Anatomy of the Grass Tribe *Isachneae* (Fam.Poaceae) and its Taxonomic significance - II

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The anatomy of the genus Isachne is presented. The taxonomic significance of anatomy in the tribe Isachneae is also discussed. The tribe Isachneae is a natural assemblage of 5 genera i.e. Isachne, Coelachne, Limnoppa, Sphaerocaryum and Heteranthoecia (not found in India). The tribe is related to Paniceae, but is distinct from true Panicoid grasses in some unique characters.

A brief historical account of work on the tribe Isachneae and observations on epidermis and anatomy of leaf and culm of *Coelachne*, *Limnopoa* and *Spherocaryum* were given in part I. The methods adopted in the present study were same as described in part I.

OBSERVATIONS ISACHNE R. BR.

1. Leaf-Epidermis-The arrangement of cells on costal zones is almost similar on the adaxial and abaxial surface, but the cells of intercostal zones on the adaxial surface are quite different from that of the abaxial surface. Both zones contain a number of different cell types which include long cells, short cells (both cork and silica cells), stomata, interstomatal cells, macrohairs, microhairs, prickle hairs, hooks and papillae.

Long cells - The intercostal zones are made up of mainly long cells. The long cells on the abaxial surface are uniform and often nearly or quite squarish or polygonal to hexagonal and with non-sinuous walls. As Metcalfe (1960) stated, term 'long cell' is rather a misnomer in this genus and other related genera, because the cells that are homologous to the long cells in most other grasses are here quite short. The long cells of abaxial surface have proved to be of little diagnostic value at infrageneric level, and species of one section cannot be differentiated from species of any other section on the basis of long cells. However, the long cells of one species often slightly differ from

that of another species in size and shape of cells and thickness of cell walls. For example, the long cells of *I. confusa* are almost of hexagonal to ploygonal and very thick-walled (Fig. 9). The cells of *I. scabrosa* are very small and there is very narrow intercostal zone (Fig. 6) while the cells of *I. lisboae* are very large and have wide intercostal zones (Fig.15). The long cells of *I. gracilis*, *I. lisboae*, *I. scabrosa*, *I. walkeri* and *I. albens* are somewhat vertically clongated while in most of the other species cells are almost equal in length and breadth. The characters of individual species are shown in Table I and Figs. 1-17 Table Fig.

The arrangement of long cells on the adaxial surface is quite different from that of the abaxial surface. In adaxial surface, long cells are of two types in the species studied.

- (i) Narrow, horizontally elongated cells with sinuous walls; these are arranged in 2 to 4 rows on either side of the costal zones (or margins of intercostal zones);
- (ii) Polygonal to hexagonal cells with non-sinuous walls; these are arranged in middle portion of the intercostal zones (Figs 18-40).

The cells of this surface also have no diagnostic value at infrageeneric level; however, they differ slightly from one species to another in size of cells and thickness of cell-walls.

