

STUDIES ON THE HISTOLOGY AND COLOURATION OF THE PERICARP OF THE SORGHUM GRAIN

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THE sorghum grain is a caryopsis. It is oval to subspherical. The embryo is fairly large and is placed at the less convex surface and more towards the base. It is acentric so that externally it is opposed to the pericarp and internally surrounded by the endosperm. The side which bears the embryo is flat and from the tip of the embryo it converges to the stylar base (Fig. 1)

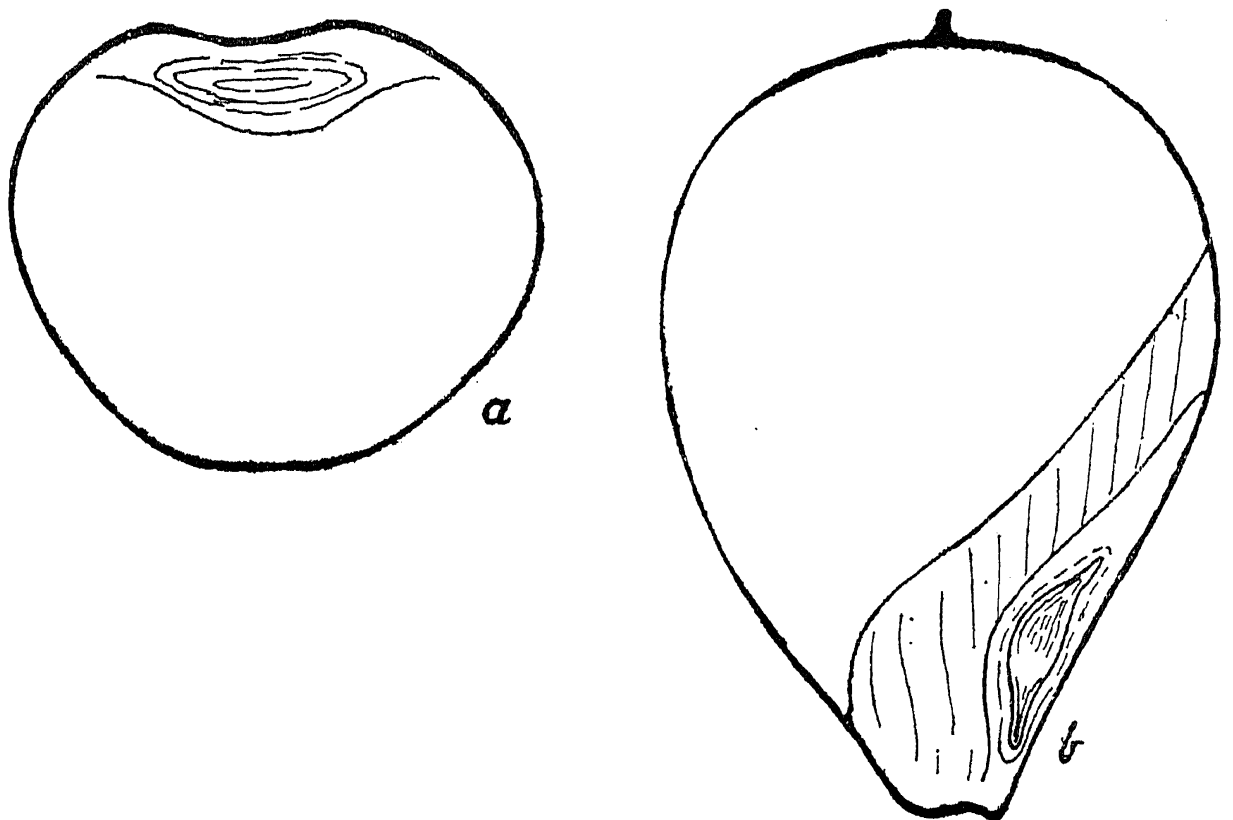


FIG. 1

Organogeny of the pericarp (Figs. 2-10)

Ovaries from the time of pollination upto the endosperm formation were fixed in Navashin's fluid and the later stages in Carnoy's, at successive stages of growth. Sections were stained in either Gentian violet-iodine or Hæmatoxylin. Types with a 'Nucellus' (Feterita) and without 'Nucellus' (A.S. 29 Periamanjil) were used in these studies.

The early stages of development were observed to be the same in both types. A young ovary is oval with two stigmatic branches typical in gramineæ. The ovule is anatropous to almost campylotropous. The funicle is broad and short, consequently the seed coat becomes unequal in length on either side of the micropyle. There are two integuments. The micropyle is formed by the inner integument, the outer one stopping far short of it. The integuments are only two layers wide but may increase in width at the chalazal end where the seed coats fit into the notch formed by the fusion of the carpel wall to form the stigmatic branches.

The nucellus is cellular, thin walled and fills up the whole of the ovule. A small beak is also found. The embryo-sac is rather small for the size of the grain and is placed somewhat deep in the nucellus. The antipodals form a tissue of 10-12 cells.

After fertilization the endosperm nuclei form a small number of free nuclei in the neighbourhood of the zygote. These form a cellular tissue by the time the zygote has undergone the second division. The endosperm thus formed is found mostly along the periphery of the embryo-sac so that a hollow tissue is formed. The expansion of the embryo-sac is very gradual. Even in a week-old grain the nucellus would not have been completely absorbed. However, in a mature grain there is no nucellus left, the absorption being complete. The deposition of starch begins in about ten days after fertilization. The aleurone is differentiated last.

The pericarp or the ovary wall is intensely green in the young stages and consists of several layers of cells. The epidermis contains a thin cutin and the walls are unthickened. The cells are rectangular in transverse sections. Immediately below this is a layer of cells which are slightly larger-lumened than the other cells. This is the hypodermis. After this is the mesocarp tissue of 9-10 layers. The innermost layers are of smaller lumen than the other mesocarp cells. There is an inner epidermis, the cells of which are very small and have no cutin. These cells towards maturity develop thickenings, become cylindrical and form the "tube cells" of the American authors (*vide infra*). The mesocarp and the hypoderm are chlorophyllous in young ovaries. The pericarp keeps pace in growth along with the embryo. The green colour is lost gradually only towards the setting in of the starch grains in the endosperm. Permanent starch may be stored in the mesocarp cells. With the maturity of the grains about $2\frac{1}{2}$ -3 weeks after fertilization, the chlorophyll is completely lost.

The integuments, as already mentioned are two. The outer one remains rudimentary and begins to disorganise very early, but remnants of it,

however, persist till even after the endosperm formation. The cells are narrow, rectangular and narrower than broad. The inner integument on the other hand grows with the developing grain. The inner layer has rectangular, more or less isodiametrical cells while the outer is longer than broad. Both layers grow in size till the formation of the endosperm, thereafter the outer layer begins to gradually disorganise. The inner layer on the other hand even at the time of the fertilization shows much larger tissue than the outer layers and grows much more in size than the outer one with the growth of the grain. The growth is most evident at the chalazal end. Towards maturity this layer in some grains becomes brown and hyaline, while in others it disorganises at maturity. Evidently it was this layer that was described as 'nucellus' by some American authors (*vide infra*). The behaviour of this layer in mature grains is more fully described later.

