachis are more or less rounded, oval or slightly elongated (Pното 7) often lobed (Figs. 13-20) and can be referred to the category of Brachysclereids or stone-cells (TSCHIRCH, 1889 and FOSTER, 1949). The cell contents may partly be the wall substance as they stain with safranin (Fig. 18). The lumen is generally round to oval in shape (Figs. 13-20). The very thick, finely lamellated secondary walls of the sclereids (Figs. 13-20) bear round or oval slit-like pits (Fig. 13) and pit-canals (Figs. 19 & 20) which run through the entire thickness of the wall. The ontogeny of the sclereids could not be studied due to the lack of younger fronds. Apart from the sclereids there are some peculiar type of thin walled cells with dark contents distributed in the ground tissue. They may be referred to as Idioblasts (Fig. 9, Photo 4) (Esau, 1962).

ANATOMY OF THE PINNA

A cross section of the pinna-shows mostly a slightly convex upper and a slightly

Text-figs. 1-10 — (cu, cuticle; epi, epidermis; epc, epidermal cell; gc, guard cells; gl, ground tissue; h, hypodermis; ib, inner bundle; id, idioblast; mt, mechanical tissue; ob, outer bundles; pa, pinna; pat, pinna trace; ph, phloem; po, pore; ra, rachis; rm, rock material; sbc, subsidiary cell; sc, sclerenchyma; scl, sclereid; xy, xylem).

^{1.} An outline sketch of the apical part of the frond with the help of the camera lucida. The venation is not shown. × 12. 2. A single pinna enlarged showing the venation. Only two bundles enter into the very base of the pinna and they divide at various levels. × 12. 3. Epidermal cells as shown by 'Duco print'. × 300. 4. A single stoma from the 'Duco print' enlarged. × 300. 5-8. Transverse sections of the rachis showing the stages of evolution of the pinna trace. Fuller explanation in text. × 20. 9. A sector of the rachis in transverse section showing the various tissues. × 60. 10. A small portion of the outer side of the outer bundles enlarged showing the sclereids. × 140.



All figures are drawn with the help of a camera lucida. $\label{eq:Text-figs.} \text{Text-figs.}, \ 11\text{-}40.$

concave lower surface (Fig. 21, Photo 8). Below the upper epidermis of smaller rectangular cells (Fig. 22, Рното 9) lies generally a single layered hypodermis, composed of slightly thick walled cells (Fig. 22, Рното 9 & 10). The palisade tissue is made up of 1-2 rows of elongated thin walled cells (Figs. 22 & 23, Photo 9 & 10). Towards the margin of the pinnae, the palisade cells are smaller in size and indistinguishable from the spongy mosophyll (Photo 9). This extends from the palisade to the lower hypodermis (Fig. 23, Photo 9 & 10) and is made up of loosely arranged more or less angular cells (Fig. 23). The vascular bundles passing through the mesophyll number 4-9 and are placed in a single row (Fig. 21, Photo 8). Earlier descriptions of the anatomy (BANCROFT, 1913; BOSE, 1953 & VISHNU MITRE, 1956 MS.) have indicated the general disposition of tissues and vascular elements in the pinnae of Ptilophyllum. But the origin of the pinna trace and their evolution into the parallel veins of the pinna have not clearly been elucidated. It was found that in the specimen described in this paper, the details could be studied definitely to some extent. Photo 5 and Fig. 5 show that the pinnatrace is single and arises from the corner of the double arc of the vascular bundles. This is gradually pushed out (Fig. 6) and abstricted off (Fig. 7) leaving a gap between the two arcs (Fig. 8, Рното 4). Only one such bundle passes into the pinna.

From the upper surface it looks as if the pinna is attached throughout its breadth. The base of the pinna is actually rounded and not auriculate (Fig. 2). The attachment to the rachis is by what appears to

