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WOOD ANATOMY OF FOUQUIERIACEAE IN RELATION TO HABIT, ECOLOGY, AND SYSTEMATICS; NATURE OF MERISTEMS IN WOOD AND BARK

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ABSTRACT

Qualitative and quantitative data are presented for wood of all species of Fouquieriaceae, the samples selected so as to cover important variables with respect to organography and age. Wood contains fiber-tracheids (plus a few vasicentric tracheids). Diffuse axial parenchyma is mostly grouped as diffuse-in-aggregates or diffuse clusters (new term), with transitions to pervasive axial parenchyma in some species. Rays are Heterogeneous Type II. These wood features are relatively unspecialized and are consistent with placement of the family in Ericales s.l. as defined in recent DNA-based cladograms. Xeromorphic wood in nonsucculent species occurs only in *Fouquieria shrevei*; the lateral branches of *F. columnaris* also have xeromorphic wood. If the preceding two instances and proliferated parenchyma of the three succulent species (*F. columnaris*, *F. fasciculata*, and *F. purpusii*) are excluded from quantitative studies, wood of Fouquieriaceae is rather mesomorphic, despite the habitats occupied by the family. This paradox is explained by the very sensitive drought deciduousness. Also, the succulent species produce water-storage parenchyma by means of expansion of rays and axial parenchyma bands. Details of these two types of meristems, as well as three other types of meristems within wood (not including vascular cambium) and four bark meristems (other than phellogen) are described; five of these meristems are newly reported for the family. Wood data permit recognition of both the three succulent and eight nonsucculent species within a single genus, in agreement with Henrickson (1972), but few wood features offer species characters. Most wood features, including the abundant reaction wood, are closely related to habit, organography, and ecology.

Key words: cambial variants, diffuse clustered parenchyma, ecological wood anatomy, Ericales, *Idria*, meristems, ocotillo, parenchyma expansion, reaction wood.

INTRODUCTION

Little published work on wood of Fouquieriaceae exists (Gregory 1994), despite the inherent interest of this distinctive family, which exhibits such diverse habits in a variety of dry habitats of Mexico and the southwestern United States (Henrickson 1969a). Data on wood anatomy was included in the thesis of Henrickson (1968), but only a portion of this fine work has been published. The plans of stems as seen in transverse sections in gross aspect have been well figured by Henrickson (1969b, 1972) and need not be repeated here. Henrickson's thesis (1968) presented both quantitative and qualitative data on the secondary xylem of the family. The wood and bark sections studied here are preparations by the author that represent new techniques, including paraffin sectioning to reveal delicate cells intermixed with sclerenchyma (Carlquist 1982), sensitive counterstaining, and scanning electron microscopy (SEM). The data presented supplement Henrickson's (1968) work, which is cited in all key respects here.

The habits of the 11 species of the sole genus now recognized (Henrickson 1972; Schultheis and Baldwin 1999) have been well figured by Henrickson (1969a). The following brief descriptions are offered to sum-

marize the surprising diversity within the family and to introduce the taxonomy of the family (data derived from Henrickson 1972):

Fouquieria subgenus *Idria*:

F. columnaris (Kellogg) Kellogg ex Curran: trees to 23 (mostly 4–16) m with an usually unbranched trunk tapering upwards, bearing numerous slender horizontal lateral branches.

Fouquieria subgenus *Bronnia*:

F. fasciculata (Willd. ex Roem. & Schult.) Nash: shrubs or small trees 2–5 m tall with 1–3 succulent trunks, branches slender, upright to diagonal.

F. purpusii T. S. Brandegee: shrubs or small trees to 5 m tall, with 1–5 tapering succulent trunks, branches slender, upright to diagonal.

Fouquieria subgenus *Fouquieria*

section *Fouquieria*:

F. burragei Rose: shrub 1–3 m tall with 2–5 twisted trunks, each bearing several branches terminating in moderately thick stems.

F. diguetii (van Tiegh.) I. M. Johnston: shrubs to 8, mostly 2–4 m tall, with a basal trunk bearing several ascending stems with divergent branches terminating in relatively thick stems.

F. formosa HBK.: trees 3–8 m tall with 1–2 basal trunks, the larger stems usually dichotomously branched and bearing numerous erect to spreading rather thick stems.

F. leonilae F. Miranda: small sparsely branched trees, 1–7, mostly 3–4 m tall, with 1–5 trunks to 2–3 m tall bearing erect to spreading branches, the youngest slender.

F. macdougalii Nash: small trees mostly 2–6 m tall with 1–4 basal trunks, much branched above, the youngest moderately slender.

F. ochoteranae F. Miranda: small trees 4–8 m tall, with 1–2 trunks 1–2 m. high, upper stems widely divergent, terminating in relatively thick stems.

section *Ocotilla*

F. shrevei I. M. Johnston: shrubs 1–2.5 m tall, the short trunk (to 15 cm tall) bearing 15–40 (rarely more) diagonal to erect moderately thick stems.

F. splendens Engelm. in Wisliz.: shrubs or small trees 2–5 m or taller, branched from near the base into 6–100 upright to (mostly) diagonal relatively thick stems (with 2–12 cm basal diameter).

Photographs convey more clearly than descriptions the distinctive forms assumed by the respective species. The habit of *F. columnaris* is easily distinguished from those of the two species of subgenus *Bronnia*, although all three may be described as succulent trees because of the thick stems (main trunks) largely composed of parenchyma. *Fouquieria columnaris* is noteworthy for differentiation between the thick main trunk and the slender horizontal lateral branches. The trees of subgenus *Fouquieria* section *Fouquieria* taper much less and do not have the parenchyma proliferation of subgenera *Bronnia* and *Idria*. Within section *Fouquieria*, however, *F. burragei* and *F. diguetii* are characteristically shrubby rather than trees. The two species of section *Ocotilla* are highly distinctive in their numerous branches that diverge from near the base of the plant; *F. shrevei* is like a somewhat dwarfed version of *F. splendens*, although the range within *F. splendens* is considerable, and three subspecies of *F. splendens* were recognized by Henrickson (1972). The nature of wood (and bark) is related to organography in part, and correlations are offered below. In dicotyledons as a whole, root wood differs from that of stem wood (Patel 1956), and Fouquieriaceae agree in that respect. The wood of thick lower stems of the succulent species has been analyzed separately from upper stems of those species. In addition, the wood of the horizontal lateral branches of *F. columnaris* is distinctive.

The relationship between wood anatomy of *Fouquieria* and ecology is not a direct one because of the presence of water-storage mechanisms, drought deciduousness of leaves, and very effective transpiration limitation by the stem periderm. All species have cortical water storage tissue, and the three succulent species have water storage within proliferated parenchyma of the secondary xylem. All species have leaves that wither during drought and are initiated rapidly after sufficient rainfall occurrences; these events can happen more than once per year. Therefore, the quantitative data on secondary xylem of Fouquieriaceae should not be expected to parallel trends reported in desert shrubs that do not have water storage mechanisms plus drought deciduousness (e.g., Carlquist 1975, p. 206). Humphrey (1935) is of the opinion that species of the family are not true succulents, an idea

supported only in that Fouquieriaceae differ from most other succulents in distribution and kinds of water storage tissue. A three-dimensional anastomosing network of water-storage parenchyma strands has been identified in the cortex of *F. splendens* stems (Scott 1932; Nedoff et al. 1985); similar tissue occurs in the cortex of the other species (Henrickson 1969c). The periderm is impervious to both water and carbon dioxide, and thus recycling of carbon dioxide is required (Nedoff et al. 1985). The so-called succulent species (*F. columnaris*, *F. fasciculata*, *F. purpusii*) not only have more axial and ray parenchyma than the species of subgenus *Fouquieria*, they have proliferation of the ray and axial parenchyma tissue (Henrickson 1969b). Although starch storage can be found in these tissues, the large cell size of this parenchyma and the relative paucity of starch in these cells suggests water storage is the primary function of these tissues. Water storage of Fouquieriaceae differs in pattern from that of Cactaceae, Crassulaceae, etc. However, commentary is appropriate on the relationship of water storage tissue to degree of xylem xeromorphy and ontogenetic mechanisms that produce that tissue in Fouquieriaceae.

Systematic relationships within the family were analyzed by means of pre-cladistic numerical methods by Henrickson (1972) and with cladistic methods based on molecular data by Schultheis and Baldwin (1999). At least some features of systematic significance occur in wood of Fouquieriaceae. Wood of the family can be compared to various placements of the family. Among the orders to which Fouquieriaceae have been most frequently assigned in more recent years are Ebenales, Ericales, Polemoniales, and Tamaricales, although earlier workers placed them with tubiflorous families (see Goldberg 1986, Table I; Thorne 1992). The discovery of iridoids in Fouquieriaceae by Dahlgren et al. (1976) led to assignment of the family to Ericales, and recent DNA data also affirms that placement. However, the cladograms based on DNA data have expanded Ericales so as to include Ebenales and Polemoniales in a new Ericales sensu lato (Morton et al. 1996; Prather et al. 2000; Soltis et al. 2000), although Tamaricaceae and allied families are assigned by recent workers to an expanded Caryophyllales (Soltis 2000).

Currently underappreciated are the kinds of meristems that occur in stems of Fouquieriaceae (no fewer than five in wood and four in bark, excluding vascular cambium and phellogen, are reported below). Therefore, a special effort has been made to describe the location and origin of these meristems and the nature and function of their products. Although Fouquieriaceae are unusual in the meristems within their wood and bark, some of these may remain to be reported in other dicotyledons, so attention to them may lead to a

better understanding of cambial variants and bark development in dicotyledons as a whole.

MATERIALS AND METHODS

Samples judged to show mature patterns were available for all species, although not all the plants sampled were of adult size. The sources of most of the samples were dried wood portions collected from plants of optimal size collected in the field by James S. Henrickson (see listing in Table 1). These wood portions are located in the wood collection of the Rancho Santa Ana Botanic Garden (RSAw). The voucher herbarium specimens documenting these wood samples, together with collection data, are given in Henrickson (1972). For the Henrickson samples, the usual sliding microtome sections proved adequate. Sections were stained with a safranin-fast green combination. Some unstained radial sections of *F. leonilae* were dried between clean slides, sputter coated with gold, and observed with an ISI WB-6 SEM at Rancho Santa Ana Botanic Garden.

Because of the admixture of soft and hard tissues in stems of subgenera *Bronnia* and *Idria*, an alternative sectioning method was used (Carlquist 1982). This method was also used on stems of *F. macdougallii*, because the tapering nature of stems in that species suggested some succulence in the stem or cortex. Histological and meristematic details are well rendered by the method cited. For the three succulent species and for *F. macdougallii*, portions were preserved in 50% aqueous ethanol. Sections were stained in a safranin-fast green combination corresponding to Foster's modification of Northen's tannic acid-ferric chloride method (Johansen 1940).

Material of *F. macdougallii* was collected 14 km S of Nacozari, Sonora, Mexico (Carlquist 8003, RSA). A relatively mature specimen (1.3 m in height) of *F. columnaris* was available from an area of Rancho Santa Ana Botanic Garden withdrawn from cultivation to make way for construction. Root material of this species came from a seedling purchased from Arid Lands Greenhouses, Tucson, Arizona. The specimen of *F. fasciculata* with a lower main stem 6 cm in diameter was purchased from Abbey Gardens (1995, at which time the Gardens were located in Carpinteria, California). The specimen of *F. purpusii* was given to me by Dr. Mark Olson and cultivated by me until the stem base was 6 cm in diameter, at which time the plant was harvested.

For all stem and root xylem samples, macerations were prepared with Jeffrey's Fluid (Johansen 1940) and stained with safranin. Macerations proved essential for determining lengths of vessel elements and fiber-tracheids, as well as for distinguishing vascentric tracheids from vessel elements and fiber-tracheids.

Measurements of vessel diameter are based on lumen diameter as seen in transection (for vessels oval in outline, long and short chords were averaged) because lumen diameter is of direct significance to conductive physiology. Vessel diameter including the wall was measured by Henrickson (1968), but lumen diameter plus twice the vessel wall thickness should equal outside vessel diameter. Henrickson's (1968) quantitative wood data are compared with mine in the discussions below. Terminology that of the IAWA Committee on Nomenclature (1964), except for the terms pervasive axial parenchyma, ray-adjacent axial parenchyma, and vascentric tracheid, which are in accordance with Carlquist (1988). The sequence of the species in Table 1 is the same as given above, and represents the sequence of subgenera and sections of Schultheis and Baldwin (2000), with species arranged alphabetically within each infrageneric group.

WOOD ANATOMY

Growth Rings

Growth rings occur in all Fouquieriaceae sampled, but in some species they are more pronounced, whereas in most they are very weakly demarcated. Perceptible growth rings are illustrated here for *F. splendens* (Fig. 1, 3), *F. formosa* (Fig. 5), *F. shrevei* (Fig. 8), *F. ochoteranae* (Fig. 11), *F. burragei* (Fig. 13), *F. diguetii* (Fig. 15), *F. columnaris* (Fig. 28), *F. fasciculata* (Fig. 39), and *F. purpusii* (Fig. 44). The most important criterion for recognizing growth rings is greater lumen diameter of vessels in earlywood (Fig. 1, 3, 4, 11, 15) or smaller diameter and/or greater abundance of latewood vessels (Fig. 8, 11, 28). In addition, axial parenchyma may appear more abundant in earlywood (Fig. 32, 39) or in latewood (Fig. 33, 34). Studies of wood of a particular plant over a period of seasons for which the moisture availability fluctuations are known are highly desirable to elucidate the role of parenchyma abundance in relation to growth ring formation.

Quantitative Vessel Element Features

The mean number of vessels per group (Table 1, column 1) shows a mean of 2.99 for subgenus *Idria*, 2.19 for subgenus *Bronnia*, and 2.32 for subgenus *Fouquieria*. The differences among these are not significant, but the relatively high figures in upper stems of *F. columnaris* (3.90) and *F. fasciculata* (3.35) are notable. The significance of vessel grouping in *Fouquieria* will be discussed below in connection with ecology.

Vessel lumen diameter (Table 1, column 2) confirms trends found by Henrickson (1968) with respect to differences between roots and stems in the nonsucculent species (see *F. splendens* in Table 1). To be sure, find-

Table 1. Wood features of Fouquieriaceae.

