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A TAXONOMIC REVISION OF THE FOUQUIERIACEAE

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INTRODUCTION

The Fouquieriaceae is a small family restricted to arid portions of Mexico and adjacent southwestern United States. It contains woody small trees and shrubs and three succulent species with greatly expanded xylem water-storage reservoirs. The family is distinguished by a number of unique characteristics including mode of spine development, extent of the hard decurrent ridges, anastomosing cortical water-storage tissue (Henrickson, 1969a) and changes in ovary placentation from flower to fruit. Numerous other xeromorphic adaptations distinguish this family from all others. Phylogenetic relationships of the family are not known. Angiosperm phylogenists have placed it in the Polemoniales, Tamaricales or Ebenales (Henrickson, 1967).

The first comprehensive taxonomic treatment of the family was undertaken by Nash (1903), who recognized two genera: *Fouquieria* with seven species and the monotypic *Idria.* Since that time four additional species have been described and considerable information has been gathered on vegetative and floral structures of two previously poorly known species intermediate between the woody species of *Fouquieria* and the succulent *Idria.* In this taxonomic revision the generic status has been revised and the family is treated as consisting of a single genus, *Fouquieria,* composed of three subgenera. The only taxonomic changes at the species level involve *F. splendens. Fouquieria campanulata* Nash (consisting of two varieties) has been changed to a subspecies of *F. splendens* Engelm. in Wisliz. and a new subspecies is designated for the southern populations of *F. splendens* in central Mexico. As the names of new taxa and combinations are valid as of the date of publication they are used throughout this paper.

In the following sections information on ecology, vegetative and floral anatomy, pollination relationships and cytology is presented or summarized. Much of this data is used in a taxometric analysis of the family. The data on phenetic relationships from this analysis serve as a guide for the taxonomic treatment of the Fouquieriaceae.

MATERIALS AND METHODS

Field studies and collections of Fouquieriaceae have been made during more than twelve excursions to various portions of Mexico from 1963 to 1972. Personal collections form the bulk of material used in this study. Specimens from the following herbaria designated by standard herbarium abbreviations (Lanjouw and Stafleu, 1964) have been studied and annotated: A, ARIZ, AHFH, CAS, DS, GH, MEXU, NMC, NY, P, POM, RSA, SD, SMU, TEX, UC, UNM, USN, WIS. The first set of my collections including voucher specimens for the present study is deposited in the herbarium of Rancho Santa Ana Botanic Garden (RSA). Duplicates have been sent to ARIZ, CAS, MEXU, MICH, NY, USN, P and others.

Prepared slides of leaf and floral material for anatomical investigation were prepared by standard paraffin procedures, stained in Safranin O, counterstained in fast green in accordance with the techniques of Johansen (1940). Methods employed in cytological and taxometric studies are discussed in the respective sections.

ACKNOWLEDGMENTS

The writer is indebted to all who contributed information, guidance and material supplies during my studies on the Fouquieriaceae, particularly to Drs. R. F. Thorne, P. A. Munz, L. W. Lenz, J. W. Carmichael, R. K. Benjamin, J. R. Hastings, R. Moran, S. Carlquist, R. Straw, E. Rutherford, R. Schlising, as well as to Messrs. Miron Kimnach, Dave Verity, Charles Glass, Bob Gustafson, Bill Lockwood and the Ed Gays. The support and assistance of Marylin Henrickson and Jennie Nelson are also greatly appreciated. Dr. P. A. Munz kindly supplied the Latin descriptions. Line drawings were made by Frances Runyan; her patience and expertise are gratefully acknowledged. Use of facilities at Rancho Santa Ana Botanic Garden and Los Angeles County Museum of Natural History made available through Drs. L. W. Lenz and F. S. Truxel is greatly appreciated. Grants from the San Gabriel and Los Angeles chapters and the National Society of the Cactus and Succulent Society of America have supported publication. Mabel Solberg and the late Mrs. Grace Henrickson have kindly financed several field expeditions. Thanks is also expressed to the curators of the above mentioned herbaria for specimen loans.

ECOLOGY AND VEGETATIVE STRUCTURES

ECOLOGY.—Plants of the Fouquieriaceae range from western Baja California, northern Arizona and eastern Texas (*Fouquieria splendens*) to southeastern Oaxaca (*F. formosa* H.B.K.). The five species of southern Mexico, *F. leonilae* Miranda, *F. ochoterenae* Miranda, *F. purpusii* Brandegee, *F. fasciculata* (Roem. et Schult.) Nash and *F. formosa* usually occur in arid portions of vegetation types designated as tropical deciduous forest and arid tropical scrub by Leopold (1950). These areas are characterized by late summer precipitation averaging 400 to 700 mm annually. *Fouquieria formosa,* however, extends into parts of Michoacan and southern Oaxaca averaging 1,000 and 300 mm rainfall respectively. Species of northern Mexico and adjacent United States occur mainly in desert habitats. *Fouquieria columnaris* (Kellogg) Kellogg ex Curran, *F. burragei* Rose, *F. diguetii* (van Tiegh.) Johnston and *F. macdougalii* Nash are centered in the Sonoran Desert in areas averaging 50 to 350 mm rainfall (Hastings and Humphrey, 1969a, b). The latter two species extend into areas of tropical deciduous forest vegetation in the Cape region of Baja California and to the foothills of the Sierra Madre Occidental in Sonora and Sinaloa—areas receiving as much as 400 to 1,000 mm annual rainfall (Tamayo, 1962). *Fouquieria splendens* is the widest ranging species of the family, extending from the Sonoran desert of Baja California and Sonora through southwestern United States to the Chihuahuan Desert and adjacent mesquite grasslands on the central Mexican plateau—regions averaging 40 to 500 mm annual precipitation. In portions of Coahuila it occurs with *F. shrevei* I. M. Johnston, the only species restricted to the Chihuahuan Desert.

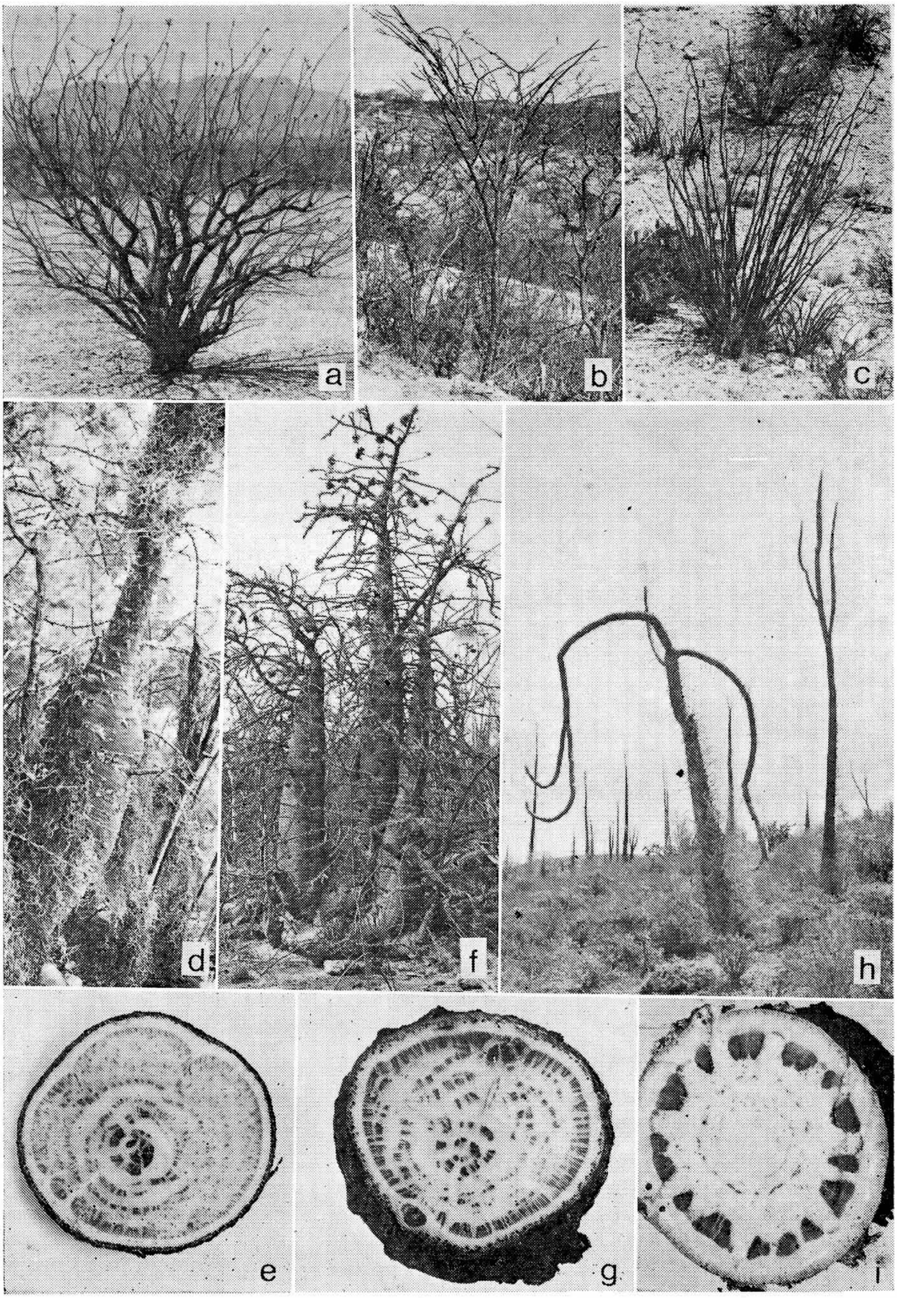
Of the eleven species recognized in the family, six can be considered narrow endemics. *Fouquieria fasciculata, F. purpusii, F. leonilae, F. ochoterenae, F. shrevei* and *F. burragei* are all known only from a few localities, though they may be locally common. Though occupying much larger ranges, *F. columnaris* and *F. splendens* ssp. *campanulata* (Nash) Henrickson can also be considered endemic to central Baja California and Durango respectively.

Several species are associated with specific edaphic conditions. Miranda (1942a) noted that *Fouquieria ochoterenae* occurs mostly on outcroppings of selenite and fibrous gypsum near its type locality. *Fouquieria shrevei* is restricted to outcroppings of nearly pure gypsum in Coahuila (Johnston, 1941). The occurrence of *Fouquieria fasciculata* with selenic and gypseous soils was also noted by Miranda (1950), while the related *F. purpusii* occurs on limestone or exposed basaltic soils (Smith, 1965). In addition, I have observed populations of *F. leonilae* and *F. splendens* ssp. *campanulata* growing on whitish, highly calcareous soils, though the latter is by no means restricted to these soils. In the Chihuahuan desert and parts of Arizona, *F. splendens* ssp. *splendens* is commonly associated with limestone outcroppings (Whittaker and Niering, 1968). In contrast, *F. diguetii, F. macdougalii, F. burragei, F. columnaris* and *F. formosa* occur on a wide range of soil types.

The effect of continual grazing and other aspects of man's impact on the environment is not known for most species. Young plants develop heavy armaments of spines which give them some protection from herbivores. It has been noted that populations of *F. splendens* may increase with heavy grazing (Whittaker and Niering, 1968; Hastings and Turner, 1965).

Ecological data are presented following the description for each species, and include vegetation associations (following Leopold, 1950), associated species, soil associations and precipitation data (from Hastings and Humphrey, 1969a, b; Vivó and Gómez, 1946; and Tamayo, 1962).

GROWTH HABITS.—The Fouquieriaceae is characterized by a wide diversity of growth habits from small woody shrubs to columnar stem succulents (Henrickson, 1969b). The basic growth form, a shrubby-small tree habit, occurs in six species: *Fouquieria ochoterenae, F. leonilae, F. macdougalii, F. diguetii, F. burragei,* and *F. formosa.* It is characterized by one or more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basal trunks bearing a series of ascending, ramifying lateral stems with horizontal to pendulous upper branches. New growth occurs in distinct long-shoot increments. Lateral stems are straight if new growth increments develop terminally but variously crooked if long-shoots develop from the margins of stem tips or from axils. Branching results from production of a pair of lateral long-shoots from a stem tip (presumably if the stem apex is damaged) or less frequently from divergent axillary long-shoots usually near the stem tip. In older plants new branches are occasionally initiated near the base of major stems. The amount of branching and general robustness of a plant varies with species but also with moisture conditions. For example, *F. diguetii* (Fig. 1a) in arid regions is often only a small shrub with few tortuous, ascending, infrequently branched stems, but in moist regions is characteristically a small tree with numerous upright branched stems. A very distinctive habit characterizes *F. ochoterenae* (Fig. 1b): lateral branches are straight and widely divergent. Branching is infrequent, accomplished either by pairs of divergent terminal shoots or subterminal axillary shoots. In either instance branches are widely divergent, giving an impression of a dichotomous branching pattern.