Long cells in costal zones (above the primary vascular

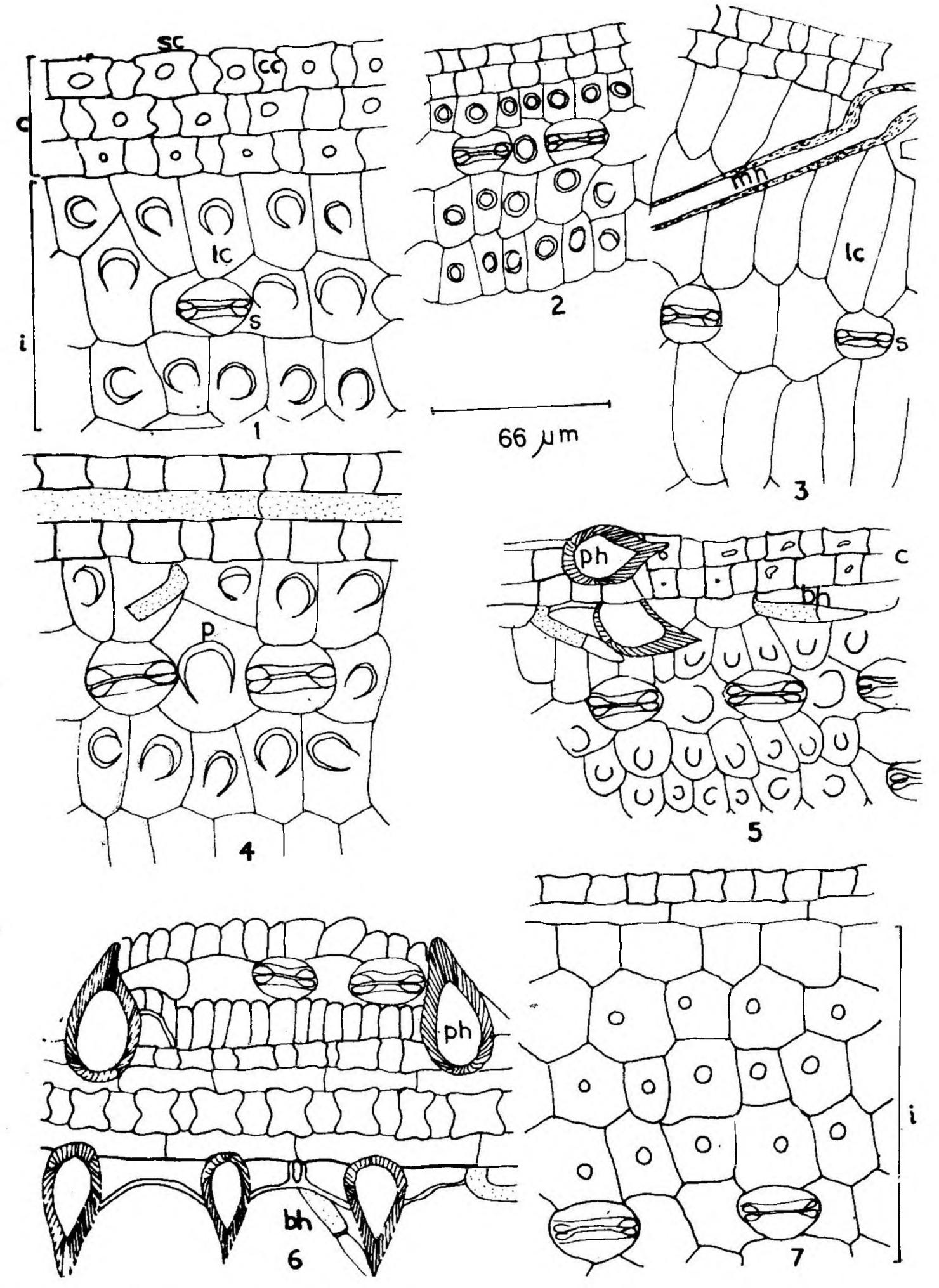


Fig. 1-7: Leaf-epidermis (abaxial surface) of *Isachne* species.

Fig. 1 *I. globosa*; Fig. 2. *I. miliacea*; Fig. 3. *I. bourneorum*; Fig. 4. *I. gracilis*; Fig. 5. *I. albens*; Fig. 6. *I. scabrosa*; Fig. 7. *I. clarkei*.

(bh - biccllular hair; c - costal zone; cc - cork cell; i - intercostal zone; lc - long cell; mh - macrohair; ph - prickle hair; p - papilla; s - stomata; sc - silica cell).