Mature pericarp.—1. The sorghum caryopsis has the pericarp fused with the seed. Winton (1902) described the structure of this sorghum caryopsis as made up of 5 layers in the pericarp, *viz.*, (i) epidermis, (ii) hypodermis, (iii) mesocarp, (iv) cross cells, (v) tube cells, and a 'nucellus' layer. In the endosperm he mentioned the aleurone and the starch cells.

Swanson (1928) mentions the same layers as Winton. He notes also the absence of the 'nucellar layer' in some types. This layer is otherwise called the 'hyaline layer' by him, and it is considered to be morphologically derived from the nucellus. He notes also that this layer when present is coloured brown. The mesocarp is starchy and it masks the brown of the nucellus, but when it is vestigial the brown colour of the nucellus is perceptible through the mesocarp. He has also measured the several tissues of the pericarp and nucellus in 18 types of grain sorghums.

Hector (1936) doubts the origin of the nucellar layer of Swanson. He concludes from evidence that it is the testa (inner integument).

Harrington and Crocker (1923) studied the structure of the pericarp in Johnson grass (*S. halepense*). They describe only the inner integument and make no mention of the nucellus layer.

Materials and Methods

Since the time of Winton (*loc. cit.*), the numerous wild and cultivated races of Sorghums have been systematically classified by Snowden (1936). Advantage was taken of the large collection at the Millets Breeding Station, Coimbatore, to make a comparative study of the typical forms in each sub-series and species of Snowden's classification. In the following is presented a classified list of the species studied:—

TABLE I

Lot Number	Sub-series and Species	Local Name and Place	Grain Colour
		WILD SORGHUMS	
Eu-sorghum			
Arundinacea—(a)	Series Spontanea		
S. 88a ..	<i>S. sudanense</i>	Guntur Farm, India	Brown
S. 207 ..	<i>S. arundinaceum</i>	S. Rhodesia	do.
S. 221 ..	<i>S. virgatum</i>	Tunis grass, Texas, U.S.A.	do.
Arundinacea—(b)	Series Sativa		
Drummondii—			
S. 102 ..	<i>S. nitens</i>	From Uganda, through Kew	do.
A.S. 5148 ..	<i>S. aterrimum</i>	Obtained as a mixture in a sample of brown corn from Odessa, U.S.S.R.	do.
Halepensis—			
S. 164 ..	<i>S. halepense</i>	Godavari, India	do.
Para-sorghums—			
S. 96 ..	<i>S. versicolor</i>	Texas, U.S.A.	Light pearly
S. 234 ..	<i>S. dimidiatum</i>	Through Sugarcane Breeding Station, Coimbatore, India	Brown
S. 250 ..	<i>S. purpureo-sericeum</i>	Through Sugarcane Breeding Station, Coimbatore, India	do.
Non-classified—			
M.S. 4357 ..	<i>S. nitidum</i>	Rangaswamikoil, Coimbatore	do.
M.S. 4360 ..	<i>S. Stapfii</i>	Maniyachi village, Koilpatti, India	do.
		CULTIVATED SORGHUMS	
Arundinacea—(b)	Series Sativa		
Guineensis—			
A.S. 683 ..	<i>S. margaritifera</i> var. <i>ovulifer</i>	N. Provinces, Sierra Leone	White pearly
A.S. 4548 ..	<i>S. guineense</i>	Tiv from Yandev, Nigeria	White chalky
A.S. 4681 ..	<i>S. conspicuum</i> var. <i>conspicuum</i>	Kimungampombo, Sanger Dt., Tanganyika	do.
A.S. 403 ..	<i>S. Roxburghii</i> var. <i>hians</i>	Talai Virichan Cholan, Coimbatore	do.
A.S. 1093 ..	do.	do.	do.

TABLE I—Contd.

Lot Number	Sub-series and Species	Local Name and Place	Grain Colour
A.S. 1092	<i>S. Roxburghii</i> var. <i>hians</i>	Talai Virichan Cholam, Coimbatore	White chalky
A.S. 1055	<i>do.</i>	<i>do.</i>	White pearly
A.S. 3819	<i>do.</i>	Jenora Josia, Patna Dt., Bihar, India	<i>do.</i> (violet)
A.S. 1008	<i>do.</i>	Khed Jonna, Vizagapatam, India	Yellow
Nervosa—			
A.S. 3783	<i>S. membranaceum</i>	Adhroo Jowar, C. Provinces, India	Pink pearly
A.S. 5219	<i>S. nervosum</i>	Yishien Shantian, Peiping, China	Light brown
A.S. 5812	<i>S. melaleucum</i>	Red durra, S. Africa	Reddish-brown
A.S. 210	<i>S. splendidum</i> var. <i>splendidum</i>	Jonna, Harivanam, Bellary, India	White pearly
Bicoloria—			
A.S. 5195	<i>S. dochna</i>	Stock feed, Kaoliang, China	Brown
A.S. 3356	<i>S. bicolor</i>	Goose-neck sorghum, U.S.A.	<i>do.</i>
A.S. 3815	<i>S. miliiforme</i> var. <i>rotundulum</i>	Juar, Bihar and Orissa, India	Reddish-brown
A.S. 4599	<i>S. elegans</i>	Jebere, Tanganyika	White chalky
Caffra—			
A.S. 4202	<i>S. coriaceum</i>	Juriba, N. Rhodesia	Reddish-brown
A.S. 4413	<i>S. caffrorum</i>	Early Kalo Sorghum, Colorado U.S.A.	Pink
A.S. 3464	<i>do.</i>	Wonder, F.C. 8986, Texas	White chalky with brown nucellus
A.S. 3998	<i>S. nigricans</i>	Karaviru, Bukoba and Behrambo, Tanganyika	Reddish-brown
A.S. 4660	<i>do.</i>	Kikuma, Tanganyika	<i>do.</i>
A.S. 5186	<i>S. caudatum</i>	Feterita, Sudan	White chalky
A.S. 4564	<i>S. caudatum</i> var. <i>faterita</i>	Kwarbiya, Sokoto, Nigeria	<i>do.</i>
Durra—			
A.S. 29	<i>S. durra</i>	Periamanjil Cholam, Coimbatore, India	Yellow, brown-mash

TABLE I—Contd.

Lot Number	Sub-series and Species	Local Name and Place	Grain Colour
A.S. 1098 ..	<i>S. durra</i>	Periamanjol Cholam, Coimbatore, India	Yellow, brown-wash
A.S. 1842 ..	<i>do.</i>	do.	do.
A.S. 2635 ..	<i>do.</i>	do.	do. (no brown-wash)
A.S. 2613 ..	<i>do.</i>	From Periamanjol Cholam crass	Brown
A.S. 1958/3 ..	<i>do.</i>	(Ears throwing brown grain mutants)	White
T. 1 ..	<i>S. cernuum</i>	Tella Jonna, Bellary, India	White pearly
A.S. 171 ..	<i>do.</i>	do.	do.
A.S. 151 ..	<i>S. subglabrescens</i>	Sakkaraguligai Jonna, Bellary, India	do.
A.S. 195 ..	<i>do.</i>	Periavellai, Coimbatore, India	White chalky
A.S. 367 ..	<i>do.</i>	Vellai cholam, Dindigul, India	White pearly, no nucellus
A.S. 389 ..	<i>do.</i>	Sen cholam, Manapparai, India	Light red
A.S. 809 ..	<i>do.</i>	Chinnamanjal Coimbatore, India	Yellow
A.S. 3672 ..	<i>do.</i>	Manjakattai cholam, Dindigul India	White pearly, red-base, red wash

The grains were soaked in water to render them soft. Free-hand sections were cut and mounted in glycerine. The measurements were done with a Zeiss X 7 ocular and X 40 objective combination. A linear micrometer was used. The data presented in the Tables (*vide infra*) represent averages of ten readings taken at random. Photographs were done with a Beck's $\frac{1}{4}$ -plate camera.