Species	Collection	Portion	1 VG	2 VD	3 VM	4 VL	5 VW	6 VP	7 FL	8 FW	9 FP	10 MH	11 MW	12 UH	13 FV	14 ME
Subgenus <i>Idria</i>																
<i>F. columnaris</i>	cult.	root	1.54	30	115	367	2.0	5	820	2.0	5	1855	2.3	312	2.23	95
	cult.	OL stem	4.47	48	33	879	2.6	9	777	6.0	9	1374	4.3	334	1.97	1279
	cult.	OU stem	3.90	32	51	468	2.5	8	1603	2.5	8	943	2.9	307	3.43	294
	cult.	H branch	2.05	20	206	448	1.5	5	777	5.0	5	1476	2.7	277	1.73	43
Subgenus <i>Bronnia</i>																
<i>F. fasciculata</i>	cult.	root	1.56	21	164	462	2.5	6	905	4.8	3	990	2.4	232	1.96	87
	cult.	OL stem	2.19	39	23	368	3.0	6–10	925	4.6	5	>1000	>10	103	2.51	624
	cult.	U stem	3.35	32	200	370	2.3	5	775	4.0	5	1326	>10	295	1.93	59
<i>F. purpusii</i>	<i>H. 2142</i>	root	1.26	40	99	542	2.0	8	1649	3.0	8	573	3.4	99	3.04	19
	cult.	root	1.90	38	75	426	2.0	5	771	2.8	6	648	2.3	282	1.81	215
	cult.	OL stem	2.80	45	46	393	2.0	7	1295	3.0	7	>1000	>10	172	3.30	384
cult.	U stem	2.30	35	74	403	2.4	7	1201	2.4	5	>1000	>10	222	2.98	191	
Subgenus <i>Fouquieria</i>																
<i>F. burragei</i>	<i>H. 2973</i>	stem	2.13	67	64	514	2.3	6	1456	5.0	8	997	3.3	101	2.83	538
<i>F. diguetii</i>	<i>H. 2228</i>	stem	2.32	70	55	556	2.5	8	1808	5.0	8	536	4.1	190	3.25	708
<i>F. formosa</i>	<i>H. 2105</i>	stem	1.85	71	34	443	2.6	7	1787	3.0	8	783	3.1	177	4.03	925
<i>F. leonilae</i>	<i>H. 2164</i>	stem	1.45	60	60	445	2.5	7	883	2.9	6	883	2.9	198	3.23	445
<i>F. macdougalii</i>	<i>C. 8003</i>	stem	3.00	46	156	284	2.3	5	931	2.8	5	548	4.6	138	3.28	284
<i>F. ochoteranae</i>	<i>H. 2114</i>	stem	2.79	49	78	457	1.8	7	1404	4.3	7	613	4.8	192	3.07	287
<i>F. shrevei</i>	<i>H. 1825</i>	stem	1.70	25	247	249	2.0	6	900	4.5	5	732	5.1	117	3.61	25
<i>F. splendens</i>	<i>H. 2587</i>	root	2.72	52	65	387	2.0	8	1402	2.7	5–12	548	4.8	157	3.63	310
	<i>H. 2327</i>	stem	3.00	35	181	341	2.3	7	1049	4.1	7	932	4.4	176	3.08	66
Subgenus, average of collections			2.32	53	104	431	2.3	7	1291	3.8	7	725	4.2	161	3.34	339

Key to columns: Collection (*C.* = *Carlquist*, *H.* = *Henrickson*; others, see Materials and Methods); Portion (*H* = horizontal; *L* = lower; *O* = outer; *U* = upper); 1 (VG), mean number of vessels per group; 2 (VD), mean lumen diameter of vessels, μm ; 3 (VM), mean number of vessels per mm^2 ; 4 (VL), mean length of vessel elements, μm ; 5 (VW), mean thickness of vessel walls, μm ; 6 (VP), mean axial diameter of pit vessel pit cavities, μm ; 7 (FL), mean length of fiber-tracheids, μm ; 8 (FW), mean thickness of fiber-tracheid walls, μm ; 9 (FP), mean diameter of fiber-tracheid pit cavities, μm ; 10 (MH), mean height of multiseriate rays, μm ; 11 (MW), mean width of multiseriate rays, μm ; 12 (UH), mean height of uniseriate rays, μm ; 13 (FV), "F/V ratio" (mean fiber-tracheid length divided by mean vessel element length); 14 (ME), "Mesomorphy Ratio" (mean vessel diameter times mean vessel element length divided by mean number of vessels per mm^2).

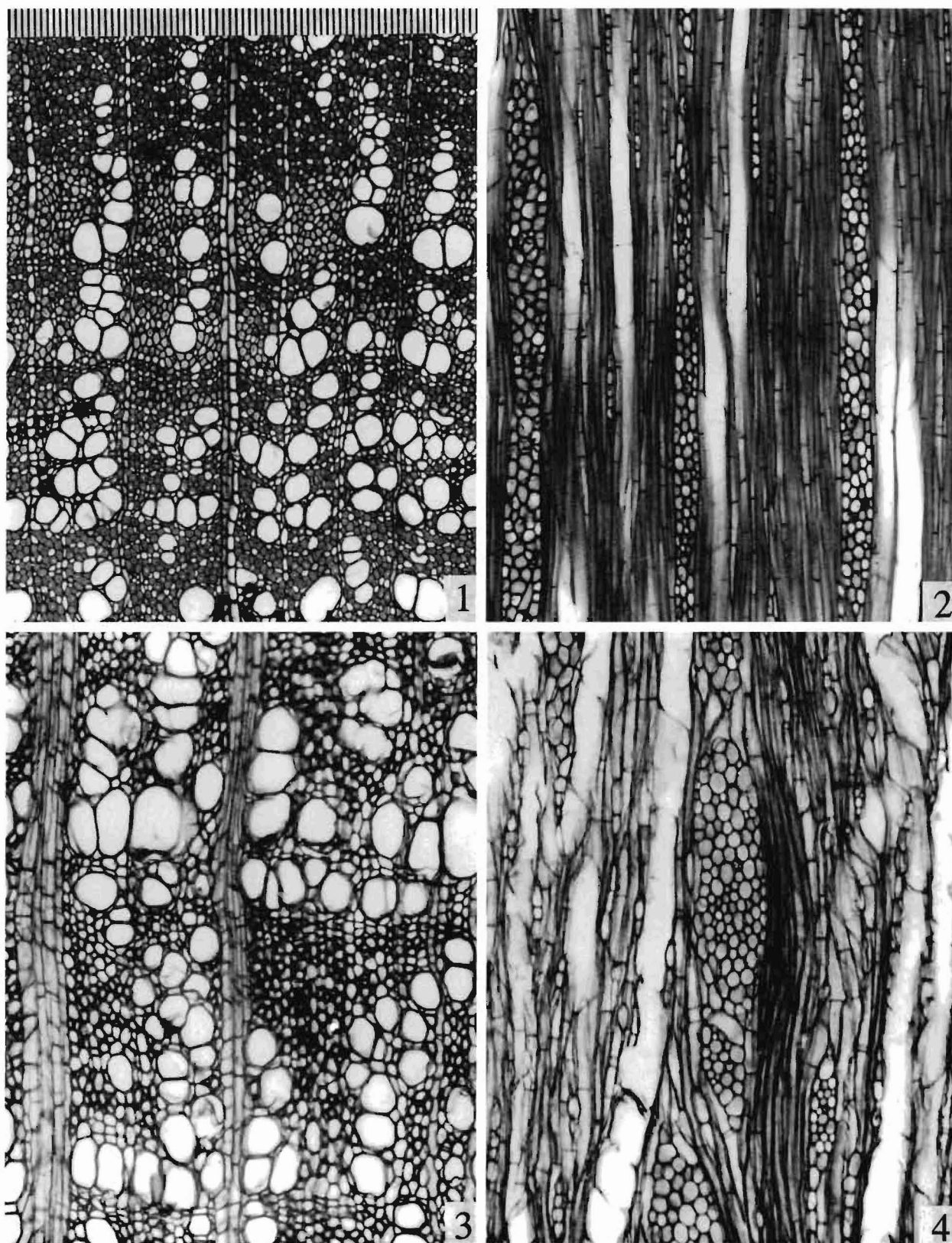


Fig. 1-4. Wood sections of *Fouquieria splendens*.—1-2. Stem sections.—1. Transection, showing fluctuation in vessel diameter.—2. Tangential section; both uniseriate and multiseriate rays are tall.—3-4. Root sections.—3. Vessels, especially those of earlywood, wider than those of stem wood vessels.—4. Tangential section. Rays wider than those of rays in stem wood. (Fig. 1-4, scale above Fig. 1 [divisions = 10 μ m].)

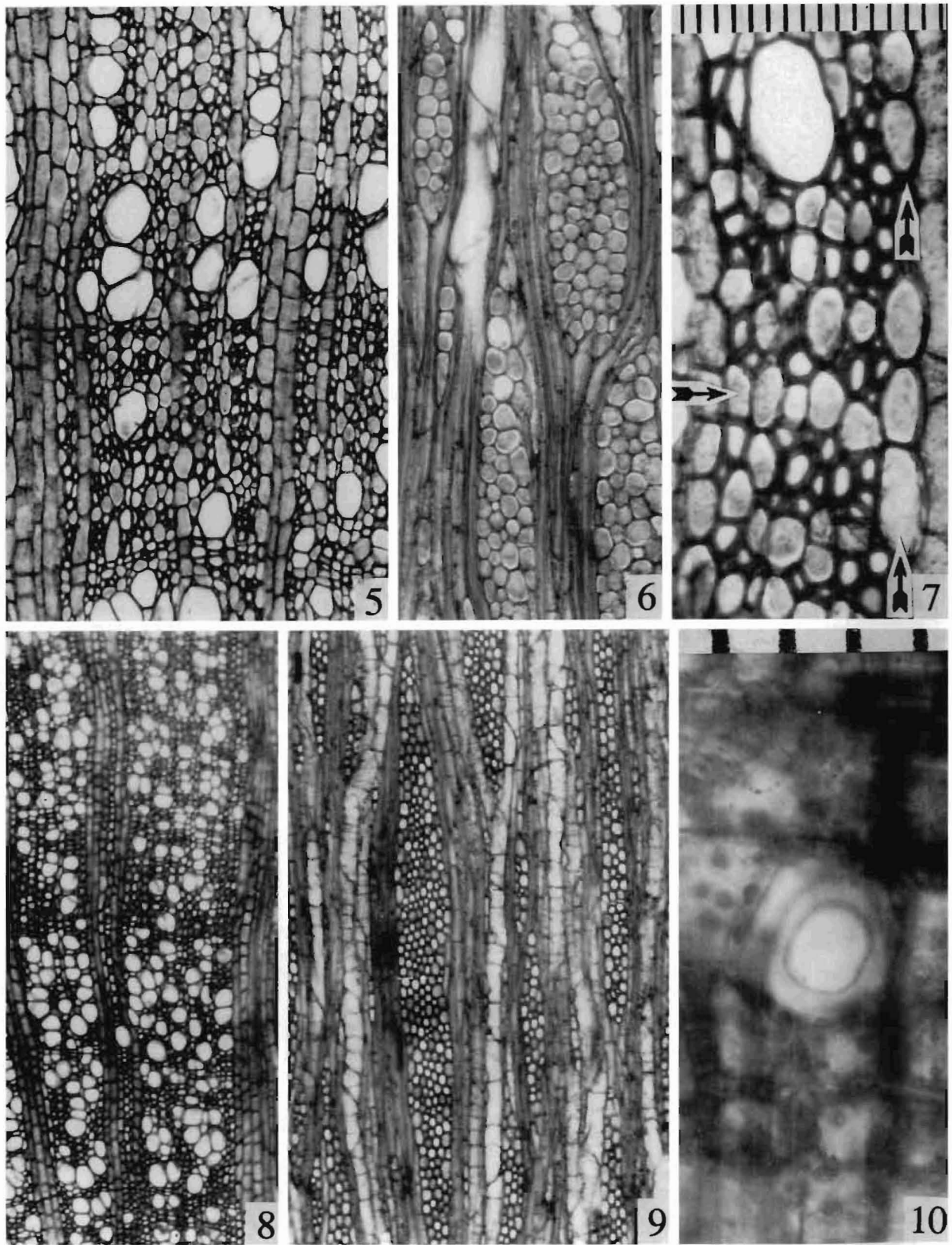


Fig. 5–10. Wood sections of *Fouquieria*.—5–7. *F. formosa*.—5. Transverse section: earlywood margin of growth ring just above the center of the photograph.—6. Tangential section; multiseriate rays are wide, starch-filled.—7. Transverse section, to show diffuse-in-aggregate axial parenchyma (horizontal arrow) and ray-adjacent axial parenchyma (vertical arrows).—8–10. *F. shrevei*.—8. Transverse section; vessels numerous, small in diameter.—9. Tangential section; multiseriate rays wide, cell size small.—10. Radial section; perforated ray cell, center. (Fig. 5, 6, 8, 9, scale above Fig. 5; Fig. 7, scale above Fig. 7 [divisions = 10 μm]; Fig. 10, scale above Fig. 10 [divisions = 10 μm].)