A derivative candelabraform or "ocotillo" growth habit—characterized by a reduced, stocky trunk bearing straight wand-like, ascending stems—occurs in *F. splendens* and *F. shrevei* (Fig. 1c). Stem elongation by terminal long-shoot increments accounts for the straight stems. Branching, either terminal or axillary, occurs only in older plants.

The remaining species are distinguished by highly parenchymatized central xylary water storage reservoirs. In *Fouquieria fasciculata* and *F. purpusii* the succulent tissue is restricted to the basal or central portion of the trunk—the terminal stems are woody (Fig. 1 d–g). Water storage tissue forms a distinct enlarged basal bole in *F. fasciculata* but extends much farther up the main stems in *F. purpusii*. In both species succulent xylary tissue gradually intrudes into upper woody stems as the reservoirs expand

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Fig. 1. Growth habits of Fouquieriaceae.—a. *Fouquieria diguetii* with shrubby habit. Near Guaymas, Sonora. (*Henrickson 1569*).—b. *Fouquieria ochoterenae* showing characteristic dichotomous branching pattern and outwardly arching stems. Near Acatlan, Puebla. (*Henrickson 2117*).—c. *Fouquieria splendens* ssp. *campanulata*. Candelabraform habit consisting of ascending straight branches is shown. Near Santiago Papasquiaro, Durango. (*Henrickson 1742*).—d–e. *Fouquieria fasciculata*.—d. Growth habit showing expanded basal trunk ca. 25 cm in diameter and slender upper woody stem. (*Henrickson 2071*).—e. Cross section of succulent basal stem ca. 14 cm in diameter, stained with phloroglucinol to show fragmented central xylem core and displaced tracheary strands among parenchymatous tissue. (*Henrickson 4331*).—f–g. *Fouquieria purpusii*.—f. Growth habit showing distribution of succulent tissue far up central stems. Plant ca. 12 ft tall. (*Henrickson 2142*).—g. Cross section of stem ca. 15 cm in diameter stained as in c showing distribution of tracheary strands. (*Henrickson 4296*).—h–i. *Fouquieria columnaris*.—h. Growth habits. Central plant has lost apex twice. Lateral branches have collapsed, bending downward and later growing upward. Background plants show characteristic erect growth. Note lateral nonsucculent branches.—i. Cross sections of central succulent stem showing spaced distribution of solid xylem and internal tracheary strands. (*Henrickson 2793*).

(Henrickson, 1968, 1969c). The two taxa are also characterized by distinctive, smooth, shiny trunks with persistent epidermis and rigid wedge-shaped segments of bark which form under the decurrent ridges.

The growth habit of *Fouquieria* (*Idria*) *columnaris* is by far the most distinctive (Fig. 1 h, i). The conical, tapering central trunk is succulent from the base to the apex where a primary thickening meristem contributes to the initial succulence (Henrickson, 1968). The thick cortex and inner parenchymatous xylem combine to form an extensive water-storage reservoir. Solid xylem forms only a small portion of the inner stem (Fig. 1i). The xylem is separated into internal tracheary strands by intrusion of nonlignified xylem parenchyma. Inner xylem parenchyma forms series of tangentially and radially oriented meristematic plates which add to the succulent tissue as they displace tracheal strands from the peripheral xylem cylinder (Humphrey, 1935; Henrickson, 1969a). Mature plants are commonly 14 or more meters tall (Humphrey and Humphrey, 1969; maximum 25 m, Humphrey, 1970) and may consist of a single unbranched or variously forked central trunk. As solid xylem forms only a small portion of the stem, stem strength is provided by internal turgor pressure. During droughts, turgor decreases and central or lateral trunks may collapse and bend downward. Distinctive series of lateral woody branches without the characteristic cortical water-storage tissue occur in spiral helices on the central succulent trunks. These may be replaced by series of short-shoot spur branches (Humphrey, 1935; Henrickson, 1969a, c).

STEM AND ROOT STRUCTURE.—Stems of Fouquieriaceae are heteroblastic, consisting of spinose long shoots bearing axillary short shoots in distinct phyllotactic patterns. Long shoots have simple petiolate leaves, often with reduced lamina. Short shoots bear fascicules of short-shoot leaves after even sparse rainfall and are much more important in over-all production of assimilates.

A number of distinct phyllotactic patterns of nodal arrangement can be distinguished in the family. In most species they provide consistent taxonomic characters; a 2/5 phyllotactic pattern characterizes *F. ochoterenae*, *F. leonilae*, *F. formosa*, a 3/8 pattern *F. purpusii*, *F. fasciculata*, and a 5/13 pattern *F. splendens* and *F. shrevei*. In contrast, stems of *F. macdougalii*, *F. diguetii* and *F. burragei* may have either 2/5 or 3/8 phyllotactic patterns. In *F. columnaris*, the thickened central stems, which have a primary thickening meristem, have a 8/21 phyllotactic pattern, while in the slender lateral branches, the pattern ranges from 2/5 to 5/13. The direction of phyllotactic helices may be constant or may occasionally reverse between successive increments.

Stems are distinguished by the elongate spines produced in association with long-shoot leaves in a manner unique to the angiosperms. The rigid fibrous tissue of the spines continues down the outer stem cortex to form distinct tapering decurrent ridges. In all but three species, the decurrent ridges completely cover young stems and are separated only by deep or shallow furrows. As stems enlarge, decurrent ridges become tangentially separated and may eventually detach from the stem. The underlying translucent periderm consisting of alternating fibrous and suberinous layers usually exfoliates from older stems in thin papery sheets. In contrast, *F. fasciculata* and *F. purpusii* have widely separated decurrent ridges. A very rigid periderm forms only under decurrent ridges—the intervening area is covered with a persistent epidermis. The variation in structure of periderm has been presented by Scott (1932) and Henrickson (1969a).

The position of decurrent ridges also affects organization of underlying cortical tissues. The anastomosing pattern of translucent furrows is reflected in the outer cortex by systems of green assimilatory tissue and series of tightly packed sclereid nests. The inner cortex consists mainly of starch storing tissue, except for a unique system of water-storage tissue which also conforms to the anastomosing pattern. The structure of stem cortex has been described for various species by Scott (1932), Reiche (1922), Humphrey (1935), and for the entire family by Henrickson (1968, 1969a). Xylem tissue forms a continuous solid core in all but three species (*F. fasciculata*, *F. purpusii*, and *F. columnaris*) which develops an extensive system of xylary water storage reservoir formed by proliferation of nonlignified xylem parenchyma (Humphrey, 1935; Henrickson, 1968, 1969c) (Fig. 1 e, g, i).

Root systems in the Fouquieriaceae are shallow but laterally extensive (Cannon, 1911). Lateral roots have relatively thickened periderm composed entirely of suberized cells. The thickened cortex contains both starch and water-storage tissue but not in an organized pattern. The cortex also develops peripheral nests of brachysclereids (Henrickson, 1969a).

LEAF ORIGIN AND STRUCTURE.—Long- and short-shoot leaves of the Fouquieriaceae, though similar in lamina structure, differ greatly in their association with the stem. Long-shoot leaves have long petioles, the abaxial side of which develops into a rigid, conical spine of variable extent (Henrickson, 1969a). The conical spine is composed of narrow, elongate fibers which continue from the spine through the underlying outer stem cortex to form the tapering, hard, decurrent ridge characteristic of the family. The adaxial portion of the petiole contains the single vascular bundle and develops into characteristic leaf petiole tissue (Fig. 2 a, b). As the long-shoot matures, an abscission layer forms between the leaf and spine tissue. The leaf tissue eventually falls away, leaving the rigid, sharp spine. Short-shoot leaves are produced in fascicles on axillary short-shoots (lateral branches which do not undergo internodal elongation). They have relatively short petioles and develop a perpendicularly oriented abscission layer near the base. They are not associated with spines (Fig. 2f).

The peculiar development of long-shoot leaves and associated spines has been described by several authors (Engelmann, 1883; Poisson, 1895; Van Tieghem, 1899; Robinson, 1904; Reiche, 1922; Humphrey, 1931). Several have regarded the spine to be of cortical origin. This interpretation is supported by the fact that (1) the fibrous tissue of the spine is directly continuous with that of the stem cortex forming the decurrent ridge, and

(2) the spine forms below the abscission layer, which is usually considered a junction between leaf and stem. If the spine is indeed formed by an extension of cortical tissue into the petiolar region, this should be revealed by a comparison of the origin of long- and short-shoot leaves. Such a comparison was undertaken with *Fouquieria burragei* and *F. columnaris* (lateral stems). The long-shoot apical meristems in both species are very slightly domed and in *F. burragei* (Fig. 2 a, b) have a maximum phase diameter of 180 μ and a minimum phase diameter of 125 μ. There appear to be three tunica layers in active apical meristems of *F. burragei* and two in *F. columnaris*. Lateral meristems are more flattened at minimal phase (Fig. 2c) and the extent of tunica is difficult to determine. In both apical and lateral meristems, leaf primordia originating at the periphery of the meristem are initiated by periclinal divisions in the second tunica and subadjacent layers in a manner characteristic of angiosperms. Leaf buttresses of both initially elongate by apical growth and later by intercalary growth to form the leaf axis. Both long- and short-shoot leaf axes are very similar in size during early stages of development. As growth continues, the basal portion of the long-shoot leaf axis expands in thickness due to a proliferation of cells dividing along many planes (Fig. 2 a, b); this is the first evidence of the eventual petiolar differences between long- and short-shoot leaves. As long-shoot leaf axes elongate, cells which eventually will differentiate into spine fibers elongate (Fig. 2 d, e) while adjacent cells divide in a plane perpendicular to the leaf axis. The long-shoot spine, therefore, is formed from cells derived from the leaf axis (petiole), and the contention of Robinson (1904) that the spine arises from a proliferation of cortical tissue into the petiole is not supported. The development of the fibrous spine-decurrent ridge structure is best described as the product of a genetically based, auxin controlled morphogenetic unit which affects both cortical and petiolar tissues, and which in turn affects the eventual position of the abscission layer.

Production of long shoots requires a large expenditure of energy and moisture and their successful formation is dependent on an adequate supply of moisture during the period of development (Darrow, 1943). If moisture is insufficient, developing long shoots may cease elongation earlier or die back entirely. Short shoots, on the other hand, can produce fascicles of leaves soon after rains without a large expenditure of energy. If moisture is available for only a brief period, the leaves abscise and another series is produced soon after the next rain (Darrow, 1943). This allows exploitation of variable moisture resources with a minimal investment of energy.