Description of the tissues

In both the wild and cultivated sorghums, the grain colour was found to dissolve to some extent in water so that the water is coloured yellow, brown or red according to the grain. With white grains the water becomes yellow tinged.

(a) *Wild sorghum* (Figs. 11 and 12-14)

The wild sorghum grains are characterised by the persistence of the integument in all of them and the vestigial nature of the mesocarp. The

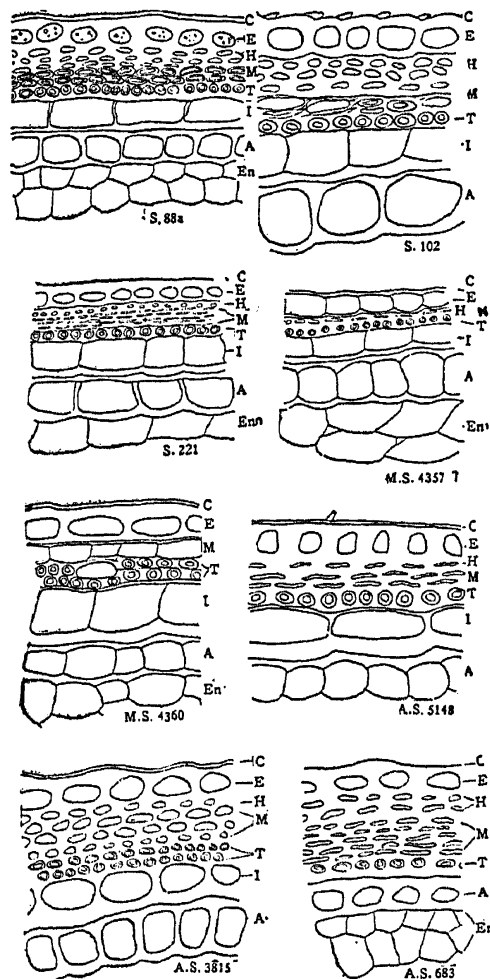


FIG. 11

pericarp is made up of (i) a very conspicuous epidermis, (ii) Hypodermis, (iii) Mesocarp (vestigial), (iv) tube cells, and (v) conspicuous integument. S. 96 has the simplest structure. The pericarp here consists of only epidermis, tube-cells and integument.

(i) The outer epidermis is one-layered. There is always a layer of cutin. The cells are oval to rectangular in transverse sections. The outer walls are generally thickened and the lumen small, but in S. 96 and S. 221, they are not much thickened and have a larger lumen. In A.S. 5148 the radial walls are much thickened. S. 234 resembles S. 96 but the contour of the grain depends on the size of the thickness of the integument. The cells are generally devoid of contents. In S. 207 the contents of the cells have a yellowish colour while in S. 250 and S. 88, they are coloured brown.

(ii) The hypoderm is generally single layered. The cells are usually much thickened so that the lumen becomes very small (almost obliterated as in A.S. 5148). The layer in extreme cases as in S. 250 and S. 221 becomes fused with the inner wall of the epidermis. It is absent in S. 96, S. 234 and M.S. 4357. The cells are generally of a uniform size but may be varying as in S. 102. It is discontinuous in S. 250 and M.S. 4360. The

cells usually are devoid of contents. The layer is commonly coloured brown or yellowish brown; in S. 207 and S. 102 the walls are yellowish.

(iii) *Mesocarp*.—This layer is generally absent in the typical wild sorghums (S. 96 and M.S. 4357). However, there is a small tissue in S. 88 *a* and S. 164. The cells are crushed and are non-starchy. In S. 207 and S. 221 it is starchy and 4–5-layered. The layer may be discontinuous and isolated mesocarp cells occur as in S. 250, S. 102 and M.S. 4360. The cells are thin-walled when starchy, otherwise they are thickened and sometimes crushed together, so that the lumen is completely obliterated as in A.S. 5148. The cells are sometimes coloured yellowish or brown especially when they are crushed together. They may have contents similarly coloured.

(iv) *Tube cells*.—This layer as already pointed out is formed mainly from the inner epidermis of the pericarp. The layer is constant in all types. This tissue is easily identified in sections by the ring-shaped, thick-walled, cells. In types like S. 96, S. 234 and M.S. 4357 the outer epidermis abuts directly on the tube cells. Very often this layer is found fused with the integument so that in many cases the cells appear as blunt protrusions of the integument. The tissue is generally 1–2-layered; cells small and coloured brown.

(v) The integument is a very constant tissue appearing next to the tube cells. It is generally composed of uniform, single-layered, large lumened cells. The cells are mostly thickened on the inner wall and to a slighter extent along the outer, while the radial walls are not thickened at all. The tissue becomes slightly wider along the chalazal and micropylar ends. In S. 234 and S. 102 the width of the tissue is very varying. S. 164 shows the widest integument in all sorghums. The cell walls in this tissue are usually coloured deep brown or yellowish brown. The cells are filled up with a homogeneous matter brown in colour. Harrington and Crocker (*loc. cit.*) find that this is tannic in nature. It may also be often devoid of contents.

A typical wild Sorghum is thus made up of a fairly massive epidermis. A hypodermal layer fused with the epidermis and usually very difficult of differentiation is found. Thereafter occurs a layer of tube cells and a very massive integumental layer. A small mesocarp may be present or may be completely absent. The wild sorghums show a uniform brown pigment in all the layers: The pigmentation deposition as well as the size of the several tissues has been given in Tables II and III.

TABLE II
Size of the Pericarp layers

Sample No.	Grain Colour	Epidermis (a)	Hypoderm (b)	Mesocarp (c)	Tube cells (d)	Integument	Total Pericarp	Aleurone
Arundinacea—		μ	μ	μ	μ	μ	μ	μ
S. 221	Brown	(a+b+c) = 11.6	11.6		3.8	9.6	25.0	13.6
S. 88a	do.	8.0	5.8	6.0	5.6	12.0	37.4	14.4
S. 207	do.	12.0	4.2	25.2	4.8	12.8	59.0	12.0
Drummondii—								
A.S. 5148	do.	(a+b) = 16.2	16.2	16.2	4.48	33.0	69.88	20.4
S. 102	do.	(a+b) = 14.4	14.4	6.0	10.0	7.4	37.8	15.2
Halepense—								
S. 164	do.	7.6	4.4	5.2	3.2	48.4	68.8	8.8
Para-sorghums—								
S. 96	Light pearly	(a+b+d) = 18.4	18.4	nil		6.8	25.2	13.8
S. 234	Brown	(a+b+d) = 10.4	10.4	nil		10.0	20.4	15.8
S. 250	do.	(a+b) = 10.8	10.8	10.8	4.8	22.0	48.4	16.0
Non-classified—								
M.S. 4357	do.	(a+b+d) = 12.0	12.0	nil		6.2	18.2	16.0
M.S. 4360	do.	12.0	6.8	nil	10.0	24.4	53.2	16.4