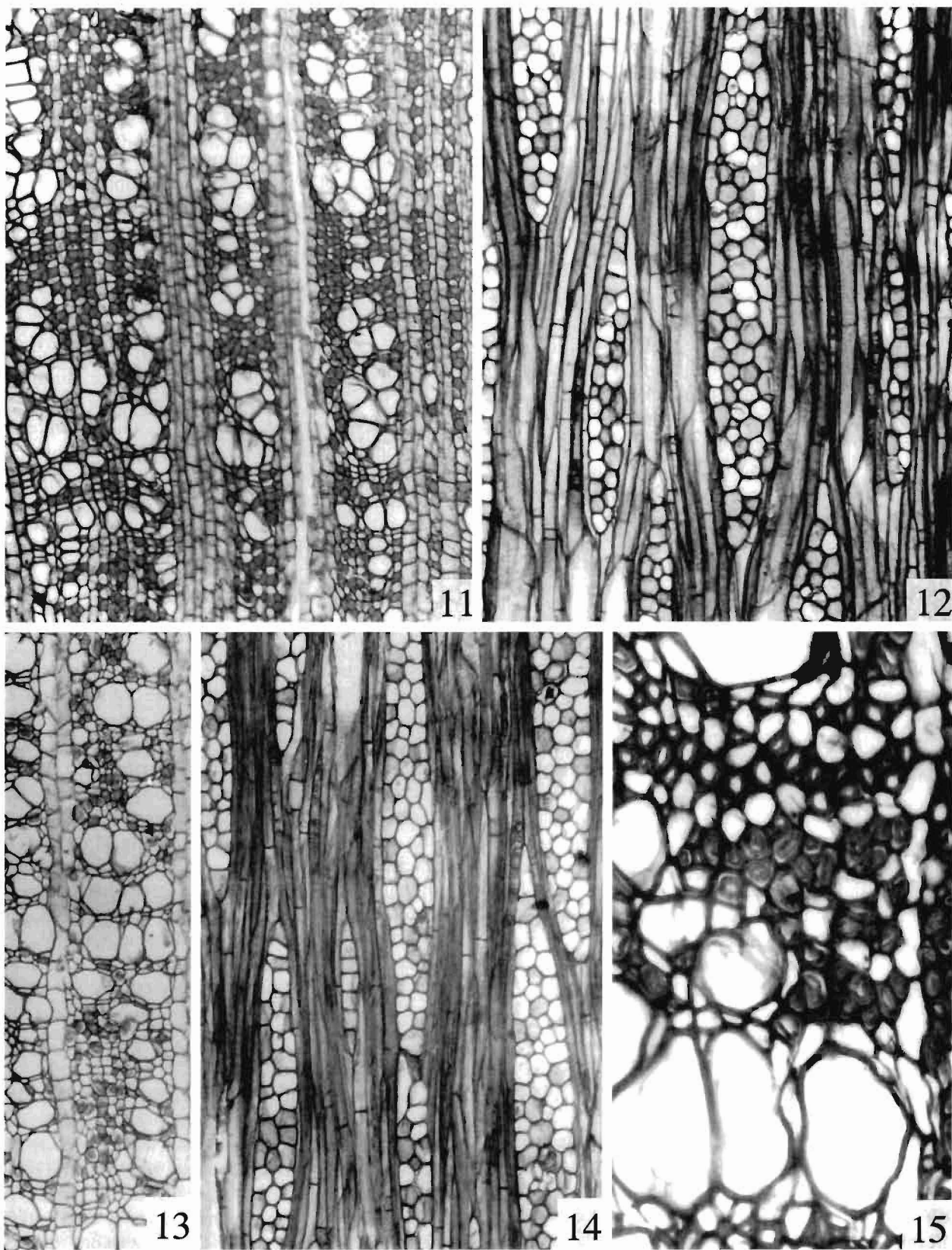


Fig. 11-15. Wood sections of *Fouquieria*.—11. *F. ochoteranae*. Transsection; vessels markedly grouped.—12. *F. leonilae*. Tangential section; wings present or absent on multiseriate rays.—13-14. *F. burragei*.—13. Transsection; parenchyma clustered diffuse transitional to pervasive; fiber-tracheids all reaction wood.—14. Tangential section; almost all ray cells are procumbent (as discerned from radial sections).—15. *F. diguetii*. Transsection; from bottom to top, wide earlywood vessels, reaction wood, normal fiber-tracheids. (Fig. 11-14, scale above Fig. 1; Fig. 15, scale above Fig. 7.)

ing roots that are comparable to stems in age, etc. is difficult: even if one has a mature individual plant available, obtaining a mature portion of both main stem and main root may not be possible. A computation of Henrickson's (1968) root vessel diameter data yields a mean of 76.0 μm ($N = 10$ collections) for the genus as a whole, whereas his stem diameter data computes to a mean of 56.3 μm ($N = 12$ collections). Henrickson's vessel diameters are not directly comparable to mine (Table 1, column 2), because mine represent lumen diameters. However, adding twice the vessel wall thickness (given in Table 1, column 5) satisfactorily converts the lumen diameter to outside vessel diameter, and our results are then very similar.

Vessel density (Table 1, column 3) is usually inversely proportional to vessel diameter in dicotyledons as a whole (Carlquist 1975), but not in *Fouquieria*. The vessel density in subgenera *Idria* and *Bronnia* fall below an inverse relationship, even though the wide ray tissue and axial parenchyma zones produced by parenchyma expansion were not included in this analysis. High vessel density (for the genus) characterizes *F. shrevei* (Fig. 8). Very low vessel density in fascicular areas may be seen in *F. fasciculata* (Fig. 39, 40) and *F. purpusii* (Fig. 44).

Vessel element length means are shown in Table 1, column 4. The mean for subgenus *Fouquieria* collections is 431 μm , which is very close to a mean calculated from Henrickson's (1968) data (stems of all species of the genus), 440 μm . The mean vessel element length for roots of all species of the genus, derived from Henrickson's data, is 460 μm . Differences in vessel element lengths of stems as compared to those of roots is clearest in subgenus *Fouquieria*, but varies within the succulent species. The longest vessel elements in the genus occur in stems of *F. columnaris*, 879 μm in my data, 713 μm in Henrickson (1968). The shortest vessel elements in both Henrickson's study and mine occur in *F. shrevei*.

Mean vessel wall thickness (Table 1, column 5) ranges from 1.5 μm in the lateral branches of *F. columnaris* (Fig. 28, 58) to 3.0 μm in the stems of *F. fasciculata* (Fig. 39). The range is not great, and most species deviate little from the means for subgenus *Fouquieria* (2.3 μm).

Lateral wall pits on vessels range upwards from 5 μm (Table 1, column 6). One curious phenomenon common in several species is dimorphism (or polymorphism) in pit size. This is shown for *F. leonilae* (Fig. 50). Larger pits appear like small perforations in sections and macerations as seen under the light microscope (Fig. 36), but SEM photographs reveal pit membranes in at least some of them (Fig. 50; Fig. 51, right). Pit dimorphism is also suggested in a vessel of *F. macdougallii* (Fig. 52, left). Pit dimorphism is com-

mon in vessels of *F. columnaris* (Fig. 36) and *F. fasciculata*.

Qualitative Vessel Features

In macerations, caudate vessel elements are common. Fibrifriform vessel elements were recorded in lateral branches of *F. columnaris* and upper stems of *F. fasciculata*. The most typical condition for vessel elements in the genus features an oblique end wall without a conspicuous tail, or with none at all. Nearly transverse end walls are less frequent (Fig. 49). Perforation plates are simple and bordered (Fig. 51, left). Two circular perforation plates at one end of a vessel element, separated by a wide band of wall material (and thus probably not a single perforation plate crossed by a bar) are infrequent, but were observed in *F. diguetii*, *F. macdougallii*, and *F. ochoteranae*. Vessel elements with double perforation plates were figured by Henrickson (1968) for *F. purpusii*.

Lateral wall pitting of vessels consists mostly of alternate pits. Some scalariform pitting was observed in *F. macdougallii* (Fig. 52, extreme left). Some pseudoscalariform pitting was recorded for *F. purpusii*. Otherwise, pits are mostly circular to oval in shape, with slitlike, or less commonly, oval to circular pit apertures (Fig. 49–52).

Vestured lateral wall pits on vessels were reported by Henrickson (1968) for all species of subgenus *Fouquieria*, but not for subgenera *Bronnia* or *Idria*. In SEM studies of two species of subgenus *Fouquieria*, *F. leonilae* (Fig. 49–51) and *F. macdougallii* (Fig. 52), I observed only nonvestured pits on vessel walls. Henrickson (1968) mentions that vesturing is sporadic within the woods in which he reports it, a pattern not characteristic of vesturing in dicotyledons as a whole (although vesturing may be somewhat more pronounced in latewood vessels in some dicotyledons). Therefore, I suspect that Henrickson may have seen droplets of secondary compounds or precipitants of some kind, a phenomenon discussed elsewhere (Carlquist 1988).

Imperforate Tracheary Elements

Pits of imperforate tracheary elements in *Fouquieria* are fully bordered, with circular pit cavities mostly about 5–12 μm in diameter and with narrowly elliptical pit apertures about the same length as the pit cavity diameter (Fig. 38). Although these pits are fully bordered, they are mostly much sparser than is typical for tracheids in dicotyledons, and therefore these cells are termed fiber-tracheids. The number of vessels per group averages above 2.41 (all collections of Table 1, column 1, averaged), a value that would not be attained in dicotyledons that have tracheids (Carlquist 1984); number of vessels per group in tracheid-bearing

dicotyledons reaches a maximum of about 1.2 vessels per group. In addition to fiber-tracheids, a small number of vasicentric tracheids was observed in *F. columnaris*, *F. fasciculata*, *F. leonilae*, *F. purpusii*, *F. shrevei*, and *F. splendens* (stem). Vasicentric tracheids were identified in macerations, in which dense pitting, fusiform shape, and absence of perforation plates could be observed clearly.

Imperforate tracheary elements with gelatinous secondary walls are common in most species (Fig. 23, all elements except in lower portion of photograph). These elements have thick walls that shrink away from the outer wall in permanent slides. Normal fiber-tracheids, by contrast, have thin walls with no shrinkage patterns (Fig. 23, approximately bottom third of photograph). As seen in macerations and longisections, the elements with gelatinous walls show splits rather than discrete circular pits. Because of these characteristics, the imperforate tracheary elements with gelatinous walls are considered reaction wood here. In some wood samples, reaction wood occurs in concentric bands (Fig. 1, horizontal strips of lighter gray cells; Fig. 15, central portion). In some wood samples, all or nearly all imperforate tracheary elements are reaction wood (*F. columnaris*, root of old seedling, Fig. 27). In some wood samples, reaction wood is scarce (Fig. 5, 6, 8). In other wood samples, normal wood is formed for prolonged periods (Fig. 16) and this lies between wide bands of reaction wood (Fig. 17). The wood of Fouquieriaceae is unusual in its abundance of reaction wood when it is compared to wood of other dicotyledons. This feature is discussed below with relationship to habit.

Mean length of fiber-tracheids (Table 1, column 7) ranges from 900 μm (*F. shrevei*) to 1808 μm (*F. diguetii*). This range is very similar to that found by Henrickson (1968), who reports a range in means from 666 μm for stems of *F. shrevei* to 1682 μm for *F. purpusii*.

The figures given for fiber-tracheid wall thickness (Table 1, column 8) exclude reaction wood. The thicknesses given average less than twice the thicknesses reported for vessel walls. The fiber-tracheids of succulent species have walls about as thick as those of the species of subgenus *Fouquieria*.

The mean pit diameter of fiber-tracheids (Table 1, column 9) shows a range similar to that of the axial diameter of lateral wall pits of vessels. The mean diameter of pits in these two cell types is about the same for the succulent species as for species of subgenus *Fouquieria*, 7 μm (Table 1, columns 6 and 9).

Axial Parenchyma

As seen in transection, axial parenchyma in the family is diffuse or some variant of diffuse—mostly the

latter. Ordinary diffuse parenchyma predominates in *F. leonilae*. In stems of *F. splendens*, a few diffuse-in-aggregates are present in addition (Fig. 1). In most species, axial parenchyma is best described as ranging from diffuse to diffuse-in-aggregates (Fig. 7, 15, 47). In main stems of *F. columnaris* (Fig. 25, 33), roots and lower stems of *F. fasciculata* (Fig. 39, 40, 42) and main stems of *F. purpusii* (Fig. 44), axial parenchyma ranges from diffuse to pervasive. These three species are the succulent fouquierias, and thus pervasive parenchyma is one aspect of succulence, but admittedly a minor element prior to occurrence of radial cell elongation. More importantly, pervasive axial parenchyma is a site for parenchyma proliferation in the succulent species, as discussed below under meristems.

Another type of axial parenchyma which may represent a radial grouping of parenchyma along ray surfaces is called ray-adjacent parenchyma (Carlquist 1988). Ray-adjacent parenchyma is illustrated here for *F. formosa* (Fig. 7).

The occurrence of intermediates between diffuse and other types of apotracheal parenchyma in *Fouquieria* includes clusters of 3–10 cells, clusters that cannot be categorized either as diffuse-in-aggregates or pervasive (Fig. 7, bottom; Fig. 17, upper left). The term diffuse clusters is proposed here for this type of axial parenchyma, with the understanding that this is an apotracheal parenchyma type.

As seen in longisections, axial parenchyma strands consisting mainly of two cells were recorded for *F. columnaris* (root of large seedling, lateral branch of young tree), *F. fasciculata* (root), *F. burragei*, *F. formosa*, and *F. macdougalii* (stems). Strands composed of two to four cells characterize most species. Strands composed predominantly of four cells, but occasionally fewer, were recorded for *F. leonilae*, *F. ochoteranae*, *F. shrevei*, and *F. splendens* (both stems and roots).

Rays

Multiseriate rays are more common than uniseriate rays in most species studied (Fig. 2, 4, 6, 9, 12, 14, 18, 22). Multiseriate rays are about as common as uniseriate rays in *F. columnaris* (lateral branches only, Fig. 29), *F. fasciculata* (root only, Fig. 43), *F. purpusii* (roots and upper stems, Fig. 48), and *F. shrevei* (Fig. 9).