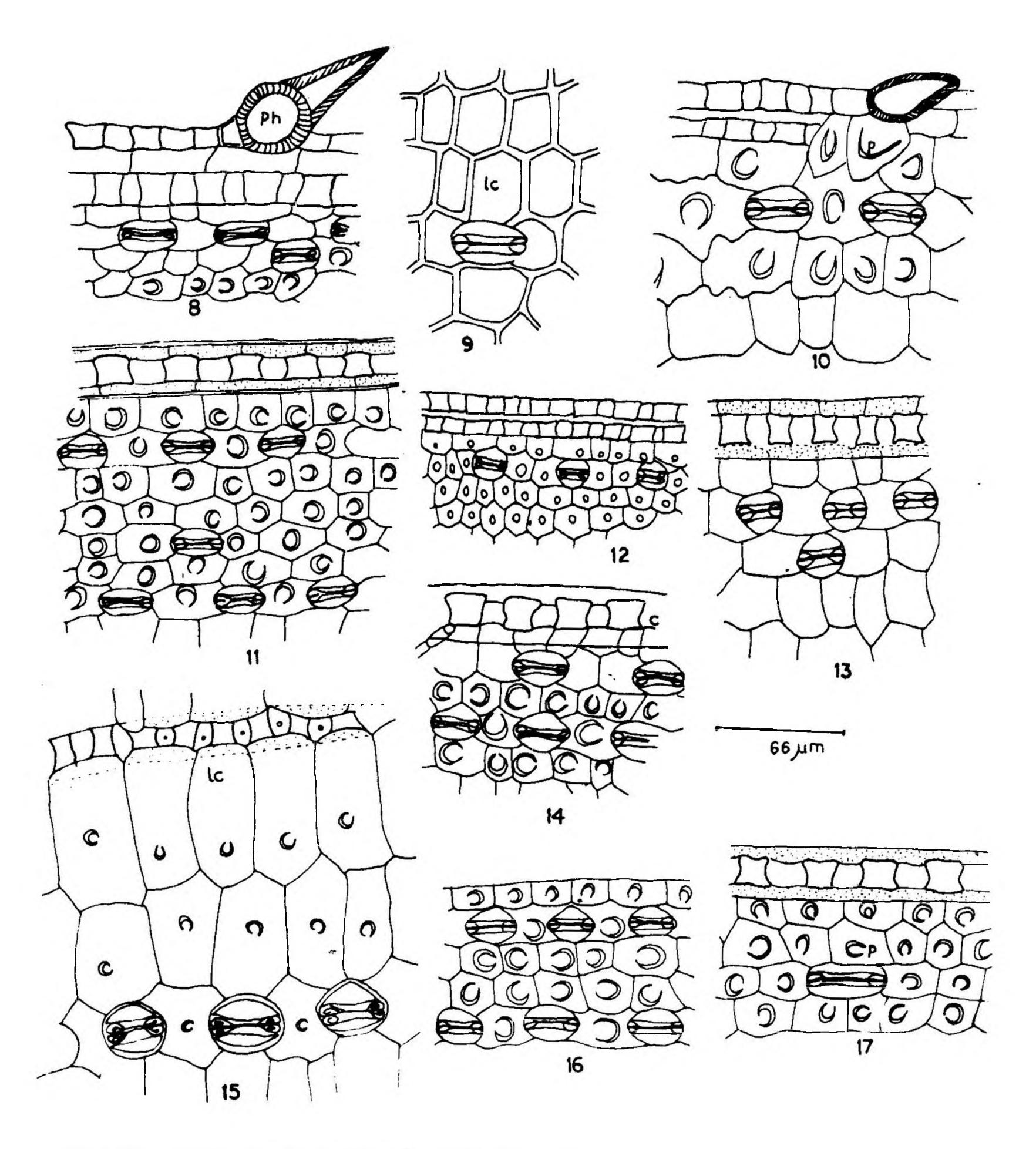


Fig. 8-17: Leaf-epidermis (abaxial surface) of Isachne species.

Fig. 8. I. himalaica; Fig. 9. I. confusa; Fig. 10. I. kunthiana; Fig. 11. I. elegans; Fig. 12. I. angladei; Fig. 13. I. walkeri; Fig. 14. I. bicolor; Fig. 15. I. lisboae; Fig. 16. I. swaminathanii; Fig. 17. I. meeboldii.

bundles) are usually thick-walled, narrow, horizontally elongated with sinuous or non-sinuous walls.

Short cells- In Isachne, short cells are present only in the costal zones (over the veins). They are classified as 'silica cells' when the cell is filled with a single silica body and as 'cork cells' when the walls give the reaction of cork. In the costal zones they are arranged in long rows commonly with alternating silica and cork cells. The long rows of short cells are often interrupted by prickle and or macrohairs. The structure of silica bodies in the state of the mature leaves is of taxonomic importance. In Isachne silica bodies are primarily cross-shaped or more or less cubical and acute angled. In I. globosa, I. elegans and I. bicolor, silica bodies are somewhat saddle shaped. These vary, in quantitative characters. There is no difference in arrangement of short cells on the adaxial and abaxial surfaces. No short cells occur in the intercostal zones.

Stomata - Stomata occur in one to several rows among the long cells in intercostal zones on both surfaces of the epidermis. The stomatal complex is made up of two dumb-bell shaped guard cells and two subsidiary cells. The subsidiary cells are low dome-shaped or rounded to triangular or with variously shaped subsidiary cells (Table 1).

Dermal appendages - There are several kinds of dermal appendages on the epidermis of grass leaves, which are generally classified as microhairs, macrohairs, prickle hairs and papillae. These appendages are found in the species of *Isachne*.

Microhairs-These, are generally much smaller, normally consist of two cells, and are referred to 'bicellular hairs'. Microhairs are absent from the leaves of typical Festucoid grasses, but are characteristic of most other groups. The wall of the basal cell of microhairs is almost always much thicker than that of the distal cell which is very thin walled, and does not readily take up stains. (It is easily damaged during preparations).

In Isachne these are present in all the species except in

I. confusa, I. meeboldii and I. lisboae. Mainly on abaxial surface of the epidermis, Microhairs commonly occur in intercostal zones, but in I. scabrosa, I. albens and I. globosa microhairs are frequent also on and along the costal zones. This is very characteristic and does not seem to have been reported earlier.

In most species, distal cell of bicellular hair is slightly shorter than the basal cell or sometimes both are equal. But in *I. kunthiana*. and *I. globosa*, the distal cell is sometimes longer than the basal (Figs. 28 -37; Table 1.).

Macrohairs - Macrohairs are usually longer than the microhairs and often form and indumentum on the leaf which is easily visible with naked eye or a hand-lens. Macrohairs also differ from microhairs in beng unicellular.

Macrohairs are present in most species of Isachne. They are short to fairly long, thick-walled with sunken bases and surrounded by cushions of large cells (Figs. 38 - 40).

Prickle-hairs - Prickle hairs are stout, thick-walled, sharply pointed cells with swollen bases. The smaller ones with more rounded base are termed as 'hooks. Prickles and hooks may both occur on same leaf or both may be absent.

Angular, strongly pointed prickles are common at leaf margins in most species of *Isachne*.

Prickles are aboundunt on the costal zones of *I. scab-rosa*, *I. albens* and *I. hir valaica* (Figs 5,6,8,). Prickles and hooks are occasionally present in intercostal zones.

Papillae - Papillae are varioulsy shapped protrusions from the outer walls of epidermal cells. One large, globose and often somewhat oblique (conical shaped) papilla occurs in each of the long cells of abaxial surface in all the species studied here except in *I. walkeri*, *I. lisboae*, and *I. gracilis*. In *I. lisboae*, one rectangular crystal like structure is present in each of the long cells; its nature could not be identified.

