NOTES.

THE DEVELOPMENT OF THE SEED-COAT OF *CARICA PAPAYA*.¹—

The seed-coat of many species of *Carica* shows a complicated structure, the highest degree of differentiation being reached in the seeds of *C. microcarpa*, *C. hastaefolia*, and *C. Papaya* (the Paupauw). Klebs² has described the constitution of the mature seed-coat in the two former species, but has not followed up its development from the unfertilized ovule—a development which in the case of *C. Papaya* shows points of interest. Material of the fruit and seeds of this species, at various stages before and after fertilization, was obtained in Angola during the recent Percy Sladen Memorial Expedition by Dr. H. H. W. Pearson, who handed it over to me for examination.

The fruit of *C. Papaya* is a one-celled berry, with seeds lining the wall. These seeds, when mature, are oval in form and about 8 mm. long. Their coat consists of two separable layers—a hard reddish-brown endotesta, covered by a soft white sarcotesta.³ The endotesta rises into irregular ridge-like outgrowths, which run down the length of the seed (Fig. 1, A) and appear in transverse section as pyramidal projections (Fig. 1, B). The sarcotesta fills up the hollows between these ridges, so that the surface of the seed, while still enclosed within the fruit, is smooth and shiny; but when it is set free, the sarcotesta quickly loses its watery contents and shrivels down into the hollows.

In the young ovule, the two integuments develop as usual, and at the time of pollination consist each of four or five layers of ordinary parenchyma (Fig. 2). Immediately after pollination, these layers begin to show the following series of changes:—

A. *The inner integument.*

The cells of the inner epidermis (*a*) are the only ones in this integument which retain their original form. As the seed matures, they enlarge, and a cuticular layer is formed on the outer side where they are in contact with the nucellus. At the same time, tannin is deposited in their cytoplasm, so that the contents of each cell become converted into a tanniferous block (Fig. 4). All the other cells in the integument begin to show sliding growth immediately after pollination (Fig. 3), the cells of the outer epidermis (*b*) elongating in a direction parallel to the long axis of the seed, while those of the underlying layers lengthen tangentially. Their walls become thickened

¹ Percy Sladen Memorial Expedition in S.W. Africa, 1908–1909; Report No. 3.

² Klebs: Beiträge zur Morphologie und Biologie der Keimung.

³ This sarcotesta was formerly described as an arillus (Baillon: Natural History of Plants, iv, 293, London, 1880).

and deeply pitted, and they are gradually transformed into characteristic sclerenchymatous fibres (Fig. 4). The epidermal fibres are elliptical in transverse section; their lumina are larger than in the underlying layers, and their walls much thicker.

B. *The outer integument.*

Immediately after pollination, this integument begins to increase in thickness, until it attains to the relatively considerable size shown in Figs. 1 and 4. This increase is due to the appearance of bands of meristem, running down the integument

FIGS. 1-4. Sections through the seed and ovule of *C. papaya*, to show the structure and development of the seed-coat. Lettering in each figure:

Inner Integument	{	<i>a</i> = inner epidermis	}	= endotesta.
		<i>b</i> = outer „		
Outer Integument	{	<i>c</i> = inner „	}	= sarcotesta.
		<i>d</i> = outer „		
		<i>e</i> = ridges of the endotesta.

A

B

FIG. 1, A and B. Median longitudinal and transverse sections of the mature seed. $\times 3$.

FIG. 2. Transverse section through integuments and nucellus of ovule before pollination. $\times 120$.

FIG. 3. The same, a short time after pollination, showing a developing ridge of the endotesta on each side of the section. $\times 120$.

in the layer immediately underlying the outer epidermis, and marking the future position of the ridges of the endotesta. By the divisions of these meristems, a ridge gradually arises along each band. These ridges, like the meristems, generally run roughly parallel in a longitudinal direction, but are often quite irregular. Two of these developing ridges are shown in transverse section in Fig. 3, and it will be noted that at the base of the depression between them, six or seven adjacent cells of the hypodermal layer have remained undivided, merely increasing in size. A similar row of about six hypodermal cells is found in transverse section at the base of each depression between the ridges, and these cells never divide, but continue to increase

greatly in size and elongate vertically, so that in the mature seed they form a pavement, six to ten cells broad, running along the bottom of these depressions (Figs. 4 and 1, B).

As these ridges develop, the cells composing them increase greatly in size, while those of the original integument remain small. The mature integument (excluding

FIG. 4. Transverse section through mature seed-coat, showing further development of the ridges of Fig. 3. $\times 60$.

the epidermal layers) thus consists of a region of cells with small lumina passing at the ridges into cells with much larger lumina (Fig. 4). As the seed-coat matures, these cells all begin to lose their contents, and their walls become thicker and rather hard (but not lignified) and take on a yellowish colour. The response of these walls to the ordinary tests for cellulose, both staining and microchemical, grows fainter, until in the mature seed only the outermost still unaltered layers give any reaction with these tests. With a solution of iodine in potassium iodide and with Schulze's

solution their yellow tinge deepens, and after treatment with iodine and sulphuric acid they become brown; this coloration in each case passing in the outermost layers into the ordinary bluish tinge of a cellulose reaction. From these facts, it seems probable that they are composed of a hardened horny variety of cellulose, like the 'reserve cellulose' described by Gardiner and Hill¹ in the endosperm of *Tamus*, and by Grüss² in that of *Phoenix* and other plants, which is also unaffected by ordinary cellulose tests, and reacts similarly with iodine in potassium iodide and with iodine and sulphuric acid. As in *Tamus*, moreover, the middle lamella is not evident in most of the walls when mature, though in the outermost layers, and fairly often among the other large cells in the ridges, it can still be recognized as a fine line. Otherwise, the layers of the walls of adjoining cells seem to coalesce to form a homogeneous intercellular matrix.

A similar transformation takes place in the outer wall of the inner epidermis (*c*), which also becomes thickened and loses its cellulose reactions. Otherwise, this epidermal layer remains unaltered, except that the cells increase in size and a crystal of calcium oxalate appears in each.

Meanwhile, the outer epidermis (*d*) is developing into the sarcotesta, which is formed entirely from this layer. Over the ridges it remains single, the cells merely increasing in size, but between the ridges the cells elongate perpendicularly, and divide several times by transverse walls. By continued elongation as the ridges of the endotesta rise up, they fill up the hollows between them, so that the surface of the seed remains smooth. In the latest stages they become separated from the endotesta towards the bottom of the hollows (Fig. 4). As the epidermis develops, its outer wall becomes much thickened and striated.

As the water in the seed-coat evaporates, the sarcotesta shrivels up, and sinks into the hollows between the ridges of the endotesta, whose thick-walled cells retain their shape. When moistened, both layers rapidly absorb water. The cells of the sarcotesta expand to fill up the hollows once more, and the outer epidermal wall swells up considerably, so that the surface of the seed becomes smooth and shiny. The cell-walls of the endotesta also expand slightly, and water replaces the air in their lumina, so that the whole seed-coat becomes a spongy reservoir for the developing embryo to draw upon.

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¹ Gardiner, W., and Hill, A. W.: The Histology of the Endosperm during Germination in *Tamus communis* and *Galium tricornis* (Proc. Camb. Phil. Soc., xi, 445-57, Pl. V, 1902).

² Grüss, J.: Studien über Reserve-Cellulose (Bot. Centralbl., lxx, 242-61, 1897).

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