Uniseriate wings on multiseriate rays are uncommon in any given species (Fig. 2, 4, 6, 9, 12, 14, 22). They are common only in roots of *F. fasciculata* (Fig. 43) and *F. purpusii* (Fig. 48). Procumbent cells predominate in multiseriate rays in most species (Fig. 2, 4, 6, 9, 14, 18, 22). The root of the seedling of *F. columnaris* was observed to have upright cells predominantly (Fig. 29), a fact likely related to the immature

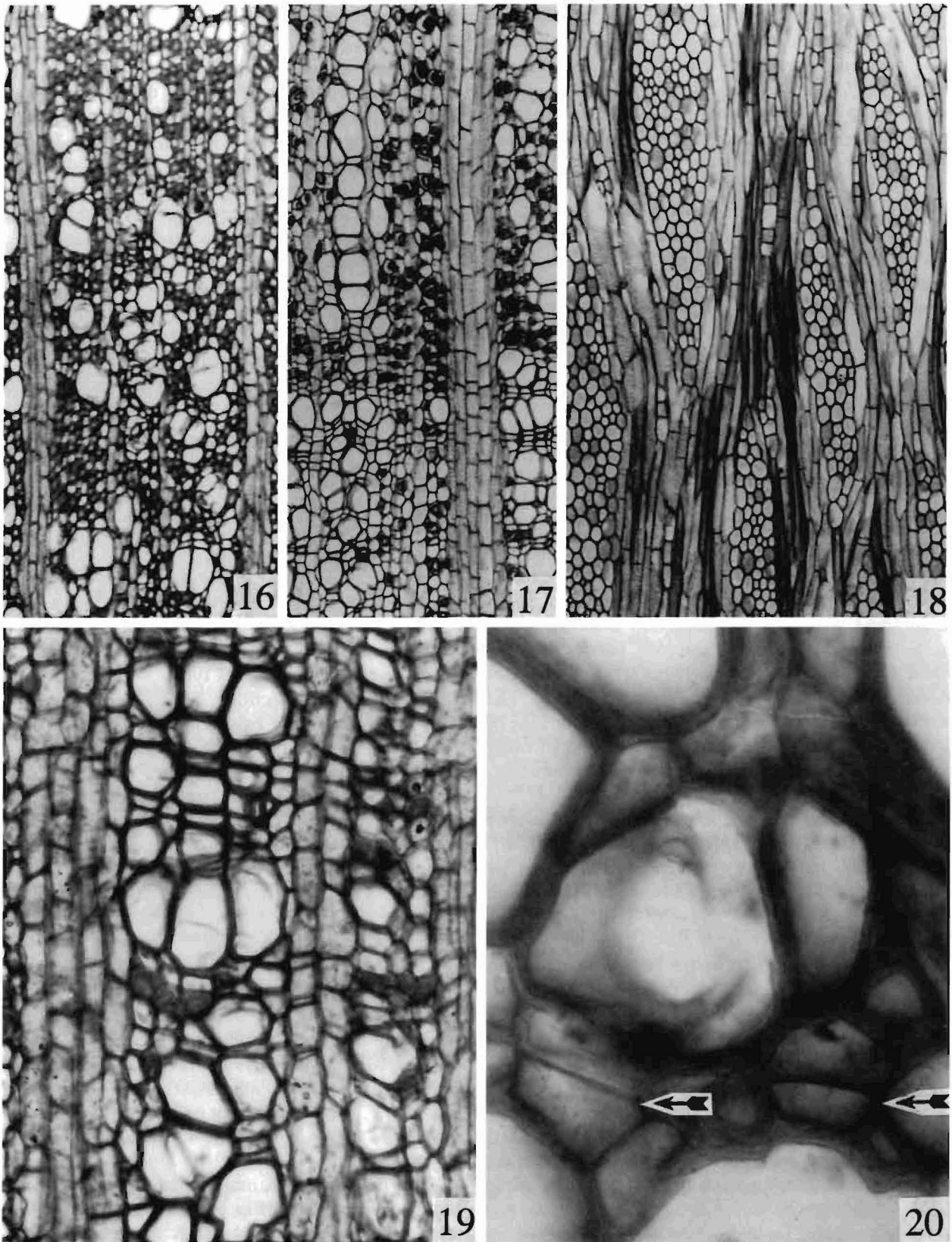


Fig. 16–20. Wood sections of *Fouquieria macdougalii*.—16–17. Transections.—16. Axial parenchyma sparse, all fiber-tracheids normal.—17. Axial parenchyma abundant, all fiber-tracheids reaction wood.—18. Tangential section; a high proportion of the wood is composed of rays.—19. Transection; axial parenchyma and reaction wood present in addition to vessel groups.—20. Transection to show, below vessel, two axial parenchyma cells in which tangentially oriented subdivisions have occurred (arrows). (Fig. 16–18, scale above Fig. 1; Fig. 19, section above Fig. 7; Fig. 20, scale above Fig. 10.)

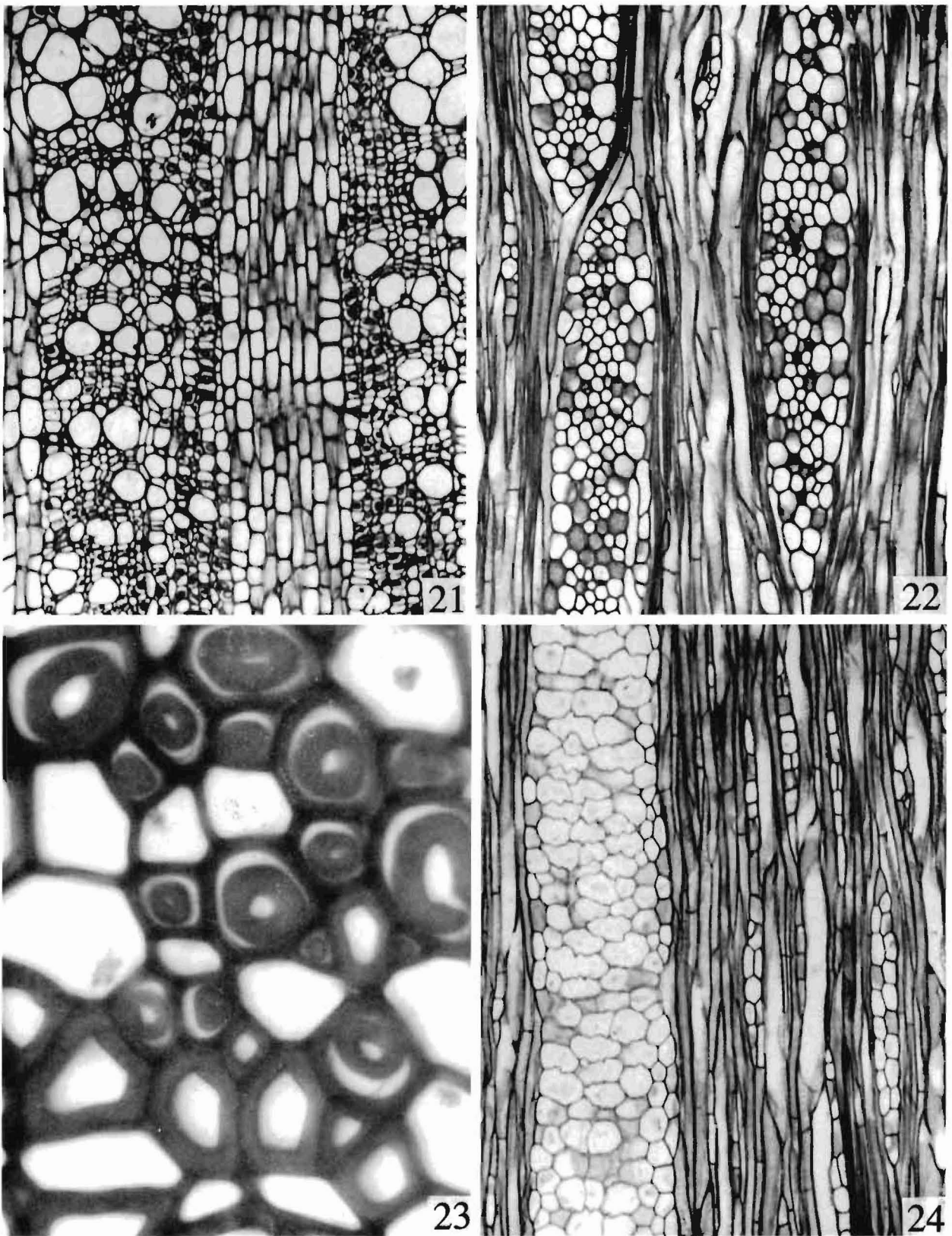


Fig. 21-24. Wood sections of *F. columnaris*.—21-22. Sections from outside of lower stem.—21. Transection; in axial xylem, parenchyma is abundant, normal and reaction fiber-tracheids about equally common.—22. Tangential section; multiseriate rays are notably wide.—23-24. Sections from outside of upper stem.—23. Transection; gelatinous fibers above, a line of normal fiber-tracheids from left to right near bottom.—24. Tangential section; radial divisions are occurring in the multiseriate ray at left, resulting in tangential widening of the ray. (Fig. 21, 22, 24, scale above Fig. 1; Fig. 23, scale above Fig. 10.)

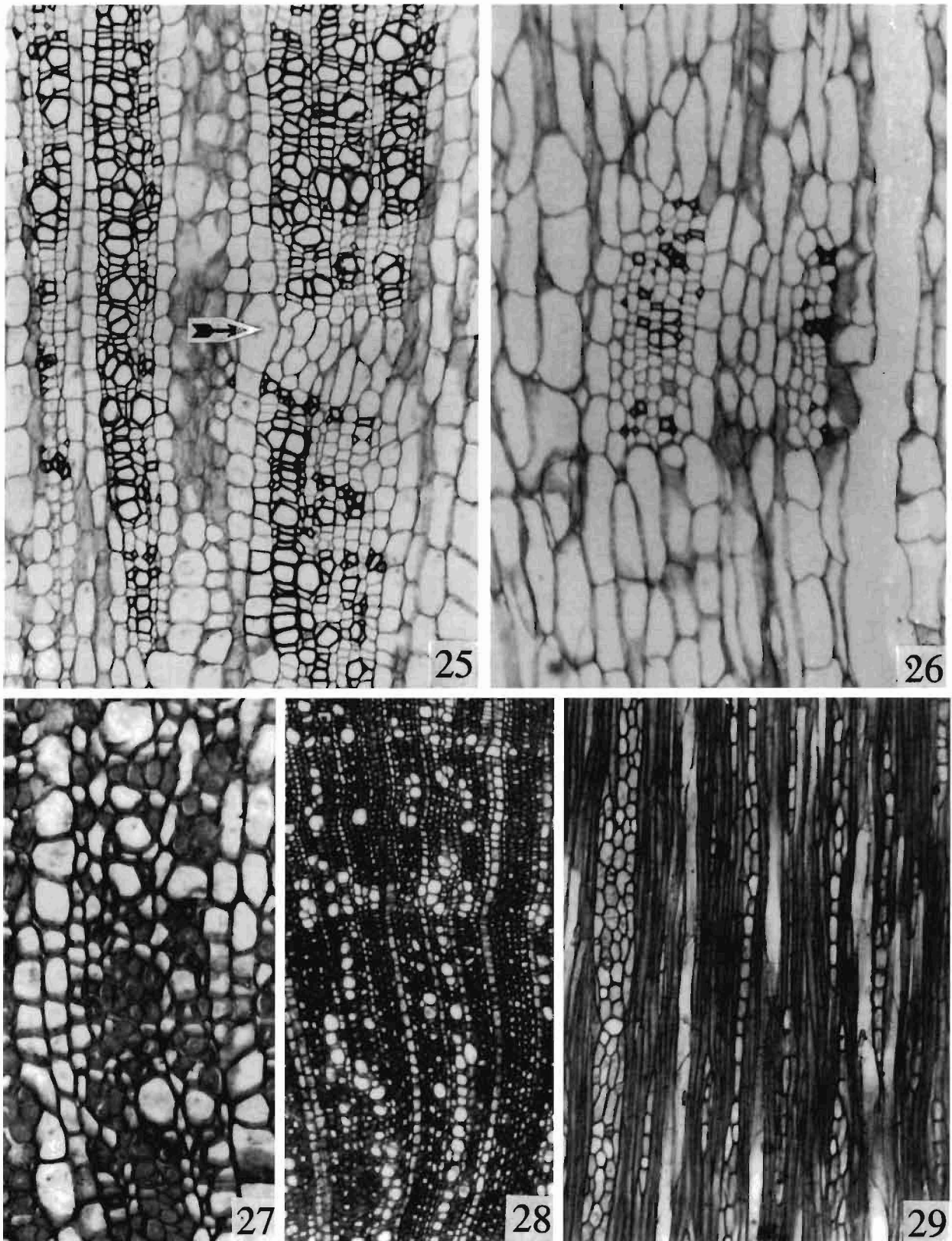


Fig. 25–29. Wood sections of *F. columnaris*.—25–26, Sections from outside of base of stem.—25. Transsection; arrow indicates a band of axial parenchyma in which radial elongation of cells is beginning.—26. Transsection, farther from outside of stem than Fig. 25, to show an isolated strand of intact axial xylem surrounded by radially elongated axial parenchyma cells (above and below it) and radially elongate ray cells, to right and left.—27. Transsection of wood of old seedling; all fiber-tracheids are reaction wood.—28–29. Wood from horizontal branch.—28. Transsection; axial parenchyma not common, vessel diameter small.—29. Tangential section; rays are narrow, composed mostly of upright cells (as discerned from radial sections). (Fig. 25, 26, 28, 29, scale above Fig. 1; Fig. 27, scale above Fig. 7.)

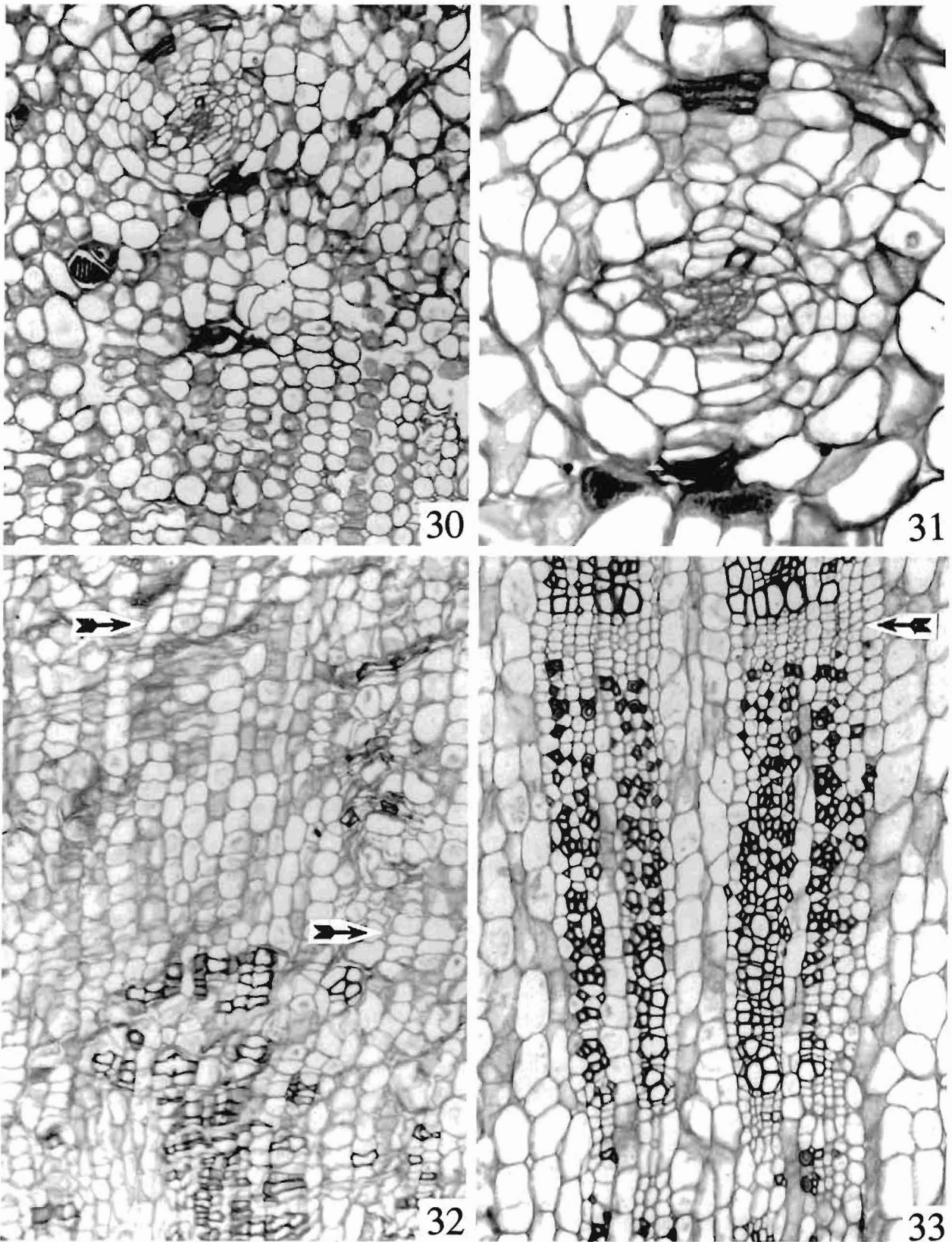


Fig. 30–33. Wood transections of *F. columnaris*.—30–32. Transections of axial cells from tissue adjacent to pith.—30. Radial files of axial parenchyma (bottom) and, above left, a strand of vascular tissue that may or may not have been separated from secondary xylem.—31. Vascular strand shown in Fig. 30, to show details of component cells and a cylinder of divisions around it that constitute a meristem.—32. Secondary xylem near center of stem; meristems producing axial parenchyma have originated (arrows).—33. Section near cambium (which would be above top of photograph) from outside of upper stem; a band of axial parenchyma that has not yet expanded is indicated by the arrow (a similar band near bottom of photograph). (Fig. 30, 32, 33, scale above Fig. 1; Fig. 31, scale above Fig. 7.)

status of this wood sample. Upright, square, and procumbent cells were about equally frequent in multiseriate rays of *F. fasciculata* and *F. purpusii*; the plants studied do not represent mature trees except for the root of *Henrickson 2142*. In rays of most species, upright cells are confined to wings and sheathing cells of multiseriate portions of multiseriate rays and to uniseriate rays. Procumbent cells can be found in occasional uniseriate rays. Thus, the rays of Fouquieriaceae should be characterized as predominantly Heterogeneous Type IIB of Kribs (1935), with tendencies to Heterogeneous Type IIA and, in the immature specimens or portions of the succulent species, tendencies to Paedomorphic Type I (Carlquist 1988).

