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ANATOMY OF PERIDERM AND CORTEX
OF FOUQUIERIACEAEJAMES HENRICKSON¹*California State College, Los Angeles*

INTRODUCTION

The Fouquieriaceae are small trees and shrubs native to arid portions of Mexico and southwestern United States. The family is treated as consisting of two genera: *Fouquieria* with 11 known species, and the monotypic *Idria*. For a brief description of the distribution, growth habits, and floral characteristics of the family, see Henrickson, 1969.

Ever since the family has been known to science, only a small number of anatomical studies have been undertaken. Van Tieghem (1899), in reporting on material collected in Baja California by Diguet, made a general and relatively incomplete description of spine formation and stem and floral morphology. He claimed his findings provided evidence of an affinity of this family with the Ebenales. Solereder (1908) in his *Systematic Anatomy of the Dicotyledons* discussed the general anatomy of *Fouquieria* and included the genus in the Tamariscaceae, where it formed an aberrant element. He included a discussion of leaf, spine, and wood anatomy. In 1922 Reiche published an account of the vegetative and floral anatomy and morphology of *Fouquieria formosa*. His work was based on study of preserved materials, and was the first to describe accurately the stem cortex, spines, etc. Scott (1932) discussed various features of the anatomy of *Fouquieria splendens* and carefully described the stem cortex and periderm. In 1935 Humphrey made a detailed study of the morphology of *Idria columnaris* and described the structure of the main trunk and secondary branches. More recently, Metcalf and Chalk (1950) presented a general review of the peculiar morphology of the family, including a brief description of the xylem.

The spines of the Fouquieriaceae are formed in association with the long-shoot leaves. Several authors have reported on this peculiar method of spine formation (Engelmann, 1883; Poisson, 1895; Van Tieghem, 1899; Robinson, 1904; Reiche, 1922; Humphrey, 1931).

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In this paper an extensive study of the anatomy and morphology of the periderm and cortex of both stem and root is presented. Only a few comments of the vascular system are made, for this aspect of my study of the Fouquieriaceae will be covered in an ensuing paper.

MATERIALS AND METHODS

During this investigation of the Fouquieriaceae, all known species were observed and collected in the field. Specimens of young and mature stems and roots were preserved in 70 percent FAA—formalin, acetic acid, 70 percent ethyl alcohol (Johansen, 1940). Microscope slides of the bark and cortex of the stems and roots were prepared by standard paraffin techniques, sectioned at 12 to 20 μ , stained in Safranin O, counterstained in fast green and mounted in canada balsam or Permount in accordance with the techniques of Johansen (1940). Thin sections of preserved material also were prepared using the sliding microtome. Most of these materials were quick frozen and sections 25 to 40 μ in thickness were cut. These were stained as above or treated with specific stains that have proved to be very useful in studies of the cortex. The latter slides were very easy to prepare and had the advantage of increasing the amount of material available for study. Both living and preserved material was studied in the case of most species. Microchemical tests were made on cortical sections of the stems and roots of several species. Phloroglucinol, potassium-iodide-iodine, Sudan IV, ferric chloride, and ruthenium red were used to test for lignin, starch, oils and fats, tannins and pectic compounds respectively (Johansen, 1940; Jensen, 1962; Bailey, 1960). Vouchers for this study are located in the herbarium of the Rancho Santa Ana Botanic Garden.

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STEM STRUCTURE

CROSS STRUCTURE.—Stems of Fouquieriaceae can be interpreted as long shoots bearing spirally arranged, petiolate long-shoot leaves (Fig. 4a). The terminal long-shoot increments vary from 1 to 9 inches in length, depending upon various environmental conditions, internal food reserves, and age of the plant, i.e., they are formed less frequently but are longer in older plants of *F. splendens* as observed by Darrow (1943). Distinct markings similar to those left by terminal bud-scale scars in other angiosperms delimit successive long shoots (Fig. 6a). Fascicles of four to eight sessile or shortly petiolate leaves are produced at the lateral nodes after each sufficient rainfall (Fig. 4b). Because lateral shoots usually are not formed at the nodal areas, these lateral nodes are designated as short shoots and their leaves as short-shoot leaves. Occasionally, in older stems long shoots will be produced by the lateral short shoots.

The developing long shoot is covered by an epidermis which is usually weathered away during the first year (Fig. 2d). Directly under the epidermis are one or two layers of slightly longer thin-walled cells which may contain tannins (Fig. 2e). Occasional epidermal cells divide periclinally as shown in Fig. 2c. A thin cuticle, which stains brightly with Sudan IV, is secreted by the epidermis. The cuticle ranges from 5 to 10 μ in thickness in the various species of woody fouquierias (Fig. 2c) and is 26 to 40 μ thick in *Idria*. In the succulent fouquierias the cuticle is initially 30 to 40 μ thick. However, it is retained permanently, as in the epidermis and in older stems the cuticle increases to a thickness of 100 to 180 μ (Fig. 2 a-b). The epidermal cells in the woody fouquierias are either isodiametric or somewhat rectangular and elongate vertically and radially (Fig. 2c). In the succulent fouquierias and *Idria* the epidermal cells are slightly papillate and are completely covered by the thickened cuticle (Figs. 2a, 10b).

In certain populations of *Fouquieria formosa* in the southern part of its range, epidermal cells may elongate and form uniseriate trichomes up to 1 mm long (Fig. 2 f-g). These trichomes are also covered with the thin cuticle. They usually weather away within the first year after formation.

The young long shoots have a distinctive appearance due to projections of the fibrous outer cortex which extend downward from the nodes and form tapering lenticular ridges (Fig. 1 a,c). The *decurrent ridges* of adjacent nodes nearly cover the surface of the young stem and in most species are separated by rather deep *furrows* which form an anastomosing pattern. In other species the furrows are poorly defined (Fig. 1e). The firm, often reddish-colored, decurrent ridges are composed of elongate fibrous cells of the outer cortex which have moderately thickened, nonlignified secondary walls (Figs. 2 d-e, 4d). The lumina of these cells are commonly filled with reddish tannins as can be shown with FeCl_3 (Jensen, 1962). These fiber-like cells are much longer than the epidermal cells and range from 110 to 350 μ in length and 15 to 25 μ in width (Fig. 4e). The walls range from 3 to 5 μ in thickness. The lumina may be prominent or reduced as the fibers collapse laterally. Prominent pits are present on their lateral walls (Fig. 2e). Their outer walls are suberized as can be shown with Sudan IV. The maximum thickness of the fibrous outer cortex varies greatly among the species and ranges from 125 to 800 μ (Table 1).

SPINE STRUCTURE AND DEVELOPMENT.—The long-shoot leaves are petiolate and have either large or reduced lamina. At the end of the growing season, the leaves wither and woody spines which developed in the lower portion of the petiole are left behind. The spine usually extends the full length of the petiole and may continue below the midrib of the leaf blade proper. Separation of the leaf from the spine occurs along an elongate horizontal abscission layer which develops in the parenchyma tissue just above the spine.

As can be seen in Fig. 4d, the petiole has a complex structure. The lower spine-forming portion consists of a cylinder of thick-walled, elongate fibers which are identical to and continuous with those of the outer cortex of the decurrent ridges of the stem. These fiber cells contain tannins, have simple

pits in their lateral walls, and range from 0.5 to 1.2 mm in length. Their length correlates directly with the length of the spine. Figure 4c shows the direct continuation of these cells with the outer cortex fibers of the decurrent ridges. A parenchymatous core continuous with the inner parenchyma cells of the stem cortex extends about two-thirds up the body of the spine. In *Idria columnaris*, however, a mass of thick-walled brachysclereids with lignified walls extends up the center of the spine in lieu of the parenchyma (Fig. 10d). Directly above the fibrous cylinder is the leaf tissue with a single broad trace which extends into the lamina. A single-layered starch sheath subtends the trace as can be seen in Fig. 4c. The broad abscission layer forms in the parenchymatous tissue just above the fibrous cylinder and extends along the entire upper surface of the spine.