After short-shoot leaves fall away, a series of immature leaves up to 1.5 mm long forms a conical bud over the lateral meristem. The outermost overlapping leaves dry out and serve as bud scales protecting the inner leaves and lateral meristem. After a rain, the inner reduced leaves quickly elongate and form a fascicle of mature leaves—often within 48 hours (Darrow, 1943). In older stems, short-shoots protrude slightly and are protected by the basal segments of short-shoot petioles. Woody stems of *F. purpusii*, *F. fasciculata* and *F. columnaris* may form short spur branches up to 5 mm in diameter and 15 mm in length. Much larger spur branches up to 7 mm in diameter

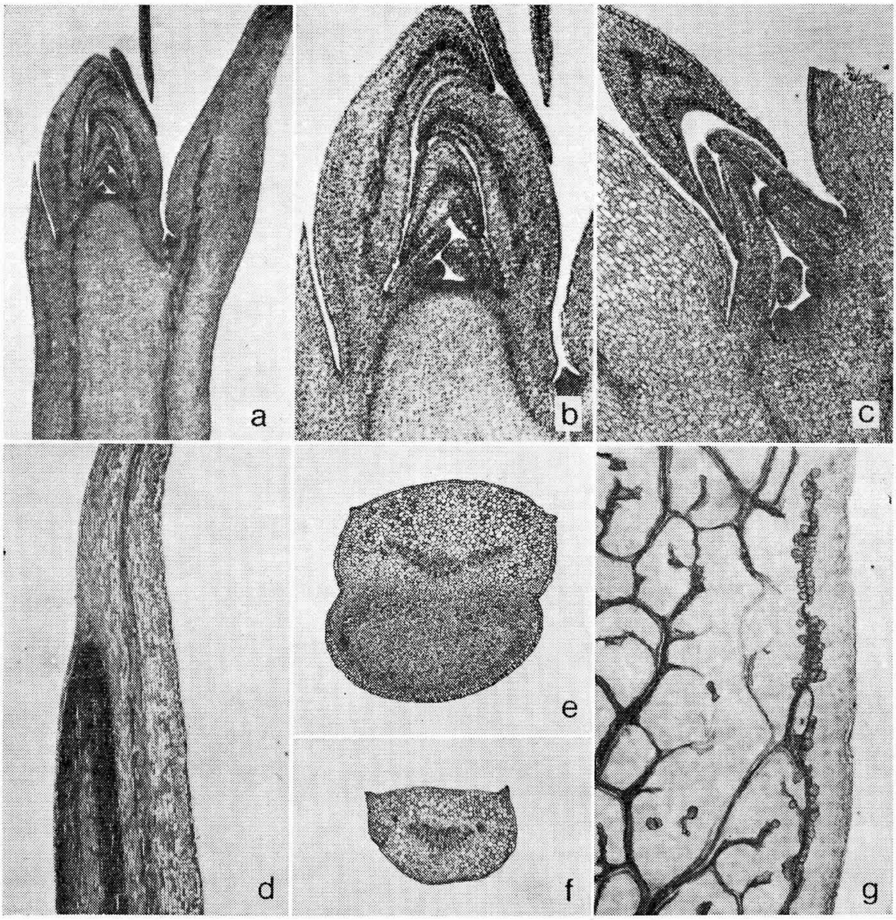

Fig. 2. Leaf development and structure.—a–e. *Fouquieria burragei.*—a–b. Longitudinal sections of stem apex.—a. Showing structure and orientation of developing long-shoot leaves. Thickened abaxial portion of petiole develops into long-shoot spine.—b. Same as a showing thickening of leaf axes.—c. Axillary short-shoot meristem and leaves. Short-shoot leaves are initially identical to long-shoot leaves but do not develop excessive basal thickening.—d. Longitudinal section of long-shoot leaf petiole showing spine and leaf portions. Note vascular strand.—e. Cross section of immature long-shoot leaf petiole. Upper half with vascular bundle continues to lamina, lower half forms conical spine. (*Henrickson 4334*).—f. *Fouquieria diguetii.* Cross section of short-shoot leaf petiole base. (*Henrickson 2046*).—g. *Fouquieria columnaris.* Cleared leaf stained to show pattern of vascular tissue along margin. Note free vein endings, characteristic water storage tracheids along marginal veins, occasional isolated tracheids within areoles. (*Henrickson 1545*).—a ×14; b ×28; c ×35; d ×13; e, f ×20; g ×30.

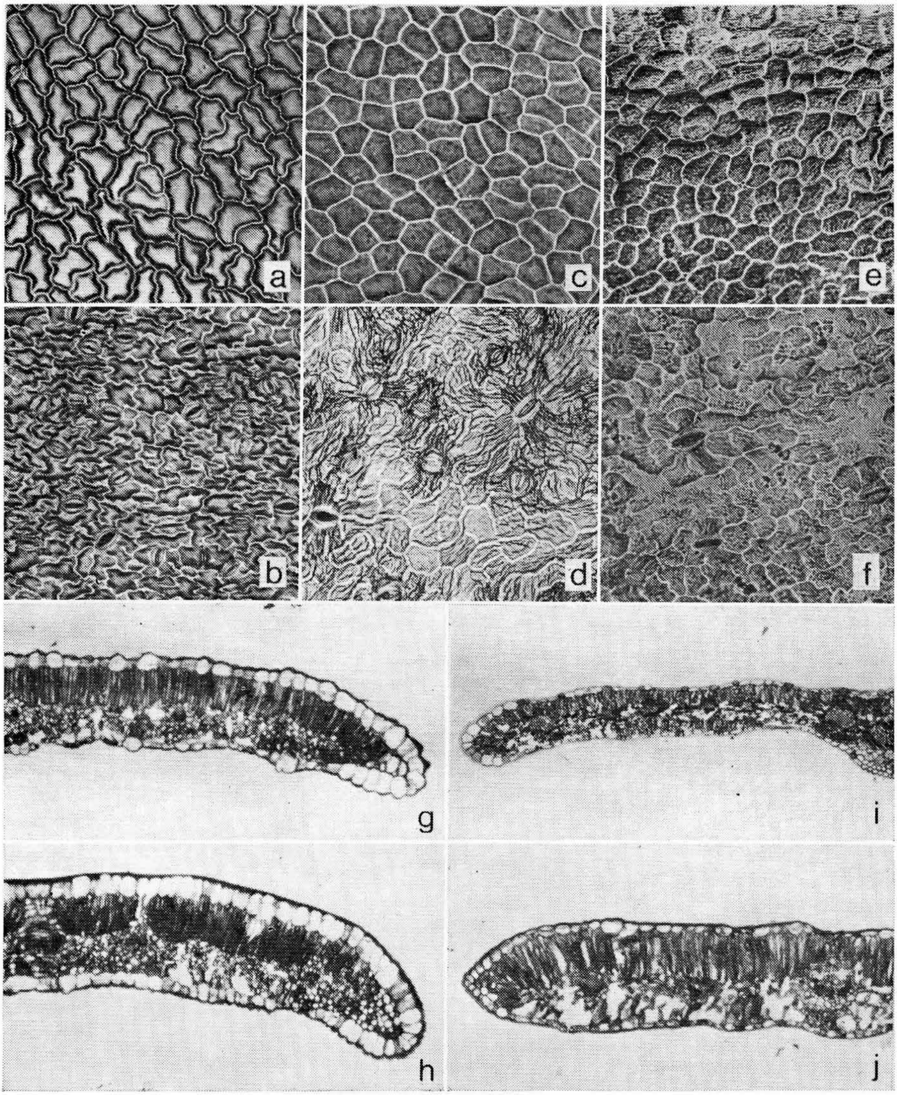

Fig. 3. Structure of dorsi-ventral leaves.—a–f. Surface relief patterns as observed from leaf peels made with Archer's Adhesive.—a–b. *Fouquieria leonilae*.—a. Ventral surface showing outline of epidermal cells and lack of stomata and cuticular relief.—b. Dorsal surface. Note smaller cells, stomata, lack of strong cuticular relief. (*Henrickson 2164*).—c–d. *Fouquieria fasciculata*.—c. Ventral surface. Note lack of stomata, punctate cuticular relief pattern.—d. Dorsal surface. Note cuticular relief pattern on ridges radiating from stomata. (*Henrickson 2171*).—e–f. *Fouquieria purpusii*.—e. Ventral surface, lacking stomata but with slight striate relief pattern.—f. Dorsal surface with striate patterns radiating from stomata. (*Henrickson 2147*).—g–j. Cross sections of short-

and 55 mm long develop on the succulent central trunk of *F. columnaris* (Fig. 30h).

While long- and short-shoot leaves within each species are basically identical in lamina structure, considerable variation in internal mesophyll structure occurs within the family. Basic hypostomatic, dorsi-ventral leaves with stomata restricted to the dorsal (abaxial or lower) side and palisade cells mainly occurring on the ventral (adaxial or upper) side characterize four species, two from subgenus *Fouquieria* (*F. leonilae, F. ochoterenae*) and two from subgenus *Bronnia* (*F. fasciculata, F. purpusii*) (Fig. 3). These four species occur in a tropical scrub vegetation of southern Mexico with a relatively uniform summer wet season and annual rainfall of 400–700 mm. They usually retain their leaves throughout the summer and only seldom produce leaves in other seasons. The adaxial or ventral leaf epidermis is without stomata and is subtended by a single layer of narrow, elongate palisade cells. The abaxial or dorsal epidermis contains stomata and the adjacent mesophyll tissue may consist entirely of spongy mesophyll (*F. leonilae*), or a short but definite palisade layer (*F. ochoterenae*), or a sparse palisade layer (*F. fasciculata, F. purpusii*) (Fig. 3 g–i). The dorsal palisade cells are usually shorter than the ventral except in *F. purpusii,* the only species with erect leaves. A spongy mesophyll layer of variable extent is present in all species. Stomata density, relative thickness of ventral and dorsal palisade and spongy mesophyll layers for these four species are presented in TABLE 1.

The only available leaf material of *F. leonilae* was obtained from plants cultivated in a greenhouse at University of California, Los Angeles. Humphrey (1935) noted greenhouse-cultivated specimens of *F. columnaris* had dorsi-ventral leaves while desert specimens had isolateral leaves. Little difference in internal mesophyll composition was noted, however, between field- and greenhouse-grown leaves of *F. ochoterenae, F. fasciculata* and *F. formosa.*

The remaining seven species have amphistomatic, isolateral leaves with stomata and palisade cells on both surfaces (Fig. 4). All but *F. formosa* occur in the more arid desert regions and receive sporadic rains averaging 100–400 mm annually and leaves may be produced several times during the year. In *Fouquieria formosa, F. macdougalii, F. diguetii,* and *F. columnaris* leaves are isolateral but not quantitatively so (Fig. 4; Table 1). Stomata are more dense on the dorsal surface, while palisade layers are noticeably thinner on the dorsal side. The palisade layers constitute about two-thirds of the internal leaf thickness except in *F. columnaris* where the much thickened leaves have an extensive spongy mesophyll layer. Leaves of *F. splendens,*

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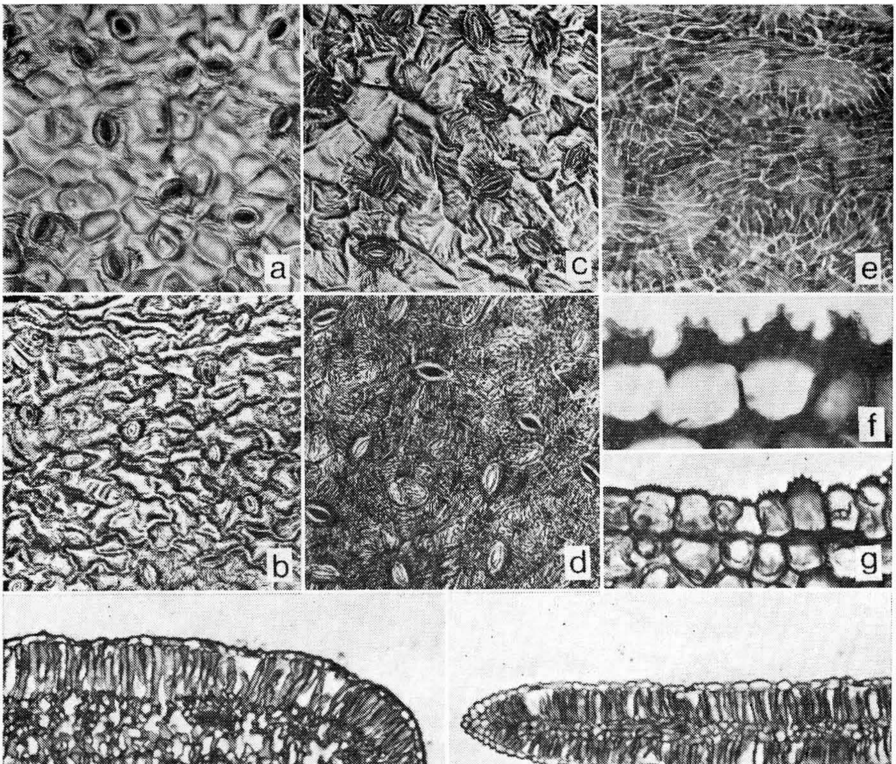
shoot leaves showing distribution of palisade and spongy mesophyll tissue and relative size of epidermal cells.—g. *Fouquieria leonilae.* (*Henrickson 2164*).—h. *Fouquieria ochoterenae.* Note large epidermal cells. Marginal cells form conspicuous scarious margins. (*Henrickson 2117*).—i. *Fouquieria purpusii.* (*Henrickson 2147*).—j. *Fouquieria fasciculata.* (*Henrickson 2171*). Leaf peels made from cultivated progeny.—a–g ×107; g–j ×48.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F. shrevei and *F. burragei* on the other hand are more quantitatively isolateral with stomata density and palisade layers equally developed on both dorsal and ventral portions (Fig. 4; Table 1). In these species about three-fourths of the internal leaf thickness consists of palisade cells.

