

THE STRUCTURE OF THE SKIN OR RIND OF THE AVOCADO

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The solution of some of the problems of avocado storage, decay and breakdown may be promoted by knowledge of the anatomy of the skin or rind of the fruit. Although studies on fruit histology and morphology have clarified certain aspects of the general problem, a more detailed study of the epidermis and its associated tissues is warranted to understand better the behavior of the fruit, both on the tree and in storage.

A general investigation on the gross structure and morphology of the avocado fruit made by Cummings and Schroeder (1) showed that differences between thick-skinned and thin-skinned fruit types resulted primarily from the amount and density of stone-cell masses located just beneath the epidermis. Varieties with thick skins, such as characterize those fruits of the Guatemalan horticultural race, have a layer of very densely packed sclerenchyma while, on the other hand, thin-skinned varieties of the Mexican horticultural race contain only small scattered groups of loosely packed, small sclerenchyma just beneath the epidermis.

The vascular system, and general histology of the flesh or pericarp and seed also are discussed. It was shown that the greater part of the cellular content of the pericarp parenchyma in the mature softened fruit consists of oil droplets. Scattered throughout the parenchyma are specialized oil cells which are distinguished by their large size and lignified, thin cell wall. These cells each contain oil in the form of a single large droplet.

Haas (2), investigating the fruit from a physiological approach, points out that length growth of the fruit is greatest near the stem end. He further shows that stomatal density is greater near the fruit apex and that considerable cork formation occurs in areas below former stoma. Stoneback and Calvert (3) investigated the general anatomy of the fruit as a whole.

MATERIALS AND METHODS

The present investigation was conducted on fresh fruit specimens of several varieties grown in the Subtropical Horticulture orchard on the Los Angeles campus. Sections for microscopic examination were cut free-hand or on a sliding microtome. Standard reagents were used for microchemical tests. Drawings were made with the aid of a camera lucida.

OBSERVATIONS

Epidermis

The skin of the avocado fruit consists of an epidermis, together with hypodermis, chlorenchyma and sclerenchyma tissues. The epidermal layer, one cell thick, extends completely over the fruit surface and is broken only by lenticel formation which eventually may develop into rather extensive corky areas (Figures 1 and 2). Such corky areas may cover some fruits to variable degrees of completeness. The epidermis consists of rather regular cells, block-shaped in cross section and irregularly polygonal in transverse section. Cell division occurs in this and most other tissues in all parts of the fruit pericarp throughout its life. Thus cell division, both radial and tangential, allows for expansion of the fruit in all planes. The development of a hypodermis one or two cells in depth generally is observed.

The outer tangential cellulose wall of the typical epidermal cell is heavily cutinized as evidenced by the staining reaction with Sudan III. This cutinization may extend laterally along the radial walls and even continue into the tangential and radial walls of the second or third cell layer below the epidermis. Such extensive cutinization is evident usually in older and mature fruit and is quite variable in extent (Figures 3 and 4).

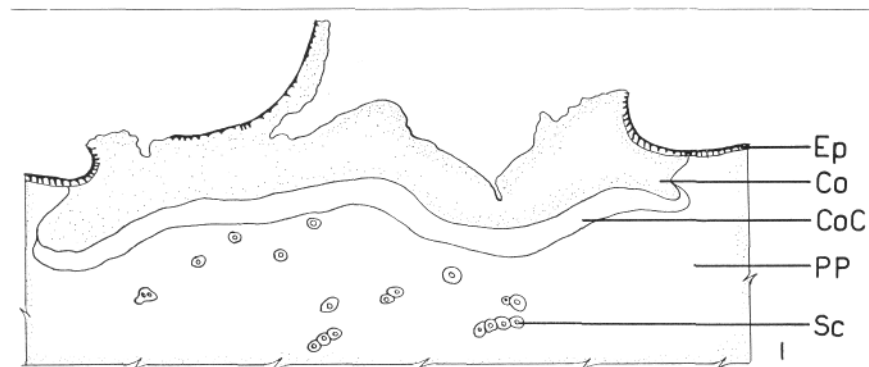


Fig. 1. Diagrammatic section through avocado fruit rind showing origin and extent of cork formation just beneath epidermis.