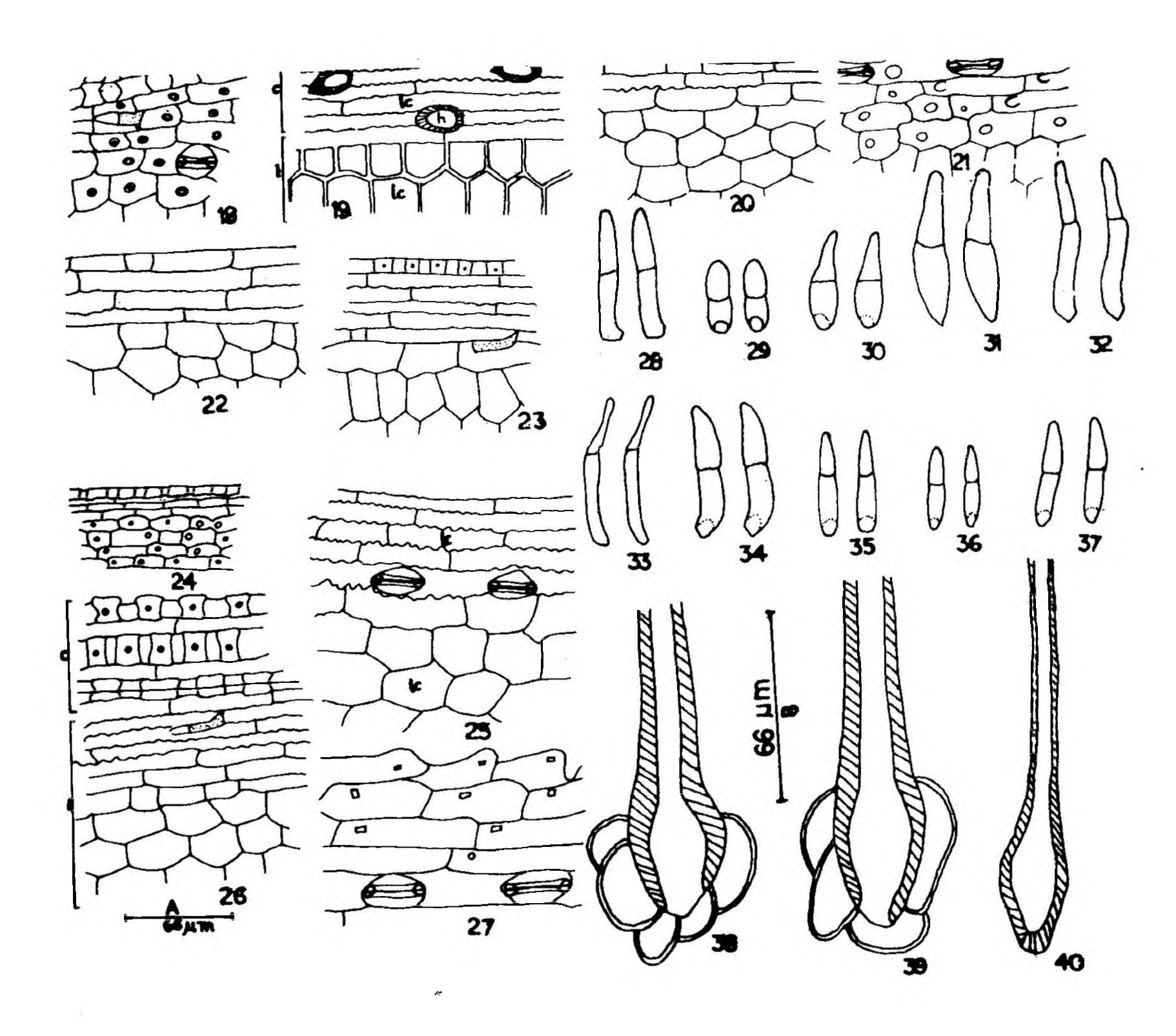


Fig. 18-40: Fig. 18-27. Leaf-epidermis (adaxial surface) of Isachne species. Fig. 18. I. globosa; Fig. 19. I. scabrosa; Fig. 20. I. albens; Fig. 21. I. clarkei; Fig. 22. I. himalaica; Fig. 23. I. walkeri; Fig. 24. I. angladei; Fig. 25. I. elegans; Fig. 26. I. swaminathanii; Fig. 27. I. lisboae; Fig. 28-37. Bicellular or micro hairs of Isachne species. Fig. 28. I. globosa; Fig. 29. I. miliacea; Fig. 30 I. gracilis; Fig. 31. I. bourneorum; Fig. 32. I. scabrosa; Fig. 33. I. angladei; Fig. 34. I. walkeri; Fig. 35. I. elegans; Fig. 36. I. bicolor; Fig. 37. I. swaminathanii; Fig. 38-40. Macrohairs of Isachne species. Fig. 38 I. swaminathanii. Fig. 39. I. bicolor; Fig. 40. I. clarkei.