Spine formation in the Fouquieriaceae appears to be unique. An understanding of the phylogenetic development of the spine can be achieved by analyzing its unique features which include: the direct continuation of the fiber cells with those of the cortex; the presence of an elongate horizontal abscission layer. Figure 3 depicts by a series of drawings the probable phylogenetic origin of the spines. Figure 3 a-b shows possible ancestral types with slightly swollen nodal areas, decurrent ridges and small rounded leaf bases. Development of an outward extension at the junction of the leaf base and cortex, resulting in an increase in the size of the leaf abscission layer and concomitant formation of a cortical projection as shown in Fig. 3c, has apparently occurred in the Fouquieriaceae. The leaf and cortical portions develop together in the petiole. The leaf portion ultimately dies and falls away leaving the hard, pointed spine. After abscission, the outer fiber cells of the spine dry and the spine becomes strong and rigid. The spine terminates in a very sharp point. The fact that the sharp spines protect the stems from herbivores would seem to explain the selective advantage of such a feature.

The length of the spines varies with the species and apparently with environmental conditions. Several species are characterized by short spines as in Fig. 3c. Occasionally, in *Fouquieria formosa* very small spines are produced (Fig. 2f). The other species have longer spines up to 3.5 cm in length. The leaf blades of these leaves are usually quite large in all species except those characterized by the ocotillo habit, where they are greatly reduced (Fig. 3e).

The spines of many angiosperms are formed by sclerification in or around the midrib of the leaf. The spine is, therefore, a modified leaf or leaf-like organ. In the Fouquieriaceae, the spine appears to be an extension of the cortex—not the leaf proper. To differentiate this type of spine from the modified-leaf type spine of other angiosperms, I shall use the term *fouquieriaceous spine* to designate the condition found in this family.

PERIDERM.—At the initiation of the first growing season after formation of the long shoot, a phellogen develops in the outer parenchymatous tissue directly under the fibrous cortex and by periclinal divisions produces several layers of thin-walled cells. The phellogen produces a narrow phelloderm layer towards the inside and a broader phellem layer on the outer side. The phelloderm cells do not have suberized cell walls as do the first formed phellem cells.

Two basic types of phellem cells are produced by the phellogen (Fig. 4 g-h). At the beginning of the growing season several layers of cells with thin, suberin-impregnated walls are produced. These cells are referred to as *suberized cork cells* after Scott (1932). The suberized walls of the cells stain brightly with Sudan IV as do the oil and fat globules in the lumina of these first formed cells. The quantity of these fats and/or oils is gradually decreased in the later-formed cells. Later in the growing season, cells with thickened cellulose walls form layers of variable thickness. These *fibrous cork cells*, as designated by Scott, have slightly suberized inner walls. The fibrous cork cells occasionally appear and stain similar to the gelatinous tracheids commonly found in the wood. In the succulent fouquierias these

Fig. 1. External appearance of young and old stems of Fouquieriaceae—a-b. *Fouquieria shrevei*.—a. Broad decurrent ridges and narrow furrows are shown in 1 year old stem.—b. Furrows expand and resin-like periderm accumulates in older stems. (Henrickson 1845).—c-d. *Fouquieria ochoteranae*.—c. Young stem. Note arrangement of decurrent ridges and compare to *F. shrevei*.—d. Mature trunk ca. 12 cm in diameter. (Henrickson 2117).—e-f. *Fouquieria leoniale*.—e. Young slender stem showing spines and inconspicuous furrows.—f. Mature trunk, 10 cm in diameter. Scaly bark characteristic of species is shown. (Henrickson 2164).—g-h. *Fouquieria purpusii*.—g. Five year old stem showing decurrent ridges, spines and short shoots which produce fascicles of leaves. The spines have been cut.—h. Mature trunk, 30 cm in diameter showing smooth areas of persistent epidermis and broadened corky decurrent ridges. (Henrickson 2141).—i-j. *Idria columnaris*.—i. Tip of main trunk showing decurrent ridges and spines of trunk and lateral stems originating from nodes.—j. Mature trunk ca. 15 cm in diameter with several short shoots produced per node. Note smooth periderm. (Henrickson 2348) and 2793 respectively. a-b, c-e $\times 0.4$; g $\times 1$; i-j $\times 0.1$; others as given.

cells develop into sclerenchyma cells. Occasionally, tannins occur in the lumina of the fibrous cork cells. Thus, after two or more seasons a definite stratification occurs in the phellem as layers of suberized cells alternate with layers of fibrous cells (Fig. 4 g-h). Subsequent modification and relative thickness of these layers account for the differences in the periderm of the species of the Fouquieriaceae.

The periderm cells are produced in definite radial series (Fig. 10e). No secondary elongation occurs subsequent to formation, but radial compaction of the phellem cells results in distortion of their distinct radial arrangement. The tablet-shaped phellem cells are roughly hexagonal in tangential outline and range from 20 to 50 μ in width and from 20 to 350 μ in length (Fig. 4f). Phellem cells are most elongated in *F. splendens* and *F. campanulata*, where they appear as short fibers; and in the succulent fouquierias, where they are elongated sclereids. They are shorter in all the other species. Those of *Idria columnaris* are the smallest in the family. The tangential dimensions of the phellem cells is given in Table 1. The amount of radial compaction that occurs in the phellem cells varies—the fibrous cells compress much less than the suberized cells.

The definite radial arrangement of the phellem cells throughout several seasons is taken as evidence that either the phellogen functions for many seasons or, if a new phellogen is produced each season, it must be formed in the phelloderm. As shown by reaction with ruthenium red, a specific stain for pectic compounds (Bailey, 1960), the phelloderm cells have large quantities of pectic compounds in their walls. These pectic compounds are not apparent in the phellogen cells proper, perhaps due to the covering of suberin compounds. Small accumulations of pectic compounds do occur in the walls of the fibrous cells which develop in the furrows.

Three types of cells ultimately compose the "outer bark:" elongate fiber-like outer cortex cells which form the ridges and spines of the young stems and the suberized and fibrous phellem cells which compose the phellem proper.

Several species of the Fouquieriaceae have distinctive periderm characteristics which are useful taxonomically. In the following section the morphology of the periderm is described and discussed. The species are, for convenience, placed into five groups which indicate phylogenetic interrelationships. Data on relative thickness of the periderm layers are given in Table 1.

FOUQUIERIA SPLENDENS and F. CAMPANULATA: The periderm morphology of *F. splendens* was discussed by Scott (1932) and my findings are generally in agreement with hers. The stems have a roughened bark consisting of thick opaque, persistent periderm under the decurrent ridges and a translucent shreading periderm between the ridges (Fig. 6a). The phellem under the decurrent leaf bases consists of thin layers of elongate fibrous periderm

Fig. 2. Epidermis of stems of Fouquieriaceae.—a-b. *Fouquieria purpusii*.—a. Persistent thickened epidermis and papillate epidermal cells of young stem are shown.—b. Same as a, but with phellem forming under epidermal layer on left. (Henrickson 2142).—c-d. *Fouquieria shrevei*.—c. Shown are epidermal cells which occasionally undergo periclinal

divisions. Note thin cuticle.—d. Cross section of decurrent ridges of developing stem. Note deep furrows, thick bands of outer cortical fibers under ridges but not under furrows. (Henrickson 1875).—e. *Fouquieria campanulata*. Vertical section of outer stem cortex showing thick walled fibers of outer cortex. Note pits and epidermis (on left). (Henrickson 1742).—f–g. *Fouquieria formosa*.—f. Young stem covered with thick vestiture of uniseriate hairs.—g. Uniseriate epidermal hairs. (Henrickson 2101). a $\times 80$; b $\times 12$; c $\times 400$; d $\times 32$; e $\times 48$; f $\times 0.8$; g $\times 28$.