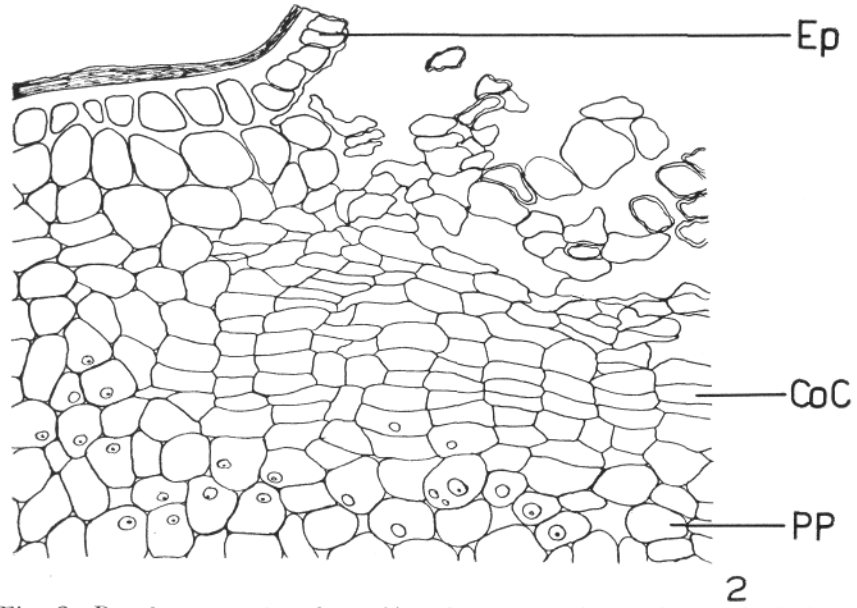


Fig. 2. Development of cork cambium in outer pericarp of avocado fruit.

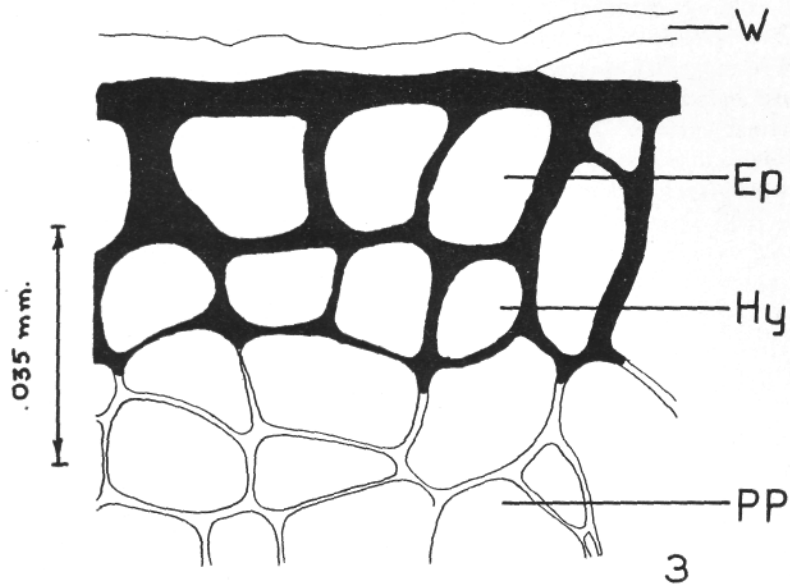


Fig. 3. Section through epidermis and hypodermis of Anaheim fruit showing extent of cutinization of cell walls in these tissues.