Guineense—													
A.S. 683	White pearly	8.0	4.4	14.4	4.0	nil	30.8	12.8					
A.S. 4548	White chalky	9.6	9.0	108.8	4.4	nil	131.8	25.6					
A.S. 4681	do.	8.6	20.0	76.0	4.0	nil	108.6	24.0					
A.S. 403	do.	11.2	11.2	88.4	6.8	nil	117.6	14.6					
A.S. 1093	do.	10.0	8.4	57.6	4.0	nil	80.0	19.2					
A.S. 1902	do.	8.6	7.2	57.6	4.6	nil	78.0	9.6					
A.S. 1055	White pearly	8.8	8.8	43.6	4.0	nil	65.2	11.0					
A.S. 3819	White violet	13.2	12.2	26.0	7.4	28.0	86.8	18.0					
A.S. 1008	Yellow	8.6	6.4	58.0	7.0	17.6	97.6	9.6					
Nervosa—													
A.S. 3783	Pink pearly	15.0	20.0	64.0	8.4	nil	107.4	18.4					
A.S. 5219	Light brown	15.6	9.4	130.8	7.6	22.8	186.2	16.8					
A.S. 5812	Reddish-brown	13.8	21.6	118.8	10.0	nil	151.0	12.8					
A.S. 210	White pearly	(a+b)	19.6	30.4	4.8	nil	54.8	17.6					
Bicoloria													
A.S. 5195	Brown	8.2	5.2	48.0	4.0	19.6	85.0	25.2					
A.S. 3356	do.	12.8	7.0	29.6	5.2	24.8	79.4	11.6					
A.S. 3815	Reddish-brown	9.8	2.6*	14.5*	6.5	23.0	56.4	11.4					
A.S. 4599	White chalky	14.0	12.0	58.8	4.4	3.6	92.8	16.0					
Caffra—													
A.S. 4202	Reddish-brown	21.6	12.8	42.8	4.6	23.2	105.0	20.8					
A.S. 4413	Pink	14.0	22.0	64.0	8.0	nil	108.0	19.2					

TABLE II—(Contd.)

Sample No.	Grain Colour	Epidermis (a)	Hypoderm (b)	Mesocarp (c)	Tube cells (d)	Integument	Total Pericarp	Aleurone
A.S. 3464	White chalky with brown nucellus	9.4	5.0	106.4	3.8	12.0	136.6	13.0
A.S. 3998	Reddish-brown	13.0	7.2	18.4	8.8	40.0	87.4	19.2
A.S. 4660	do.	12.8	18.0	36.5	8.8	62.0	138.0	12.0
A.S. 5186	White chalky	11.2	10.4	116.4	4.4	28.4	170.8	23.6
A.S. 4564	do.	12.2	13.0	103.2	13.6	36.4	178.4	23.6
Durra—								
A.S. 29	Yellow, brown-wash	13.4	14.0	61.2	8.4	nil	97.0	20.0
A.S. 1098	do.	15.2	4.0	23.6	4.0	nil	46.8	14.4
A.S. 1842	do.	11.4	30.2	36.4	15.6	nil	93.6	17.2
A.S. 2635	Yellow, no brown-wash	14.2	25.6	31.6	6.8	nil	78.2	16.0
A.S. 2613	Brown	13.2	9.6	34.4	4.0	50.4	111.6	24.4
Cernuum—								
T. 1	White pearly	11.8	11.6	28.8	9.2	nil	61.4	20.4
A.S. 171	do.	8.0	8.0	20.4	4.4	nil	40.8	20.0
Subglabrescens—								
A.S. 151	do.	8.8	10.8	33.6	6.4	nil	59.6	10.4
A.S. 195	do.	14.0	14.8	101.2	8.0	nil	138.0	21.2
A.S. 367	do.	11.4	3.4	38.0	4.4	nil	57.2	13.2
A.S. 389	Light-red	14.2	6.2	34.4	9.2	nil	64.0	15.2
A.S. 809	Yellow	16.6	10.4	27.4	12.0	nil	66.4	18.2
A.S. 3672	White pearly, red base	11.8	12.8	39.6	7.8	nil	73.0	13.2

* Average of (12).

TABLE III
Colour Deposition in the Pericarp of the Sorghum Grain

Sample No.	Seed Colour	Epidermis	Hypodermis	Mesocarp	Tube cells	Integument	Aleurone
Arundinacea—							
S. 88a ..	Brown	Outer wall light yellow	Light yellowish	Brownish or yellowish contents	Yellow to brown	Brown	No colour
S. 207 ..	do.	Walls yellow, contents yellowish	Walls yellowish	Walls yellowish	Brown	do.	do.
S. 221 ..	do.	Light brown	Light brown	Yellowish-brown	do.	Outer wall intense brown, inner wall pale brown	do.
Drummondii—							
A.S. 5148 ..	do.	Yellowish-brown	Yellowish-brown	do.	do.	do.	do.
S. 102 ..	do.	Yellow	Light yellow	Light yellow	Brownish-yellow	Brownish-yellow	do.
Halepensea—							
S. 164 ..	do.	Brown, outer wall reddish-brown	Walls brown	Walls brown	Brown	Brown	do.
Para-sorghums—							
S. 96 ..	Light pearly	Brown	nil	nil	do.	do.	do.
S. 250 ..	Brown	Brownish-contents	Similar to epidermis	(Not continuous layer)	do.	do.	do.
S. 234 ..	do.	do.	Not conspicuous	nil	do.	do.	do.

TABLE III—(Contd.)

Sample No.	Seed Colour	Epidermis	Hypodermis	Mesocarp	Tube cells	Integument	Aleurone
Non-classified—							
M.S. 4357	Brown	Brown	Same as epidermis	nil	Brown	Brown	No colour
M.S. 4360	do.	Walls deep brown	Brown	Brown	do.	do.	do.
Guineense—							
A.S. 683	White pearly	Yellowish	No colour	No colour	Yellowish	nil	do.
A.S. 1548	White chalky	No colour	do.	do.	No colour	nil	do.
A.S. 4681	do.	do.	do.	do.	do.	nil	do.
A.S. 403	do.	Yellowish	Yellowish	do.	Yellowish	nil	do.
A.S. 1093	do.	No colour	No colour	do.	do.	nil	do.
A.S. 1902	do.	Light yellow	Light yellow	do.	Light yellow	nil	do.
A.S. 1055	White pearly	Walls pale yellow	Yellowish	do.	do.	nil	do.
A.S. 3819	(Violet)	Yellowish	do.	do.	Yellowish	Brown	do.
A.S. 1008	Yellow	Yellowish-brown	Yellowish-brown	Yellowish	Dark brown	do.	do.
Nervosa—							
A.S. 3783	Pink pearly	Pale reddish-brown with yellowish-brown contents	Pale reddish-brown	Rarely coloured	Yellowish	nil	do.
A.S. 5219	Light brown	Brownish-yellow	Brownish-yellow	Wall very light yellow	Brown	Deep brown	do.