TABLE 1. *Distribution of bark characteristics in young and mature stems of Fouquieriaceae.*²

SPECIES	COLLECTION	STEM AGE, YEARS	TOTAL DIAMETER, mm	PITH DIAMETER, mm	XYLEM RADIUS, mm	BARK THICKNESS, mm	CAMBium TO STARCH SHEATH, THICKNESS, mm	CORTEX THICKNESS, mm	PERIDERM THICKNESS, RANGE, mm	CORTICAL SCLEREID NESTS, THICKNESS, mm
F. splendens	Henrickson 1830	1	6.7	1.3	0.2	2.6	0.13	2.4	0	0.1
F. splendens	Henrickson 2322	40	62	2.5	20	8	2.8	3.2	1.2-3.5	0
F. campanulata	Henrickson 1742	1	5.2	1.1	0.2	1.5	0.2	1.3	0	0.1
F. campanulata	Henrickson 1742	15	17	1.2	6.5	2	0.55	0.9	.5-1	0
F. shrevei	Henrickson 1825	1/10	8	1.4	0.5	2.2	0.3	2	0	0.2
F. shrevei	Henrickson 1825	15	32	0.5	9	4.6	0.9	2	1.5-2.2	0.3
F. burragei	Henrickson 2173	1	5.2	3	1.5	2.3	0.15	2.2	0	0.13
F. burragei	Henrickson 2173	25	46	3	18	5	1.8	2.3	0.9-1.4	0.8
F. diguetii	Thorne 32679	2	5.7	1.8	0.7	1.4	0.2	1.2	0	0.13
F. diguetii	Henrickson 2228	30	74	3	28	5	3	1.5	0.4-1.8	0.7
F. macdougalii	Henrickson 1560	1	4.5	2	0.2	2.8	0.1	0.7	0	0.07
F. macdougalii	Henrickson 2391	60	90	2	35	9.3	4.5	4.2	0.4-1.8	1.3
F. formosa	Henrickson 2157	1	4.3	1.4	0.25	1.2	0.13	1.5	0	0.14
F. formosa	Henrickson 2157	40	62	2.2	24	7	3.2	4.3	0.5	1.5
F. leonilae	Henrickson 2164	2	5.7	0.8	1.2	1.2	0.25	0.9	0	0.3
F. leonilae	Henrickson 2164	35	79	1	37	8.3	2.2	5.3	0.25	2
F. ochoterenae	Henrickson 2117	1	5.7	1.9	0.25	1.6	0.15	1.8	0	0.17
F. ochoterenae	Henrickson 2117	40	60		37	6.3	2.4	3.5	.4-2	1.8
F. purpusii	Henrickson 2142	1	4.3	0.7	0.65	1.3	0.25	1.4	0	0
F. purpusii	Henrickson 2142	50	1650	3	770	5.1	2	3.9	0-7	1.8
F. fasciculata	Henrickson 2071	2	5.3	1.1	0.25	1.6	0.15	1.6	0	0
F. fasciculata	Henrickson 2071	25	90	1	41	4.7	0.7	4.0	0-3	1.7
I. columnaris	Verity —	1	31	18	1.1	4.8	0.75	4	0	1.4
I. columnaris (central trunk)	Henrickson 2238	40	3250	30	110	16	4	15.5	0.1	6
I. columnaris	Henrickson 2313	1/5	1.5	0.35	0.08	0.5	0.02	0.5	0	0
I. columnaris (lateral stem)	Henrickson 1545	25	18	4	4	3	1.8	0.7	0.3-0.7	0.25

²The term bark refers to all portions outside the cambium and includes phloem, cortex and periderm. Measurements and distribution of characteristics are given for both mature stems and young stems, usually under one year of age. Symbols refer to the following: 0 not applicable; — absent or not developed; + present, moderately developed; ++ frequent, well-developed; n negative starch sheath; s sclereid nests associated with primary phloem fibers; ? not known.

40 to 170 μ thick alternating with thinner layers of radially compressed suberized cork cells 30–50 μ thick. As the overlying decurrent leaf bases are persistent, many alternating layers accumulate. The periderm formed in the ever expanding furrows consists of the same alternating layers of cells but the thickness of each layer is greatly increased (Fig. 5a). The fibrous periderm layers increase to 400 μ thick and the layers of suberized periderm cells increase to about 50–150 μ in thickness. The lumina of the outer suberized cells contain fatty compounds which are progressively less apparent in the inner suberized cells.

Fig. 3. Phylogenetic development of fouquieriaceous spine from ancestral types shown in a and b with raised decurrent ridges and horizontally oriented abscission layer. The fouquieriaceous spines are interpreted as cortex extensions developing with the long-shoot leaf resulting in formation of elongate abscission layer. In more specialized 'species,' lamina size is reduced as seen in e.

The waxy periderm of the furrows is ruptured as the stem increases in diameter and is constantly weathered away leaving ragged margins along the persistent ridges. Usually only 2 to 4 layers of the translucent periderm remain between the ridges which allows light to pass through to the underlying chlorenchymatous cortex.

FOUQUIERIA SHREVEI: The periderm of this species is unique in its "resinous" character (Fig. 1b). The decurrent leaf bases consist of a thick layer of woody cortical fibers under which accumulate several layers of fibrous cork cells with collapsed cellulose walls surrounded by a thin suberin layer (Fig. 5b). The periderm formed under the persistent ridges is of a woody texture. The periderm between the decurrent leaf bases consists of radial series of thin walled, partially collapsed, suberized cells which accumulate large quantities of a waxy, rust-brown, "resinous" material which in older stems has a texture of hard translucent plastic. As the periderm does not peel off or flake away, large quantities accumulate in which deep furrows eventually develop. When the "resinous" periderm is dry in older or dead stems it cracks like dry pine resin. Dry chips of the material stain with Sudan IV which

Fig. 4. Spine and periderm morphology.—a. *Fouquieria ochoteranae*. Developing long-shoot with obovate leaf blades and elongate petioles. Leaf portion of petiole exceeds subtending spine portion. (Henrickson 2117).—b. *Fouquieria diguetii*. Fascicles of secondary leaves at nodes are shown in two year old stem. Note spines.—c. *Fouquieria shrevei*. Longitudinal section through long shoot petiole. Note direct continuation of

cortical fibers between stem and spine, vascular bundle of leaf and subtending starch sheath (arrow). (Henrickson 1825).—d-e. *Fouquieria splendens*.—d. Cross section through base of long-shoot petiole. Cylinder of elongate fibers continuous with decurrent ridges with parenchymatous core forms spine. Above is parenchymatous leaf tissue with single broad trace. Abscission layer forms between fibrous spine and parenchymatous leaf tissue.—e. Elongate cortical fibers as seen in maceration. (Henrickson 2459).—f. *Fouquieria diguetii*. Paradermal peeling of phellem cells. (Henrickson 2228).—g. *Fouquieria macdougalii*. Alternating layers of thin walled suberized cork cells and fibrous cork cells are shown. Bottom thin walled layers are phellogen and phelloderm. Note cortical sclereids below. (Henrickson 2456).—h. *Fouquieria campanulata*. Periderm under decurrent ridge showing thickening of suberized and fibrous cork cell layers toward margin. (Henrickson 1742). a $\times 0.6$; b $\times 1$; c $\times 5$; d $\times 20$; e $\times 40$; f $\times 400$; g $\times 60$; h $\times 30$.

shows it is composed of waxes and suberized compounds. A layer of chlorenchymatous tissues develops in the outer cortex under the translucent periderm. Mucilaginous materials as well as chloroplasts were noted in the underlying phelloderm layers.