Walls of ray cells are relatively thin (1.0 to 2.0 μm) and lignified in most species (Fig. 2, 4, 6, 9, 12, 14, 18, 22, 29, 35, 37). Nonlignified ray cells can be found commonly in rays of the succulent species (Fig. 24, left; Fig. 25, 26, 33, 39, 40, 41, 44, 45). Lignification of rays may occur slowly. The pitting shown in a *F. columnaris* ray section (Fig. 35) is that of a vessel wall portion, but the underlying ray cells are lignified, and thus the occurrence of half-bordered pit pairs is assumed. Henrickson (1968) reported nonbordered pits among ray cells in the family. This is commonly true, but bordered pits often occur on the tangential walls of ray cells in *F. columnaris* (root of seedling, lateral branch of young tree). *F. formosa*, *F. ochoteranae*, *F. shrevei*, and *F. splendens* (stems). In earlier studies, pits among ray cells were observed in face view and thus borders were frequently overlooked. If one views sections of ray cell walls, borders are commonly seen in many dicotyledons (Carlquist 1988, Fig. 6.13.4). In some ray cells that have appear to have lignified relatively tardily, pits resemble primary pit fields in their range of sizes (Fig. 34).

Perforated ray cells were reported by Henrickson (1968) in *F. ochoteranae* and *F. shrevei*. I can confirm the presence of perforated ray cells in *F. ochoteranae* and *F. shrevei* (Fig. 10) and I observed them also in *F. burragei*. Although some workers have reported perforated ray cells as though they are characteristics of systematic importance, these cells seem to relate to ontogeny and location in rays (Herendeen and Miller 2000), and thus may be expected in other species of *Fouquieria*.

Quantitative features of rays are given in Table 1. Multiseriate ray height is greatest in the succulent species, but averages less than 1,000 μm in species of subgenus *Fouquieria* (column 10). Ray width (column 11) is not especially great in the family as a whole, despite the occurrence of wide rays in some species (e.g., Fig. 4, 6, 18, 22, 41, 45) In *F. columnaris*, the portions surveyed were relatively nonsucculent, and thus the rays within woodier areas (= areas derived from fascicular xylem, excluding major multiseriate

rays) are reflected. In *F. fasciculata* and *F. purpusii*, the younger plants studied show less differentiation between woodier secondary xylem and secondary xylem containing large rays extending to the center of the stem, so greater ray width is evident for those two species. Uniseriate ray height (column 12) is relatively short, reflecting the fact that most uniseriate rays are one to five cells in height.

Tyloses

Tyloses were observed in vessels of *F. columnaris* (lateral branches), *F. burragei*, and *F. splendens* (stems). The tyloses observed all bear only primary walls.

Crystals

The full range of crystal distribution in *Fouquieria* is shown in the radial section of an upper main trunk of *F. columnaris* (Fig. 37). At top in this photograph, some ray cells are subdivided into pairs of cells each of which bears a rhomboid crystal. At left, below, is an upright ray cell, subdivided into four cells, each of which bears a large rhomboid crystal ("chambered crystals"). An axial parenchyma strand subdivided into crystal-bearing cells is at center, below, in Fig. 37 (vertical arrow). In those species that bear crystals in ray cells, upright rather than procumbent cells contain crystals. Crystal-containing cells are most often subdivided. In the case of either rays (Fig. 37, 56) or axial parenchyma that contain crystals, subdivisions are achieved by means of primary walls. A large rhomboidal crystal may appear to be unaccompanied by smaller crystals (Fig. 54). However, the illustration of a subdivided axial parenchyma cell of *F. formosa* (Fig. 57) shows rhomboids of various sizes.

In addition to rhomboidal crystals, sphaerocrystals were observed in *F. leonilae* (Fig. 53), *F. burragei*, and the lateral branches of *F. columnaris*. Druses (Fig. 55, above) were also observed. The differences between druses and sphaerocrystals have not generally been appreciated, but are given elsewhere (Carlquist 1988; in press). In a given subdivided cell, more than one of the three crystal formations may be present. For example, in subdivided axial parenchyma of *F. leonilae*, druses plus rhomboids or sphaerocrystals are present.

The systematic and organographic distribution in wood of Fouquieriaceae observed in the present study is as follows (AP = axial parenchyma, R = rays; portions studied in Table 1): *F. columnaris*, rhomboids in AP, R (Fig. 37) of outer upper stem, rhomboids and sphaerocrystals in AP of lateral branch; *F. fasciculata*, rhomboids sparse in AP, R of stem; *F. burragei*, rhomboids and sphaerocrystals in AP, R; *F. diguetii*, rhomboids of various sizes in AP, R; *F. formosa*, rhomboids

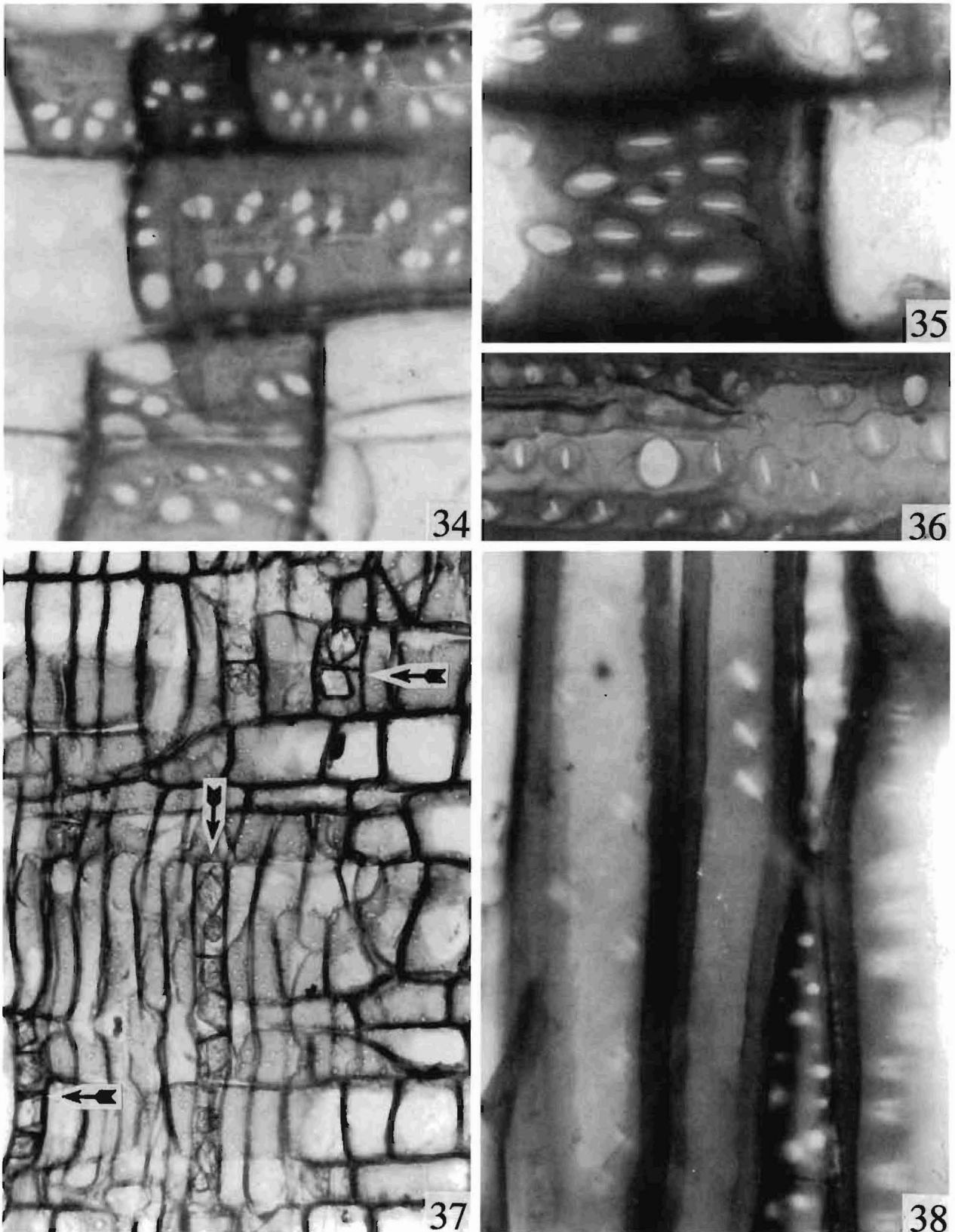


Fig. 34–38. Wood sections of from outer portion of a lower (Fig. 36, 37) and an upper (Fig. 34, 35, 37) main stem of *F. columnaris*.—34–35. Radial sections.—34. Ray cells showing recently lignified walls; unligified cell walls at left and right, below.—35. Vessel side of vessel-to-ray pitting, showing oval alternate pits.—36. Vessel wall from tangential section; one large and numerous smaller pits are present.—37. Radial section to illustrate crystals in subdivided upright ray cells (horizontal arrows) and in a subdivided axial parenchyma strand (vertical arrow).—38. Fiber-tracheid from tangential section, showing three pits, to right of center (vasicentric tracheid with numerous pits out of focus at left). (Fig. 34–36, 38, scale above Fig. 10; Fig. 37, scale above Fig. 7.)

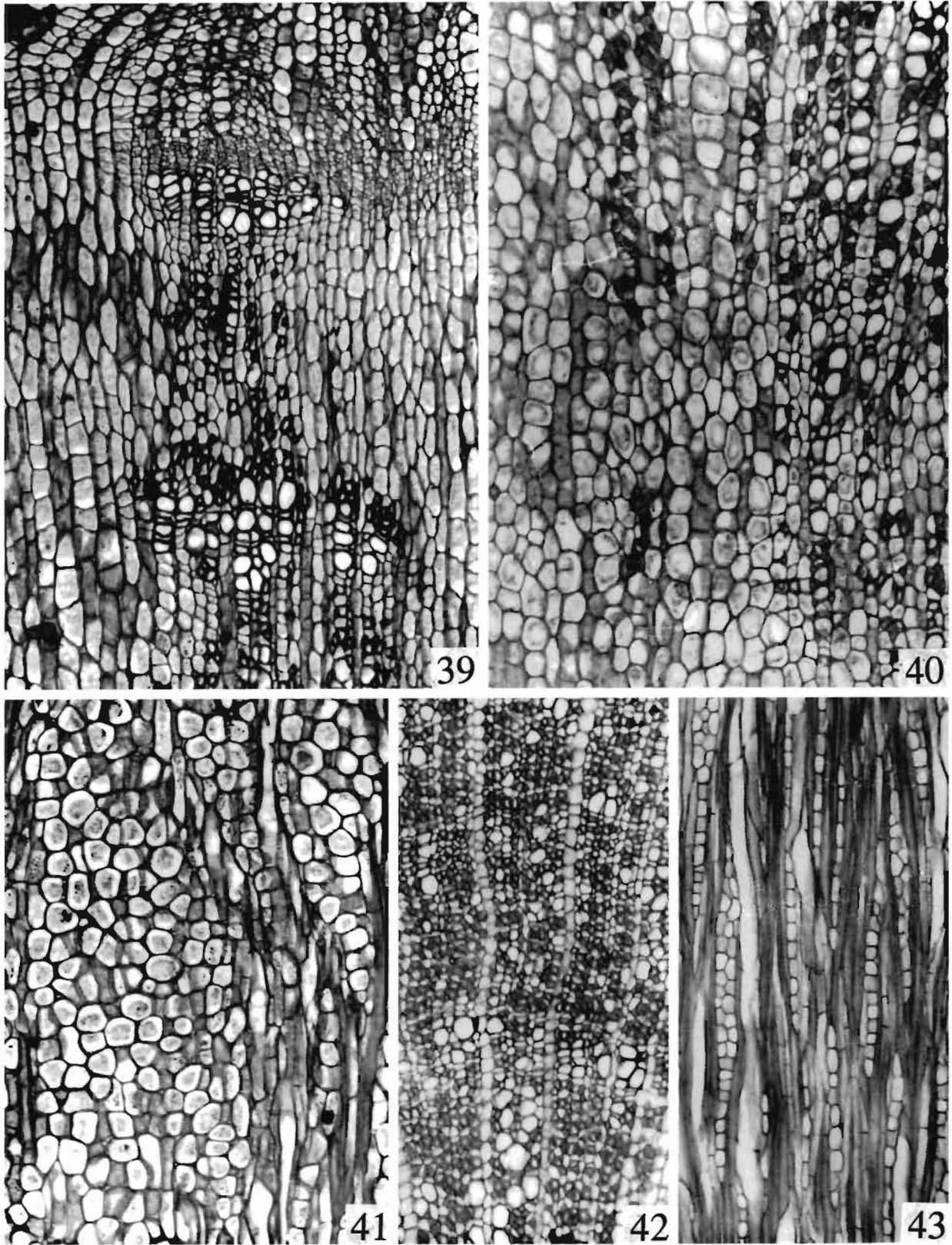


Fig. 39–43. Wood sections from stem (Fig. 39–41) and root (Fig. 42, 43) of *F. fasciculata*.—39. Transection (secondary phloem at top) to show that distribution of vessels, axial parenchyma, and fiber-tracheids tends to be in bands rather than at random.—40. Transection; axial parenchyma is abundant, below, especially at left, where it is difficult to distinguish from ray parenchyma.—41. Transection; rays are notably wide, contain starch.—42. Transection; axial parenchyma sparse compared to that of stem wood.—43. Tangential section; rays narrow compared to those of stem. (Fig. 39–43, scale above Fig. 1.)

of various sizes, AP, R (Fig. 57); *F. leonilae*, sphaerocrystals, druses, and rhomboids in AP (Fig. 55), R; *F. ochoteranae*, rhomboids sparse in R; *F. shrevei*, rhomboids sparse in R. The above reports represent new records as compared to the listings of Henrickson (1968). However, Henrickson reported rhomboids in the roots of *F. diguetii*, which were not studied here. Extensive study of woods of the family would probably yield a few new records. The apparent absence of crystals in *F. splendens* is noteworthy at present. Crystals occur in bark of all species of *Fouquieria* (Henrickson 1969c).