A.S. 5812	..	Reddish-brown	Reddish-brown	Reddish-brown	No colour	Dark purple	nil	do.
A.S. 210	..	White pearly	Yellowish contents	Same as epidermis	do.	Yellow	nil	do.
Bicoloria—								
A.S. 5195	..	Brown	Brown	Brown	do.	Brown	Brown	do.
A.S. 3356	..	do.	Yellowish-brown	Same as epidermis	do.	do.	Dark brown	do.
A.S. 3815	..	Reddish-brown	Yellowish	Yellowish	Yellowish	Dark brown	Reddish-brown	do.
A.S. 4599	..	White chalky	No colour	No colour	No colour	No colour	nil	do.
Caffra—								
A.S. 4202	..	Reddish-brown	Reddish-brown	Reddish-brown	Light reddish-brown	Deep reddish-brown	Deep reddish-brown	do.
A.S. 4413	..	Pink	Brown	Brown	No colour	Yellow	nil	do.
A.S. 3464	..	White chalky with brown nuvellus	No colour, occasionally light reddish-brown	Same as epidermis	do.	Light reddish-brown	Deep reddish-brown	do.
A.S. 3998	..	Reddish-brown	Brown	Brown	Brown	Brown	Brown	do.
A.S. 4660	..	do.	do.	do.	do.	Dark brown	do.	do.
A.S. 5186	..	White chalky	No colour	No colour	No colour	No colour	Reddish-brown	do.
A.S. 4564	..	do.	Very light yellow	Very light yellow	do.	do.	Yellowish-brown	do.
Durra—								
A.S. 29	..	Yellowish-brown	Yellow	Yellow	do.	Yellow	nil	do.
A.S. 1098	..	Yellow, brown-wash	Walls yellow, contents yellow	do.	do.	do.	nil	Walls yellowish

TABLE III—Contd.

Sample No.	Seed Colour	Epidermis	Hypodermis	Mesocarp	Tube cells	Integument	Aleurone
A.S. 1842	Yellow, brown-wash	Walls yellow	Yellow	No colour	Yellowish-brown	nil	No colour
A.S. 2635	Yellow, no brown-wash	Yellow	do.	do.	Intense yellow	nil	do.
A.S. 2613	Brown	Brown	Brown	Walls brown	Blackish-brown	Yellowish-brown	do.
A.S. 1958/3	do.	Brownish-yellow	Very light brown	No colour	Brownish-yellow	Brown	do.
A.S. 1958/3	White grain mutant	No colour	No colour	do.	No colour	nil	do.
Cernuum—							
T. 1	White pearly	Walls light yellow	Walls light yellow	do.	do.	nil	Walls very light yellow
A.S. 171	do.	do.	do.	do.	Walls very light yellow	nil	No colour
Subglabrescens—							
A.S. 151	do.	do.	do.	do.	do.	nil	do.
A.S. 195	White chalky	No colour	No colour	do.	Yellowish	nil	do.
A.S. 367	White pearly	do.	do.	do.	do.	nil	do.
A.S. 389	Light red	Walls red	Light red	Sometimes red-wash, else nil	Red	nil	do.
A.S. 809	Yellow	Deep yellow walls	Deep yellow	One layer only yellow	Slight yellow	nil	Slight yellowish
A.S. 3672	White pearly, red-base, red wash	Light reddish-brown, in places where colour is present, otherwise no colour	Light reddish-brown, as in epidermis	No colour	Reddish-brown as in epidermis	No colour	No colour

(b) *Grain Sorghums* (Figs. 11 and 15–19)

Mature grains from typical varieties in each sub-order have been examined. Out of the 31 sub-orders of Snowden (*loc. cit.*) only 10 have been omitted. In some of the more important ones as in the Durra, Caffra and Roxburghii more than one sample has been examined.

The grain is made up of the same layers as the wild ones. In transverse sections the caryopsis is oval. The central portion of the grain is occupied by the white endosperm. The pericarp forms a thin lining round this white endosperm. The width of the pericarp increases towards the embryo, which is placed towards the flatter side of the grain. Very little endosperm tissue occurs between the embryo and the pericarp externally. In the longitudinal sections the pericarp increases again at both the micro-pylar and the chalazal ends of the grain.

(i) The epidermis is the least varying of all the layers. The cutin is generally thin and discontinuously deposited. The cells are rectangular. The thickening may vary considerably. Extremes are found in the same sub-order. Usually they are thickened on the outer and radial walls. In some cases the lumen becomes almost obliterated owing to the thickening. Nor is this character restricted to either chalky or pearly grains alone. The epidermal cells often have granular contents.

(ii) The hypoderm is usually single-layered and much thickened. The cells are usually small and the lumen narrow. The thickening is generally on all the four walls. Very often the layer becomes hard to distinguish from the thickening of the epidermal wall (A.S. 3556). It may often contain 2–3 layers of cells. Granular contents may sometimes be present. In A.S. 3464 the cells are filled with a homogeneous material.

(iii) Mesocarp is generally a parenchymatous tissue of varying numbers of layers. This tissue usually has 5–6 layers of cells but 10–14 layers of cells are not uncommon. The deposition of the starch in these layers depends upon the variety. In the same sub-order both starchy and non-starchy forms may occur. The predominantly starchy ones are usually not coloured. The non-starchy ones are either pale-yellow or brownish coloured. The outermost 2–3 layers often becomes thick-walled and non-starchy (A.S. 210, A.S. 2635 and A.S. 1902). This is more common in the pearly grains. Cases in which the innermost 2–3 layers become thickened also occur. This thickening leads to the reduction in the cell-lumen and very often the cells are found jammed together.

(iv) *Tube cells*.—This layer has elongated cylindrical cells more or less

from the inner epidermis of the pericarp and a few layers immediately above it. Winton (*loc. cit.*) mentions a layer of cross cells. These are probably some of the last layers of the mesocarp cells since the only definitely different tissue next to the mesocarp is the one formed by the cylindrical tube cells. The tissue contains usually of a single layer of cells, but sometimes two to three layers may be found (A.S. 1902 and A.S. 5186). These cells are constant in all types. In A.S. 210 the cells are found to be large, whereas in A.S. 3464 they are very small. In A.S. 4564 the tissue is not continuous. Quite often the inner epidermis remains unthickened and the tube cells may be seen in different stages of formation.

(v) *Integument*.—The integument does not occur in all types. It is absent in most of the white, yellow or red grains but always found in browns. In certain white grains as in A.S. 5186 and A.S. 3819 it is present, then the grain takes on a light blue tint or violet. The cells are large and brown. Generally they are filled up with a homogeneous brown substance, so that the individual cell walls are difficult to be distinguished. The layer appears as a single continuous sheet. The inner walls are much thickened. The radial walls are very thin. The outer ones are thickened slightly. Generally there is only one layer but as in A.S. 1008 two layers may be present. This is probably both the layers of the integument persisting. In certain types the cell lumen does not contain any deposits and remains empty (A.S. 5195). The colouration becomes much diluted in such types. In some of the white grains as in A.S. 4548 and A.S. 4599 the integument is incompletely absorbed so that isolated strips of cells may be found here and there, sometimes much crushed. These cells were found to be entirely free from colouration (Fig. 18).

The sizes of the different tissues are given in the annexed Table II.