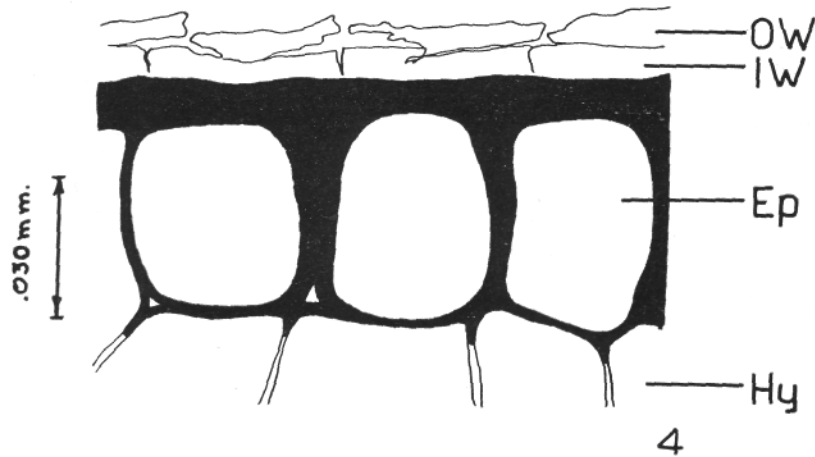


Fig. 4. Section through epidermis of Fuerte fruit showing cutinization of epidermal cell walls and development of wax layers on outer surface of cuticle. Note fissure in wax layers over each radial wall. Ep—epidermis, Hy—hypodermis, PP—pericarp parenchyma, Co—cork, CoC—cork cambium, Sc—Sclerides (stone cells), W—wax layer, OW—outer wax layer, IW—inner wax layer.

The tangential surface of the epidermis outside the cuticle is overlain with a dense and rather uniformly thick layer of wax which covers the uninterrupted epidermal surface. This primary layer of wax measures approximately 6 microns in thickness and is more or less continuous and homogeneous. A second and outer layer of wax overlying the primary layer is frequently distinguishable. This secondary layer is more irregular in general appearance and is characterized by irregular patches of wax and by deep and irregular fissures and by the fact that it is rubbed off easily. These two waxy layers, apparently of the same chemical nature, dissolve readily in carbon tetrachloride or xylene. The addition of potassium iodide and sulfuric acid to sections which previously have soaked in Sudan III causes the outer tangential epidermal wall to become intense red and leaves the wax layers colorless or clear. Morphologically, the outer wax layer has a rough and irregular surface and has many fissures and scalings of variable thickness. The inner wax layer is, in comparison, more uniform in thickness with cracks approximately over each radial wall of the subtending epidermal cells.

The detail and minute structure of the wax layer which constitutes the greater part of the cuticular cover is not discerned under ordinary treatments. When very thin tissue slices are soaked in concentrated potassium iodide and then treated with dilute sulfuric acid and followed by more concentrated sulfuric acid the true fibrillar nature of the waxy layer can be observed (Figure 8). This treatment causes the wax layer to appear as a series of minute wax rods or fibrillae which extend outward at right angles to the outer tangential surface of the epidermal cells. The many minute secretory pores which exude the wax fibrillae can be traced through the outer tangential cell wall to the protoplast along the inner surface of the epidermal cell. The fibrillar nature of the outer secondary wax layer is not delineated easily because the wax rodlets become fused and distorted. Likewise the irregular scaling and fissures which develop in this layer destroy the structural pattern of the fibrillae. The removal or destruction of these protective waxy

layers makes the fruit surface more susceptible to attack by fungal and bacterial infections or may result in physiological disturbances as the result of desiccation or bruising of the underlying tissue.