be an exceedingly short petiole like structure which cannot be satisfactorily demonstrated. Into this evidently passes the single pinnatrace referred to above and divides into two. Fig. 24 shows these two bundles cut transversely in a rather obliquely sectioned basal part of a pinna. Figs. 25-34 represent transverse sections at different progressive levels in the pinna. It will be seen that the multiple bundles disposed more or less in a parallel manner in the adult pinna are the result of repeated dichotomy of a single trace that passes into the base of the pinna. This is confirmed by Fig. 2, which shows the venation in surface view. Fig. 34 shows the maximum number of veins encountered in the middle of the pinna. The tip of the pinna contains four veins almost the same that is found near the base. The vascular bundles are collateral, exarch with poorly preserved phloem and well preserved xylem elements (Fig. 35, Рното 10), which are scalariformly thickened and are quadrangular to hexagonal in section. A parenchymatous sheath (Fig. 35, Photo 10) surrounds the vascular bundle. Just as in the rachis here also sclereids or stone-cells are found in a row in the palisade region (Fig. 36) and occur scattered in the spongy mesophyll, where they are confined mostly to the vascular bundles (Fig. 37). They are also slightly elongated with thick, lamellated, pitted, lignified secondary walls (Figs. 38 & 39). Such stone cells have been described by Sahni in the leaf bases and peduncle of Williamsonia sewardiana (1932). The lower epidermis has rectangular cells and bears a number of papillae which are generally 2-3 celled (Fig. 40, Рното 10). Sectional

Text-fics. 11-40 — (ct, cell content; epi, epidermis; ffb, fungal fruit body; gt, ground tissue; h, hypodermis; l, lumen; lep, lower epidermis; mt, mechanical tissue; p, pits; pc, pit canal; ph, phloem; pl, palisade; pp, papilla; ps, parenchyma sheath, sc, sclerenchyma; scl, sclereid; sm, spongy mesophyll; sw, secondary wall; upe, upper epidermis; vb, vascular bundle, xy, xylem).

^{11.} A portion in between the outer bundles enlarged to show the distribution of sclereids and sclerenchyma. × 140. 12. A vascular bundle shown on an enlarged scale. × 140. 13-20. Different types of sclereids from the rachis. × 300. 21. Transverse section of the pinna. × 32. 22. A portion of the pinna showing the upper epidermis; hypodermis; and palisade cells enlarged. × 140. 23. A sector of the transverse section of the pinna enlarged to show the vascular bundle. × 140. 24-34. Transverse sections of the pinna at the different progressive levels. × 20. 25. Represents the base of the pinna with only two bundles. × 20. 26. Represents a section through the middle part of the pinna showing the maximum number of vascular bundles. × 20. The other figures show varying numbers of vascular bundles due to the dichotomy of the veins. Further explanation is in text. 35. A single vascular bundle of the pinna shown on enlarged scale. × 300. 36. The marginal region of the pinna in transverse section showing a row of sclereids below the hypodermis. × 140. 37. A vascular bundle from the pinna showing the sclereids in the bundle sheath. × 140. 38-39. Sclereids from the pinna. × 300. 40. A portion of the lower epidermis and papillae enlarged. × 300.

views of the stomata could not be clearly made out, but surface "Duco prints" show the stomata and the epidermal cells but not very clearly the papillae. In some of the air spaces, which are obviously caused by decayed cells, as well as in other parts of the pinnae and rachis, there can be recognized a number of fungal fruit bodies (Fig. 23) which measure $10~\mu$ in diameter and contain similar spores measuring $0.3~\mu$ in diameter.

DISCUSSION

The specific name Cutchense was first given by Morris (1840) to certain pinnate fronds from Cutch, India. Seward in 1900 recognized for the first time the organic connection of the leaves of Ptilophyllum cutchense to a cycadean trunk which was later on named as Bucklandia indica (SE-WARD, 1917). In 1920 Seward and Sahni instituted a comprehensive species P. acutifolium to include almost all the detached leaves of Ptilophyllum known from India. Sahni in 1932 reconstructed Williamsonia sewardiana and pointed out that the leaves till then known as P. cutchense associated with Williamsonia sewardiana were similar to those borne on the stem of Bucklandia indica. Sahni and Rao in 1933 for the first time separated P. cutchense from P. acutifolium on some of the morphological and cuticular features of the pinnae as seen in some specimens from the Rajmahal Hills. These features were further confirmed by Ganju (1946) and Jacob and Jacob (1954). A number of new species of Ptilophyllum have been described by Ganju (loc. cit.), Bose (1953), Jacob and Jacob (loc. cit.) and Vishnu Mittre (1956) (see TABLE 1). P. amarjolense the new species instituted by Bose (1953) includes, according to him, two types of fronds with morphological and cuticular features comparable to those of P. cutchense and P. acutifolium. P. amarjolense is separated from the above two species in the possession of the following features. It differs from P. cutchense (1) "in having also pinnae with acute tips like those of P. acutifolium"; (2) "in having a very variable width of the lamina and having slightly falcate pinnae at the apical region of the frond and also in the widest fronds"; and (3) its association with a new species of Bucklandia, Bucklandia sahnii.