FOUQUIERIA MACDOUGALII, *F. DIGUETII*, *F. BURRAGEI*, *F. OCHOTERENAE*, *F. LEONILAE* and *F. FORMOSA*: The periderm of these six species is basically similar but the species differ in such features as degree of furrow development in the young long shoots and the retention of the decurrent ridges on mature stems. The furrows are well developed in *F. ochoterenae* (Fig. 7a) but much less so in other species (Fig. 6f). This particular characteristic will also vary within a species. The diameter of the long shoot stem also varies between and occasionally within a species. In larger stems the grey woody ridges become separated by broad areas of smooth waxy, usually bronze colored, translucent periderm to which the underlying chlorenchymatous cortex often imparts a greenish cast.

The periderm under the decurrent leaf bases consists of alternating layers of collapsed suberized cork cells and fibrous cork cells 25–75 μ thick (Fig. 5c). Between the ridges both layers increase in thickness to 100 and 150 μ respectively. The outer suberized cells collapse radially and often serve as an abscission layer as the outer layers of periderm peel off in thin papery sheets. Usually only the accumulation of 2 to 4 seasons remains on the stem. Widely spaced dot-like lenticels occur in the translucent periderm of all species. In the larger stems of *F. leonilae*, *F. macdougalii*, and *F. formosa* the decurrent ridges and nodes ultimately are eliminated and a smooth unbroken papery periderm is formed (Figs. 1f, 5d). In *F. diguetii*, *F. burragei* and *F. ochoterenae* the decurrent leaf bases are retained permanently becoming widely separated in older stems (Fig. 1d, 5c).

FOUQUIERIA FASCICULATA and *F. PURPUSII*: The succulent fouquierias are distinctive in the permanent retention of their epidermises over all the stem areas except the corky decurrent ridges (Figs. 1 g–h, 2 a–b). As the stems increase in size the papillate epidermis expands by anticlinal divisions and continues to secrete a cuticle which ultimately becomes 100 to 180 μ thick. The resulting trunk is smooth and shiny. The chlorenchymatous tissue of the outer cortex imparts a bright green color to the stems and trunks.

A phellogen develops under the decurrent leaf bases and forms a highly specialized, very hard periderm consisting of two types of cells. The suberized cells apparently have formed thickened secondary walls which contain pectin and variously unknown orange colored compounds. These form into broad bands 200 to 400 μ thick which alternate with irregular tangential bands of thick walled sclereids 100 to 500 μ thick. These cells are apparently derived from the fibrous cork cells characteristic of the woody fouquierias. The sclereid cells are somewhat compressed and range from 140 to 200 μ long and 50 to 80 μ wide. They have partially lignified walls 5 to 30 μ thick with numerous simple or ramiform pits.

The resultant periderm is very rigid. In *F. purpusii* broad wedge-shaped enations are formed as the width of the phellogen increases with the stem

(Figs. 1h, 5e). In older trunks of *F. fasciculata* a thin periderm consisting exclusively of suberized cells may form over limited areas.

IDRIA COLUMNARIS: The large trunk of this species is covered with a thin periderm composed exclusively of suberized phellogen cells. A phellogen forms under the epidermis and decurrent leaf bases after the first year and produces a thin layer of small compressed phellem cells $20\text{--}40\ \mu$ in diameter. As the phellem accumulates the epidermis and decurrent leaf bases and spines fall from the young central trunk. The phellem cells are constantly weathered away and only a thin layer of phellem cells $150\text{--}300\ \mu$ thick remains on the mature trunk (Fig. 5f). The periderm is yellowish in color but in some specimens the chlorenchymatous cortical tissue imparts a greenish cast to the trunk. The periderm of lateral stems of *Idria* also consists entirely of suberized phellem cells which may accumulate to a thickness of $600\ \mu$ or more (Fig. 10e).

Fig. 5. Diagrammatic representations of periderm showing changes in thickness of phellem cell layers under and between decurrent ridges in mature stems.—a. *Fouquieria campanulata* type. Both fibrous and suberized layers increase in thickness between ridges and are weathered away.—b. *Fouquieria shrevei* type. Cells under decurrent ridge have thicker walls and form narrower layers than those between ridges. All cells contain suberin.—c. *Fouquieria diguetii* type. Several years accumulation of phellem remains under decurrent ridges but only 2 to 5 years remains between ridges.—d. *Fouquieria formosa* type. Decurrent ridges fall away and continuous thin periderm is produced. Outer layers peel away in thin sheets.—e. *Fouquieria purpusii* type. Phellogen only produced under decurrent ridges. Elsewhere epidermis is persistent. Suberized cells have thickened walls, fibrous cells have lignified thickened walls and can be called sclereids.—f. *Idria columnaris* type. A thin layer of suberized cells is formed which continuously weathers away. ca. $\times 10$.

INNER STEM CORTEX.—The stem cortex inside the fibrous cortex, which forms the hard covering over the young stems, is specialized for the following: assimilation of food materials; support and protection; and storage of starch and water. The parenchymatous cells of the cortex directly under the translucent periderm contain chloroplasts and function in assimilation of food materials. Immediately below the assimilation tissue is a layer of sclereid nests which may give support to the cortex and in some cases may protect the inner succulent tissues from gnawing animals. The bulk of the cortex is parenchymatous and stores variable quantities of starch and water. Situated in the cortex is an anastomosing network of cells which differ anatomically and physiologically from the surrounding starch storing cortex cells. These water-storage cells or tissue, as designated by Scott (1932), rarely store starch and may function as an intercortical water and sugar transport system. The inner boundary of the cortex is marked by a starch sheath. Within the starch sheath lies the “pericycle” and the phloem, much of which is parenchymatous. The functional phloem occupies only a narrow band near the cambium. The conductive elements in the older phloem are mostly obliterated and lie in thin tangential bands surrounded by axial parenchyma. Several species possess primary phloem fibers and also may have associated phloem sclereids forming large nests. In the following section each portion of the cortex is described and discussed in greater detail. Table 1 shows the distribution of the characters mentioned.

CHLORENCHYMATOUS TISSUE.—In all the species of the Fouquieriaceae a layer of chlorenchymatous tissue occurs in the outermost parenchymatous cortex. The amount formed is directly dependent on the amount of light which passes through the translucent periderm or epidermis. In young stems the chlorenchymatous tissue is less developed under the decurrent stem ridges than in the areas covered by the translucent periderm. Therefore, the assimilatory tissue is arranged in an anastomosing pattern—a direct inverse stamp of the overlying opaque ridges (Fig. 6b). As the stems enlarge the assimilatory tissue increases in extent as the decurrent ridges are separated. The depth of the assimilatory tissue varies from 100 to 700 μ . The cells are rounded, 20 to 50 μ in diameter and generally are smaller than the starch storing cells of the inner cortex. The cellulose walls are sometimes slightly thickened. The chloroplasts, 6 to 10 μ in length, are flattened and lie along the walls of the cells. Oil globules often are contained within these cells. Scott (1932) and others have reported layers of collenchyma cells under the periderm. These were not observed in my material.

In the succulent fouquierias large oil droplets to 10 μ in diameter are common in the cells of the chlorenchymatous tissue. In most species, however, the oil globules are smaller and less frequent. Cuboidal crystals of calcium oxalate are also found in this tissue. Those cells containing crystals usually lack chloroplasts. The assimilatory tissue extends inward to the broad layers of sclereid nests and rarely beyond.

Fig. 6. Cortex structure.—a-c. *Fouquieria splendens*.—a. External features of stem with decurrent ridges separated by ragged translucent periderm.—b. Outer cortex directly under periderm showing effect of periderm translucence on chlorenchyma development.