Endosperm.—The endosperm consists of (1) the starch cells which form the bulk of the tissue and (2) the aleurone cells which are specialised from the outermost layers of the endosperm.

The starch cells are hexagonal to rectangular, thin walled, large cells filled with large simple starch grains. The endosperm towards the aleurone is sometimes filled with smaller grains in addition to the large starch grains. These are similar to the aleurone grains. The layers appear horny in texture when the starch grains are compact and when less compact they form a floury endosperm.

The aleurone cells are smaller and very regular. The grains are globular and somewhat smaller than the endosperm starch grains. The largest aleurone cells ($24\ \mu$ – $20\ \mu$) have been found in Caffra (A.S. 5186) and Durra

The wild sorghums are all coloured brown and show a distribution of colour in the tissues which is closely similar to the cultivated ones.

A table giving the distribution of colour in the different tissues is appended (Table III).

The size of the pericarp when considered group by group according to Snowden's classification gave no definite clue to the relationship of the families. It was on the other hand seen that within every group the same variations could occur. The epidermis and the tube cells as already noted were found to be the least variable amongst the several groups. Even the wild sorghums gave the same size variations.

The hypodermis and mesocarp on the other hand are much more variable. The size of the pericarp is more or less directly proportional to the sizes of these tissues. The hypoderm may increase by a layer or two. The mesocarp itself is very varying according to the presence or absence of the starch grains. When filled with starch the cells have wide lumen and the walls are thin. In the non-starchy grains the mesocarp is less developed and secondly the tissue is collapsed or crushed so that it becomes compact and narrow. In many grains the mesocarp may be narrow but starchy, the grains here being rather small. In many of the pearly grains this condition is common. In the predominantly starchy, chalky grains the starch grains are large and the tissue very wide. Thus the size of the pericarp becomes proportional to the size of the mesocarp tissue.

The integument is also found to be confined to no particular group. It appears both in the starchy and non-starchy grains. The presence of this layer does not much influence the size of the other layers of the pericarp and seems to be inherited as an independent one.

Of the cultivated sorghums A.S. 683 and A.S. 3815 come nearest to the wild sorghum type, but in *Margaritifera* the integument is wanting (Fig. 11).

In the case of grains reported as Pseudomutations (Ayyangar *et al.*, 1939; Sieglinger, 1940), the brown grains appearing in the purely white grained panicles have a brown integument while the white grains occurring in a purely brown-grained head do not possess this tissue though the parental grains have the tissue. Grains showing striping of brown and white colours also occur. The sections of such grains showed the absence of the integument in the white portions and its presence in the coloured areas (Fig. 19).

In some of the white grain crosses the F_1 was found to be brown. The same experience was found also in crosses between (i) yellow grains with

brown-wash crossed with white chalky and (ii) yellow grains with brown-wash and yellow grains without brown-wash. The parents as well as the F₁ grains were examined for colouration. In Table IV is given the sizes of

TABLE IV
F₁s and Parents

A.S. Number	Epi-dermis	Hypo-dermis	Meso-carp	Tube-cells	Integu-ment	Total of pericarp	Aleu-rone
171 White pearly ..	8.0	8.0	20.4	4.4	nil	40.8	20.0
1902 White chalky ..	8.6	7.2	57.6	4.6	nil	78.0	9.6
F ₁ 3914 Brown ..	11.2	6.4	46.8	5.6	46.8	70.0	12.6
195 White chalky ..	14.0	12.0	101.2	8.0	nil	138.0	21.2
403 do. ..	11.2	11.2	88.4	6.8	nil	117.6	14.6
F ₁ 5597 ..	13.8	7.2	66.0	8.4	40.8	95.4	11.6
1098 Yellow with brown-wash ..	15.2	4.0	23.6	4.0	nil	46.8	14.4
403 White chalky ..	11.2	11.2	88.4	6.8	nil	117.6	14.6
F ₁ 5600 ..	12.0	5.4	14.2	10.8	40.8	42.4	11.6
1842 Yellow with brown-wash ..	11.4	30.2	36.4	15.6	nil	93.6	17.2
2635 Yellow with no brown-wash ..	14.2	25.6	31.6	6.8	nil	78.2	16.0
F ₁ 3926 ..	14.4	10.0	23.6	14.4	28.8	62.4	10.8
367 White pearly ..	11.4	3.4	38.0	4.4	nil	57.2	13.2
3464 White chalky with brown 'nucellus' ..	9.4	5.0	106.4	3.8	12.0	136.6	13.0
F ₁ 6515 ..	16.4	12.0	89.6	6.8	21.2	146.0	12.8

the several tissues of the pericarp in the parents and F₁s. It was found that all the parents lacked the integument, except A.S. 3464 whereas the F₁s showed well-developed integuments (Figs. 15-17), thus showing that complementary factors are responsible for the manifestation of the integument. Vinall and Cron (1921) and Sieglinger (1924) have obtained a 9:7 ratio for Brown:White grains. Sieglinger (1933) has shown that Brown 'nucellus' to no Brown 'nucellus' is 3:1. This cross is similar to the cross A.S. 367 × A.S. 3464 examined here, but the other crosses are between

parents without integuments. Ayyangar *et al.* (1936) found an absolute linkage between blackish purple of sheath and glume and 'nucellar' brown.

In the above crosses it was also noted that when the two parents differed widely in the number of layers of cells in the mesocarp tissues the F_1 tended to be like the parent with lower number of layers. The cells with starch grains however depend on the amount of tissue left unthickened. The size of the layer does not seem to indicate the number of layers of cells, since the width of the individual cells may vary with the amount of starch deposited.

The sorghum pericarp could be divided primarily into starchy and non-starchy mesocarp. The integument occurs irrespective of the mesocarp being starchy or not. The main colours as found in sections are—(i) yellow, (ii) brown, and (iii) red. In the white grains there is always a very light yellow colouration natural to the cell walls. The reds and browns have always a yellow background. Some of the red have a mixture of brown colour while some of the browns are reddish browns. The colour is found primarily in the epidermis, hypodermis, and the tube cells. The mesocarp is coloured when the layer is non-starchy or when the walls are thickened. Sometimes when the colouration of the other tissues is very intense the mesocarp also takes on the same colour. The integument except in two cases already mentioned are coloured brown, whenever present. Complementary factors are responsible for the occurrence of this tissue.

Summary

1. The histology of the pericarp of wild and cultivated races of sorghum have been described.

2. The organogeny of the pericarp has been studied. The tube cells were found to arise from the inner epidermis of the pericarp while the integument was from the inner integument and not from the nucellus. The latter is completely absorbed.

3. The wild sorghums are characterised by a very thin pericarp consisting of only epidermis and tube cells and sometimes a very small tissue of mesocarp. An integument is always present. All wild sorghums are brown coloured.

4. The cultivated sorghums have similar layers to the wild ones but the number of layers is greater. The grains could be distinguished into two main groups (i) starchy and (2) non-starchy. The integument is found only in some grains and absent in all others. The grains with the integument are generally brown.

5. The colour of the pericarp is found mostly in the epidermis, hypodermis and the tube cells. The integument is always coloured brown and the tube cell is also coloured similarly whenever an integument is present. The mesocarp is rarely coloured.

