California Avocado Society 1942 Yearbook 27: 56-64

Anatomy of the Avocado Fruit

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This report is a brief summary of an anatomical study of the avocado fruit begun by the senior author in 1940 as part of a general study of the structure, chemical composition and physiological behavior of this fruit undertaken at the request of the California avocado industry. In 1941 the problem was taken over by the junior author. More complete and detailed reports on this portion of the study will appear in appropriate technical journals. Several reports already have been made on other phases of the general study.*

Stoneback and Calvert (3) have made a cursory study of the avocado fruit, and Haas (1,2) mentions a few anatomical features as they are related to the physiological reactions of the fruit. Aside from these, practically no references exist in the literature concerning the anatomy of this fruit.

This report deals with the anatomy of the Fuerte avocado fruit and of five other commercial varieties selected because of pronounced differences in certain structural characteristics. For the purpose of this study the Fuerte is considered to be a typical fruit, for presumably it combines the characteristics of the Guatemalan and Mexican horticultural races. The other varieties studied were Leonard, Leucadia, Nabal, Carlsbad and Nimlioh.

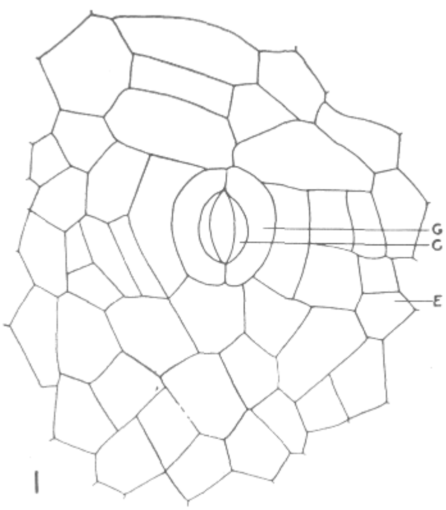
The avocado fruit is a berry of one carpel containing a single seed. The mature Fuerte fruit is noticeably asymmetrical at the apex as a result of differential growth on opposite sides. The pericarp consists of three layers; the exocarp, which comprises the skin or rind, the fleshy mesocarp, which is the edible portion of the fruit, and a thin inner layer next to the outer seed coat, the endocarp (Fig. 14). The following description of the fruit tissues refers to the Fuerte variety except where others are specifically mentioned.

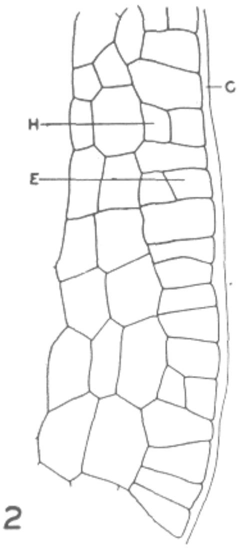
The exocarp is made up of epidermal, parenchyma and sclerenchyma tissues and is the layer which is removed when the fruit is peeled. A relatively thin cuticle forms a wax-like film over the surface of the fruit. Beneath this film is an epidermis of one layer and a hypodermis of one to three layers of brick-shaped cells (Fig. 2). Suberin is present in the outer tangential and radial walls, and the cell contents include chloroplasts, starch, oil and tannin. Stomatal openings level with the surface may be seen in this layer in young fruits (Fig. 1). In older fruits, however, many of the stomata have been forced outward by lenticel formation beneath them and are no longer visible. The lenticels appear on the surface of the fruit as slightly raised white or gray patches which remain parenchymatous and usually do not break through the epidermis (Fig. 11). The color is due to the many, large intercellular spaces of the lenticel region. A slight amount of cork is formed in some lenticels near the apical end, a condition considered by some growers to be an indication of fruit maturity. The distribution of the lenticels is not uniform for they are more numerous on the shorter side and also toward the apex of the fruit. This results from the differential growth of the fruit as a whole, so that on the "longer" side and at the stem end where growth is greatest (2) the lenticels are more widely separated.

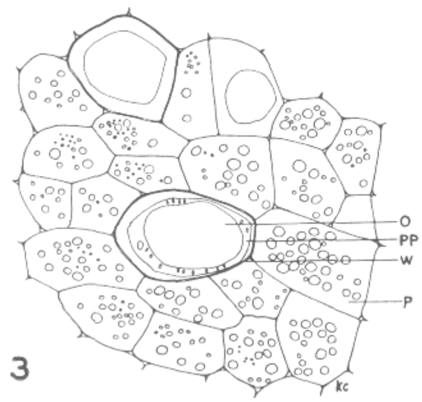
In contrast to the Fuerte and some of the even smoother Mexican varieties, the rinds of the Carlsbad and Nimlioh are rough in texture due to the cork which forms in the lenticels. The epidermis is ruptured and several lenticels may coalesce to form large, rough, corky patches. In the case of these thicker-skinned varieties, part of the roughness in texture is due to underlying sclerenchyma tissue as well as to abundant cork formation.