Note dark lines around nodes.—c. Anastomosing network of water storage tissue (white) of inner cortex is shown. (Henrickson 2549).—d-e. *Fouquieria ochoterenae*.—d. In young stems sclereid nests form only under furrows, water storage tissue forms under sclereid nests. Note primary phloem fibers.—e. Xylem and scattered primary phloem fibers are shown. (Henrickson 2117).—f. *Fouquieria diguetii*. 1 year old stem stained with IKI. Note distribution of water-storage tissue, single leaf trace and formation of periderm layers. (Henrickson 2228). a-c $\times 1$; d-e $\times 67$; f $\times 8$.

CORTICAL SCLEREIDS.—Massive groups of tightly packed, thick-walled brachysclereids are present under the translucent periderm and are separated from it by the thin layer of chlorenchymatous tissue (Fig. 9 c,d,f). The sclereid nests are initially present only under the furrows separating the decurrent ridges (Fig. 6d; 7a) but will form a solid, firm layer as the stems enlarge and the area of opaque periderm is proportionally reduced. If the decurrent ridges are lost with age, the sclereid nests will be continuous around the stem (Fig. 9 a–b). The sclereid nests are not consistently present in the stems of *F. splendens* and *F. campanulata*. The largest nests of sclereids are found in the trunk of *Idria columnaris*, where they commonly are 4 mm in diameter and in older trunks may increase to 5 mm in tangential and radial thickness and 18 mm or more vertically. In the genus *Fouquieria* they rarely exceed 2 mm in diameter.

The sclereid nests continue to increase in size at the expense of the adjacent parenchyma cells. Also, new sclereid nests are continuously added outside earlier-formed sclereid nests as the stem expands in diameter (Fig. 9c). Sclereid cells are the same size as cortical parenchyma cells from which they are derived and are mostly isodiametric or slightly broadened tangentially (Fig. 8c). The latter are formed from parenchyma cells which have stretched tangentially as the stem expands in diameter. The thickened, lignified walls, which often exceed 15 to 20 μ in thickness, are traversed by ramifying pits about 2 μ in diameter. The lumina of the sclereids are small—about one-third or one-fourth the total diameter of the cells. The thickness of the bands of sclereids varies with the species and usually is greater than 1 mm. The lumina of the sclereids often contain cuboidal crystals (Fig. 8d) that are half as large as the whole sclereid. Infrequently, amorphous, druse-like crystals may also occur in the same cells. When two or more cuboidal crystals occur in the same sclereid they may be separated by a lignified septum. Occasionally crystals are incorporated into the thick wall of the sclereid—the lumen is separate from the crystal (Fig. 8d). Other cells containing crystals have collapsed, non-thickened cell walls. From the pattern of sclerification observed in relation to the crystals and the density of the crystals around the sclereid nests, one can conclude that the crystals were present in the cells prior to their sclerification.

In *Fouquieria fasciculata*, the sclereid nests in the young stem follow the pattern found in the woody fouquierias. *Fouquieria purpusii*, however, forms no outer cortical sclereids until after the first year. Because the sclereid nests are closely packed they function as a hard cylinder which may protect the thick succulent underlying tissue. In the central trunk of *Idria columnaris* the sclereid nests form a very thick cylinder even in the young stems (Fig. 9 d,f). In some young individuals from 1 to 3 meters tall, only a small amount of wood is accumulated near the cambium. Still, these individuals are firm and appear quite strong. The question arises, to what degree does this thick cylinder of sclereid nests support the trunk? I believe that sclereid-nest cylinders add greatly to the strength of the central trunk. The strength is, of course, basically dependent upon the turgidity of the surrounding parenchyma cells. When the turgidity is lost in the central trunk it often leans far to one side. The sclereid nests may also function in deterring gnaw-

ing rodents. Also, the presence of saponin compounds in the cortex (Rodríguez Hahn, 1954) would explain why rodents rarely damage the trunks.

WATER STORAGE TISSUE.—In the outer cortex directly under the sclereid nests is an anastomosing network of parenchymatous tissue conspicuously different from the surrounding cortex cells (Figs. 6c; 7b; 9c). Scott (1932) termed this the water-storage tissue, as it does not usually store starch. It apparently functions in transporting water and sugars to the developing leaves. The cells of the water-storage tissue generally are larger and have slightly thinner walls than the adjacent cortical cells (Fig. 8 b,e-f). Fre-

Fig. 7. Cross sections of stems of Fouquieriaceae.—a–b. *Fouquieria ochoterenae*. Young stems.—a. Section stained with phloroglucinol showing lignified outer cortical sclereid nests under furrows. Primary phloem fibers and xylem elements are also conspicuous.—b. Section stained with IKI showing starch-free water storage tissue under furrows. (Henrickson 2117).—c. *Fouquieria fasciculata*. Five year old stem stained with phloroglucinol to show heavy band of sclereids which develop between primary phloem fibers. Note lack of cortical sclereids. Water storage tissue in cortex can also be seen. (Henrickson 2071).—d. *Fouquieria macdougallii*. Older stem 6.5 mm in diameter stained with IKI showing starch in xylem rays and cortex. Note water-storage tissue and stratification in periderm under decurrent ridges. (Henrickson 2391). a–b $\times 8.5$; c $\times 9.2$; d $\times 9$.

quently, the size difference is quite conspicuous, but this is not consistently so. The average tangential diameter of both the water-storage cells and cortical parenchyma cells is given for all species in Table 1. In both tissues the cells are somewhat elongated tangentially, reflecting the tangential stretching which occurs as the stems expand.

Within the water-storage cells are globules of oil, 5 to 12 μ in diameter, which stain brightly with Sudan IV (Fig. 8a). Oil globules are not restricted to these water-storage cells but occur with less frequency throughout the cortex. Starch, which is commonly stored in the surrounding cortical cells, is conspicuously lacking in the water-storage tissue. In fresh stems the Fehling's test gives a deep copper-red precipitate indicating the presence of reducing substances; probably sugars which are lacking in the neighboring cortical cells (Jensen, 1962).

In young stems the water-storage tissue conforms to the pattern of the assimilation tissue and the sclereid tissue—an anastomosing network (Fig. 6c). The nodes of the network lie just above the nodes of the stem. As the stem enlarges, the water storage system also becomes more extensive. In most species it retains its anastomosing pattern but the strands broaden, becoming 3 to 5 mm broad tangentially while generally remaining less than 2 mm thick radially (Fig. 9 a,c). In other species and occasionally in the species characterized by the above pattern, the small strands seldom exceed 5 mm in tangential breadth (Fig. 9b).

In several species a peculiar anomaly of the water-storage tissue was observed in which cork cells similar to those produced in the periderm were formed by an internal cork meristem at the outer margin of the water-storage tissue. Oil droplets were prevalent in the suberized cork cells. In some cases the cork was restricted to the center of the water-storage cells. In all instances the corky tissue was not extensive in that it was found only in isolated regions of the cortex. It may be a response to wounding.

STARCH STORAGE CELLS.—The cortical cells between the sclereid nests and the starch sheath have cellulose walls 1 to 1.5 μ thick and function in the storage of both starch and water. These cortex cells are noticeably larger than the peripheral chlorenchyma cells. Initially the cells are isodiametric, but as the stem expands they are stretched tangentially. The cells divide by anticlinal vertical divisions as the stems increase in diameter. Occasionally as the cortex thickens, radially arranged inter-cortical meristematic plates produce tangentially oriented series of cells on both sides. These meristems are most apparent in the very thick cortex of *Idria columnaris*.