The occurrence of isolateral leaves in a group with basic dorsi-ventral leaves suggests an evolutionary change towards greater xeromorphy (Shields, 1950). Species with dorsi-ventral leaves occur in tropical scrub vegetations with a moderate, relatively reliable annual rainfall. Species with more isolateral leaves occur in relatively arid deserts (except *F. formosa*) where rain is more sparse and sporadic. This change is accompanied by an increase in palisade tissues from about one-half of the internal leaf tissue in dorsi-ventral leaves to about three-fourths in isolateral leaves. As the arrangement of chloroplasts in palisade cells increases the assimilatory capabilities of the leaves by exposing more chloroplasts to sunlight (Shields, 1950), plants dependent on sporadic rain could produce larger quantities of assimilates during the brief periods with leaves. As these plants may go a year or more without rain, this becomes a significant factor in their survival.

A single arc of vascular tissue extends from the vascular cylinder (Fig. 2 e, f) (a unilacunar, one-trace node) and this branches in a pinnate venation pattern. Minor venation consists of closed areoles with free vein endings. Isolated tracheids or clusters of tracheids were observed rarely in areoles in most species (Fig. 2g). Major veins and veinlets at the distal periphery of leaves commonly are associated with numerous, enlarged, pitted water-storage tracheids. Bundle sheath extensions consisting of elongated parenchymatous cells lacking chlorophyll occur on the midrib of all species—usually to the leaf tip. They also extend to major lateral veins in *F. formosa, F. leonilae* and *F. macdougalii,* and continue to the larger areoles in *F. ochoterenae.* Bundle sheaths and extensions often contain druses (rarely also cuboidal crystals) of calcium oxalate. Special strengthen-

Fig. 4. Structure of isolateral leaves.—a–e. Surface relief patterns as observed from leaf peels made with Archer's Adhesive.—a–b. *Fouquieria splendens.*—a. Ventral surface; cuticular relief restricted to radial series from stomata. (*Henrickson 7087*).—b. Dorsal surface with general striate pattern. (*Henrickson 7088*).—c. *Fouquieria formosa.* Dorsal surface showing strong open relief pattern. (*Henrickson 2171*).—d. *Fouquieria burragei.* Dorsal surface with dense relief pattern. (*Henrickson 7092*).—e–f. *Fouquieria columnaris.*—e. Fine striate-reticulate cuticular relief pattern is shown.—f. Cross section of epidermis showing high cuticular ridges and thickened outer cell wall. (*Henrickson 7089*).—g. *Fouquieria macdougalii.* Cross section of epidermis showing cuticular ridges and thin cell walls. (*Henrickson 7090*).—h–m. Cross sections of short-shoot leaves showing relative distribution of palisade layers and spongy mesophyll.—h. *Fouquieria columnaris.* Note equal thickness of palisade and spongy mesophyll layers. (*Henrickson 1545*).—i. *Fouquieria burragei.* (*Henrickson 4334*).—j. *Fouquieria shrevei.* Note very broad scarious margins composed of epidermal and mesophyll cells. (*Henrickson 1825*).—k. *Fouquieria formosa.* Dorsal palisade layer is poorly developed. Note stomata in ventral and dorsal epidermis. (*Henrickson 4325*).—l. *Fouquieria splendens.* Note nearly complete isolateral structure of leaf. (*Henrickson 4029*).—m. *Fouquieria macdougalii.* Note thinness of leaf and unicellular trichomes. (*Henrickson 2448*).—a–d ×107; e–g ×825; h–m ×48.

ing tissues (collenchyma and sclerenchyma) are lacking, but in *F. fasciculata*, *F. purpusii* and *F. ochoterenae*, elongate fiber-like tracheids and occasional phloem fibers with walls to 3 μ in thickness are present in major veins.

Epidermal cells are tabular to somewhat isolateral in shape and are rounded, angular or wavy as seen in paradermal view (Figs. 3 a–f; 4 a–e). Dorsal and ventral epidermal cells are equal in thickness in all species except *F. ochoterenae* which has much larger ventral epidermal cells. The outer wall is usually slightly thickened, but is particularly so in *F. shrevei* (13 μ). Cuticle layers are surprisingly thin, exceeding 2–3 μ only in *F. purpusii* (4–4.5 μ), *F. columnaris* (5 μ) (Fig. 4f), and the dorsal surface of *F. ochoterenae* (4–7 μ). Cuticular relief patterns formed by narrow ridges 1.5–6 μ in height are common (Fig. 4g). The patterns are variable both inter- and intraspecifically. The ventral surfaces of dorsi-ventral leaves are without relief or are slightly punctate (Fig. 3 a, c, e). Relief patterns on stomatiferous epidermises vary from small series of ridges radiating from the margins of guard cells (with other cells smooth, Fig. 4a), to heavier radiating ridges (with other cells slightly to heavily striate with parallel but meandering ridges either localized in a mosaic pattern or continuous, Fig. 4d). In *F. columnaris* and *F. ochoterenae* (dorsal surface only) the outer tangential cell walls are greatly thickened in the center and relief consists of branched ridges radiating from the centers to the margins of the cells (Fig. 4 e, f). In all species, cuticular relief is more extensive on the dorsal leaf surface (Table 1). Unicellular trichomes characterize certain populations of *F. formosa*, *F. macdougalii* and are rare in *F. burragei* and *F. diguetii*. They are usually more frequent on the basal portions of the dorsal leaf surface.

Stomata are diffuse in distribution (but lacking over major veins) and have no specially arranged subsidiary cells; they are anomocytic. Stomata density which usually decreases in larger leaves, is given in Table 1. In isolateral leaves with well-developed palisade layers stomata are subtended by gaps in the palisade layer.

Scarious leaf margins formed entirely by epidermal cells or by a combination of epidermal and mesophyll cells occur in all species. The scarious margins are most conspicuous (to 1 mm wide) in *F. shrevei* (Fig. 4j) and *F. ochoterenae* (Fig. 3h) where they consist of epidermal and mesophyll cells. They are least conspicuous or often absent in *F. columnaris* (Fig. 4h). In older leaves, scarious margins may turn reddish as anthocyanin pigments accumulate.

REPRODUCTIVE STRUCTURES AND POLLINATION

INFLORESCENCE.—The Fouquieriaceae is characterized by a wide variety of inflorescence types ranging from simple indeterminate spikes to complex determinate panicles (Fig. 5). The basic inflorescence type appears to be an indeterminate panicle with determinate lateral paniculate branches. From

TABLE 1. *Distribution of leaf blade characteristics of Fouquieriaceae.*[1]

	SURFACE	LEAF TYPE D-V dorsi-ventral I isolateral	STOMATA DENSITY per mm²	CUTICULAR RELIEF 0—lacking 1—punctate 2—near stomata 3—slight throughout 4—heavy throughout 5—radiating per cell	LEAF THICKNESS TOTAL in μ	EPIDERMIS, μ	PALISADE, μ	SPONGY MESOPHYLL, μ	PERCENT MESOPHYLL IN PALISADE	PERCENT VENTRAL PALISADE	BUNDLE SHEATH EXTENSION 1—midrib only 2—midrib-major veins 3—midrib to minor veins	FIBERS IN VASCULAR BUNDLE + present; – absent	CUTICLE THICKNESS, μ
F. leonilae	V	D-V	0	0	240–280	30–45	95–105	82–95	51–55	100	2	–	3.4
2164	D		117–164	2		23–32	0						2.3
F. ochoterenae	V	D-V	0	0 (1, 3)	290–350	38–67	90–125	70–110	45–53	69–74	3	+	2
2117	D		86–122	5 (2, 3)		25–38	40–47						**4–7**
F. purpusii	V	D-V	0	0 (1)	140–295	12–23	45–90	22–77	65–80	48–59	1	+	4.5
2147	D		62–70	2 (1, 3, 4)		12–24	43–90						4.5
F. fasciculata	V	D-V	0	1 (2)	285–330	23–38	120–130	60–125	64–76	67–76	2	+	3.5
2071, 4331	D		79–102	2 (0, 1)		19–30	40–80						3.5
F. formosa	V	I	25–39	2 (3)	320–410	30–40	110–175	55–95	72–84	58–70	2	–	2
2171, 4300	D		54–140	2, 3		25–40	65–90						2
F. diguetii	V	I	27–90	3 (2, 1, 4)	360–380	20–25	110–125	110–125	62–66	55–58	1	–	1
4371, 7091	D		49–109	4–2 (1)		20–25	87–95						1
F. macdougalii	V	I	44–55	2 (1)	150–315	18–25	55–145	38–62	67–77	62–70	2	–	2
2448, 7090	D		150–161	3, 4 (2)		12–25	23–60						2
F. columnaris	V	I	48–62	5	390–510	19–23	100–154	120–190	53–64	52–57	1	–	5
1545, 7089	D		68–83	5		12–25	90–115						5
F. burragei	V	I	79–85	4	220–380	30–35	62–90	38–63	71–82	50–69	1	–	3
4334, 7092	D		77–86	4		19–28	50–87						3
F. splendens	V	I	77–117	3, 4	155–250	15–35	40–100	38–44	67–83	52–57	1	–	2
4029, 7087-8	D		88–98	4, 3		19–32	37–90						2
F. shrevei	V	I	74–93	4, 3	305–400	17–38	78–140	100–130	60–70	50–52	1	–	2
1825	D		75–94	4, 3		20–38	70–140						2

[1] Species arranged from those most dorsi-ventral (*F. leonilae*) to those most isolateral (*F. shrevei*). Data for ventral (V) or adaxial surface presented above data for dorsal (D) or abaxial surface. Stomata density measured by occular grid 0.96 mm². Cuticular relief: most common characteristics listed first (infrequent characteristics in parenthesis). Stomata density and cuticular relief data from leaf peels made with Archer's adhesive from outdoor-cultivated plants. Thickness measurements also from prepared slides of field-collected material. Herbarium voucher number (Henrickson collection) for collections used given below specific epithets.

this, indeterminate racemes and spikes as well as determinate panicles with paniculate (subgenus *Bronnia*) or spicate (subgenus *Idria*) lateral branches have been derived.

The occurrence of indeterminate and determinate inflorescences at first implies a basic difference of paniculate versus cymose organization (Rickett, 1944; Troll, 1964). But such is not the case in the Fouquieriaceae. All complex inflorescences in the family have a basic paniculate structure with lateral branches and pedicels arranged in a helical 3/8 or 2/5 phyllotactic pattern—decussate branching patterns characteristic of cymose inflorescences do not occur. The main difference between these indeterminate and determinate inflorescences appears only to be the direction of maturation of the central inflorescence axis. Inflorescences of most species are characterized by an acropetal pattern of maturation and are indeterminate. In *Fouquieria fasciculata* and *F. purpusii* (subgenus *Bronnia*) and *F. columnaris* (subgenus *Idria*), however, the terminal flower of the central axis matures first and subsequent development follows in a basipetal direction.

Inflorescences are bracteose. All lateral branches and pedicels are subtended by caducous bracts, and a pair of bracts occurs on all but the terminal pedicels of central and lateral axes as shown in Fig. 5 a–d. The caducous bracts are often large and conspicuous on developing inflorescences where they may have a protective function.

Phyllotactic arrangement of lateral branches or flowers on a central inflorescence axis is often not consistent. Branches may be arranged in a 3/8 phyllotactic pattern near the base but in a 2/5 pattern in more narrow terminal portions, or 2/5 (or less frequently 3/8) throughout.

Lateral branches of all paniculate inflorescences are determinate and peduncles are arranged in a 2/5 phyllotactic pattern as illustrated in Fig. 5 b–e. Lateral branches may consist of spikes (often panicles of spikes) in *F. columnaris* (Fig. 5e), racemes in *F. macdougalii*, *F. diguetii* (Fig. 5b), or panicles of various degrees of branching in *F. splendens*, *F. fasciculata*, *F. purpusii* and *F. burragei* (Fig. 5 c, d).

Inflorescence size and development of lateral branching is strongly affected by environmental factors. For example, with heavy rainfall, *F. macdougalii* and *F. diguetii* may produce large, much branched paniculate inflorescences, but in a dry season the same plants may produce much reduced inflorescences that are paniculate at the base and racemose above or racemose throughout.

The racemose inflorescences of *F. ochoterenae* (and occasionally in *F. shrevei*) and spicate inflorescences of *F. leonilae* and *F. formosa* are very similar in appearance, as pedicels of racemose inflorescences are very short. Flowers are arranged in a 2/5 or 3/8 phyllotactic pattern depending on the diameter of the rachis. All but the terminal flowers are subtended by a triad of caducous bracts as shown in Fig. 5a. The greatest reduction of inflorescence occurs in *F. shrevei* where solitary or paired flowers (in reduced racemes) are borne at the upper nodes of a stem as shown in Fig. 18a.