Starch

Spherical or oval starch grains or various kinds of starch grain remnants (identifiable by presence of air-filled hila) were observed in rays and axial parenchyma of all species. Starch grains are shown here for axial parenchyma of *F. macdougallii* (Fig. 52). Liquid-preserved material more often yields grains that are relatively intact. Preparations made from dried wood samples show various kinds of starch remnants. Presumably, starch will vary in quantity according to season and growth or flowering activity. A special type of starch-bearing tissue is discussed below for *F. macdougallii* (Fig. 60, 61). In the succulent species, some large parenchyma cells assumed to be water-storage cells contain starch, so the two functions are probably variously combined in parenchyma cells.

MERISTEMS

Fouquieriaceae have an amazing roster of types of meristematic activity in stems and roots, in addition to vascular cambia and phellogen. These meristems deserve special attention because they form a series of phenomena unequalled by other families of dicotyledons. The most obvious of these involve proliferation of axial and ray parenchyma in the succulent species, thereby breaking axial xylem into segments. The products of this proliferation have been figured photographically for stems as seen in gross aspect by Henrickson (1969a, 1959b, 1972), and these appearances do not need repetition here. However, the use in the present study of a method that can reveal thin-walled meristematic cells well in tissues that also include sclerenchyma or other lignified cells (Carlquist 1982) has permitted detailed analysis of the histology of these and other types of meristems in Fouquieriaceae.

1. Axial Parenchyma Expansion

In the three succulent species, tangential bands of axial parenchyma undergo tangential divisions that constitute meristems (Fig. 46, lower left); these cells then expand, mostly in a radial direction (Fig. 25). The

increase in volume achieved in stems in this manner features cell expansion more than cell division, but an appreciable number of cell divisions may be seen. In order for this meristematic action to occur, there must be pre-existing bands of axial parenchyma in fascicular areas of the wood. Fibers and vessels are absent or uncommon in these parenchyma bands. Clear examples of axial parenchyma bands in *F. columnaris* are at the top and at the bottom of Fig. 33. A band in the process of expansion is shown in Fig. 25. Examples from the other succulent species have been presented as Fig. 39, Fig. 40 (bottom), and Fig. 44 (the fiber-free zone of fascicular secondary xylem). Ultimately, as a result of expansion of the axial parenchyma bands, strands or bands of intact axial secondary xylem, like the one shown in Fig. 26, are separated from each other by radially elongate axial parenchyma cells. The ray cells adjacent to the radially elongating axial parenchyma cells also elongate radially in a coordinate fashion (Fig. 25, 26). The fascicular strand shown in Fig. 26 consists of fibers and axial parenchyma (the latter not radially enlarged within the strand), and vessels are absent. Some such isolated strands do contain vessels, however—vessels that presumably are still functional and in contact with a conductive network (the displacement does not seem drastic enough to break vessels). Rifts may form among parenchyma cells (Fig. 26, right) as a way of adjustment to the expansion process.

2. Ray Expansion

The histological basis for fracturing apart of fascicular secondary xylem segments is shown here in Fig. 45 (a tangential section) and Fig. 46 (a transection). Radial longitudinal divisions are evident in both of these figures. Tangential elongation of ray cells, resulting in widening of the ray, is evident near the top of the large ray in Fig. 46.

One must stress that expansion in ray width and in radial width of axial parenchyma bands is coordinated. Both of these processes occur simultaneously and segments of "fibrous" wood are separated from each other in an orderly fashion, so that radial plates and tangential bands of parenchyma form a functional interconnected network of water storage tissue, intercalated within a conductive system (vessels and associated imperforate tracheary elements) apparently capable of storing water in and withdrawing water from the proliferated parenchyma.

3. Formation of Secondary Parenchyma Tissue in the Stem Center

Cambia that produce axial parenchyma in old secondary xylem are present in the centers of older stems of *F. columnaris*. This secondary parenchyma forma-

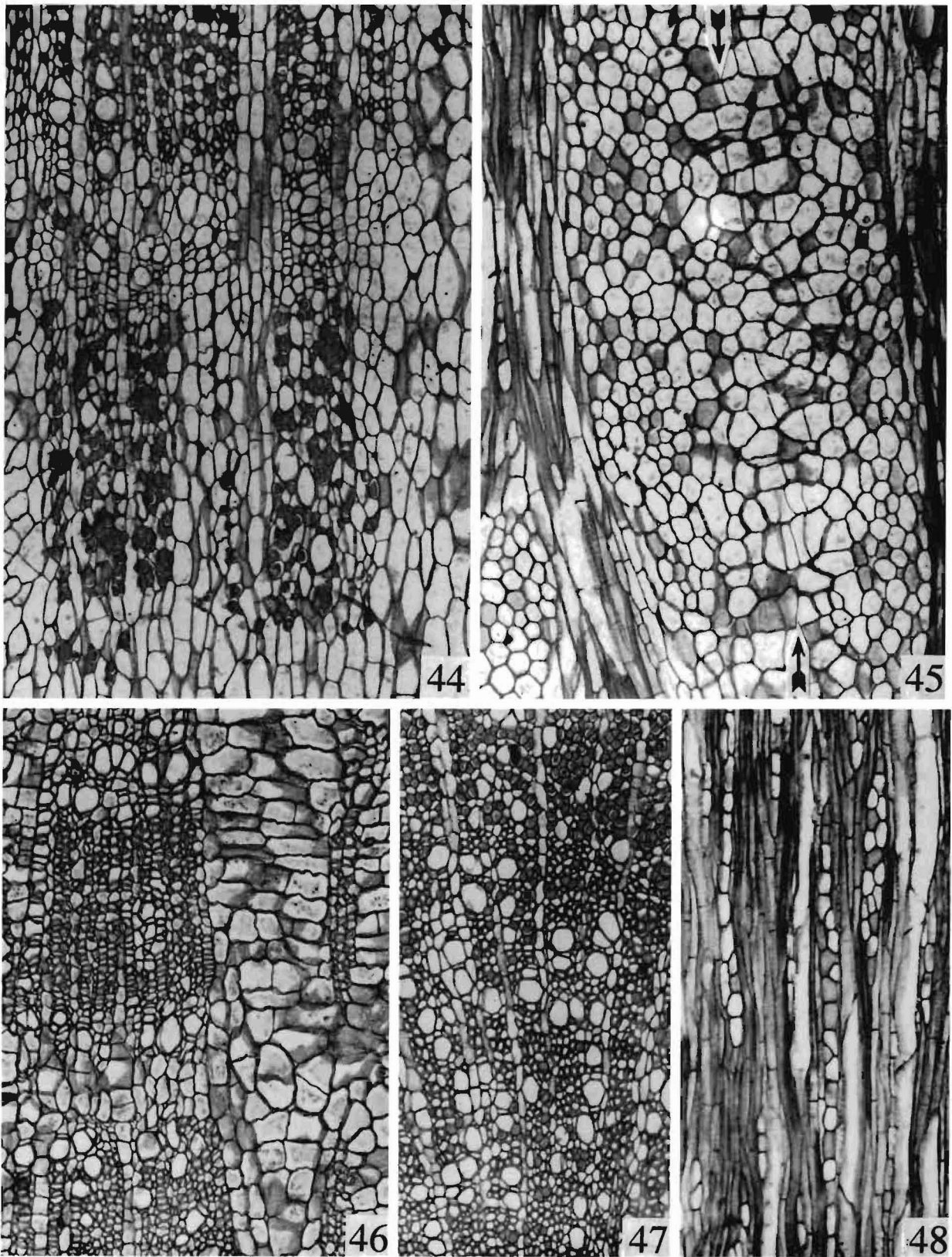


Fig. 44-48. Wood sections from outside of main stem (Fig. 44-46) and root (Fig. 47, 48) of *F. purpusii*.—44. Transection, showing bands of axial parenchyma (elongated axial parenchyma at bottom) and reaction wood (in lower half of photograph).—45. Tangential section; radial divisions are beginning in central portion of rays (area between tips of the arrows).—46. Transection; multiseriate rays (right), showing radial divisions; a few tangential divisions are occurring in axial parenchyma band, lower left.—47. Transection; axial parenchyma sparse.—Fig. 48. Tangential section; rays narrow. (Fig. 44-48, scale above Fig. 1.)

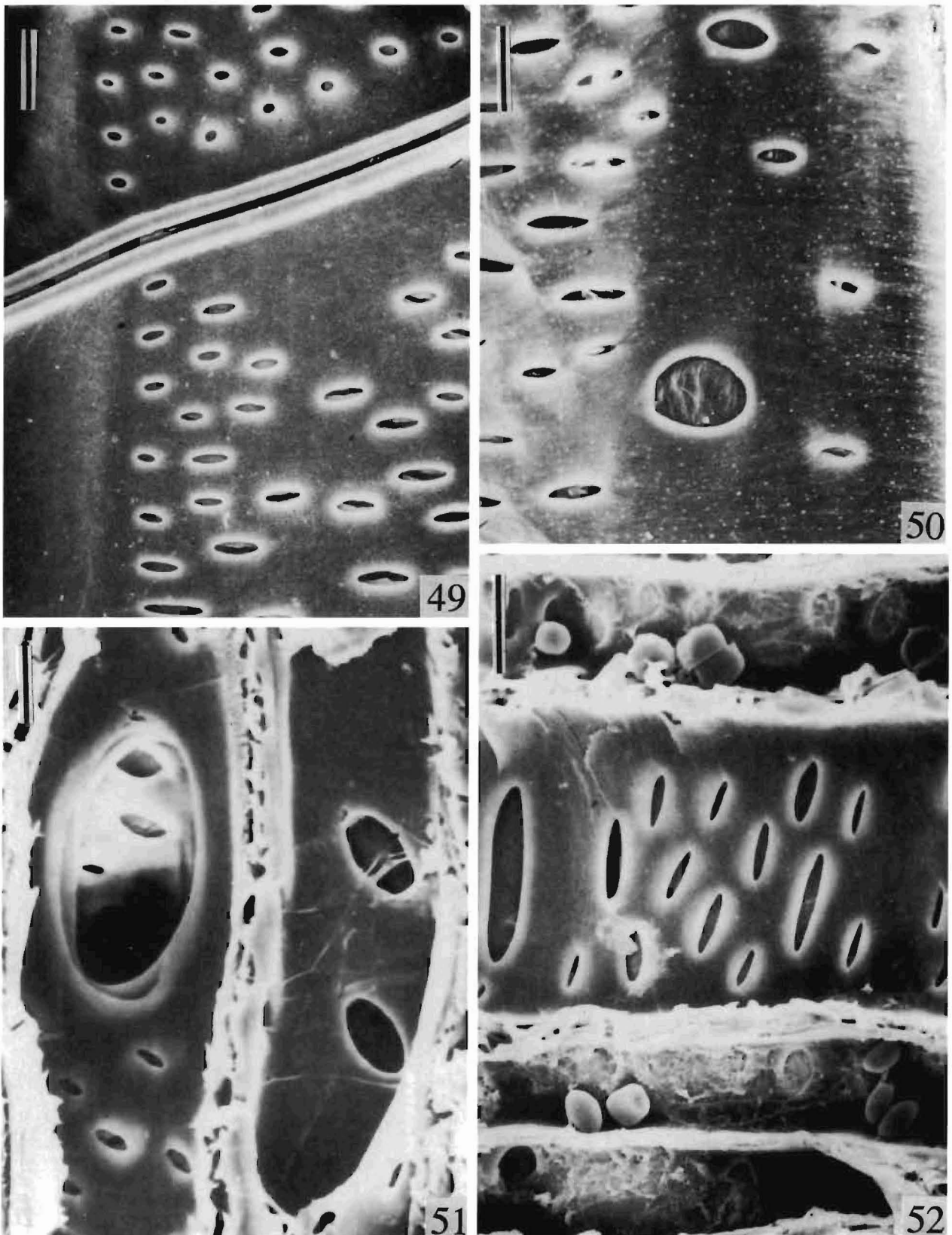


Fig. 49–52. SEM photographs of pitting and perforations in vessels from wood sections.—49–51. *F. leonilae*, radial sections.—49. Lateral wall pitting of two adjacent vessel elements (perforation plate diagonal, above).—50. Wall of vessel, showing one large and numerous smaller pits.—51. Small perforation plate, above left; in vessel at right are a pair of large pits or else small perforation plates.—52. *F. macdougalii*, radial section, axis of vessel oriented horizontally; alternate to pseudoscalariform pitting on vessel; axial parenchyma above and below the vessel contains starch grains. (Scales at left in each figure = 10 μ m.)