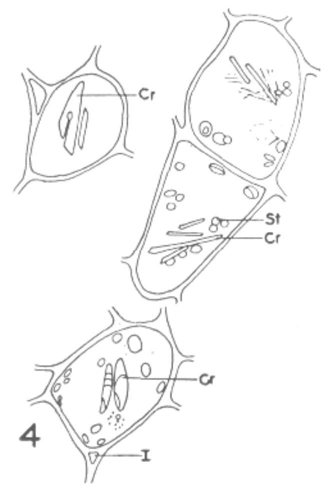
*Appleman, D. and I. Noda. Biochemical studies of the Fuerte avocado fruit. Calif. Avocado Soc Yearbook 1941: 60-63. 1941.

*Biale, J. B. Climacteric rise in respiration rate of the Fuerte avocado fruit. Amer. Soc. Hort. Sci Proc. 39: 137-142. 1941.









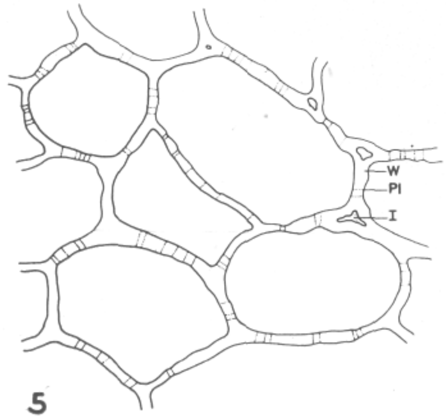
All figures except Fig. 123 are taken from mature Fuerte fruits.

Fig. 1. Surface view of epidermis and stoma. E, epidermal cell; G, guard cell; C, cutin.

Fig. 2. Transverse section through outer exocarp. C, cuticle; E, epidermis; H, hypodermis.

Fig. 3. Idioblast and parenchyma of mesocarp. P. parenchyma cell; O, oil drop; PP, protoplasn W, wall of idioblast.

Fig. 4. Mesocarp parenchyma cells containing starch grains and calcium oxalate crystals. Cr, calciu oxalate crystal; St, starch grain; 1, intercellular space.



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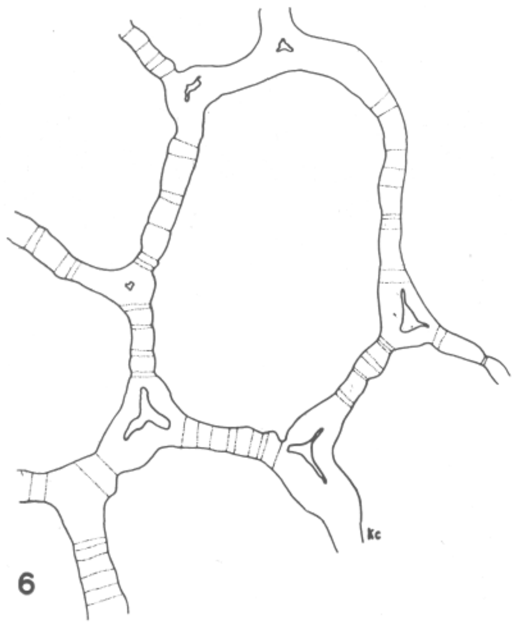

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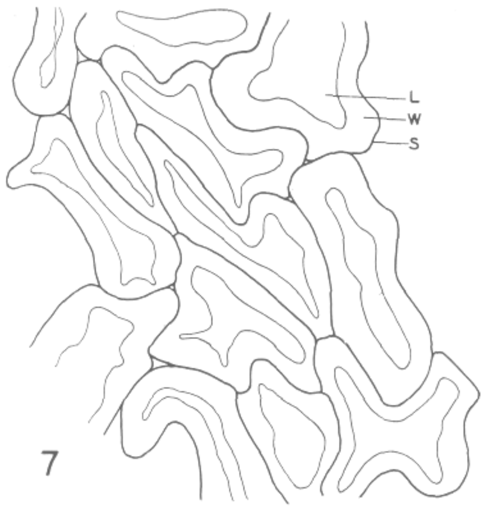
Fig. 5. Mesocarp parenchyma cells showing plasmodesmata. W, wall of two adjoining cells; Pl, plasmodesma; I, intercellular space.

Fig. 6. Cotyledon parenchyma cell showing plasmodesmata.