(h – hook; other abbreviations explained in previous Fig.) Scale A: for Fig. 18-27. B for Fig. 28-40.

Table 1 Epidermal characteristics on abaxial surface of isachne species

Species*	Voucher Specimens	Intercostal Zone		Stornata		Microharis or Bicellular hairs	
		Lon	ng Cells	Size	Shape of	Size (J	ım)
		Size (µm		(µm)	subsidiary Cells	Basal cell	Distal cel
1	2	3	4	5	6	7	8
I. globosa (Thunb.) O.Ktze.	Ved Prakash 330	(13) 17-33 X 26 -40 (50)	Almost cubical to polygonal (hexagonal) with thin non-sinuous walls	26-33 X 23-30	Somewhat trianglular, or variable	(i) 17 - 23 (ii) 10	(i) 17 - 26 (ii) 10
I. miliacea Roth ex Roem. et Schult	Deka 13730	13-17 X 20-23	11 11	23 X 17	**	10 - 17	7 - 10
I. gracilis C.E. Hubb.	Ved Prakash 332	10-23 X 36-63	Vertically elongated with thin non-sinuous walls	23-26 X 20	Variable	23 - 26	20 - 23
1. bourneorum Fischer	Bourne 1280	23-30 X 23-33	Almost cubiccal to polygonal (hexagonal) with thin non-sinuous walls	33-40X23-26	11	23 - 2 6	23 - 26
I. albens Trin	Ved Prakash 208	10-23 X 13-26	n n	26-30 X 17	" "	23 - 2 6	(10) 17-20
I scabrosa Hook f.	Ved Prakash 256	7-13 X 10-17	Very small, narrow, vertically elongated with thin & non-sinuous walls	23-30 X 17-20	Somewhat low dome shaped	26 - 36	13 - 23
I. clarkei Hook.f.	Ved Prakash 187	17-33 X 23-33	Almost cubiccal to polygonal (hexagonal) with thin non-sinuous walls	30-33 X 17-23	Somewhat trianglular, or variable	20 - 23	17
I. himalaica Hook. f.	Ved Prakash	17-30 X 13-17	77	20-26 X 13-17	Variable	17 - 20	13 - 17

	1	1	7
I. confusa Ohwi.	S. Kurz. s.n.	-17-33 X 17-33	Hexagonal to polygonal with very thick & non-sinuous walls
1. Kunthiana (Wight et Am. ex Steud.) Thw	Ved Prakash 103	17-33 X 17-26	Rectangular or cubical to polygonal with thin slightly sinuous or non-
. angladei Fischer	Ved Prakash 91	13-17 X 10-17	sinuous walls Almost cubical to polygonal (-hexagonal) with thin non-sinuous walls
I. walkeri (Am. ex Steud.) Thw	Ved Prakash 139	10-30 X 20-26	н н
I. lisboae Hook. f.	Ved Prakash 347	17-33(46) X33-99	Vertically clongated, narrow with thin & non sinuous walls
1. elegans Dalz.	Ved Prakash -349	13-43 X 17-23	Almost cubical to polygonal (-hexagonal) with thin non-sinuous walls
I.bicolor . sw	Ved Prakash 346	17-26 X 13-26	11
aminathanii Ved Prakash & Jain)	Ved Prakash 337	(10) 17-33 X 17-23	11
I. Meeboldii	Meebold 107	17-33 X 17-26	17

^{*} sequence of species is according to putative relationship.

(-) = absent

33-36 X 17-16	61 44	(-)	(-)	
40-43 X 20-26	P1 11	17 - 26	17 - 30	
17X13	17 21	33	20 - 23	
23-26 X 20-23		23-26	20	ANA
33-40 X 23-33	Somewhat triangular to low dome- shaped or	(-)		ANATOMY OF ISA
26-30 X 17-20	variable " "	17-20	10	ISACHNEAE.II.
23 X 17 - 20	**	17	13-17/	
26-30 X 17-20	, ,,	17	13 - 17	
33-40 X 17	Low dome- shaped to paralled! sized	(-)	(-)	