6. An examination of the F_1 and parents of some of the crosses revealed that while both the parents had no integuments at all, the F_1 had an integument indicating complementary factors.

7. On examination of pseudomutation grains and grain chimera it was seen that whenever there was a brown colour there was an integument present and absent when the grain was not brown.

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EXPLANATION OF ILLUSTRATIONS

FIG. 1. Diagrammatic. *a*, cross-section; *b*, longitudinal sections of sorghum grain. The black outer layer represents the pericarp. \times about 8.

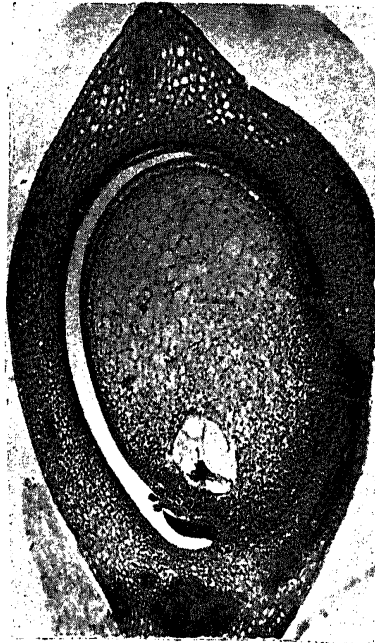
FIGS. 2-10. Organogeny of the pericarp. Reduced in reproduction by T, tube cells; I, Integument. FIG. 2. A. S. 29 young ovule showing the embryo-sac, inner integuments and the micropyle. \times 150. FIG. 3. do. Embryo-sac with the zygote, shows the micropyle formation by the inner integuments only. \times 80. FIG. 4. do. Older grain showing an increase in the layer of the integuments at the place of the fusion of the pericarp. \times 450. FIG. 5. do. The zygote surrounded by an endosperm tissue. The inner layer of the inner integument much enlarged. \times 40. FIG. 6. do. Older grain magnified to illustrate the growth of the inner layer of the inner integument and the resorption of the outer integument. The inner epidermis of the pericarp is beginning to thicken. \times 450. FIG. 7. do. The integument well grown. The inner epidermis of the pericarp rounding off to form the tube cells. \times 450. FIG. 8. do. The inner epidermal layer thickened and formed into tube cells. \times 450. FIG. 9. do. Ovary much advanced, the nucellus completely absorbed. Inner integument alone is left, cross layers not yet formed. \times 300. FIG. 10. Feterita—showing the well-developed inner integument which later turns brown. Nucellus still present. \times 40.

FIG. 11. Diagrammatic sketches of sorghum grain transverse sections. A.S. 3518 and A.S. 683 two cultivated sorghums coming nearest to the wild sorghums, C, cutin, E, epidermis, H, hypodermis, M, Mesocarp, *En*, endosperms. Names of varieties found in Text-Table I.

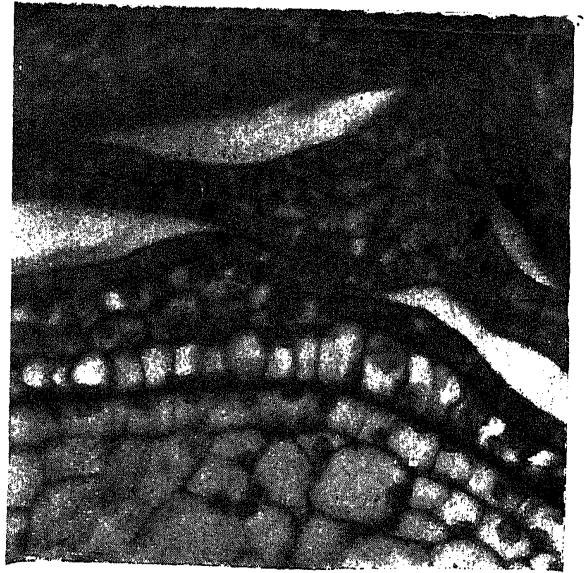
FIGS. 12-21. Transverse sections of sorghums. Reduced in reproduction by Letterings as in Fig. 11. FIG. 12. *S. versicolor* no mesocarp, large aleurone, integument present. $\times 300$. FIG. 13. *S. dimidiatum*, unequal development of inner integument, large aleurone. $\times 300$. FIG. 14. *S. halepense* largest integument. $\times 300$. FIG. 15. *S. arundinaceum*—Starchy mesocarp. $\times 300$. FIG. 16. *S. purpureosericeum*—mesocarp discontinuous. $\times 300$. FIG. 17. A.S. 171 Tella Jonna—white pearly. Shows general structures of typical pearly grain. Mesocarp thick-walled, narrow, non-starchy, no integument. $\times 300$. FIG. 18. As. 1902—T. V. Cholan—white chalky. Shows the general structure of typical chalky grains. Mesocarp very broad and starchy, no integument. $\times 300$. FIG. 19. A.S. 3915 F_1 of A.S. 1902 \times A.S. 171. Integument present, mesocarp more like A.S. 171 but more starchy. $\times 300$. FIG. 20. A.S. 4599—grain showing the colourless integument. $\times 250$. FIG. 21. A.S. 5519/2—striped grain (brown and white) from pseudomutant heads—brown in white. Shows the development of patches of integument (*a*) and no integument (*b*).