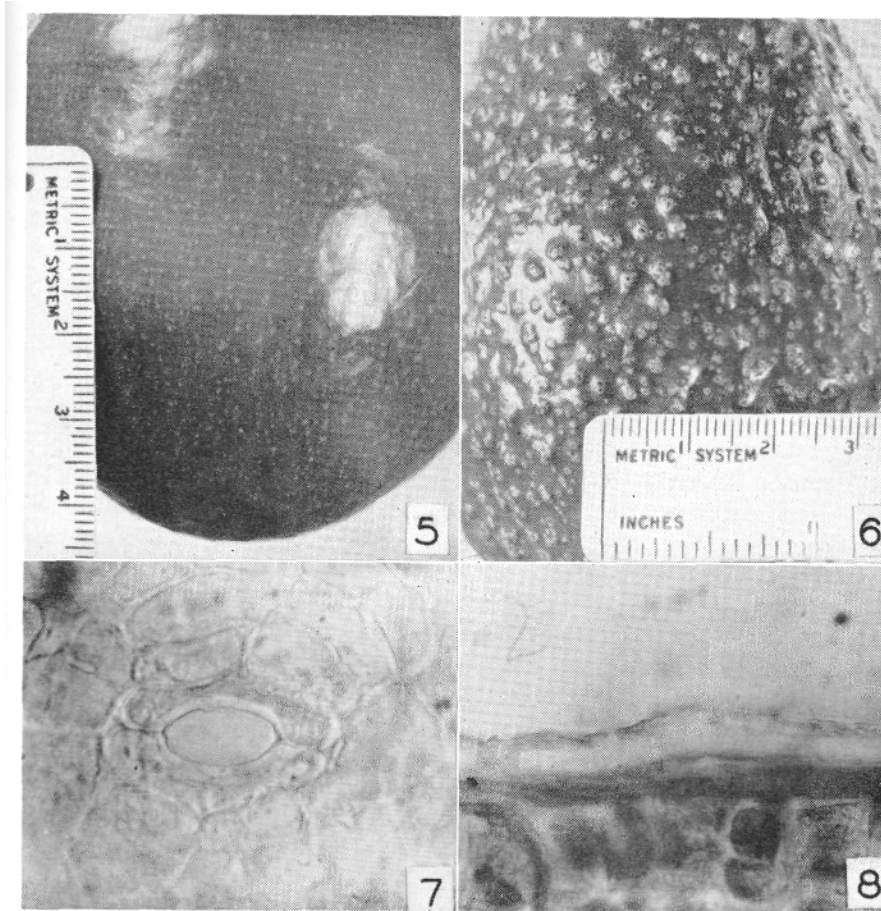
Stomata

The stomata of the avocado fruit are quite regular in general morphology. They consist of a pore surrounded by two simple guard cells which have a thickened cuticle on the inner radial surfaces (Figure 7). A typical stomata measures 21 microns long by 14 microns wide with a pore opening approximately 10 microns in length. The stomata normally are level with the epidermal layer.

Stomatal density over the fruit surface varies considerably within a given fruit and between fruits of different shapes, varieties, and horticultural races. A casual observation of most avocado fruits indicates that the greater density of stomata is at the apical or styler end. Differences in stomata density between the basal and apical ends, however, varies with the form of the fruit, the spherical forms having smaller differences than long-necked or pyriform types. Such uneven distribution results from a greater amount of growth or stretching in the "neck" or stem-end region during the period of fruit development in long-necked types. Increase in size of fruit in the spherical type results from growth more uniformly distributed throughout the fruit, hence a more even distribution of stomata is observed.

Stomata can easily be observed on the fruit surface under relatively low magnification. The pores appear as tiny white dots in most cases rather well differentiated from the otherwise smooth, homogenous cuticle. Stomata are also restricted to the elevated mounds of tissues in those fruits which have a rough or pebbled surface as is characteristic of many varieties of the Guatemalan horticultural race. Thus varieties such as Hass and Dickinson have stomata concentrated in groups on the elevated surfaces of the rind (Figure 6), whereas in smooth skin varieties such as Duke (Figure 5), the stomata are more uniformly distributed over the relatively smooth surface. Immediately beneath each stomata is a mass of cells characterized by extensive intercellular spaces. Such tissue facilitates the gaseous exchange between the subsurface tissue and the external atmosphere through the stoma. Each stomata is thus subtended by aeration tissue which appear as a white dot to the unaided eye. Hence stomata in a given area can be detected merely by counting the white dots in that area.

The determination of stomatal density is easily made with the aid of a dissecting microscope. The fruit surface can be marked off in square centimeters at various desired points or over the whole fruit surface and the number of stomata counted in each square centimeter of surface.



- Fig. 5. Surface view of Duke avocado fruit showing smooth skin and rather even distribution of stomata.
- Fig. 6. Surface view of Lyon avocado fruit showing stomata concentrated in elevated areas of skin surface.
- Fig. 7. Surface view of open stomata in avocado fruit with guard cells and adjacent epidermal cells.
- Fig. 8. Section through cuticle and wax layer of avocado fruit epidermis following treatment with potassium iodide and sulfuric acid showing fibrillar nature of wax layer.

Stomatal density determination were made on a number of representative varieties by actually counting all stomata on one half of the bilaterally symmetrical fruits. The fruit surface area was determined by carefully removing the skin in small sections, tracing the outline of these sections on heavy paper and weighing the traced areas. Knowing the area per given weight of paper the total area of the tracings was calculated approximately. Typical determinations are given in Table I.