It differs from *P. acutifolium* in (1) its "pinnae have rounded upper basal corner and they are not decurrent"; (2) in not having the sinuous walls in the upper epidermal cells; and (3) in having only 2-4 stomata in each band.

Ptilophyllum nipanica (VISHNU MITTRE, 1956 MS), based upon just three pinnae, shows a number of morphological and anatomical resemblances with Ptilophyllum cutchense, yet it is regarded by Mittre as distinct from Ptilophyllum cutchense on the following grounds: (1) falcate with pointed apex of the pinnae; (2) the presence of polar thickenings and papillae on the guard cell and (3) in the absence of nonstomatiferous bands in the stomatiferous region of the pinnae.

It seems to us that the cuticular and morphological variations shown by these two species, *Ptilophyllum amarjolense* and *Ptilophyllum nipanica*, are insufficient to separate them as different species. They may as well be regarded as variants of either *Ptilophyllum cutchense* or *P. acutifolium*. More specimens with a fuller display of morphological and cuticular character are needed before anything definite could be stated about these species.

A very intriguing situation has arisen on account of the discovery of the type specimen of *Ptilophyllum cutchense* Morris. Through the kind courtesy of Dr. Bose we were able to see the photographs of the original specimen of *Ptilophyllum cutchense* Morris as figured in Grant (1840).

The Ptilophyllum species represented by this figure looks more like P. acutifolium and not at all like the species which have all along been regarded as P. cutchense or compared to it. Further, the type specimen does not show cuticular features. In view of this a fundamental doubt is raised whether the specific name cutchense has been correctly applied after Morris. We are therefore not referring our specimen definitely to the species cutchense. We refrain from any further comments as Dr. Bose is reviewing all the Indian Ptilophyllum fronds in an exhaustive monograph.

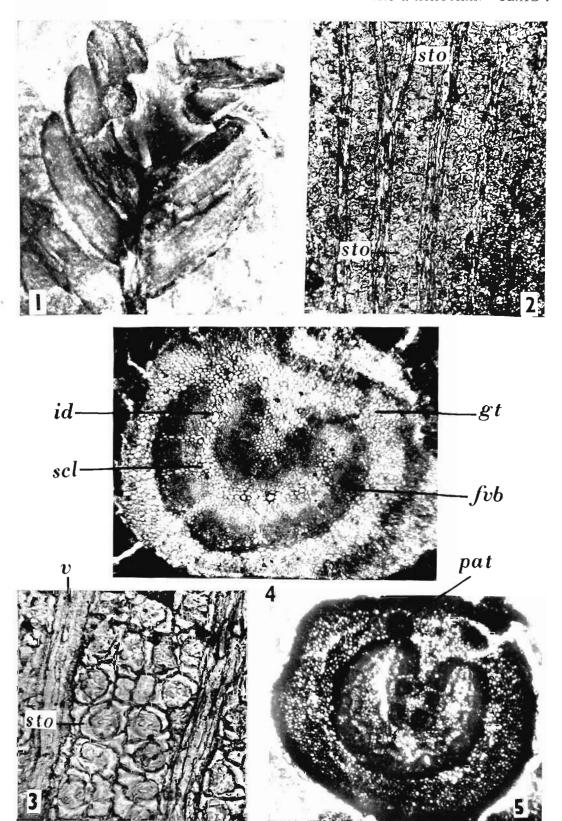
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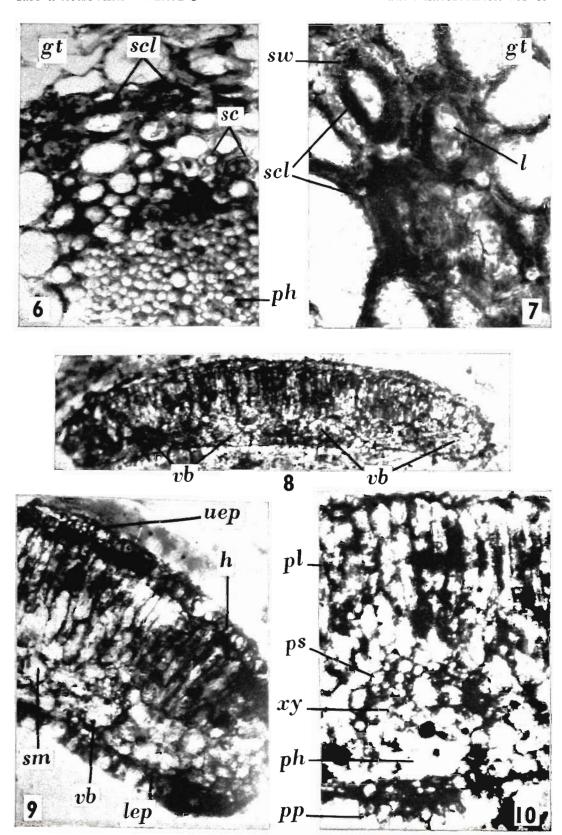
We are greatly indebted to Dr. M. N. Bose for showing his slides, photographs and specimens, examining our specimens and discussing certain points. We are