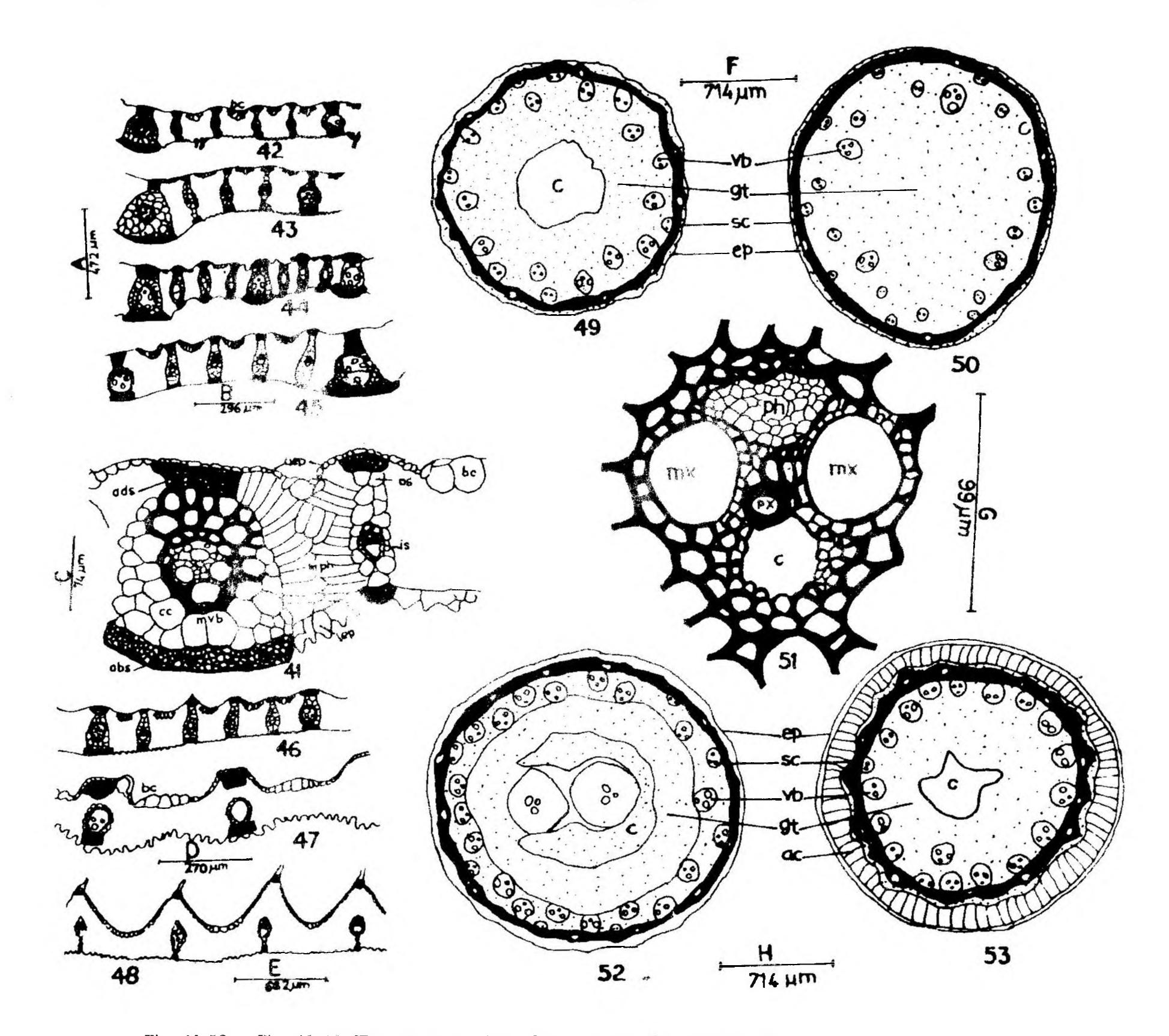


Fig. 41-53: Fig. 41-48. Transverse section of leaf-blades of Isachne species.

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Fig. 41, 42. I. Swaminathanii; Fig. 43. I. Globosa; Fig. 44. I. himalaica; Fig. 45. I. scabrosa; Fig. 46 I. bicolor; Fig. 47. I. confusa; Fig. 48. I. lisboae; Fig. 49-53. T.S. of culms of Isachne species. Fig. 49. I. globosa; Fig. 50. I. swaminathanii Fig. 51. Vascular bundle of I. scabrosa (basic type). Fig. 52. I. scabrosa; Fig. 53. I. albens.

(abs – abaxia¹ sclerenchyma girder; ads – adaxial sclerenchyma girder bc – bulliform cell; c – cavity; cc – colourless cell; ep – eperdermis; gt – ground tissue; is – inner sheath of V.B.; os – outer sheath of V.B.; lep – lower epidermis; mph – mesophyll cells (chlorenchyma); mvb – main V.B.; pvb – primary V.B.; sc – sclerenchyma; svb – secondary V.B.; uep – Upper epidermis; vb – vascular bundle).

Scale A for Fig. 42-44, 46. B. for Fig. 45. C. for Fig. 41. D for Fig. 47. E for Fig. 48. F. for Fig 49-50. G for Fig. 51. H for Fig. 52-53.

In adaxial surface, papillae are absent in most of the species; however, in some species like *I. globosa*, *I. angladei*, *I. clarkei* and *I. swaminathanii*, papillae are present but smaller in size than those of abaxial surface.

2. Leaf-Anatomy: The general character of transverse section of 14 species of *Isachne* is presented. The voucher specimens are the some as for epidermal structures.

Chlorenchyma- The ground tissue of the blade, the mesophyll, is made up of thin-walled chlorenchyma cells. The arrangment of chlorenchyma is very characteristic and similar in all species of *Isachne*. The cells of chlorenchyma are very long, narrow, some what loosely and distinctly radially arranged but not as in Chloridoid and Panicoid grasses (Fig. 6A).