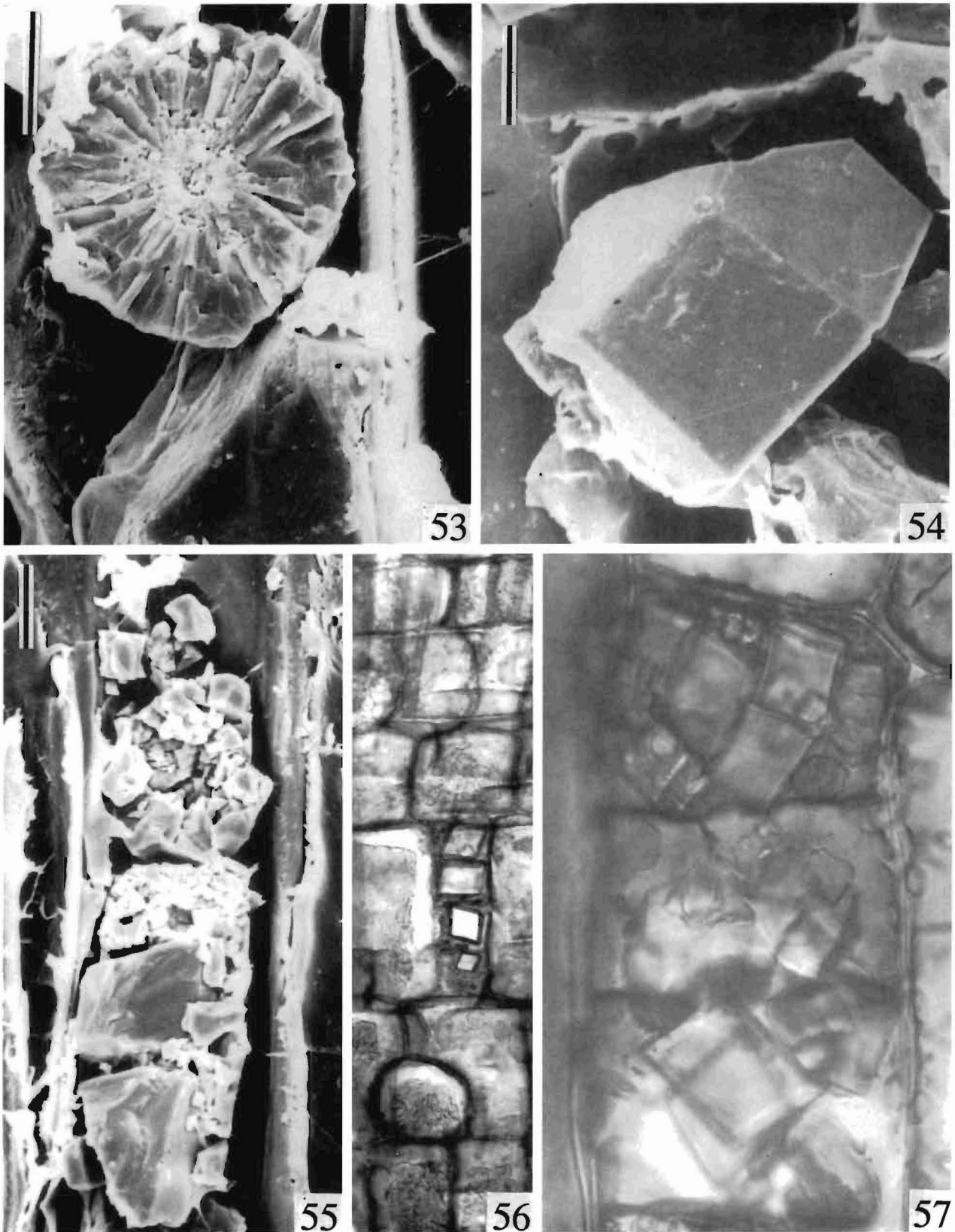


Fig. 53–57. SEM photographs (Fig. 53–55) and light microscope photographs (Fig. 56, 57) of crystal-bearing cells from wood sections of *Fouquieria*.—53–55, *F. leonilae*, radial sections.—53. sphaerocrystal (and portion of a rhomboid crystal, below) from a subdivided axial parenchyma cell.—54. Rhomboid crystal from ray cell.—55. Two fractured rhomboid crystals with smaller rhomboid crystals, below, and a fractured druse, above, from an axial parenchyma cell.—56. *F. diguetii*, four rhomboid crystals in a subdivided upright ray cell.—57. *F. formosa*, numerous rhomboidal crystals of various sizes in axial parenchyma cell subdivided by primary walls. (Fig. 53–55, scale at left = 10 μm ; Fig. 56, scale above Fig. 7; Fig. 57, scale above Fig. 10.)

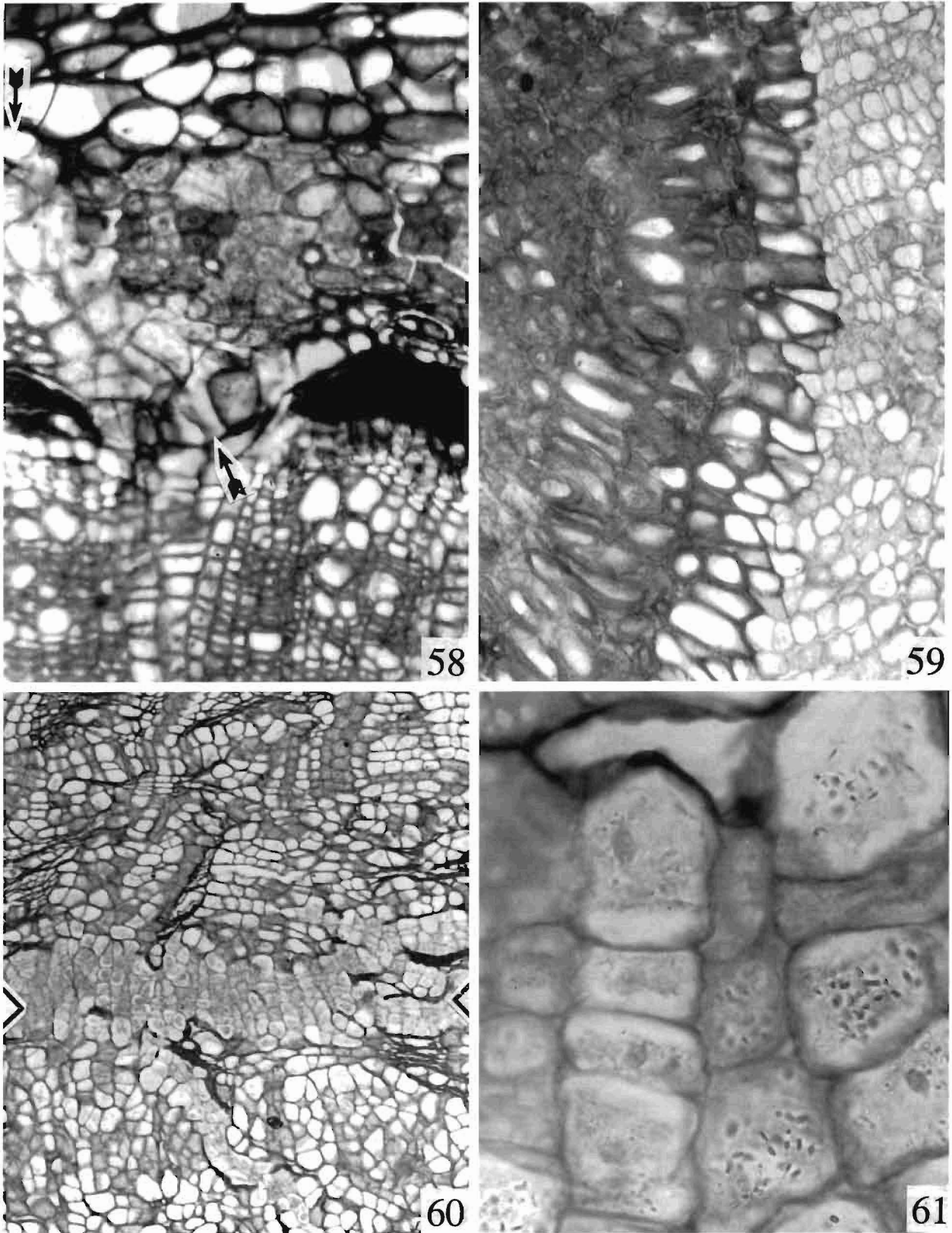


Fig. 58–61. Bark transections of *Fouquieria*.—58–59. *F. columnaris*.—58. Inner cortex and (below) outer secondary xylem from lateral branch; dividing parenchyma cells occupy the gap in sclerenchyma cylinder indicated between arrows tips.—59. Bark from outside of lower stem, showing portion of a sclereid nest, left, to which a meristem (right) is adding cells maturing into sclereids; the meristem also adds parenchyma cells to right.—60–61. *F. macdougalii*, section in outer phloem region.—60. Band (with branches) of secondary parenchyma, indicated by arrow tips at left and right.—61. Portion of secondary parenchyma band, to show radial files indicating recent derivatives of a meristem, left, and starch-rich more mature cells, right. (Fig. 58, 60). (Fig. 58, 58, scale above Fig. 78; Fig. 60, scale above Fig. 1; fig. 61, scale above Fig. 10.)

tion can form extensive orderly rows (Fig. 30, bottom). The axial parenchyma formed in the inner stem is free from vessels and fiber-tracheids—understandably so, because forming new conductive tissue or mechanical tissue that cannot be connected to pre-existing conductive or mechanical cells is unlikely. In fact, old conductive cells and even thin-walled fibers in the central core of the stem of *F. columnaris* are often crushed and nonfunctional. The radial rows of axial parenchyma originate as bands of tangential divisions such as those shown in Fig. 32 (arrows). Some of these tangential bands of new axial parenchyma are interspersed between zones of crushed parenchyma (Fig. 32, top). The stem of *F. columnaris* studied was that of a young tree, and probably represents a process found in mature trees (although further studies are necessary). My material of *F. fasciculata* and *F. purpusii* was not old enough to reveal origin of secondary parenchyma by means of meristems of this sort.

4. Cylindrical Meristems Around Vascular Strands

At the periphery of the pith of older stems of *F. columnaris*, there are strands of vascular tissue around which meristems form (Fig. 30 for location; Fig. 31 for histological details). The center of these strands appears composed of phloem because the cells are small in diameter and lack secondary walls. Sieve plates were not observed. The strands also contain tracheary elements as well as parenchyma derived centripetally from the cylindrical cambium. These tracheary elements (Fig. 31, top) have pitting like that of vessel elements, and several perforation plates were observed in them. The strands around which cylindrical meristems form probably still function in conduction, otherwise only parenchyma would be added to them. Certainly elsewhere in the stem center, crushed vessels were observed. The strands that are surrounded by cylindrical meristems may not be true pith bundles. I did not observe any pith bundles in transections across the entire diameter of a young stem of *F. columnaris*. The strands surrounded by meristems may be derivatives of inner portions of secondary xylem on the margins of the pith. Pith parenchyma is characterized by presence of scattered tannin idioblasts, and the strands with cylindrical meristems were not within the zone of tannin idioblasts. The stems available of *F. fasciculata* and *F. purpusii* were not old enough to reveal strands of this sort.

5. Occasional Late Divisions in Axial Parenchyma

In rotary microtome sections of liquid-preserved wood of *F. macdougalii*, tangentially oriented primary walls were observed (Fig. 20, arrows). These primary walls contrast with the lignified walls of the axial parenchyma cells within which they are formed. This is

taken as evidence of the relatively late timing of these divisions, and shows that the divisions did not take place in the vascular cambium. These divisions were not common in the material examined. A search for instances of this phenomenon would be useful, especially in plants of nonsucculent species of *Fouquieria* that bear somewhat swollen bases. My sections of one such base of a young *F. diguetii* plant revealed secondary xylem with more axial parenchyma and fewer fiber-tracheids in zones of secondary xylem than is normal in wood of the nonsucculent species, but without any apparent meristematic action.

6. Cortical Water Storage Tissue Meristems

Scott (1932) showed that in the stems of *F. splendens*, strands of water storage tissue occur in the cortex. Scott (1932, Fig. 7) showed that these strands form a cylindrical network. Scott's findings were confirmed by Nedoff et al. (1985). In addition, they showed that in older stems of *F. splendens*, meristems apparently adding to the water-storage strands encircle each of these strands. These meristems apparently add a modest quantity of cells to the water-storage strands. The meristems surrounding water-storage strands are not illustrated here because the illustrations of Nedoff et al. (1985) are clear and need not be duplicated. Strands of water-storage tissue such as reported in *F. splendens* have been reported by Henrickson (1969c) in stems of *F. columnaris*, *F. diguetii*, *F. ochoteranae*, *F. purpusii*, and *F. shrevei* and in roots of all species of *Fouquieria*, but his illustrations did not show whether meristems surround the water-storage strands.

7. Sclereid Band Maintenance Meristems

Bands or plates of brachysclereids occur in the stem and root bark of various species of *Fouquieria*. In lateral stems several years old of *F. columnaris*, a single band of sclereids is present (Fig. 58, the darker cells in the band are intercalated phloem fibers). As the secondary xylem of the lateral branches increases in diameter, the continuity of the sclereid cylinder in the cortex is potentially disrupted. However, older lateral stems of *F. columnaris* (Henrickson 1969c, Fig. 10f) have two concentric unbroken cylinders of brachysclereids, separated by a cylinder of parenchyma. To maintain integrity as the stem expands, the sclereid cylinders must have a mechanism for addition of sclereids derived from living cells. As shown in Fig. 58, left, discontinuities do form within the sclereid band. These discontinuities are invaded as rapidly as they form by dividing cortical parenchyma cells which may be considered a type of meristem. Derivatives of these rather diffuse and fragmented meristems mature into sclereids (cells intermediate between parenchyma and brachysclereid cells can sometimes be seen in these

areas). The integrity of the sclereid band is thereby maintained.

8. Sclereid Nest Meristems in Bark of Succulent *Fouquierias*

In the three succulent species of *Fouquieria*, there are large sclereid nests (spherical to oval in shape) at the periphery of the stem, internal to the periderm. Some of these sclereid nests become rather large—up to 5 mm in diameter in my material, but probably larger in larger specimens in the wild or in cultivation. The sclereid nests are not so large in stem portions near the tip of the stem, so one would expect addition of sclereids to the nests by some mechanism. In transverse and radial sections of older stems, files of meristematic cells radiating from the surfaces of the sclereid nests were observed (Fig. 59). Because the preparation method used permits one to obtain sections in which unbroken continuity between delicate meristem cells and thick-walled brachysclereids can be demonstrated, one can establish ontogenetic sequences and determine the products of this meristematic action. The meristems occur on all surfaces of sclereid nests, but cell division appears more active on the radial longitudinal faces of the sclereids than on the outer tangential or inner tangential faces of the sclereid nests. Centripetally, the meristem adds brachysclereids to the nests. The fact that files of sclereids with progressively thicker walls extend from the meristem to the portion of the sclereid nest in which cells are arranged randomly shows that the sclereids in files were derived from the meristem. The randomly arranged isodiametric sclereids are in an arc at extreme left in Fig. 59, whereas the sclereids derived from the meristem are elongate and form in files leading outward to the meristem. The centrifugal products of the meristem are parenchyma cells. This added parenchyma presumably permits addition in circumference of the stem, since the limited quantity of sclereids added to the stem does not appear sufficient to account for the circumference increase, although enlargement of the sclereid nests likely plays a subsidiary role.