Papillae

CHARACTERS	Pillophyllum culchens Morrets 1840	Ptilophyllum vulchense Feistmental (1876 & 1877)										
		P. cutchense		the statement of the party and the same of		Ptdophyllum cutchense Feist Bancroft 1913	P. et. entchense McCl. Sp. Sahnt & Rao (1933)	P. (f. cutchen McCl. Sp. Garrio (1946)	P. culchense Morris, Jacob & Jacob 1954	P. amarjoleusi Bose (1953)	P. nipanica Vishav Mitter (1956)	Puliphyli, myt. P. cutchense, DESCRIBED IN THIS PAPER
Form and arrangement of pinnae on the frond	"Fronds pinnate; pinnae closely approximated, linear, lanceolate, more or less elongate, imbricate at the base, attached obliquely; base semicircular or rounded."	apex and base, leaflets short, oblique, subalter- nating, imbricate or		"Frond very slender and narrow, leaflets short and narrow, whole aspect fern like."	their whole length."	pinnae decrease in size	"Pinnae are relatively short and have a rounded apex."	Finna short, stoat with rounded tip	Agrees with Fristmental's description.	Fragments of the fronds measuring 0.4 to 4.5 cm. in breadth, tapering very gradually below and more suddenly at the apex. The leaves are imparipinate, fwo types of pinnae, one having mostly oblong, short rounded apices resembling P. euthorisis and the other widest fronds in which pinnae are slightly falcate with more or less acute tips, resembling P. euthofitim. Upper basal corners of the pinnae are rounded, while the lower basal angles are not rounded.	"A fragment of a frond 5-6 mm, long and 8-10 mm, broad with the puna overlapping with each other, disposed in 2 rows, taleate with pointed apex and with upper and lower round corners at the proximal region."	3 pairs of paintae seen in the fronds, fragments 1.4 cm long and 1 cm, broad, pinnae short 2 num, broad and 6.7 num, long with rounded apex. They are sub-opposite-lightly overlapping, obliquely pla, ed. The base of the pinnae is rounded.
Veins	"Equal, slender, paral lel" .	"Distinct, radiating from the base and fork- ed towards the apex."		-	~	Parallel and apparently end blindly. Dichoto- mies occur even in the upper parts of pinnae.	-	_	Same as Feistmental's description.	"Distinct, nearly parallel and branching at all levels."	"Lateral years are very few 3-5 in number and occasion- ally dichotomising."	4-8 nearly parallel veins, di- chotomising at all the levels
No. of cells over the veins	-	-	_	-	_	_	4 rows of elongated epi- dermal cells.	3 rows of elongated epi- dermal cells	Cells with slightly sinuous walls.	3-4 rows of much elongated epider- mal cells over each vem.	_	Generally 4 rows of clongated epidermal cells
Epidermal cells		_				_			"Squarish or rectangular cells having thin looped walls in both upper and lower epidermis."	The upper epidermal cells are clongated and the lower epider- mal cells are irregular in shape with thin sinuous walls having a few folds	mat cells are squarish to	shape with sinuous walls
Distribution of stomata	_	-	-			-	_	Close in distribution.	No uniformity in distri- bution.	Orientated more or less at right angle to the veins.	"Stomata are evenly placed to contiguous, irregularly ar- ranged, transverse to oblique in orientation."	Orientated more or less a right angles to the veins.
Prequency of the stomata per sq. mm.			_	****	, –	_	-	-	100 sq. mm.			100-110/sq. mm.
Size and shape of the stomata	· —	_		-	_	_	_	! Round	Sunken, vary much in size, $36 \times 66 \ \mu$, $50 \times 49 \ \mu$, $50 \times 70 \ \mu$, $60 \times 66 \ \mu$	Dimension of the guard cells 43 \times 34 \times	$38\text{-}51\mu \approx 35\text{-}45~\mu$ (including subsidiary eclls).	Sunken, slightly vary in size 43-58 $\mu > 36\text{-}57~\mu.$
No, or stomata per band	u —		-			_	Usually two, sometimes three rows.	Two to three rows.	Two to four rows	Two to four, usually 3, very rarely 5	_	2-3 rows of stomata
Marginal cells	_ ·		_	_		-		Non-stomatal narrow region.	Non-stomatal and non- papillate region with 4-5 rows of cells.		Non-stomatal rectangular cells.	Non-stomatal and non-papil- late more or less rectangular to clongated cells.
Papillae		-	_	_		_			1-3 in the epidermal cells.	-	Seen even in the guard cells.	1-3 in epidermal cells.
Inatomy of Rachis Epidermis.	-	_	_	-	phrap	_		-		Upper layer of rectangular cells		Not preserved properly.
Hypodermis		_	_	_			_	_	-	6-7 celled, thick walled cells	22	6-7 celled thick walled cell with contents.
Ground tissue	-			_		_			-	Isodiametric or oval cells with in- tercellular spaces between them	Round to oval parenchymatons cells with frequent inter- cellular spaces.	Isodiameteic found to ova- cells with sometimes inter- cellular spaces.
Vascular hundles		***	_	-	and .	-	-	-		Double series in the form of t Maximum number of bundles 46 or even more. Xylem in all bundles pointing inwards.		t-shaped double series bundles number 25-32. Xylen pointing inwards.
Pinna Epidermis		_		-	-	-	_		_	Small rectangular cells.	Rectangular cells.	Single layered.
Hypodermis					Man-		-	-	-	Single layered slightly thick walled cells which are bluntly tapering inwards.	Single layered more or less isodiametric cells.	Single layered slightly thick walled cells.
Palisade cells	-	_	_	_	-	-	-		_	Narrow, clongated, single layered.	. Single tayered cells.	Narrow, elongated thin waller single layered cells.
Spongy Mesophyll	-4-	-	_	-	_	-	_	_	-	Loose cells.	Loose and spongy.	Slightly loose cells
Vascular bundles				_	_	_	_			Situated in between the meso- phyll and lower hypodermis. Xylem on the upper side phloem on the lower side.	form tracherds.	 4-8 situated between the mesophyll and lower hypedermis. Collateral, endared bundles with scalariforn thickening of the xylem elements.