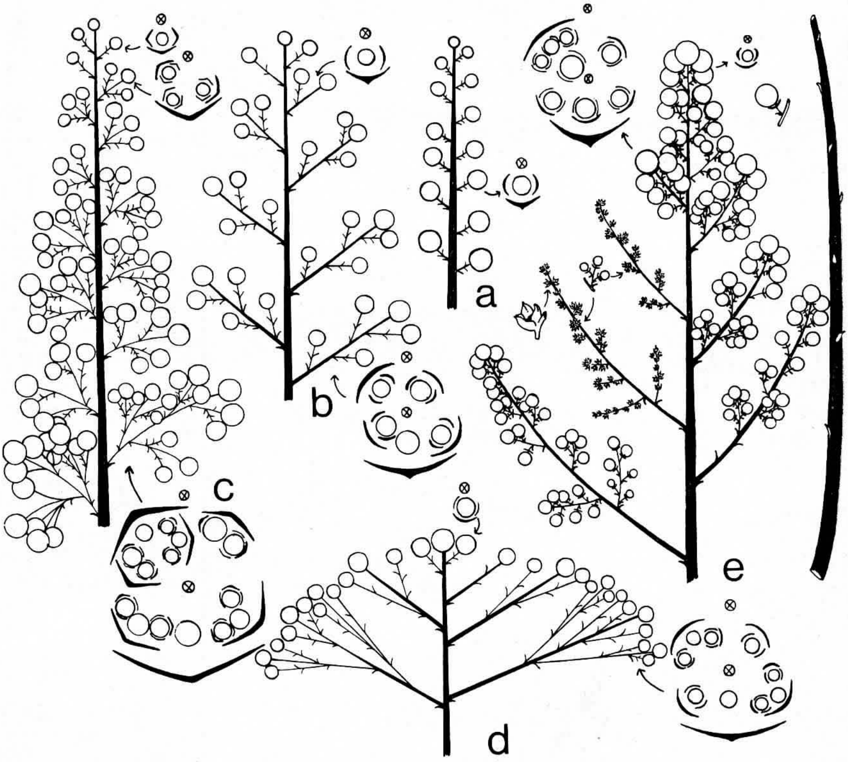
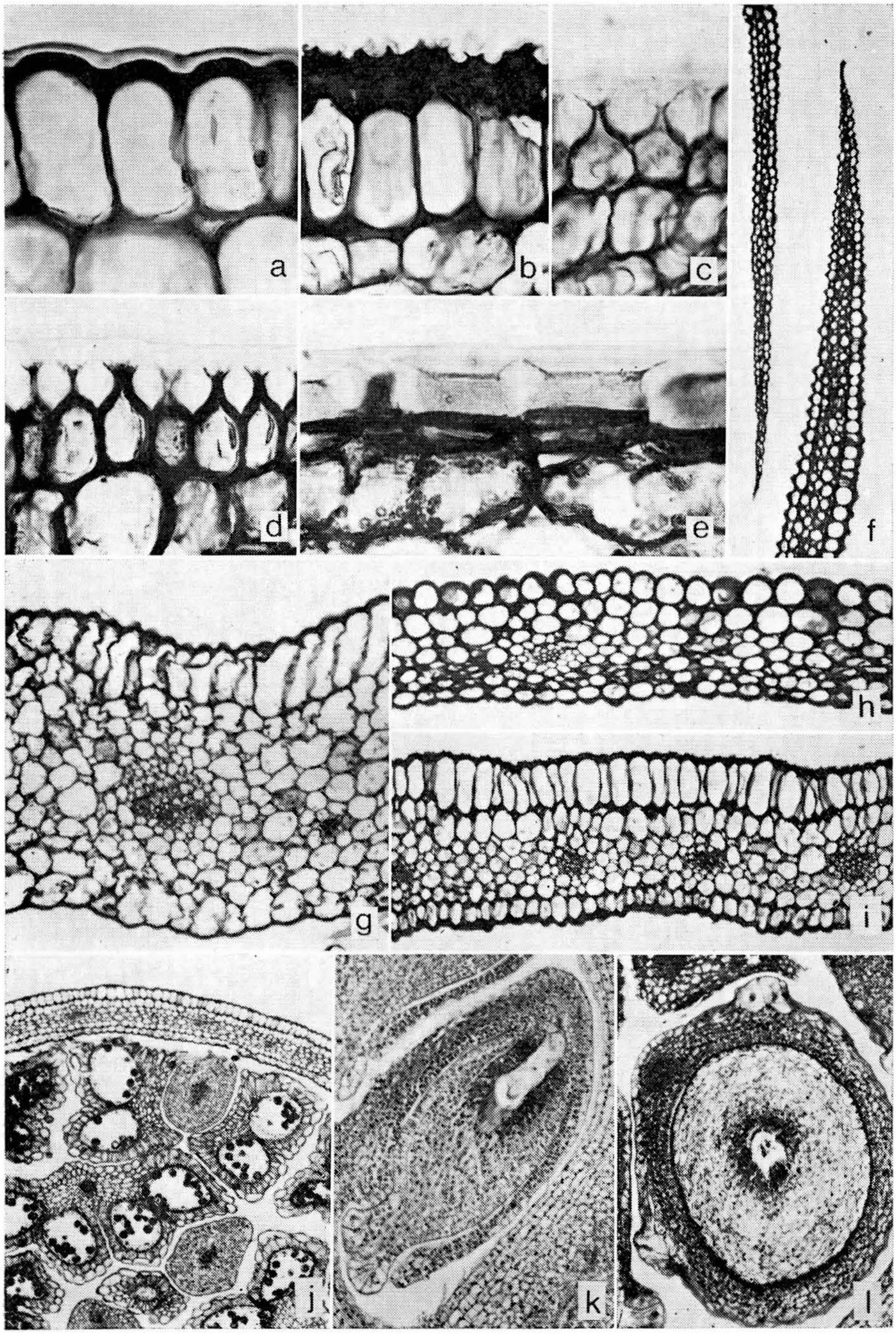


Fig. 5. Diagrams of inflorescence characteristics of Fouquieriaceae.—a. Indeterminate raceme showing position of three bracts on all but terminal flower. Racemes or derivative spikes are characteristic of *Fouquieria ochoterenae, F. leonilae, F. formosa.*—b. Indeterminate panicle with determinate lateral branches showing distribution of bracts. Characteristic 2/5 phyllotactic arrangement of flowers shown for lower lateral branch. Characteristic of *F. macdougalii* and *F. diguetii,* and somewhat reduced in *F. burragei.*—c. Much-branched indeterminate paniculate inflorescence with determinate lateral branches characteristic of *F. splendens* showing branching pattern and distribution of bracts. Spiralled 2/5 phyllotactic arrangement of flowers, bracts illustrated for upper two and lower branches.—d. Determinate corymbose paniculate inflorescence with determinate lateral branches characteristic of *F. purpusii* and *F. fasciculata.* Arrangements of flowers on upper and lower lateral branches shown at lower right.—e. Large determinate paniculate inflorescence characteristic of *F. columnaris* showing distribution of flowers and bracts. Center two branches on left side drawn to show actual sessile position of lateral bracts. *Conventions:* Flowers represented by circles, size of circles indicate relative maturation—larger circles (flowers) mature before smaller. Phyllotactic arrangement of lateral branches on rachis and flowers on peduncles is *not* shown. Phyllotactic arrangement of flowers, bracts on lateral bracts indicated in supplementary "floral" diagrams. Axis of inflorescence represented by encircled x.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FLOWER STRUCTURE AND HISTOLOGY.—Flowers of the Fouquieriaceae are bisexual, actinomorphic and are characterized by a basic pentamerous perianth and androecium and a three-carpellate superior ovary. The detailed structure and histology of the flowers of the Fouquieriaceae are presented below. Significant intraspecific differences—particularly those of phylogenetic or taxonomic importance—are emphasized.

SEPALS.—The five, persistent, strongly imbricate sepals are arranged in a spiral 2/5 phyllotaxy and are borne at successively higher levels on the receptacle. They range from lance-ovate to broadly orbicular-reniform in outline, acute to rounded or emarginate, often apiculate at the apex and cuneate to cordate at the broad base. In most species the outer two sepals are slightly smaller, and more lance-ovate than the inner, orbicular sepals. The outer sepals are greatly thickened at the base and extend over the constricted pedicel apex as shown in Figs. 7d; 10a. The sepals gradually thin from the base towards the broad, overlapping scarious margins. The sepals contain a parenchymatous mesophyll of thin-walled cells which are progressively larger and may contain chloroplasts near the abaxial surface. The mesophyll diminishes greatly in extent towards the scarious margins where it eventually diminishes entirely; the outermost portion of the scarious margin may consist of only two layers—the outer and inner epidermis (Fig. 6f). In the inner, protected sepals, the inner epidermis also diminishes and is eventually lost, occasionally leaving only a single outer epidermic layer at the extreme margin.

Stomata are not present on the sepals. The epidermis consists entirely of axially elongated cells covered with a smooth, shiny cuticle of variable thickness. Considerable intraspecific variation occurs in the shape and composition of epidermal cells. In all species the abaxial and occasionally the adaxial tangential walls are much thicker than lateral walls, and outer portions of the abaxial walls are impregnated with cutin. The most simple epidermal structure occurs in *Fouquieria splendens*. Here the epidermal

Fig. 6. Flower histology of Fouquieriaceae.—a–e. Sections of abaxial sepal epidermal cells.—a. *Fouquieria splendens*. Note slight thickening of outer tangential wall and uniform thickness of cuticle. (*Henrickson 3199*).—b. *Fouquieria shrevei*. Note great thickening of outer tangential wall and thin cuticle. (*Henrickson 3120*).—c–d. *Fouquieria burragei*.—c. Transverse sections of epidermis showing characteristic wedge-shaped crest with thin protoplasmic wings. Note very thick cuticle. (*Carter 4906*).—d. Older cells with thickened walls closing off abaxial crest. (*Lenz s.n.*).—e. *Fouquieria leonilae*. Longitudinal section of sepal epidermal cell showing elongate structure of abaxial crest. (*Henrickson 2164*).—f. *Fouquieria splendens* ssp. *campanulata*. Cross section of sepals showing characteristic tapering scarious margin. (*Henrickson 1742*).—g–i. Cross sections of petals, abaxial surface uppermost showing association of petal thickness and cell size.—g. *Fouquieria ochoterenae*. (*Henrickson 2117*).—h. *Fouquieria columnaris*. (*Moran 11890*).—i. *Fouquieria splendens* ssp. *campanulata* (*Henrickson 1742*).—j. *Fouquieria burragei*. Cross section of flower showing petal and tetrasporangiate anthers. (*Lenz s.n.*).—k–l. *Fouquieria macdougalii*. Ovule.—k. Longitudinal section of ovule showing thin outer integument, thick inner integument forming micropyle, epistace, etc.—l. Cross section of ovule showing development of seed membrane trichomes from outer integument. Note vascular strand in outer integument, thickened inner integument. (*Henrickson 1560*).—a–e ×390; f ×75; g–i ×120; k ×97; l ×84.

cells have a moderately thickened, slightly convex outer wall covered with a uniform cuticle 4–5 μ thick (Fig. 6a). The related *F. shrevei* also has a uniform cuticle 3–6 μ thick but the outer tangential primary wall is greatly and often irregularly thickened as shown in Fig. 6b. A similar thick-walled epidermis occurs on the inner sepal surface and may also extend to the corolla, filament and style surfaces. The remaining species have epidermal cells with broad to very narrow wedge-shaped outer walls. The thick cuticles have smooth outer surfaces and highly irregular inner surfaces, and range from 10 to 30 μ thick (Fig. 6 c, d). These outer epidermal walls are characterized by a series of conspicuous protoplasmic extensions which radiate outward from the margins of the cell wall into the cuticle. In young cells these extensions have direct connection with the cytoplasm but this is lost as outer walls increase in thickness (Fig. 6d). The extensions probably function in deposition of the thickened cuticle. Epidermal cells of the inner sepal surface are usually smaller, more tabular in outline and are covered by a thin cuticle 3–6 μ in thickness.