The quantity of starch in the cortex naturally varies throughout the season. Starch is most abundant after the rainy season during which the plants

Fig. 8. Anatomical features of stem cortex.—a-b. *Fouquieria ochoterenae*.—a. Water-storage tissue stained with Sudan IV showing large oil globules.—b. Section stained with IKI showing junction of water-storage tissue (above) and starch storing tissue (below). Note differences in cell sizes. (Henrickson 2117).—c. *Fouquieria macdougalii*. A typical sclereid nest of thick-walled brachysclereids is shown. (Henrickson 1560).—d. *Fouquieria formosa*. Crystals of calcium oxalate are commonly included within the crystals. (Henrickson 2157).—e-f. *Fouquieria purpusii*. Cortex of mature stem.—e. This section shows size difference between water-storage tissue and starch storing cortical cells. Note

widely spaced xylem segments and wedge-shaped obliterated phloem.—f. Water-storage tissue occurs in small packets in middle of cortex. Xylem below, sclereid nests above. (*Henrickson 2142*). a $\times 240$; b $\times 40$; c $\times 200$; d $\times 240$; e $\times 27$; f $\times 24$.

have been in full leaf. At this time the stem cortex is filled with starch. When excessive amounts are present, some starch grains even were noted in the water-storage tissue. The rest is stored in parenchyma cells throughout the cortex of the stems and roots, including the chlorenchyma and in the phloem and xylem axial and ray parenchyma as well as the pith. As the starch is hydrolyzed it is first taken from the water-storage tissues, then the surrounding cortical parenchyma of both the stem and root, the phloem, the pith and lastly from the xylem parenchyma. Consistently less starch was stored in the cortex of the roots than in the stems as the starch in the root cortex apparently is used before that of the stem.

The starch grains are variously shaped and range from 5 to 25 μ in diameter. The grains may be spherical, plate-like to lenticular. The variation in shapes is probably due to the degree of hydration. Crystals are common in the cortex. In addition to starch, quantities of water are stored in the cortex. As the water stored varies throughout the growing season, so does the volume of the cortex. During periods of extended drought the volume of the cortex is so reduced that horizontal lacunae form within the cortex and relieve the pressures caused by the shrinking cells (Fig. 9g). Cortical lacunae are not present in all species. They were particularly evident in *F. ochoterenae* and *F. shrevei*.

STARCH SHEATH.—The inner border of the cortex is defined by the starch sheath which is visible in almost all species. However, when starch is abundant in the cortex the sheath becomes difficult to distinguish. Often in such cases a cylinder of cells lacking starch is observed forming a pattern just inside the starch sheath. The cells constituting the starch sheath are not always connected end to end but form an uneven layer occasionally two cells thick in some areas. No Casparian strip was observed.

PHLOEM.—In most species primary phloem fibers, which often exceed 1000 μ in length, are found at the outer portions of the obliterated phloem in younger stems (Figs. 6 d-e, 7a). The phloem fibers have thick, lignified walls and frequently are found in groups of 5 to 15. As the stem enlarges, these groups of fibers are separated tangentially. In the young stems of *F. fasciculata* sclereids form between the pockets of primary phloem fibers and form a continuous cylinder of sclerenchyma (Fig. 7c). More sclerenchyma is added as the stem continues to increase in diameter. In *F. purpusii* an inner series of sclereid nests occasionally forms, but only in older stems. The structure of the phloem and phloem rays will be discussed in detail in another paper.

Fig. 9. Gross morphology of stems.—a. *Fouquieria formosa*. Mature stem stained with phloroglucinol. Note thick layer of cortical sclereids and continuous band of water-storage tissue (darker layer directly under sclereids). The sclereids are not under decurrent ridges. (Henrickson 2157).—b. *Fouquieria leonilae*. This section stained with phloroglucinol shows band of cortical sclereids and scattered arrangement of water-storage tissue. (Henrickson 2164).—c. *Fouquieria purpusii*. Section of cortex of mature trunk stained with IKI to show water-storage tissue. Note cuticle, large sclereid nests, phloem and widely separated segments of xylem.—d. *Idria columnaris*. Right half of picture stained with IKI to show distribution of water-storage tissue and distribution of starch.

Left half of picture stained with phloroglucinol shows cortical sclereid nests. (Henrickson 1545).—e. *Fouquieria splendens*. Mature stem showing water-storage tissue (dark patches) and thick periderm. Note development of heartwood. (Henrickson 2322).—f. *Idria columnaris*. Broad cortex of mature trunk ca. 30 cm in diameter. Note small accumulation of xylem and massive sclereid nests. (Henrickson 2346).—g. *Fouquieria ochoteranae*. Small stem 1 cm in diameter showing chambered pith and horizontal lacunae in cortex. (Henrickson 2117). a-b $\times 0.8$; c $\times 6$; d $\times 1.2$; e $\times 1$; f $\times 0.9$; g $\times 1.3$.

LATERAL BRANCH OF *IDRIA COLUMNARIS*.—The cortex of the lateral branch of *Idria* is distinctly different from other species of the family, for it lacks the anastomosing water-storage tissue and large quantities of sclerenchyma form in the inner cortex and outer phloem in older stems. A continuous cylinder of thick-walled cells occurs in the outer cortex. This layer, ca. 200 μ thick, is composed of 3–5 layers of cells that are 40 to 65 μ in diameter, 120 to 250 μ long, and have walls 4.5 to 7 μ thick. These cells compose the decurrent leaf bases and the areas separating them. Under the decurrent leaf bases a mass of elongate lignified fibrous cells occurs beneath the outer layer of cells. These cells range from 500 to 800 μ in length, are 25 to 35 μ in width, and extend from the cortex into the base of the spine (Fig. 10a). These lignified fibers occupy the center of the spine in contrast to the parenchyma found in the fouquierias. Inside the broad layer of thick-walled cortical cells under which the phellogen develops, lies a distinctive band of inner cortex cells (Fig. 10c). In the slender lateral long shoots of the seedlings, the inner portion of the cortex—6 cell layers and 100 to 125 μ in thickness—is composed of a homogeneous band of parenchyma cells with slightly thickened cellulose walls. In contrast to the outer cortical cells, these cells lack Sudan IV positive compounds. As the stem matures and the cortex expands to about 600 μ in thickness, patches of sclereids 200 to 300 μ thick form a broken ring in the outer cortex under the periderm (Fig. 10f). The outer parenchymatous cortex cells contain chloroplasts, whereas the inner cortical cells store quantities of starch and have progressively fewer chloroplasts. Crystals are common throughout the cortex. Of great interest, however, is the fact that no water-storage tissue develops in this relatively thin cortex. This is the only instance where the water-storage tissues are lacking in either stem or root.

Contiguous with the inner margin of the cortex is a nearly continuous cylinder of primary phloem fibers. These fibers, 1 to 1.5 mm long are of 15 to 20 μ in diameter, have lateral slit-like pits, 2 to 5 μ long. In the young stems the fibers form a continuous cylinder 1 to 3 cells in thickness (Fig. 10 c–g). In older stems the fibers are broken up into packets of 8 to 20 fibers and are separated by parenchyma cells which soon sclerify and form a solid ring of sclerenchymatous tissue. Parenchyma cells internal and external to the phloem fibers also sclerify and ultimately a band of sclerenchyma 50 to 100 μ in thickness forms (Fig. 10 f–g). The lignified sclereids surrounding the primary phloem fibers are large in diameter (25 to 50 μ) and have walls 8 to 12 μ thick.

Fig. 10. Structure of lateral stems of *Idria columnaris*.—a. Lateral stem bearing fascicles of short shoot leaves. Note lack of furrows.—b. Papillate epidermis of young stem. Note underlying layer of tannin filled cells.—c. Cross section of young lateral stem. Note outer layer of cortex consisting of suberized cells, and inner layer consisting of non-suberized parenchyma cells. A single line of primary phloem fibers can be seen within cortex.—d. Cross section of young lateral stem through decurrent ridge showing outer cortex of fibrous cells surrounding a central mass of fibers with lignified walls. These fibers extend into the base of the spine.—e. Cross section of periderm of lateral stem consisting exclusively of suberized cells. Note yearly increments.—f. Cross section of bark of large lateral branch. Xylem at base, periderm at top. Distinctive features include thin cortex consisting of outer band of sclereids with inner band of parenchymatous cortex (water-storage tissue is lacking); and an inner band of sclerenchyma develops around primary

phloem fibers, in both phloem rays and obliterated phloem.—g. Longitudinal section with xylem on left. Note thin lignified walls of scattered clusters of ray parenchyma and long primary fibers. (a–e—*Henrickson seedling*, W.2315; e–g—*Henrickson 1545*). a $\times 0.8$; b $\times 240$; c $\times 47$; d $\times 52$; e $\times 60$; f–g $\times 72$.