Vascular bundles - Three types of vascular bundles are present in most species of *Isachne*. The first is the main vascular bundle (MVB); it is the largest vascular bundle in the leaf, is solitary and is present in the midrib of the blade. This vascular bundle (MVB) is of baise type (Metcalfe, 1960) and is characterised by having two conspicuous metaxylem vassels on either side of the protoxylem and clearly differentiated xylem and phloem (Figs. 41, 42). However, MVB is not recognisable in some species of Isachne such as I. lisboae, I. confusa, I. bourneorum, I. miliacea and is not so conspicuous in *I. kunthiana* and *I. clarkei*. The other two types of vascular bundles of the lamina, which are relatively small, may be distinguished as primary vascular bundles (PVBs) and seondary vascular bundles (SVBs). The PVBs are larger and almost similar to MVB, and are separated by 2-7 SVBs. The SVBs are the smallest; often there are no metaxylem vessels, but xylem and phloem can be differentiated. The proportion and arrangement of these three (or two) types of vascular bundles are different in various species (Figs. 41-48).

Bundle sheaths - The vascular bundles are usually surrounded by one or two bundles sheaths. When there are two, the outer sheath (OS) is made up of

large, usually thin-walled cells. The inner sheath (IS) is composed of small, thick-waklled, sclerenchyma fibres. In *Isachne* the inner sheath is scarcely differentiated (not well developed) and often either not visible or visible only in the upper half of the bundle. The OS which is well developed and does not contain chloroplast, is made up of single or multilayered parenchymatous cells which mostly have extensions of large colourless cells, reaching to, and forming girders with the adaxial and abaxial sclerenchyma (Figs. 41-46). In *I.confusa* and *I. lisboae* the OS does not have extension of colourless cells adaxially (Figs. 47,48). The OS is mostly complete, but is interrupted abaxially in *I. confusa*, and both adaxially and abaxially in MVB of *I. scabrosa* by an extension of sclerenchyma.

Sclerenchyma - In grass leaves, usually the sclerenchyma provide mechanical support. They follow the course of the vascular bundles in the form of subepidermal longitudinal strands or girders. The term 'strand' is used when the sclerenchyma does not extend inwards from the epidermis to make contact with the bundle sheaths while the term 'girder' is used when the slerenchyma extends from either or each epidermis to the bundle-sheaths.

In the genus *Isachne* all the three (or two) types of vascular bundles are mostly accompanied by abaxial and adaxial sclerenchyma girders. The only exceptions are I. lisboae and I. confusa in which vascular bundles are accompanied by sclerenchyma girders abaxially and sclerenchyma strand adaxially (Figs 47, 48). In most cases, the sclerenchyma do not extend inwards sufficiently to make sclerenchyma girders, but outer sheaths have large extensions of colourless cells forming girders. The MVB and PVB are mostly accompanied by anchorshaped girders i.e. the adaxial girder is narrow and tall and abaxial girder is wide and short (Figs 41-46). The SVBs are accompanied by small abaxial and adaxial girders, in which sclerenchyma groups are more or less equal or inversely anchor-shaped. The amount of sclerenchyma fibres and thickness of cell-walls differ in various species.

Bulliform cells: Bulliform cells are colourless cells

which occur on the adaxial epidermis. They are mostly well differentiated, quite large and arranged in regular groups (Figs 41-48). In *I. lisboae* the bullifrom cells are not so large and not well-differentiated. The cells of abaxial epidermis mostly protude outward due to presence of papillae.

Abaxial and adaxial surfaces - In all species of Isachne, the adaxial surface has slight to moderately tall, wide, rounded ribs and shallow to deep furrows (Figs. 41-48). The ribs and furrous are very conspicuous in I. lisboae and I. confusa. The sclerenchyma groups and bulliform cells are always arranged alternately in ribs and furrows respectively. The abaxial surface is commonly flat or with very slight furrows.

The above observations show that the leaf-blades of most *Isachne* species are similar anatomically, but *I. confusa* and I. *lishoae* are anatomically very distinct from other species.

3. Culm-Anatomy - We examined the T.S. of culms of 5 species of Isachne viz. I. albens, I. globosa, I. scabrosa, I. swaminathanii and I. walkeri. The culm of 1. albens shows aquatic character in that the epidermis is subtended by a circle of large intercellular cavities separated from one another, by radiating strips of par enchymatous cells, which are bounded on the outer side by single layered and on inner side by a ring of 1-3 layers of very thick-walled sclere nchyma (Fig. 53). In other species, the epidermis is subtended by 1-3 layers of small, thin-walled cells, followed by a singlelayer of cells resembling an endodermis, separating thin walled tissue from a sclerenchyma ring, consisting of about 2-6 layers of very thick-walled cells. In I.swaminathanii, the peripheral parenchymatous tissue is interrupted by selerenchyma fibres of vascular bundles which reaches up to the epidermis. Ground tissue on the inner side of the sclerenchymatous ring consists of large, thin walled cells (somewhat thickwalled in I. albens and extends to the large cavity at the centre of culm (Figs. 49,52,53). But in I. swaminathanii, there is no cavity at the centre and the ground tissue forms the solid centre of the culm (Fig. 7B). In I. scabrosa, there are two vascular bundles at the centre

filling into U shaped cavity; in this species the ground tissue is made up of two distinct zones; i.e. the outer zone is of thin-walled cells and inner zone is of thick-walled cells (Fig. 52). Outermost vascular bundles are arranged in a circle at the outer boundary of the sclerenchymatous ring, Some of them being connected to the epidermis by girders of sclerenchyma. Remaining vascular bundles are in 2-3, more or less distinct, circles, some bundles being at the inner boundary of the sclerenchymatous ring; others are more deep in the inner thin-walled ground tissue. Usually the individual vascular bundles are almost circular or oblong and of basic type (Fig. 51).