PETALS.—The corolla consists of five connate petals forming a cylindrical to slightly ampliate tube. The imbricate lobes may be inflexed, erect to tightly reflexed in position and range from oblong-ovate to orbicular in outline, emarginate to acute or apiculate at the apex and cuneate to cordate at the broad base. Lobes have narrow scarious margins. Petals range from 110 to 300 μ in thickness. They are thinnest in *F. fasciculata, F. splendens, F. purpusii,* and thickest in *F. ochoterenae, F. diguetii* and *F. formosa.* All corollas are 8–10 cells thick—the relative thickness is mainly a result of cell size (Fig. 6 g–i). A thin cuticle covers the outer and inner epidermal cells and may be smooth or have a slight relief pattern consisting of small parallel ridges. The outer epidermal walls are slightly thickened, particularly in *F. shrevei.*

ANDROECIUM.—Stamen number is variable in the family. Seven species are characterized by ten stamens while the remaining four species show high variability in stamen number—(10–)14–18(–23)—and will vary greatly even within an inflorescence. Studies of floral vascularization provide evidence that the ten-stamened condition is basic (see below) and the additional stamens are vascularized by a branching of an original ten stamen traces. In *F. fasciculata* and *F. purpusii* the five stamens alternate with the petals, are often longer, and their anthers may be arranged outside of the inner, opposite anthers, giving an impression of two whorls of five stamens each (Fig. 29). In all species, however, stamens are borne from the receptacle in a single whorl and the only disparity between alternate and opposite stamens is in their arrangement in the bud, which is in turn reflected in recently opened flowers. Flowers with numerous stamens have the anthers compacted at various levels within the bud. In all species stamens are exserted to variable levels.

Stamens receive vascular traces directly from the receptacle and while not epipetalous, filaments are very slightly connected to the adaxial petal base and fall from the spent flower with the corolla tube. While the upper part of a filament is straight and cylindrical, the lower 4–6 mm segment is more squarish to rectangular in transverse section and tends to arch toward the style above the ovary. In *F. splendens* this arch continues as a short ligule or spur to 1 mm long which nearly closes off a distinct chamber above the ovary (Fig. 22 c, g). The basal arching portion of the filament bears unicellular trichomes. They extend from the outer (abaxial) sides of the filaments 1–2 mm above the base, around to the inner (adaxial) side at the upper arch, where they occasionally exceed 1.5 mm in length. The trichomes are commonly covered with nectar which probably is drawn up between the filaments from the ovary base by capillary action. The trichomes thus present the nectar to flower visitors at a point 2–5 mm above the ovary. This separation of the ovary and nectar would provide the ovary a degree of protection from damage by beaks of feeding hummingbirds. In flowers with shorter open corolla tubes (*F. shrevei, F. burragei*) the numerous trichomes fill the flower center and probably function to a great extent in reduction of nectar evaporation.

The structure of the anther is relatively uniform throughout the family. Anthers are oblong-lanceolate in outline, distinctly cuspidate at the apex and cordate with two rounded lobes at the base. The anther is dorsifixed and the filaments extend between the basal lobes and enter the anther about one-fourth way above the base. The anthers are tetrasporangiate, and dehisce introrsely along two lines extending almost the entire length of the anther (Fig. 6j). As the anthers dry they tend to curl backward (abaxially) completely exposing the yellow pollen.

Anther wall development has been studied and it follows the dicotyledonous-type pattern (Davis, 1966). The anther wall consists of a persistent epidermis, an endothecial layer of enlarged cells with fibrous thickened walls, an ephemeral middle layer which initially increases to 2–3 layers and an inner tapetal layer. The tapetum is glandular or secretory in nature. It initially consists of a layer of enlarged densely staining cells which become increasingly vacuolate as the anthers mature; it usually breaks down by the time anthers open. Microspore mother cells undergo simultaneous cytokinesis and produce tetrahedral tetrads. Pollen grains are shed as single-celled monads. They are tricolporate, eureticulate, subtectate and are associated with yellowish oils. They have been described in detail previously (Henrickson, 1967).

GYNOECIUM.—In mature flowers ovaries are 1.5–2 mm high and about 1.2 mm in diameter. The basal solid portion of the ovary is nectariferous and consists of tightly packed cells with dense cytoplasm (Fig. 7a). A sweet nectar is secreted through a series of stomata around the ovary base. In young flowers the ovary walls range from 120 to 180 μ (9–12 cells) in thickness and consist entirely of thin-walled cells. The ovary is one-loculed and contains three parietal septiform placentae which extend almost to the center of the ovary, dividing the locule into three sections. In the upper four-fifths of the ovary the inner septal margins are adjacent but not united and placentation is parietal (Fig. 7c). In the lower portion of the ovary the

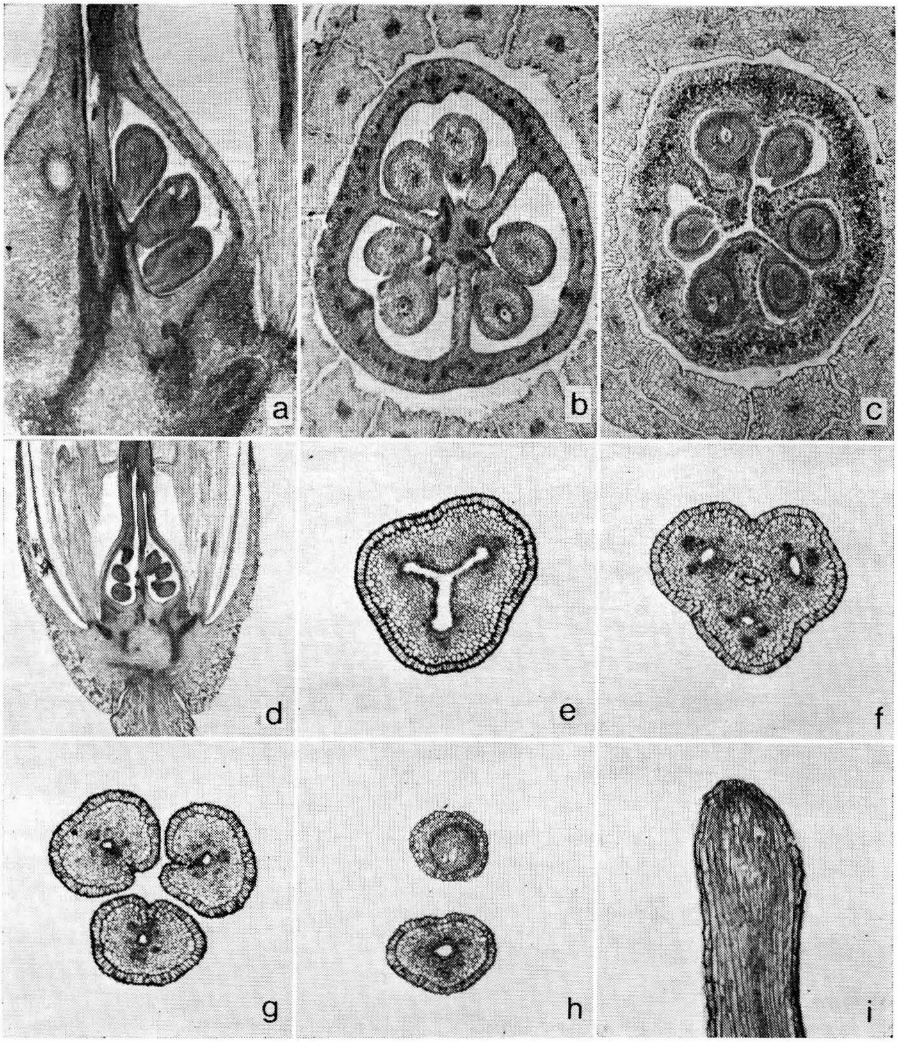

Fig. 7. Gynoecial structure of Fouquieriaceae.—a–b. *Fouquieria splendens* ssp. *campanulata*.—a. Longitudinal section of ovary showing septum on left, locule with three ovules on right. Note connection of central placenta at ovary base. (*Henrickson 3184*).—b. Cross section of basal ovary with axial placentation. Note distribution of carpel wall traces. (*Henrickson 2017*).—c. *Fouquieria diguetii*. Cross section of middle ovary with parietal placentation. Transition from basal axial to parietal placentation shown in a. (*Thorne and Henrickson 32679*).—d. *Fouquieria splendens* ssp. *campanulata*. Longitudinal section of flower showing arrangement of perianth, filaments with adaxial spur and gynoecium. Note connection of locule with stylar canals. (*Henrickson 3184*).—e–h. Cross sections of style showing open stylar canals.—e. *Fouquieria diguetii*. Basal style. (*Thorne and Henrickson 32679*).—f. *Fouquieria splendens*. Mid style just

inner septal margins unite into a central axile placenta (Fig. 7b). The ovary then has both parietal and axile placentation and the region of transition is shown in Fig. 7a. Ovules are borne at the inner septal margins, the lowermost from the axile portions of the placenta. Ovule number is quite variable. Most species have 14–18(–20) ovules but *Fouquieria ochoterenae* and *F. leonilae* commonly have only six or occasionally 12 ovules. The ovules are about 0.5 mm long, anatropous, and tenuinucellar (Fig. 6 k, l). The inner integument surrounds a thin nucellar tissue and forms the micropyle as it protrudes beyond the outer integuments. Ovules have distinct raphes containing a single procambial strand. Structure of the ovule, and embryo sac and features of embryogenesis have been presented by Johansen (1936) and Kahn (1943). Distinctive features include a nucellar epistace and lateral haustoria on the mature megagametophyte.

The ovaries have single terminal styles, which are three-branched usually in the upper half. Styles are exserted in varying degrees in all species except *Fouquieria columnaris* where they are much reduced and included. The three medial carpel wall (dorsal) traces continue into the style. Traces contain both annular and helically thickened tracheids and phloem elements and tracheids extend to about 0.5 mm of the style tip. The style contains an open central stylar canal formed by the abaxial surfaces of three conduplicately folded carpels. The open canal, continuous with the ovary locule (Fig. 7d), is three-winged at the base of the style and divides with the style branches in the manner shown in Fig. 7 e–h. The stylar canal is lined with a single continuous layer of stigmatoid tissue consisting of cells with enlarged, dark-staining nuclei. The stigmatoid tissue does not continue into the inner ovary wall. The stigmatic area is restricted to the adaxial or terminal portion of the style branch and can be distinguished externally by a series of papillate hairs. The passage of the open stylar canal is blocked at the stigmatic region by proliferation of enlarged, vacuolated stigmatoid cells (Fig. 7 h, i).

FRUIT.—The fruit is a dry, loculicidal dehiscent capsule containing a large parenchymatous central axis and 5–18 broad, winged seeds (Fig. 9). The lance-ovate capsules are subtended by persistent sepals and range from 18 to 30 mm in length, 4–7 mm in maximum diameter. The ovary begins enlargement soon after separation of the petals, stamens and style. Increase in size occurs entirely by cell enlargement which begins at the ovary tip and proceeds in a basipetal direction. By the time the carpels extend above the surrounding sepals, terminal cells have reached their maximum size and those of the middle wall layers have differentiated into thick-walled sclereids. Sclerification also proceeds in a basipetal direction, and occurs before

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below style branches. (*Rutherford s.n.*).—g. *Fouquieria shrevei*. Mid style branches. (*Henrickson 3120*).—h. *Fouquieria splendens* ssp. *breviflora*. Section at tip of style branches. Upper stigma lobe shows closure of stylar canal by stigmatoid tissue. (*Henrickson 3147*).—i. *Fouquieria splendens* ssp. *campanulata*. Longitudinal section of stigma showing stigmatoid tissue which blocks stylar canal. (*Henrickson 3184*).—a ×25; b–c ×28; d ×8.4; e–h ×37; i ×53.