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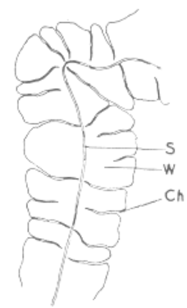

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Fig. 7. Surface view of stone cells of outer seed coat. L, lumen of cell; W, wall; S, suberin layer of wall.

Fig. 8. Cross section through a portion of two stone cells of outer seed coat showing channels in walls and suberin layer between cells.

Fig. 9. Surface view of tannin cells of outer seed coat. T, tannin cell; I, intercellular space.

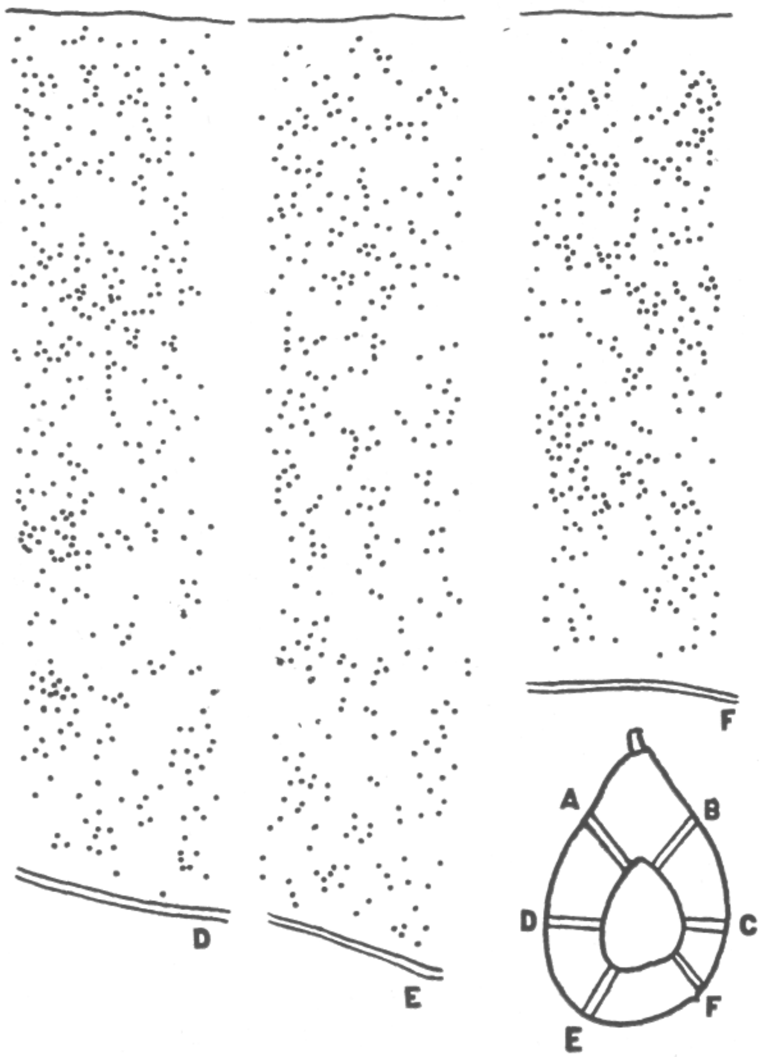

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Fig. 10. Transverse sections of pericarp showing distribution of idioblasts. Each dot represents an idioblast. Sections D, E and F enlarged from corresponding sections on fruit diagram in lower right corner.

Beneath the epidermal and hypodermal layers, but still a part of the exocarp of the typical Fuerte fruit, lie several layers of parenchyma cells. These cells are isodiametric in form, measure approximately 40 microns in diameter and contain chloroplasts, some oil and tannin. Next inside this parenchymatous tissue and limiting the exocarp on the inner surface is an interrupted layer of sclerenchyma tissue (Fig 13). In the Fuerte, as in other relatively thin-skinned varieties, this layer consists of a few isolated, slightly lignifled stone cells separated by parenchyma. The thick-skinned varieties, in contrast, contain large numbers of strongly lignifled stone cells which are in part responsible for the brittle texture of the rinds. Most of these stone cells remain attached to the skin when the fruit is peeled and form the dividing line between skin and flesh.

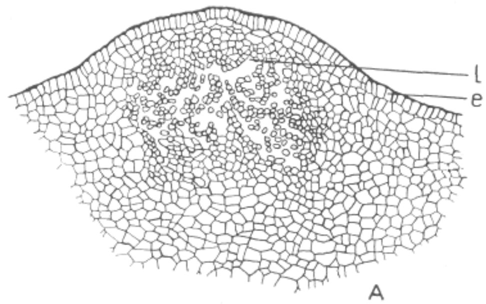

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Fig. 11. Section through a lenticel. L, intercellular space; e, epidermis.