TABLE I

Variety	Fruit Weight gr.	Fruit size cm.	Surface area cm. ²	Total Stomata	Stomata per cm. ²
Lodge	144	9.0 x 6.1	118.8	32,776	275.8
Mayapan	326	8.6 x 8.6	311.3	8,926	28.6
Hass	253	11.0 x 7.0	195.3	13,882	71.0
Mexicola	—	5.0 x 4.3	51.0	3,343	65.4
Fuerte	107	8.5 x 5.2	123.8	13,682	110.6
Itzamma	339	14.0 x 7.3	—	13,960	—
Duke	146	10.0 x 5.7	138.3	5,960	43.1
MacArthur	475	15.2 x 8.3	380.0	9,660	25.4

A wide range in variation of total stomata between fruits of different varieties is evident upon examination of Table I. The widest differences among those specimens examined was between the varieties Lodge and Duke. Both of these fruits were of approximately the same weight (144 and 146 grams) and size (9.0 x 6.1 cm. and 10.0 x 5.7 cm.), but differ slightly in surface area (118.8 and 138.3 cm²), yet the total stomata in Lodge is about 5.5 times that of Duke. The actual average of stomatal density in Lodge is 6.4 times that of Duke regardless of the slight difference in surface area.

While the precise number of stomata varies between individual fruits, the fact remains that the magnitude of stomatal density between varieties is in general quite different. The range of variation between individual fruits of a given variety may be observed in Table II. Thus Fuerte shows a range from 106.6 to 130.9, whereas Hass varies from 60.3 to 75.6.

In another set of observations stomata counts were made on a strip of fruit surface 1 cm. wide traversing the fruit from stem to apex on opposite sides along the axis of symmetry. The average stomata density determined from such counts is given in Table II.

TABLE II

Variety	Average number stomata per cm. ²	Variety	Average number stomata per cm. ²
Hass	60.3, 71.0, 75.6	Ganter	207.8
Lyon	55.7	Blake	206.6
Itzamma	54.3	Lodge	275.8
Dickinson	52.6	Topa Topa	442.6
Nabal	48.3	Duke	56.0, 65.4, 43.1
Mayapan	41.0, 28.6	Puebla	107.4
Anaheim	29.9	Fuerte	110.6, 119.6, 106.6
Sharpless	23.3		

It is evident that the varieties tend to fall into groups based on average density of

stomata. Varieties of the Guatemalan horticultural race have in general fewer stomata per unit surface than do those of the Mexican race. Fuerte, presumably a variety of the Guatemalan-Mexican hybrid race is somewhat intermediate in regard to this character, as is also the variety Puebla. The latter has several horticultural and other botanical characters which additionally suggest hybrid origin. An exception to this general grouping is Duke. This variety is classified by most horticultural criteria as a member of the Mexican race, but considering the stomatal index it should belong to the Guatemalan group for it has fewer stomata than any of the Mexican types. Actually it has fewer stomata than many of the typical Guatemalan varieties.

The normal function of stomata is to provide for the liberation of the products of respiration from the internal fruit tissues and to admit oxygen from the surrounding atmosphere. Transpiration or water loss from fruit is governed to some extent by the number and nature of stomata. The high density of stomata around the apical end of the fruit apparently provides some means by which physiological processes are carried on more intensively in that area. Such acceleration of respiration and possibly the ease of moisture loss and gaseous exchange results in the early development of cork tissue in the styler end of the fruit as the result of breakdown of aeration tissue beneath the stomata. The formation of periderm or cork tissue in the styler end of the fruit is pronounced in some varieties and is characteristic of others.

It is a general observation that fruits of certain avocado varieties under normal conditions show differential physiological development. Some fruits may soften at the styler end many days before the stem end becomes soft. This is especially true of fruits of the Mexican race. The premature physiological breakdown of the styler end as indicated by the penetration of dyes into the fruit has been demonstrated by Haas. The greater concentration of stomata and subsequent lenticel formation at the apex may be a factor in the differential physiological behavior observed between the apical and basal portions of the avocado fruit.

LITERATURE CITED

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