The phloem in the young stem is typical of the family. In older stems, however, the phloem-parenchyma cells become sclerified to within about 250 to 500 μ outside the cambium. The lignified sclereids range from 50 to 125 μ in diameter and have walls ranging from 4 to 15 μ in thickness. Some phloem-parenchyma cells have thin, lignified walls (Fig. 10g). Many of the sclereids are elongated tangentially and crystals are commonly present in their lumina. This is the only instance of sclerification of axial and ray phloem parenchyma in the stems of the Fouquieriaceae, although it does occur in the root phloem of several species.

The detailed morphology of the phloem and xylem will be covered in a later work. It is sufficient to mention at this time that the xylem appears to show particular adaptations for increased conductivity to compensate for the reduced succulence of the cortex.

The pith of the lateral branches of *Idria* varies from 0.5 to 1.2 mm in diameter. The cells, formed from the ground meristem and arranged in vertical rows, are flattened vertically and range from 20 to 45 μ in horizontal diameter. In older stems, their slightly thickened walls are lignified and form a solid hard pith. Cuboidal and druse-like crystals may also accumulate in certain cells.

The central trunk of *Idria columnaris* is distinctive in many ways. A primary thickening meristem surrounds the apical meristem which results in the formation of a greatly expanded stem (Humphrey, 1935). The pith ranges from 2 to 3 cm in diameter. The outer bark (phloem and cortex) is initially about 5 mm in thickness but increases to about 20 mm in the mature trunk. The xylem of the central stem enlarges markedly due to an extensive proliferation of xylem parenchyma. This also occurs in a similar manner in *Fouquieria fasciculata* and *F. purpusii*. The structure of the pachycaulous central trunk will be dealt with in greater detail in a later paper.

ROOT STRUCTURE

Tissues in roots of Fouquieriaceae are similar to those in stems. However, because nodes and internodes are lacking in roots, tissues are not arranged into definite anastomosing patterns. The morphology of the root periderm, cortex and phloem are discussed in detail in the following paragraphs. Certain interspecific anatomical differences are given in Table 2.

The primary root, 200 to 500 μ in diameter, consists of an epidermis, a thickened cortex, and a narrow endodermis surrounding a thin pericycle and the xylem and phloem in a diarch arrangement. As the root matures, a cork cambium develops in the cortex and produces a layer of periderm. The parenchyma cells of the cortex within the periderm will divide and ultimately differentiate into sclereids, or parenchymatous storage tissue. The endodermis is not distinguishable in the older roots. In general, the maturation and development of the roots is like that of typical dicotyledons. The bark (including cortex) in mature roots 4 to 5 cm in diameter is quite succulent and ranges from 5 to 9 mm in thickness from the cambium to the outer surface. The extensive shallow root system functions in storage of food reserves and water as well as support and conductivity.

ROOT PERIDERM.—The root periderm, which begins as a continuous band, consists of a poorly defined, inner, thin layer of phelloderm consisting of 3 to 7 layers of non-suberized cells and a broad outer layer of suberized phellem which may become quite extensive in older roots (Fig. 11e). In contrast to the stem, only one kind of phellem cell is produced by the root phellogen—the suberized cell with its thin suberin impregnated walls. The fibrous, thick-walled cells of the stem are lacking in the root periderm (Fig. 11f).

As in the stem phellem, the quantity of fats and/or oils which accumulates in the lumina of the phellem cells varies within a season's increment. These substances are more prevalent in the first-formed cell layers of a seasonal increment and become progressively less abundant in the later-formed cell layers. Tannins also appear to be present in the phellem cells. Between 6 and 15 layers of phellem cells are produced per seasonal increment.

The suberized cells are basically isodiametric, about 30 to 80 μ broad, but due to radial pressures exerted by the growing stems and the soil, they compress radially and form tablet-shaped cells (Fig. 11f). The cells are roughly hexagonal in tangential outline and in some species may be slightly elongated parallel to the axis.

The phellem cells of successive increments are arranged in distinct radial series (Fig. 11f) and as in the stem, the phellogen probably remains active for many seasons.

The outer cell layers of a seasonal increment usually will collapse completely and form a thin impervious layer. The inner, later-formed cells of the increment may either collapse completely and add to the outer layer or remain only partially collapsed and ultimately serve as a type of abscission layer which is broken as the roots expand in diameter. In the latter case, the bark will consist of many thin, paper-like layers which will easily slough off upon handling. This is the case in the younger roots of *F. campanulata* and *F. splendens*. In most other species, however, there are fewer, thicker layers of impervious periderm which overlie one to three seasons' accumulation of partially collapsed cells. The periderm in both cases rarely exceeds 3 mm in thickness. The outer periderm is usually a dark reddish-brown color due to the accumulation of tannins and/or the oxidation of materials in the outer cells. In mature roots of *F. macdougalii* and young roots of *Idria columnaris* a very thick, soft periderm is formed as large quantities of partially collapsed cells accumulate under the outer impervious layer (Fig. 11e). This bark was as much as 3.8 mm thick in the roots of *F. macdougalii*.

ROOT CORTEX.—The thickened root cortex contains three types of cells: sclereids, water storage and starch storage cells. Their arrangement is less precise than in the stems and occasionally it is difficult to distinguish between the two types of parenchyma cells. In young roots, the most conspicuous portion of the cortex is the thick central band of sclerenchyma cells. Only a few rows of parenchyma cells occur on both sides of the sclerenchyma cells. As the root cortex enlarges, the parenchyma cells on the inside form the bulk of the parenchymatous cortex. In the mature root the

first-formed sclereid nests lie near the periderm (Fig. 11d). Occasionally, however, parenchyma cells outside the sclereid nests also divide periclinally and some of the first-formed sclereid nests will remain in the middle of the cortex (Fig. 11b). The sclereids have thick, lignified secondary walls with simple, ramiform pits. The sclereid nests increase in size by the addition of adjacent parenchyma cells and, as in the stems, crystals commonly are incorporated into the sclereid nests. The outer sclerenchyma cells are often broader tangentially than radially, reflecting the shape of the parenchyma cells from which they were derived.

In some species the first-formed sclereid nests do not increase greatly in size which results in a scattered distribution of sclereid nests, e.g., *F. campanulata* (Fig. 11 a-b). In other species a continuous layer is formed under the periderm. The outer sclereid nests may become quite large. In *F. leonilae* sclereid nests 0.6×2.3 mm were observed. The outer sclereid nests in the roots of *Idria columnaris* often exceeded 4 mm in tangential diameter. In those species with a thick cortex, new sclereid nests may form in the middle of the cortex. More frequently, however, inner sclereid nests form near or in the obliterated phloem, where cortical parenchyma, phloem ray parenchyma and vertical phloem parenchyma may undergo sclerification (Fig. 11c). The segments of vertical phloem parenchyma are septate and each undergoes sclerification independently of the other. Again, crystals are commonly present in these sclereids. The inner sclereid nests were observed in mature roots of *F. diguetii*, *F. macdougallii*, *F. leonilae*, and *F. ochoteranae* and *Idria columnaris*. In *F. splendens*, *F. campanulata*, *F. shrevei*, *F. purpusii* and *F. fasciculata* only the original sclereid layer exists in the mature root. No material was available of the roots of *F. formosa* and *F. burragei*. In some species three layers of sclereids were observed. An outer thick layer, a thinner layer in the middle of the cortex and an inner layer partially associated with the phloem.