The flesh of all varieties of avocado fruits exhibits a cellular structure of considerable uniformity. The bulk of the mesocarp is composed of isodiametric parenchyma cells, among which are scattered specialized oil-containing cells (Fig. 3). The vascular system forms a network throughout this region (Fig. 12). Evidences of recent division of mesocarp parenchyma cells are found in fully ripened fruits, indicating that increase in volume of the fruit results from cell division throughout the life of the fruit. The typical parenchyma cell measures about 60 microns in diameter, has a thin cellulose wall and contains oil which appears in the form of small droplets in sectioned tissue. In addition, chloroplasts are present in all of these cells, calcium oxalate crystals in some (Fig. 4), and a small amount of starch may occur, although this substance is usually found, in the Fuerte variety, only in young developing fruits.

Outstanding among the parenchyma cells are the larger, specialized oil-containing cells, which will be referred to as idioblasts. These are distributed fairly uniformly through the mesocarp, and in volume make up about two percent of the total edible portion of the fruit (Figs. 3, 10). A typical idioblast measures 80 microns in diameter. The walls are four microns in thickness in contrast to 2.5 microns for parenchyma walls, and contain, in addition to cellulose, a substance which does not dissolve upon treatment with concentrated sulfuric acid. This substance probably is suberin. Occasionally some of these thickened walls give positive indications of the presence of lignin in addition to the suberin-like layer. Another point of difference between the idioblasts and parenchyma cells is the physical state of the oil drops. Oil in the idioblasts occurs as a single, large drop which fills the cell, while the oil in the surrounding unspecialized cells takes the form of many small droplets (Fig. 3). Color reactions with microchemical reagents and pH indicators also point to a difference between the type of oil in these cells.

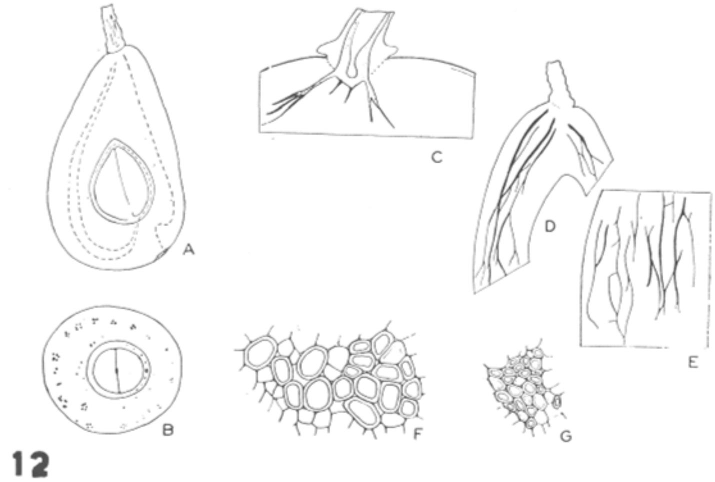

Fig. 12. Vascular system of pericarp and seed coat. A, diagram of the strands which enter style and seed coat; B, cross section of fruit showing unequal distribution of strands; C, vascular tissue of pedicel attachment region; D, longitudinal median section through stem end of fruit; E, tangential section through mesocarp showing anastomosing of strands; F, cross section of xylem elements in thick side of fruit; G, cross section of xylem elements in thin side of fruit, same scale as F.

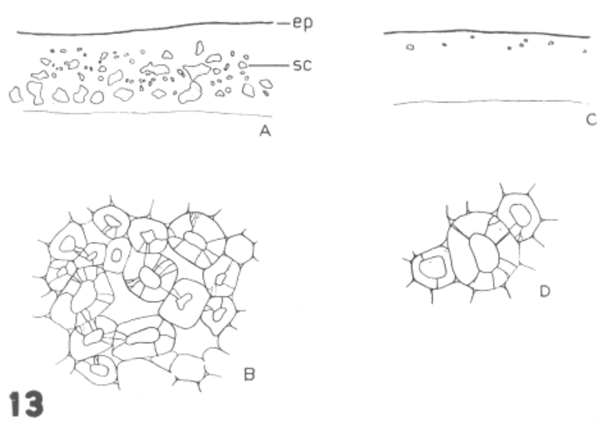

Fig. 13. Comparison of sclerenchyma tissue in exocarps of thin and thick-skinned fruits. A, transverse section through exocarp of Nabal variety; B, detail of group of stone cells as seen in A; C, transverse section through exocarp and part of mesocarp of Fuerte variety; D, detail of group of stone cells as seen in C. ep, epidermis; sc, sclerenchyma or stone cells.