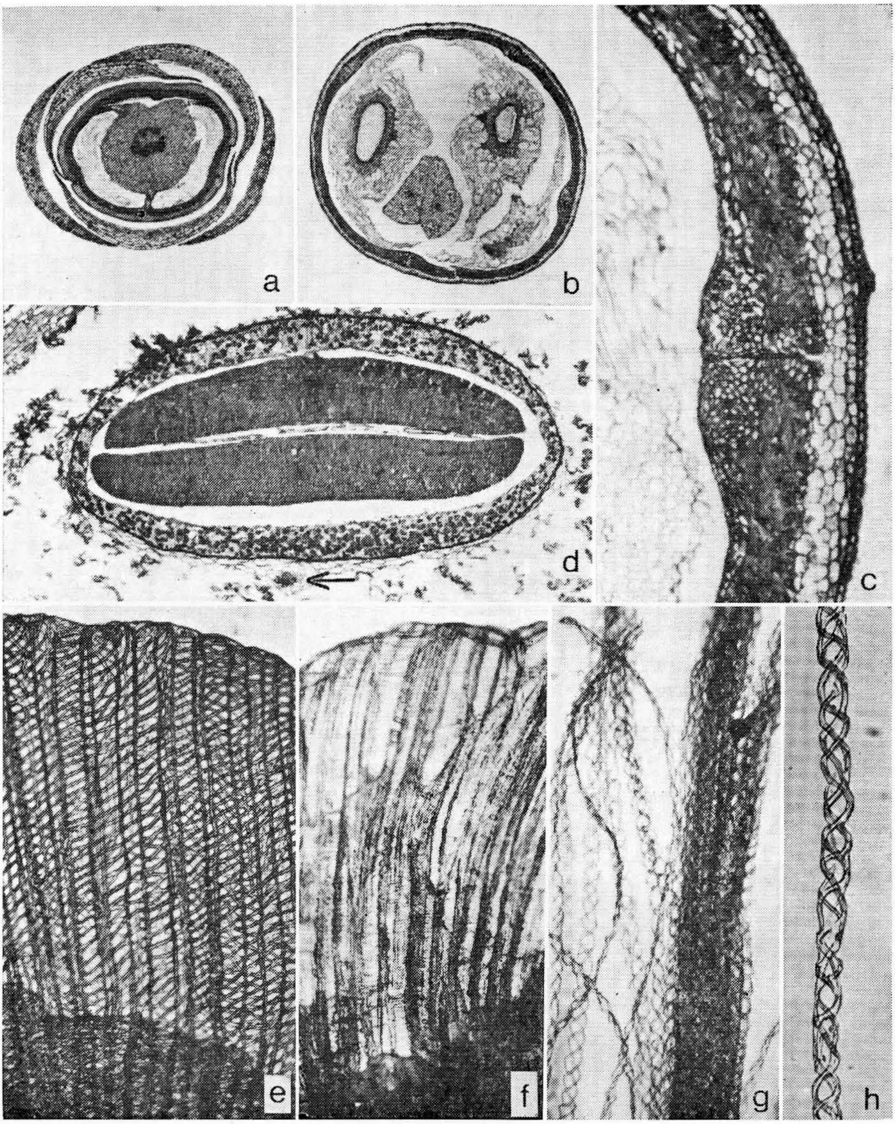

Fig. 8. Fruit and seed structure of Fouquieriaceae.—a. *Fouquieria splendens* ssp. *campanulata*. Cross section of base of young fruit showing sepals, fruit wall, enlarged placential axis and septa. (*Henrickson 1742*).—b–c. *Fouquieria shrevei*.—b. Cross section of aberrant young fruit with four carpels, two expanded placentae and two large seeds. Note adaxial vascular strand, mass of epidermal hairs around seed. Placental regions normally fill center of fruit.—c. Cross section of carpel wall showing zone of dehiscence. Wall consists of outer parenchymatous and inner sclerenchymatous tissue.

the tissue extends beyond the protecting sepals. After the capsule reaches its full size, sclerification continues through the middle layer to the base of the capsule and often into adjacent inner layers of the pericarp wall. The basipetal pattern of differentiation affects the fruit shape. Terminal portions sclerify when young (small) while basal portions have opportunity to enlarge considerably before maturing. At maturity the pericarp wall consists of an outer parenchymatous layer 3–5 cells thick, a medial band of sclereids, 3–5 cells (60–125 μ) thick, an inner parenchymatous layer 1–2 cells in thickness, and an outer and inner epidermis, the outer of which consists of much larger cells and has a distinct cuticle (Fig. 8 b, c). The thick-walled sclereids form a continuous layer except along the dorsal traces where a narrow, radially-oriented series of thin-walled cells forms the eventual zone of dehiscence shown in Fig. 8c. This zone is marked by the distinct expansion of the sclereid layer on each side. As the capsule dries, the outer parenchymatous wall layers contract, placing an outward stress on the three valves of the capsule. This causes their separation at the narrow zone of dehiscence. As the capsule continues to dry the valves reflex outward allowing dispersal of the large winged seeds. That dehiscence is actually caused by shrinkage of the outer wall layer can be demonstrated by placing open capsules in water where they reclose.

Maturation of the ovary into fruit is accompanied by certain apparent changes in placentation. At flowering, the ovary has three central parietal placentae borne at the inner margins of the thin septa (Fig. 7 b, c). As ovary and ovules enlarge, the three septa are broken and the three central placentae fuse into a common three-angled central column as their constituent cells enlarge (Fig. 8 a, b). The parenchymatous column fills much of the central cavity of the fruit and compresses the developing seeds against the pericarp wall. It is interesting that while the ovary has parietal placentation, the fruit has a single central column which would appear to be derived from an ovary with free-central or axile placentation. This has caused some confusion in the early taxonomic history of the family. Kunth (Humboldt, Bonpland and Kunth, 1823) placed fruiting and flowering specimens of two species in separate genera partly due to apparent differences in placentation.

SEEDS.—The flattened seeds have conspicuous membranous wings and contain a small embryo and a thin layer of endosperm. Seeds range from 8 to 20 mm in total length and range in number from 5 to 18 per capsule. The

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(*Henrickson 1969*).—d. *Fouquieria splendens* ssp. *breviflora.* Cross section of mature seed showing two cotyledons with procambial strands, scant endosperm, embryo sac wall, vascular trace (arrow). Membrane trichomes mostly removed in preparation. (*Henrickson 3147*).—e–h. Seed membranes.—e. *Fouquieria burragei.* Outer seed membrane consists of two layers of flattened trichomes forming characteristic anastomosing pattern of wall thickening. (*Henrickson 4334*).—f. *Fouquieria fasciculata.* Outer seed membrane with two layers of flattened trichomes with slight to no wall thickening pattern. (*Henrickson 2071*).—g–h. *Fouquieria shrevei.*—g. Outer seed membrane composed of thick mats of cylindrical hairs shown teased apart.—h. Single seed membrane trichome showing characteristic three helical thickenings. Membrane hairs are almost identical to those of *Fouquieria splendens.* (*Henrickson 3120*).—a ×8.5; b ×8; c ×5; d ×37; e–g ×45; h ×65.

seed wing is formed from unicellular trichomes derived from outer integument epidermis. The pattern of trichome development and wall thickening varies considerably and provides taxonomically useful characters. In most species elongate trichomes develop only in a narrow lateral zone 6–8 cells thick extending from the micropylar end to the ovule tip (Fig. 6 l). The other ovule epidermal cells merely expand as the ovule enlarges and have a tabular shape at maturity (Fig. 9c). The basal portion of the membrane consists of 6–8 layers of cells. The inner layers are progressively longer than the outer and the membrane thins and consists of only two cell layers at the periphery. In most species marginal trichomes are distinctly flattened and are marked with a perpendicular, often anastomosing network of wall thickenings as shown in Fig. 8e. This anastomosing network is, however, usually poorly developed in *F. fasciculata, F. purpusii* and *F. columnaris* (Fig. 8f). In contrast, seed membranes of *F. splendens* and *F. shrevei* consist of thick

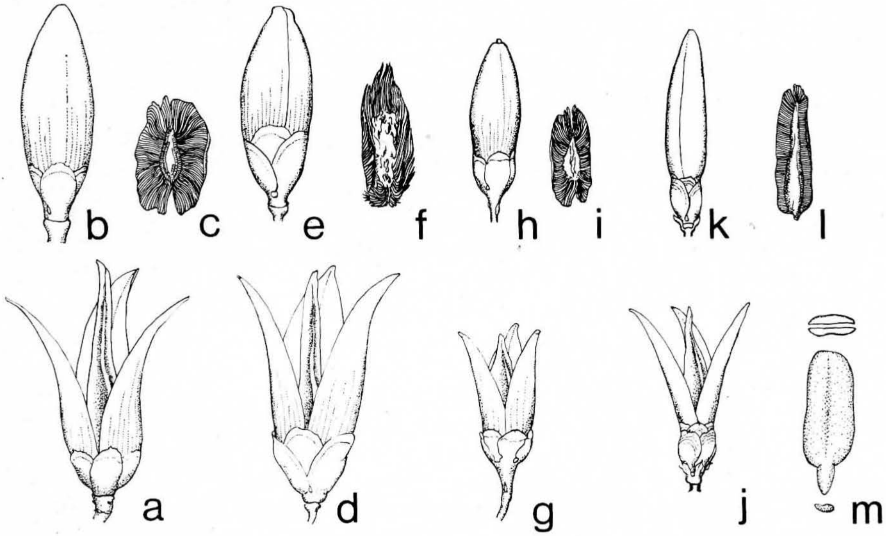

Fig. 9. Fruits and seeds of Fouquieriaceae.—a–c. *Fouquieria burragei.*—a. Dehisced fruit showing central three-cornered placental structure as it appears in dry fruit.—b. Mature fruit before dehiscence.—c. Seed with characteristic broad membrane composed of flattened trichomes. (*Henrickson 4334*).—d–f. *Fouquieria splendens.*—d. Dehisced fruit.—e. Mature fruit.—f. Seed with membrane of matted cylindrical hairs. (*Henrickson s.n.*).—g–i. *Fouquieria fasciculata.*—g. Dehisced fruit.—h. Mature fruit.—i. Seed with broad thin membrane of flattened hairs. (*Henrickson 2077*).—j–l. *Fouquieria columnaris.*—j. Dehisced fruit.—k. Mature fruit. Note narrow outline.—l. Seed with broad margin of flattened hairs. (*Harbison 10–1963*).—m. *Fouquieria burragei.* Embryo showing surface view and section of cotyledons and hypocotyl. (*Henrickson 4334*).—a–l ×1.5; m ×4.3.

mats of narrow trichomes with a distinct series of three spiraled wall thickenings (Fig. 8 g, h). Similar trichomes form over the entire seed surface but only those in a broad lateral band greatly elongate and contribute to the membrane.

The inner 3–5 cell layers of the outer integument remain as a thin layer of parenchymatous cells around the embryo sac. This layer is traversed by a single vascular bundle along the adaxial seed surface. The bundle develops from the procambial strand which enters through the funiculus.

After fertilization the resulting zygote enters a resting stage and is pushed towards the micropyle by the enlarging embryo, which grows at the expense of the nucellar and inner integumentary tissue (Johansen, 1936). The embryo sac is filled with large endosperm cells with thin walls and scanty cytoplasm. As the embryo develops, the central endosperm cells disintegrate and only a thin layer of smaller cells remain along the embryo sac margin. In the mature seed the endosperm is practically negligible, consisting of a thin layer of 4–5 cells (50–70 μ) thick on the inner surface of the seed coat (Fig. 8d). The cells have a dark staining cytoplasm and show a positive reaction with alloxan indicating proteinaceous contents (Jensen, 1962). The cells disintegrate as the seeds germinate and the proteinaceous contents are not present in the spent seed coat.

Embryogenesis conforms to the Asterad Type (Johansen, 1936; Davis, 1966) and the mature embryo consists of a basal, short hypocotyl about 1 mm long and two oblong-elliptical flattened cotyledons 4–5 mm long. As the seed germinates, the hypocotyl-radicle greatly elongates forming a long hypocotyl and root axis. The cotyledons borne at the top of the hypocotyl develop chloroplasts and spread apart to become the first leaves. Development of mature growth forms from the seedlings has been described by Henrickson (1968).

FLORAL SIZE VARIATION.—Flower size often varies slightly or noticeably among individuals of a population. This is particularly apparent regarding the diameter of corolla tube, sepals and young stems. An example of such intrapopulation variation is presented in Table 2 where data obtained from two adjacent plants of *Fouquieria splendens* ssp. *campanulata* var. *albiflora* Henrickson allows comparison of floral and stem features.

TABLE 2. *Comparative measurements of adjacent plants of* Fouquieria splendens *ssp.* campanulata *var.* albiflora (*Henrickson 3184*).