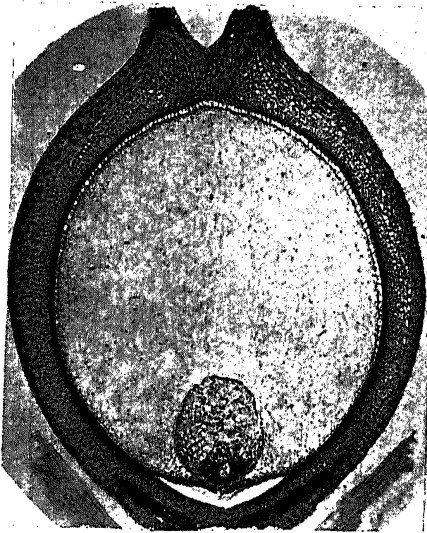
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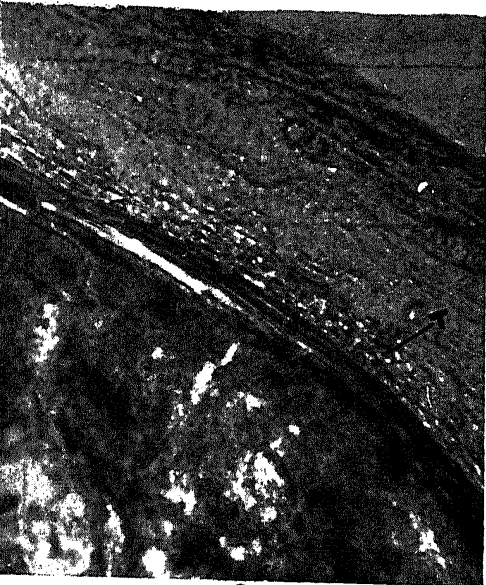
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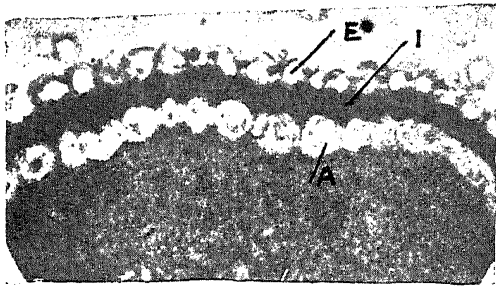
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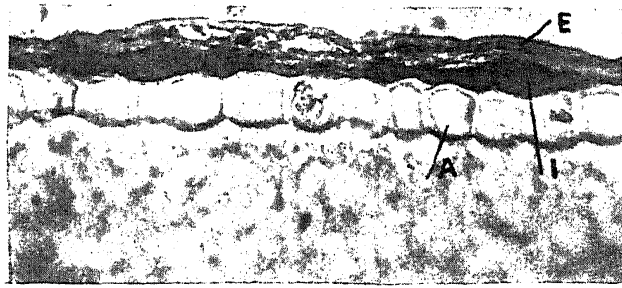
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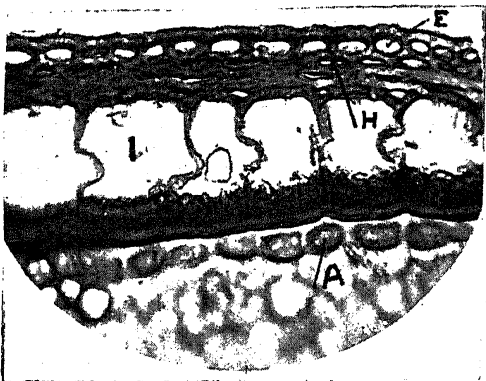
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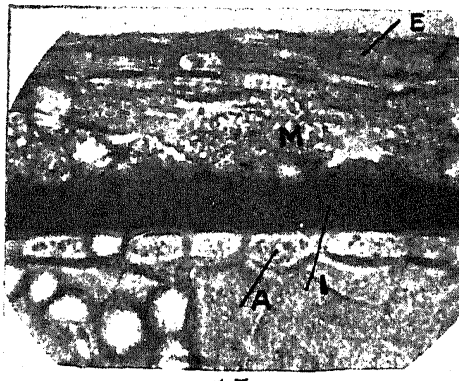
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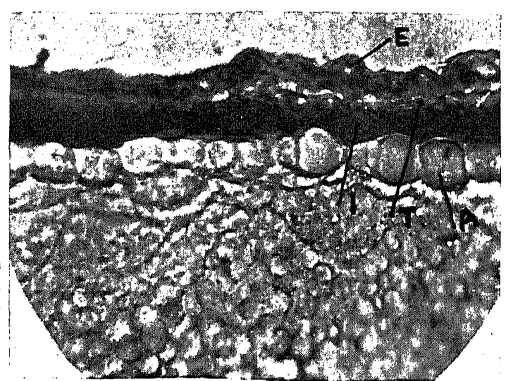
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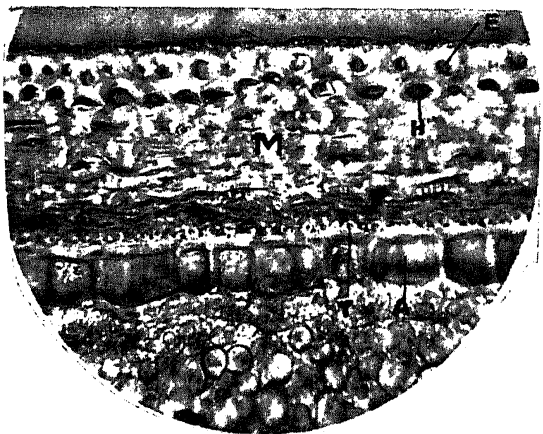
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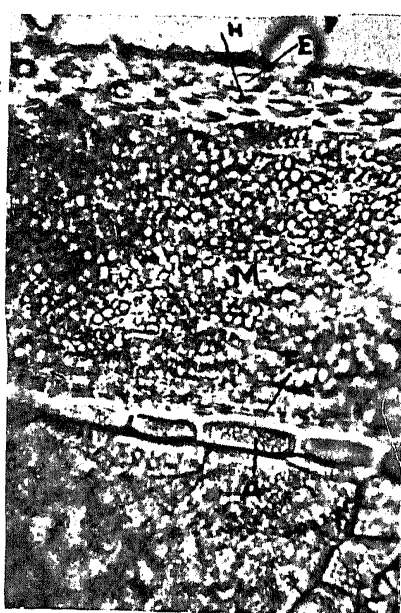
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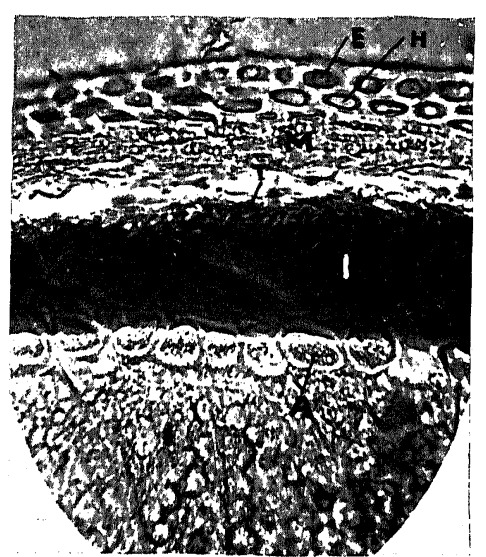
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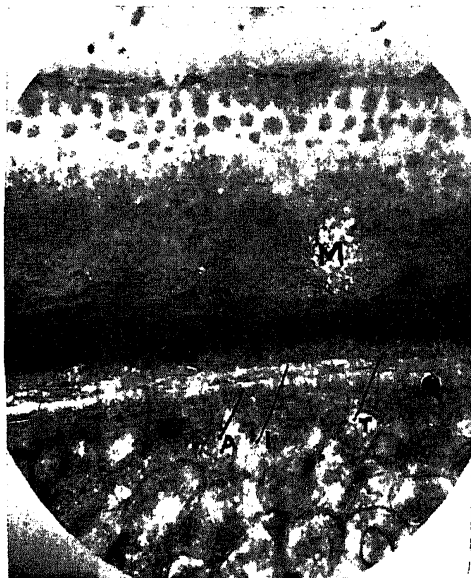
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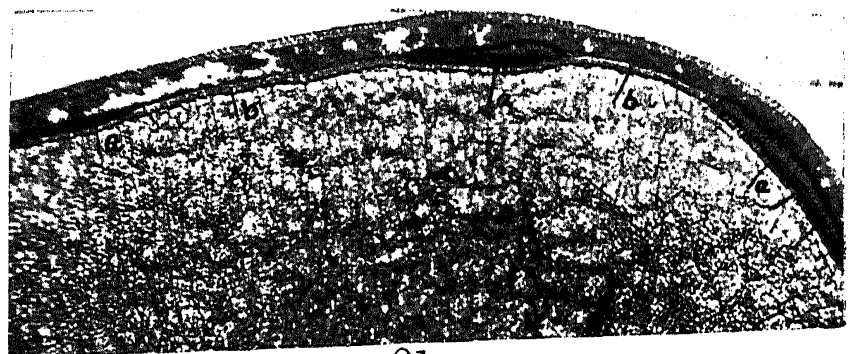
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