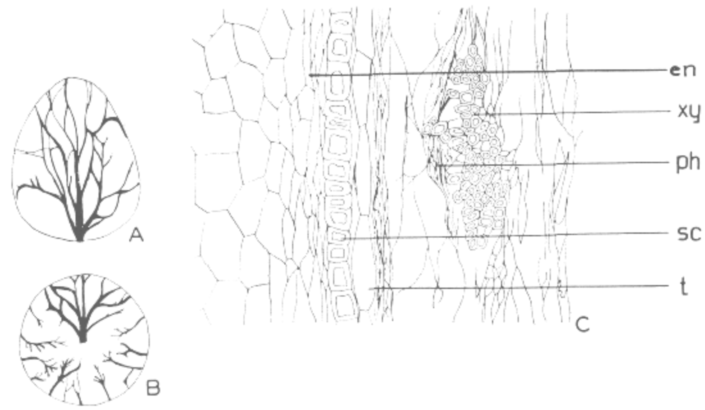

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Fig. 14. A, surface view of vascular system of the seed coats; B, same as A, end view; C, cross section through endocarp and seed coats. en, endocarp; xy, xylem; ph, phloem; sc, stone cell; t, tannin cell.

The vascular or conducting system of the fruit permeates the mesocarp in an asymmetrical pattern, a fact which is linked with the asymmetry of the fruit as a whole (Fig. 12-A-B). The seed develops slightly off center, so that there is a "thicker" side to the pericarp from the stem end to the apex of the fruit. In the pedicel tip and continuing a short distance into the fruit beyond the pedicel attachment, the vascular tissue forms a solid cylnder (Fig. 12-C). At this point it breaks up into six major strands which divide, redivide and anastomose until the entire mesocarp is penetrated by the vascular network. The thicker side of the fruit contains more of the original six strands than does the thinner side (Fig. 12-D). Some of the bundles on the thinner side end blindly toward the apex of the fruit and some lead to the stylar point. Those of the thicker side coalesce near the apex and from there enter the seed coats as a single strand (Fig. 12-A). Within the seed coats continuous branching with some anastomosing of the finer veins again occurs until a network of conducting tissue surrounds the embryo (Fig. 14-B). The xylem of the veins in the fruit consists principally of strongly lignified spiral and annular primary elements and of scalariform and simple-pitted vessels. The veins appear as the stringy and sometimes dark fibrous material which remains when the fruit softens.

The endocarp, or inner layer of the fruit, consists of a few rows of parenchyma cells which are smaller and somewhat more flattened than the adjoining cells of the mesocarp (Fig. 14-C). These cells lie directly against the outer seed coat and may adhere to it when the seed is removed from the fruit. Cells of the endocarp contain fewer chloroplasts, starch grains, oil droplets and crystals than do those of the mesocarp.

The large, conspicuous seed of the avocado is made up of two fleshy cotyledons and a centrally attached plumule, hypocotyl and radicle, the whole surrounded by two papery seed coats closely adherent to each other. There is no endosperm left in the seed at maturity. The outer layer of the outer seed coat consists of one to five layers of stone cells which are irregular in shape with heavy, deeply pitted, lignified walls. A suberin layer occurs at the middle lamella (Pigs. 7, 8). Underlying the stone cells is a layer of large, highly irregular cells which are filled with tannin (Fig. 9). A typical cell measures 118 by 302 microns. Underneath these are several layers of small parenchyma cells of the same general irregular shape as the larger tannin-filled cells next to them. A few oil-bearing cells similar to the idioblasts of the fruit are distributed among these smaller parenchyma cells.

The cotyledons are formed of undiflerentiated parenchyma tissue interspersed with occasional idioblasts. Starch is the main storage material of the cotyledons and is present in great abundance. The large size of the cotyledon parenchyma makes them especially favorable for observing plasmodesmata connections between the cell protoplasts (Fig. 6). These connections may also be seen in the mesocarp parenchyma and stone cells of the fruit (Fig. 5).

The vascular system of the embryo consists of several strands running in groups parallel to the flat surface of the cotyledons. At the point where the hypocotyl joins the cotyledons, the vascular strands of the latter coalesce into a single bundle which supplies the hypocotyl and radicle, and remains in these structures as a complete cylinder.

The writers wish to thank Dr. P. M. Scott of the Botany Department for her valuable assistance during the course of this study.

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3. Stoneback, W. J. and H. Calvert. Histology and chemistry of the avocado. Amer. Jour Pharm 95: 598-612. 1923.