1-3 celled on the lower side.





indebted to Dr. Miss Malaviya for examining our slides and confirming the presence of sclereids. Our grateful thanks are due to the authorities of Birbal Sahni Institute

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EXPLANATION OF PLATES

(All photographs are from untouched negatives)

PLATE 1

- (fvb, fibrovascular bundles, gt, ground tissue, id, idioblast; pat, pinna trace; scl, sclereid; sto, stomata; v, vein.
- 1. The apical portion of the frond enlarged. $\times 9.9.$
- 2. 'Duco print' of the lower epidermis showing the distribution of the stomata and veins. \times 153.6.
- 3. An enlarged portion of the same showing the arrangement of the stomata. \times 173.
- 4. Transverse section of the rachis showing the bundles arranged in a double c-shape. \times 6.
- 5. Transverse section of the rachis showing the origin of the pinna trace from the corner of the stele. \times 4.9.

PLATE 2

(gt, ground tissue; h, hypodermis; l, lumen;

- lep, lower epidermis; ph, phloem; pl, palisade; pp, papilla; ps, parenchyma sheath; sc, sclerenchyma; scl, sclereid; sm, spongy mesophyll; sw, secondary wall; uep, upper epidermis; vb, vascular bundle; xy, xylem.
- 6. Magnified portion of a section of the rachis showing sclerenchyma and sclereids. \times 286.6.
- 7. Magnified view of the sclereids showing their lamellated walls. \times 580.5.
- 8. Transverse section of a pinna showing the palisade tissue and a row of vascular bundles. \times 28·3.
- 9. Margin of the pinna enlarged showing the palisade and spongy mesophyll tissues and vascular bundle. \times 172.6.
- 10. Magnified portion of a section of the pinna showing palisade tissue, vascular bundle and papillae. \times 191.4.