9. Secondary Starch Sheath Meristems in Bark

A starch sheath external to water storage tissue has been identified in cortex and bark of *Fouquieria* (Scott 1932; Henrickson 1969c). Cell divisions within the starch sheath zone of the cortex of *F. columnaris* were reported by Henrickson (1969c). In the present study, liquid-preserved material permitted study of secondary starch-sheath formation in *F. macdougallii* (Fig. 60, 61). A meristem originates in parenchyma of the outer secondary phloem. The secondary starch sheath is not a continuous ring around the bark in the sense of periderm, but is a discontinuous cylinder from which short

plates branch (Fig. 60). Growth of the secondary starch sheath produces crushing of cells adjacent to the sheath, permitting one to see the secondary starch sheath more readily by the crushed cells outlining it in places. The meristem produces cells both to the outside and to the inside of the stem (Fig. 61, left). These cells soon become filled with starch (Fig. 61, right). The cells of the secondary starch sheath are more densely filled with starch than are parenchyma cells just outside of and adjacent to the secondary starch sheath. Because of its association with secondary phloem, the secondary starch sheath is located toward the inside of the bark, which is thick in mature *F. macdougallii* plants, and there is no evidence of secondary starch sheath formation in outer bark.

CONCLUSIONS

Habit and Organography

The term succulent is applied to the main stems of *F. columnaris*, *F. fasciculata*, and *F. purpusii*, and undoubtedly these stems do contain greater quantities of water per vertical unit than stems of subgenus *Fouquieria*. Such succulents as cacti or cactiform euphorbias, by contrast, have most of their water storage tissue not in wood, but rather in primary cortex and in pith. Transverse sections of the tip of the main stem of *F. columnaris* reveal relatively wide pith and moderately wide cortex, and on this basis that species would probably be considered a succulent. However, young stems of *F. fasciculata* and *F. purpusii* have slender young stems with little water storage in cortex and pith. In mature individuals of all three species, most of the water storage tissue is proliferated axial and ray parenchyma. I know of no other genus in which succulence is achieved by means of these patterns of parenchyma expansion.

The presence in the abovementioned species of some wide rays and some axial parenchyma bands prior to marked cell enlargement in these regions could be considered a precursor form of succulence. Wide axial parenchyma bands (without unusual cell enlargement) can be found in nonsucculent dicotyledons such as *Ficus*, and wide rays characterize nonsucculent families such as Proteaceae.

Wood in subgenus *Fouquieria* clearly reflects the woody habit of subgenus *Fouquieria*. Some of the species have moderately thickened trunks, notably *F. burragei*, *F. diguetii*, and *F. macdougallii* (Henrickson 1969a, 1972). The width of trunks in these species is not achieved by ray or axial parenchyma meristems that confer succulence to subgenera *Bronnia* and *Idria*. The wood of *F. burragei* (Fig. 13), *F. diguetii*, and *F. macdougallii* (Fig. 16, 17) can contain zones of pervasive axial parenchyma rather than diffuse-in-aggre-

gates axial parenchyma and this may add moderately to water-storage capacity.

Another curious characteristic of wood of the genus probably related to the various habits is the presence of large quantities of reaction wood. Reaction wood was recorded in roots and stems of most species, and had the genus been more thoroughly surveyed, very likely reaction wood would have been found in all species. Absence of reaction wood is reported for stems of *F. shrevei* (Fig. 8, 9) and for the lateral branches of *F. columnaris* (Fig. 28, 29). These instances may be related to the relatively light weight of branches: the lateral branches of *F. columnaris* are nonsucculent and limited in diameter, and the habit of *F. shrevei* is that of a shrub of moderate dimensions, like a downsized version of *F. splendens*. If weight is a factor in presence of reaction wood, most *Fouquieria* species have growth forms that would provide a correlation, for main trunks or branches or both are rather thick and heavy compared with the slender stems of such desert shrubs as *Larrea*. If reaction wood is a way of maintaining position of a trunk or branch, heightened water content in wood or in cortex and thick sclerenchymatous bark in *Fouquieria* would intensify the value of reaction wood. If reaction wood corrects leaning, "overcorrection" is likely in view of the constant seasonal changes in water content. Thus, sites of reaction wood formation might constantly shift within the stems. Abundance of reaction wood is characteristic of succulent and semisucculent species of *Euphorbia* (Carlquist 1970). Presence and distribution of reaction wood in succulents is in need of investigation.

The prominence of fibrous tissue in *Fouquieria* suggests that the family is basically woody. The ratio of lengths between fiber-tracheids and vessel elements (Table 1, column 13) is high, and this may be one indicator of a woody ancestry.

Wood of roots in *Fouquieria* is more mesomorphic than that of stems, as revealed in the comparative data of Henrickson (1968) cited above and the data for *F. splendens* in Table 1. Roots in dicotyledons as a whole generally have vessel elements that are wider and longer than those of stems (Patel 1956). Wider and longer vessel elements are criteria of wood mesomorphy (Carlquist 1975). Wood of roots in Fouquieriaceae shows little or no evidence of succulence, in contrast with the succulent roots of other woody plants of dry regions, such as most Moringaceae, some Cucurbitaceae, etc.

Ecology

The water-storage capacity of stems of nonsucculent species of *Fouquieria* is limited. This may be related to the extremely responsive nature of drought decid-

uousness of leaves in the genus. Leaves can wilt and fall in a matter of a few days when moisture availability falls, and new leaves can be initiated soon after a rain. *Fouquieria* habitats characteristically have rather brief wet periods, sometimes several per year, often separated by long dry periods. Cortical water storage tissue may not support persistence of foliage. Rather, Scott (1932) mentions that cortical water storage tissue of *Fouquieria* contains sugars and oils. Certainly axial and ray parenchyma in the genus are rich in starch. Storage of sugars, oil, and starch may support rapid and massive flowering and fruiting, and may also be involved in the rapidity with which leaves can be produced.

Xeromorphic woods have relatively narrow vessels, numerous per unit transection, and short vessel elements (Carlquist 1975). According to those criteria, woods of *Fouquieria* are relatively mesomorphic. The value for the Mesomorphy Ratio of nonsucculent *Fouquieria* species given in Table 1, column 14 is 399, and when all species are averaged, the value is 343, not much lower. Values in this range characterize dry tropical trees and mesic shrubs (e.g., *Pittosporum*, Carlquist 1981), whereas a sampling of desert shrubs yields the value 20.9 and chaparral shrubs the value 66.7 (Carlquist and Hoekman 1985). Two values in *Fouquieria* within the range of dryland shrubs are those of the lateral branches (but certainly not main trunks) of *F. columnaris* (43) and stems of *F. shrevei* (66). The lateral branches of *F. columnaris* are mechanically strong and not at all succulent, and the relatively small size of *F. shrevei* shrubs reflects a drier habitat than does the larger size of shrubs in habitats with greater water availability.

With the exception of those two low values within the genus, Mesomorphy figures for *Fouquieria* are relatively uniform (Table 1, column 14). The wood of the succulent species was analyzed so as to exclude the proliferated parenchyma. Thus, the wood of the succulent species is essentially that of the nonsucculent ones, discounting the added parenchyma. However, the presence of a few vasicentric tracheids and moderately high numbers of vessels per group in the genus tend to indicate moderate but not pronounced degrees of xeromorphy when compared to values for those features in dicotyledons native to southern California (Carlquist and Hoekman 1985).

The fact that the wood of Fouquieriaceae is mesomorphic, with exceptions noted, reflects the exceptional efficiency of drought deciduousness and the effectiveness of transpiration reduction provided by thick waxy periderms. In effect, Fouquieriaceae are shrubs of temporarily mesic habitats, and the wood reflects the wet periods in those habitats. Thanks to highly responsive drought deciduousness and to the exceptionally efficient sealing via periderm against water

loss during dry periods, Fouquieriaceae can be considered mesomorphic trees and shrubs that have mechanisms to survive long dry periods by shutting down photosynthesis, water uptake, and transpiration; and by deferring flowering and fruiting. In deserts of southern California, one can observe that *Fouquieria splendens* can survive a series of dry years by growing not at all, not flowering, and producing foliage on short shoots only and then only when brief moist periods occur.

Phylogeny and Systematics

A good modern monograph of the family has been offered by Henrickson (1972), whose system is followed in the present study (see Table 1). Henrickson's dendrograms and numerical taxonomic analyses, based as they are on a wealth of macromorphological information, are essentially the starting point for concepts of interspecific relationships. Henrickson's (1972) dendrograms show arrangements similar to the molecular-based cladograms of Schultheis and Baldwin (1999). The constructs of both authors show an early separation of the succulent species from subgenus *Fouquieria*. Does this equate to primitiveness of the succulent habit within the genus? Despite the results of his dendrograms (which attempt to depict similarities rather than phylogenetic histories), Henrickson (1972) finds that "*Fouquieria leonilae* and *F. ochoteranae* have the greatest number of basic characteristics that can reasonably be considered primitive in the family, e.g., both are diploid ($2n = 24$), they have dorsiventral leaves, united single traces to each sepal, ten stamens, and 6(–12) ovules per ovary. They are possibly remnants of the basic line of the family."

Where wood anatomy is concerned, the primary phylogenetic question to be asked is whether the habit of parenchyma proliferation in the three succulent species is a primitive character state within the genus. This parenchyma proliferation is not found in any families considered to be related (see below) and perhaps not even elsewhere in dicotyledons, unless in a different form. The possibility that parenchyma proliferation is a symplesiomorphy for the family, and has been lost in the ancestors of subgenus *Fouquieria* is conceivable. The occurrence of a few tardy divisions within axial parenchyma cells of *F. macdougallii* does not offer much support to this concept, because these few divisions are not likely a remnant of the parenchyma proliferation of the succulent species, but a separate phenomenon. If this hypothesis were the correct one, one would have to imagine that the genus basically has the ability for formation of wide rays and axial parenchyma bands and for proliferation of this parenchyma, but also one must suppose that the production

of these formations can and has been suppressed genetically in subgenus *Fouquieria*.

The alternative hypothesis is that parenchyma proliferation is a synapomorphy uniting *F. columnaris*, *F. fasciculata*, and *F. purpusii*. This hypothesis is consistent with the midpoint-rooting tree illustrated by Schultheis and Baldwin (1999, Fig. 4). The three succulent species together branch away from the remainder of the family. The presence of cortical sclereid nests surrounded by meristems in the three succulent species would be another potential synapomorphy for this branch. There are several autapomorphies within *F. columnaris*, certainly: the distinctive lateral branches that undergo limited increase in diameter, highly xeromorphic wood, absence of water storage tissue, and concentric cycles of bark sclereids represent a syndrome of autapomorphies.

No anatomical feature examined in the present study links *F. fasciculata* and *F. purpusii* independently of *F. columnaris* except for absence of the putative *F. columnaris* autapomorphies listed above. Therefore, recognition of *Idria* as a monotypic genus is not supported by information offered here, nor does recognition of three genera seem warranted. The taxonomic treatment of Henrickson (1972) is supported.

Weed features within subgenus *Fouquieria* offer some features of specific significance, but none that would clarify interrelationships within the subgenus. The small size of wood cells in *F. shrevei* is distinctive. Presence or absence of particular crystal types may be species characters (e.g., no crystals have been found in wood of *F. macdougallii* or *F. splendens*), but further investigations are required before these character states can be designated with certainty.

Relationships of Fouquieriaceae

A review of present concepts has been offered in the Introduction. Molecular papers have now narrowed the orders to which Fouquieriaceae are considered closely related. Sympetalous families as a whole are no longer considered to group with Fouquieriaceae, but some sympetalous families have emerged as probably close to Fouquieriaceae. Of the families traditionally assigned to Tubuliflorae, only Polemoniaceae are now considered close to Fouquieriaceae (Prather et al. 2000; Soltis et al. 2000; Thorne 2000). Both Morton et al. (1996) and Soltis et al. (2000) include Fouquieriaceae in an expanded version of Ericales, in which many genera and families formerly placed in Theales and Ebenales as well as the traditional Ericales are included. The idea of an ericalean placement first attained prominence with the discovery that iridoid compounds in *Fouquieria* are like those in Ericales (Dahlgren et al. 1976).

Data from wood anatomy that can be cited as fa-

voring placement of Fouquieriaceae in Ericales sensu lato include unspecialized character states: fully bordered pits on fiber-tracheids (albeit sparser than those on tracheids); diffuse axial parenchyma (or a modified form, such as diffuse-in-aggregates), and Heterogeneous Type II rays (for discussion of the phyletic status of these character states, see Carlquist 1988).

The proposed position of Fouquieriaceae within Ericales s.l. varies. The cladograms offered by Prather et al. (2000) and by Soltis et al. (2000) are not congruent, although they have much in common. Sampling of more species within Ericales s.l. will doubtless lead to refinements in DNA-based cladograms, with consequent better understanding of the placement of Fouquieriaceae. Ericales s.l. are stereotypically considered plants of mesic and often acidic habitats. One can hypothesize that mutations and time have been sufficient for ancestors of Fouquieriaceae to shift into new edaphic and climatic preferences. The adaptation of Fouquieriaceae to areas of marked seasonal drought is shown above to be minimal in terms of quantitative wood features, but distinctive compensations (sensitive drought deciduousness, impervious periderm, succulence in the species of subgenera *Bronnia* and *Idria*) seem overriding, necessitating minimal alterations in wood to xeromorphy. One can also question the stereotypes of edaphic and climatic preferences of Ericales. For example, the phenomenal success of *Arctostaphylos* (Ericaceae) in arid areas of the southwestern United States has involved adaptation to prolonged seasonal drought and to soils not notably acid.

Nevertheless, Fouquieriaceae represent a series of remarkable adaptations to seasonally very arid areas of North America. Preconceptions that Fouquieriaceae must be derived from or related to plants also capable of life in dry and even saline habitats, such as Tamaricaceae and Frankeniaceae (see Goldberg 1986) may have influenced earlier workers, but the evidence supporting a placement within Ericales s.l. now seems difficult to dispute. Tamaricaceae and Frankeniaceae are now referred to a redefined Caryophyllales s.l. (see Soltis et al. 2000). The remaining questions involve not so much ordinal location of Fouquieriaceae, but refinement of ideas concerning which families should be included in that order and how those families are cladistically arranged within the order.

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