Significantly, distribution of the sclereid nests is not necessarily constant throughout the roots of a species. For example, in *F. campanulata*, some sections showed a complete cylinder of sclereids whereas other sections were devoid of sclereid nests (Fig. 11 a-b). Again, primary phloem fibers were observed in only a single specimen of one species. Whether they are not common or simply were not observed in the other species due to chance sampling is not known.

Water-storage tissue is also present in the roots of all species. The constituent cells are identical to those of the stem and generally are larger than the neighboring, starch-storing cells. In the young roots their presence is often difficult to detect but as the root enlarges they form a continuous or broken layer under, or less frequently above, the sclereid nests (Fig. 11e). Oil droplets are present in the water storage cells as in the stems, but the quantity of oils in this tissue and in the adjacent starch-storing tissue is generally greater than in the stems. In a small root of *F. purpusii* it was noted

Fig. 11. Root structure.—a-b. *Fouquieria campanulata*.—a. Longitudinal section of young root, xylem at base, periderm above. This section lacks cortical sclereids.—b. Cross section of same root as in a. Note cortical sclereids. (Henrickson 1742).—c. *Fouquieria*

macdougallii. Cross section of old root showing developing of sclereids in vertical parenchyma of obliterated phloem. (Henrickson 2356).—d. *Fouquieria diguetii*. Cross section of bark of mature root stained with IKI showing thick periderm, scattered cortical sclereid nests and phloem. Water-storage tissue is not discernible. (Henrickson 2391).—e. *Fouquieria shrevei*. Cross section of mature root cortex. Note thick periderm, sclereid nests and distinctive water-storage tissue. (Henrickson 1825).—f. *Fouquieria macdougallii*. Cross section of periderm showing radial series of suberized cells. (Henrickson 2356). a $\times 22$; b-c $\times 28$; d $\times 4$; e $\times 5.5$; f $\times 60$.

that bark tissue had formed in water-storage cells in certain portions of the root cortex. This tissue was similar to that found occasionally in the stems and definitely was a response to wounding.

The remaining cortical cells around the sclereid nests and water-storage cells are the starch-storing cells. In addition to starch, they often contain large and/or small oil globules and crystals of calcium oxalate. The crystals are more common near the sclereid nests and in and around the obliterated phloem. The quantity of starch stored in the roots appears less than the

TABLE 2. *Distribution of certain bark characteristics in young and mature roots of Fouquieriaceae.*³

SPECIES	COLLECTION		TOTAL DIAMETER, mm	XYLEM DIAMETER, mm	BARK THICKNESS, mm	PERIDERM THICKNESS, mm	OUTER SCLEREID LAYER, THICKNESS, mm	INNER SCLEREID LAYER, THICKNESS, mm
<i>F. splendens</i>	Henrickson	2322	65	47	9	2	0.7	—
<i>F. campanulata</i>	Henrickson	1742	3.5	1.6	1	1.2	0.2	—
<i>F. campanulata</i>	Henrickson	1742	12	4	4	0.5	—	0.3-0.7
<i>F. campanulata</i>	Henrickson	1742	32	27	5	0.5	0.1	—
<i>F. shrevei</i>	Henrickson	1825	4	2	1	0.5	0.3	—
<i>F. shrevei</i>	Henrickson	1825	38	28	5	1	0.3-0.5	—
<i>F. diguetii</i>	Henrickson	2391	70	60	5.7	0.4	1.2	0.5
<i>F. macedougalii</i>	Henrickson	2391	10	8	1.1	0.3	0.06	—
<i>F. macedougalii</i>	Henrickson	2356	65	47	9	3.8	0.6	0.2
<i>F. leonilae</i>	Henrickson	2164	7.5	4.5	1.5	0.2	0.15	—
<i>F. leonilae</i>	Henrickson	2164	40	30	5	0.5	0.6	0.4
<i>F. ochoterena</i>	Henrickson	2117	14	11	1.5	0.8	0.2-0.35	—
<i>F. ochoterena</i>	Henrickson	2117	70	61	4.6	1.4	0.3-0.6	0.3-0.4
<i>F. purpusii</i>	Henrickson	2142	7	5.5	0.8	0.5	0.15	—
<i>F. purpusii</i>	Henrickson	2142	19	14	2.5	0.3	0.5	—
<i>F. purpusii</i>	Henrickson	2142	50	38	5.8	1.5	.4-.8	0.3-0.7
<i>I. columnaris</i>	Henrickson	1545	4.2	1.8	1.2	0.7	0.2	0.05
<i>I. columnaris</i>	Henrickson	1545	11	3.6	3.7	2	0.6	—
<i>I. columnaris</i>	Verity		80	64	8	1.5	1.5	—

³ Not all species are represented. Symbols refer to the following: — absent, not applicable; + present.

quantity stored in the stem cortex of the same plant, for perhaps the starch is used-up first in the root. In all cases concentration of starch proved much higher in the xylem parenchyma than in the root cortex.

The phloem of roots is similar to that of stems. It also occurs in wedge shaped segments. The only exceptional difference is the sclerification of the parenchyma cells around and between the obliterated phloem in some species (Fig. 11c). The outer phloem rays dilate tangentially first by tangential stretching and later by vertical anticlinal divisions of the phloem

CORTEX THICKNESS, mm	PHLOEM THICKNESS, mm	SCLERENCHYMA IN OBLITERATED PHLOEM, PRESENCE	TANGENTIAL DIAMETER WATER STORAGE CELLS, μ	TANGENTIAL DIAMETER STARCH STORAGE CELLS, μ	PHLOEM CELLS, LENGTH, μ	PHLOEM CELLS, WIDTH, μ
2.7	4.5	—	100-160	70-80	110-120	60-110
0.6	0.3	—	40-80	70-120	90-110	40-60
2.5	0.8	—	—	60-100	120-150	80-100
3.5	1	—	100-120	80-120	120-210	30-40
0.25	0.15	—	—	50-80	80-130	70-120
3	0.9	—	100-120	50-75	100-120	80-110
3.5	2	—	120-160	70-90	100-125	70-80
0.45	0.25	—	60-80	50-60	90-150	40-50
1.8	2.9	+	70-150	40-90	70-120	50-70
0.5	0.8	+	40-60	60-80	120-150	45-60
2	2.5	+	80-110	80-100	120-160	80-100
0.4	0.25	—	—	30-50	130-230	40-50
2.3	1.1	+	80-110	50-80	80-140	40-50
0.25	0.1	—	—	40-60	120-150	50-60
1.9	0.5	—	100-130	70-90	150-200	70-80
2.5	1.7	—	80-150	70-120	120-190	60-100
0.4	0.2	+	—	—	80-140	50-90
0.9	0.7	—	80-110	60-75	80-120	70-80
3.7	2.8	—	100-140	50-60	60-110	45-60

ray cells or occasionally by the adjacent phloem parenchyma. Occasionally the vertical phloem parenchyma separating the layers of obliterated phloem divides periclinally, further separating the segments of obliterated phloem.

SUMMARY

The anatomy and morphology of the stems and roots of the twelve known species of the Fouquieriaceae has been described and discussed in detail. Among the distinctive anatomical characteristics of the family are: the heteroblastic organization of stem shoots; the long fibrous decurrent leaf bases and spines which develop in association with the leaves; the layered periderm of two cell types, suberized and fibrous; the retention of the epidermis over part of the stems in the succulent fouquierias; the structure of the cortex which consists of an outer thin chlorenchymatous layer, a thick layer of sclereid nests, and a thick inner layer of starch storage tissue through which permeates an anastomosing network of water storage tissue. The distinctive anatomy of the lateral stems of *Idria* is also discussed. The anatomy and morphology of the vascular system and the origin of the succulent xylem tissue will be discussed in a later work.

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