Usually the vascular bundles nearest to the centres of the culm are much larger than those next to the epidermis. In small vascular bundles, the metaxyler vessels are not conspicuously larger in diameter than the neighbouring cells.

Isachneae, namely Isachne R.Br. Coelachne R.Br. Limnopoa C.E. Hubb., Sphaerocaryum Nees ex Hook. f. and Heteranthoecia stapf are closely related anatomically and form a natural and distinct group. The leaf structure of these genera is panicoid in nature but stands apart from the typical panicoid grasses in certain features. We support Metcalfe's (1960) view in recognising Isachneae subtype under panicoid group in anatomical grouping. The anatomical characters are not very useful at infrageneric level or for identifying species since they overlap in characters among species, but they are very useful for seeing relationships among the genera. The diagnostic characters are the following.

Short cells Over the veins, usually in rows of more than 5 cells long; these usually absent between the veins; silica bodies roughly cross shaped, more or less cubical or rectangular with concave side and acute angled; long cells between the veins (on abaxial surface) relatively very small (ca. equal in length and breadth), squarish, hexagoanal to polygonal, usually with non-sinuous walls (shape and arrangement of long cells on the adaxial surface are quite different

rom that of the abaxial surface)papilla mostly one arge, globose (conical in shape) present in each of the long cells; bicellular microhairs mostly present with almost equal basal and distal cells; stomata with variable subsidiary cells; vascular bundles motly of three types and conspicuously angular in outline; bundle sheath inner scarcely differentiated in some species; outer well developed single or multi-layered of large colourless parenchyma cells and often reaching to and forming girders with the abaxial and adaxial sclerenchyma; mesophyll cells very long and narrow (elongated), somewhat loosely (tending to be spongy) and distinctly radially arranged but not as in Chloridoid and Panicoid grasses.

The above characters show that the tribe Isachneae is panicoid in most characters but it does differ somewhat by certain features from true paincoid grasses. The small, cubical intercostal long cells with papillae, narrow, elongated and radially arranged mesophyll cells and nature of outer bundle sheath are very characteristic of this tribe and make it distinct from all other Panicoid grasses. In Paincoid grasses (as well as in Festucoid grasses) the long cells are usually horizontally elongated with sinuous walls and mesophyll cells are not so elongated and radially arranged as in the tribe Isachneae.

The tribe Isachneae is distinctly primitive morphologically as well as ecologically, since it bears often 2 fertile florets and is hygrophyllous in tropics and subtropies. Hence, the tribe may be considered primitive anatomically. The conspicuous features of this tribe, i.e. nature of intercostai long cells and shape and arrangement of mesophyll cells may be considered as primitive features in anatomy. On the basis of certain features of leaf structure, especially the shape and arrangement of the mesophyll cells and nature of outer bundle sheath the tribe Isachneae appears to be related to Lasiacis (a tropical American grass genus, and primitive memeber of tribe Paniceae). But in Lasiacis, the silica bodies are mostly dumb-bell shaped (Davidse, 1978) while these are roughly cross shapped in Isachneae.

from Lasiacis. In gross morphology, the genus Lasiacis has the typical characters of tribe paniceae and thus it differs from Isachneae in structure and articulation of spikelet.

Potztal (1952) stated that the genus Sphaerocaryum should be transferred from the tribe Isachneae to sporoboleae, because it possesses the characteristic bicellular microhairs whose lower cell is sunken among the epidermal cells and the spikelets are with 1floret and 1- nerved 1- lemma, as often found in sporoboleae. Tateoka (1957) reported that the characteristic bicellular hairs are found in a species of Coelachne (C.japonica Hack.) but do not aways infer a relationship to sporoboleae and same is true of bicellular hairs of Sphaerocaryum. Moreover, the other anatomical features (arrangement of short cells shape of silica bodies, shape of long cells shape and arrangement of mesophyll cells, nature of vascular bundles and morphological character (i.e. disarticulation of spikelets above the glumes) are quite similar to Isachneae. Consequently, as Tateoka (1957) and Metcalfe (1960) pointed out, Potztal's (1952) view is not acceptable.

The tribe *Isachneae* is a natural assemblage of 5 genera; Isachne, Coelachne, Limnopoa Sphaerocaryum and Heteranthoecia which show resemblance in most characters and constitute well defined natural group. The tribe Isachneae, although apparently related to paniceae-panicoideae but is distinct from true panicoid grasses in some unique morphological as well as anatmoical characters (Ved Prakash & Jain, 1984).

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