	Plant A	Plant B
Average flower diameter[1, 2]	4.03 mm	3.41 mm
Average stamen number[1]	16.7	13.9
Young stem diameter	6.5 mm	3.8 mm
Cortex thickness	1.06 mm	0.75 mm
Pith diameter	0.85 mm	0.64 mm

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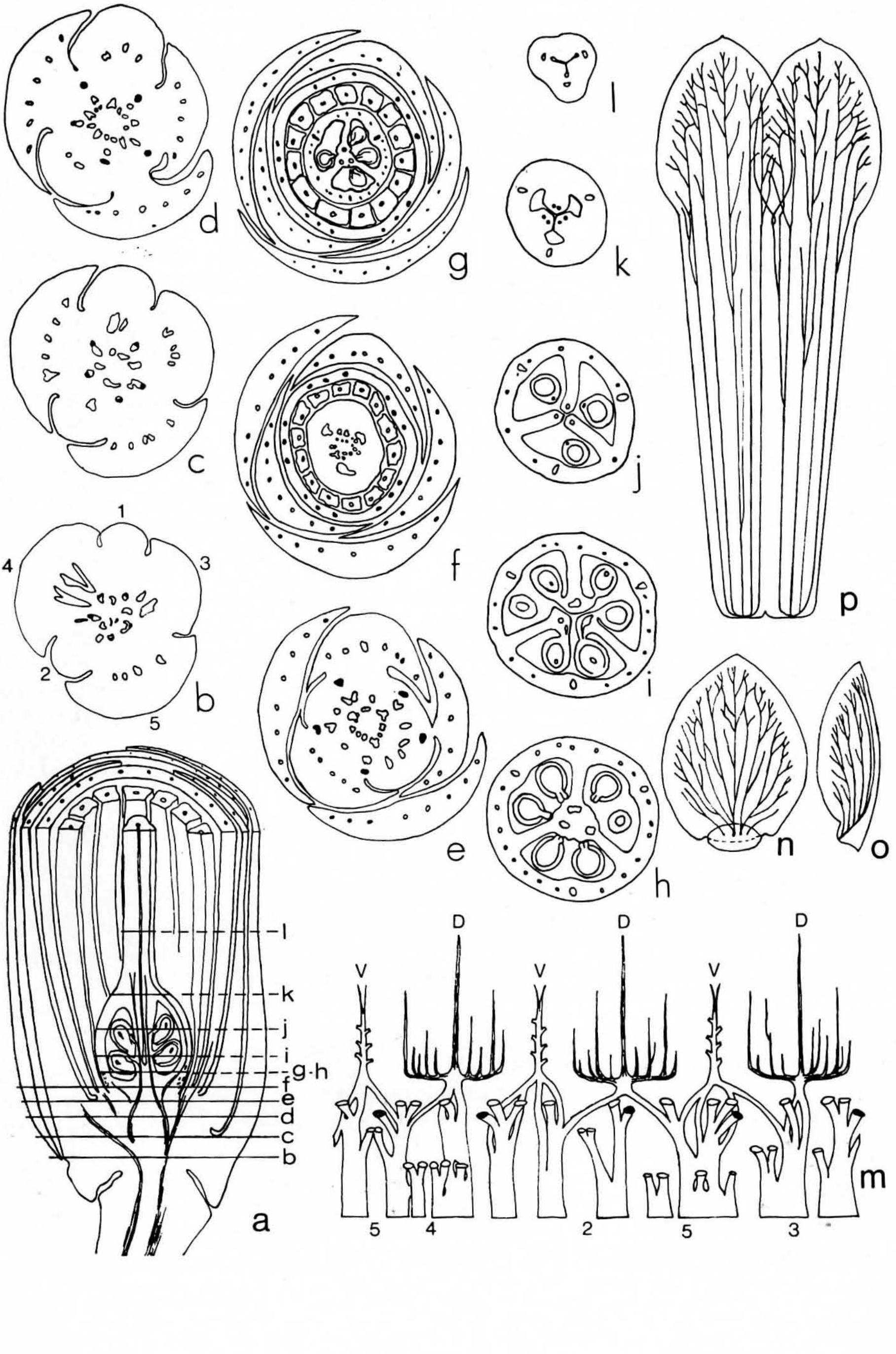
[1] $n=20$

[2] maximum diameter of sepals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The strong correlation of flower and stem dimensions is immediately apparent. Anatomical studies of both longitudinal and transverse sections of mature flowers reveal that the flowers and stems differ in *number* of constituent cells, not cell size. There apparently is genetically based variability in the number of cell layers derived from the apical initials which is reflected in both floral and vegetative derivatives—an instance of plieotropy. Stamen number also varies with flower diameter. Variation in total corolla tube length also occurs over the entire range of *F. splendens* (Figs. 24–26). This again is a quantitative difference. Longer corollas are merely composed of a greater number of cells. The total number of cells, however, to some extent may be influenced by moisture conditions at the time of development.

FLORAL VASCULARIZATION.—Patterns of floral vascularization for all 13 species and subspecies of the Fouquieriaceae have been determined from serial transverse and longitudinal sections of fully mature buds. While venation patterns are typical of dicotyledonous flowers with compound superior ovaries, certain intraspecific dissimilarities have contributed greatly to an understanding of phylogenetic relationships and trends within the family. The patterns of floral vascularization are described below and illustrated with *F. splendens* in Fig. 10.

Vascular tissue in the upper pedicel consists of a cylinder of about ten separate vascular bundles enclosing an often sclerified pith and surrounded by a narrow band of cortical fibers which terminates at the base of the flower. As the imbricate sepals are arranged in a spiral 2/5 phyllotaxy, sepal traces diverge from the central vascular cylinder at successively higher levels in the receptacle at points opposite the sepals. The vascular traces may originate from the center of an initial vascular bundle and may be associated with a closed or open gap, or they may originate from the margin of the initial bundle which then merely branches. In *Fouquieria ochoterenae* and *F. leonilae* all sepals receive a single trace from the central cylinder. In all other species, however, sepal traces range from 1 to 5, with the outer sepals receiving a larger number of traces (4–5) than the inner sepals (3–1) (Fig. 10 b–d). The more extensive outer sepal vascularization would appear to correspond to greater moisture requirements of the exposed outer sepals which completely enclose the inner sepals. As one would not expect a decrease in sepal vascularization to occur in such a xerophyic group, and as

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Fig. 10. Floral venation of *Fouquieria splendens* ssp. *splendens*.—a. Longitudinal section of basal portion of mature flower showing general path of vascular tissue from receptacle, distribution of perianth, ovules, etc.—b–l. Diagrammatic transectional views of flower (b–g) and ovary-style (h–l) at points indicated in a. Sepals are numbered in b to indicate relative position and 2/5 phyllotaxy. Eventual petal traces solid, others shown in outline only. Sections a, h–j show transition from basal axial to upper parietal placentation. Note large stylar canals in k–l.—m. Diagram of horizontally extended vascular tissue of flower cut between sepal 5 and 3 showing traces to 5 sepals as indicated by numbers, petals (solid), stamens (open) and to ovules (ventral traces) and carpel wall, dorsal trace (D) continues into style.—n–o. Venation pattern of cleared outer sepal.—n. Face view.—o. Side view.—p. Venation pattern of two petals. Note anastomosis of veins in lobes. (*Henrickson 2549*).—a–g ×8; h–l ×16; n–o ×4.4; p ×3.1.

all leaves receive single traces, it appears most reasonable to consider the single-traced sepals as a basic condition and the variable, increased vascular supply an adaptive advancement. The vascular bundles ramify and occasionally anastomose in the sepals as illustrated in Fig. 10 n, o. They do not extend into the scarious margins.

At a level just above the divergence of the uppermost sepal trace, a series of five petal traces—or in *F. splendens, F. shrevei* and *F. columnaris* combined petal-sepal traces—diverge from the central vascular bundles at a point alternate to the sepals. These traces either ascend directly to the base of the petal or branch into petal and stamen traces. At the petal base, the traces ramify into 3(–4) vascular bundles which continue up the petal and ramify and occasionally anastomose as illustrated in Fig. 10p.

In all but two species an initial series of ten stamen traces diverge from the central cylinder at a level just above the petal traces; of these, five are alternate and five are opposite the petal traces (Fig. 10 d, e). They will hereafter be referred to as the *alternate* and *opposite* stamen traces. In the seven species with ten stamens per flower, the ten stamen traces ascend directly into the bases of the filaments. In the taxa characterized by more numerous (12–23) stamens, the initial ten traces ramify either after or *as* they diverge from the central cylinder. In *Fouquieria splendens* and *F. shrevei* the five opposite stamen traces which are initially associated with the petal traces usually branch into two or occasionally three stamen traces to account for the increased stamen vascularization. The five alternate traces usually do not ramify or only occasionally branch into a pair of traces. A somewhat similar vascular pattern was observed in *F. burragei* flowers but the stamen traces, which diverge outward far above the petal traces, branch *as* they diverge from the central vascular cylinder. This branching usually occurs only in the opposite traces—the five alternate traces remain single. In these flowers what appears a simultaneous divergence of all (e.g., 15–18) traces is merely a delayed proliferation from the initial ten traces. In other flowers (even on the same inflorescence) pairs of alternate stamen traces diverge from separate gaps between two adjacent opposite stamen traces. This is then a numerical increase in initial stamen traces (i.e., more than ten initial traces). *Fouquieria formosa* also follows a similar pattern with ten or more separate initial stamen traces caused by an increase in number of alternate sepal traces.

There are then two general groups of taxa with more than ten stamens per flower. *Fouquieria splendens* and *F. shrevei* have ten initial stamen traces, five of which (the opposite traces) usually diverge from the central cylinder with the petal traces before branching. In contrast *F. burragei* and *F. formosa* have ten or more initial stamen traces caused by both a basic increase in alternate traces and by branching of the five opposite traces as they diverge from the central cylinder. The basic difference between the two groups would seem to indicate independent derivations from decandrous stock. The fact that the increase in stamen number is accompanied by branching of ten initial stamen traces is significant and overwhelming evidence that the ten-stamen condition is basic to the family.

Above the level of stamen-trace divergence the remaining vascular bundles of the central cylinder arrange into three large peripheral bundles and an inner loosely organized alternate series of bundles which in most species forms an open cylinder. The outer traces are the carpel wall or dorsal traces, while the inner are the placental or ventral traces of the tricarpellate compound ovary. At the ovary base the three outer bundles abruptly diverge outward and each ramifies greatly to form a series of 6–12 lateral carpel wall bundles and a larger medial bundle—the dorsal carpel trace. Most of the small lateral carpel wall bundles do not extend to the apex of the ovary and in the mature flower consist of procambial strands which will differentiate as the fruit wall develops. The dorsal carpel traces continue from the ovary into the style and extend to the tip as the stylar traces (Fig. 10 h–m).

The inner vascular bundles organize into three groups and enter into the inner placental margins of the carpel septa at the base of the carpel where they constitute the ventral carpel traces (Fig. 10 f–l, m). Each trace is a double structure composed of ventral traces of two adjacent carpels. As they extend up the placenta, 2–6 bundles extend into the funiculi of the ovules. The ventral traces continue to the ovary top where they ultimately branch into two or three bundles (Fig. 10 k–m). In most species the dorsal and ventral bundles remain separate as they enter the ovary but occasionally a trace from the ventral bundles will extend outward to the ovary wall. The dorsal and ventral traces greatly increase in extent as the ovary matures into fruit.

POLLINATION.—The Fouquieriaceae exhibits considerable diversity in those floral features (e.g., corolla size and color) commonly associated with specific pollination relationships. Both ornithophily and entomophily occur in the family. Hummingbird visitation has been observed to red tubular flowers of *Fouquieria splendens* ssp. *splendens* (Grant and Grant, 1966), *F. diguetii*, *F. macdougalii* and *F. formosa*. It has also been observed but to a limited extent in *F. splendens* ssp. *campanulata* and *F. splendens* ssp. *breviflora* Henrickson. Although not observed in the field it is also expected to occur in *F. leonilae*. Each of the above has flowers borne in terminal inflorescences where areas for perching are not readily available. In contrast, *F. ochoterenae* produces short upright inflorescences along larger stems which permit visitations by perching birds (e.g., yellow grossbeaks and doves). All other species have short, whitish flowers and less specialized insect visitors. Visitation to *F. shrevei*, *F. burragei* and *F. purpusii* has not been observed in the field but a wide array of insects has been observed on the flat-topped inflorescences of *F. fasciculata*. A large number of bees has been recorded visiting the sweet-smelling flowers of *F. columnaris* by Humphrey and Werner (1969). Carpenter and bumble bees obtain nectar from several species either legitimately or by cutting through the corolla tube base of longer flowers.

All species are characterized by long exserted stamens. In most, the three-branched style is also exserted and terminal stigmas are situated among the lower, introrse anthers. In *F. macdougalii* and *F. diguetii,* however, stigmas are stationed above the anthers at all times, a factor which would apparently favor outbreeding. In contrast, *F. columnaris* has reduced, included styles. In all species a sweet nectar is produced from nectaries around the ovary base. Grant (1958) reports that the flowers of *Fouquieria splendens* ssp. *splendens* are self-compatible and, as the stigmas are situated at the same level as the anthers, it seems reasonable that they are capable of self-fertilization. There is evidence that *F. macdougalii, F. diguetii* and *F. columnaris* are also self-compatible as isolated cultivated plants set seed. Self-fertilization, however, probably does not occur since styles are stationed above the anthers in the first two species, and are included and protected by inwardly folded petals in *F. columnaris.*

CHROMOSOME CYTOLOGY

CYTOLOGY.—The first report of chromosome numbers in the Fouquieriaceae was made by Johansen (1936), who in his embryological investigations of three species of the family reported $n=8$ for *F. splendens,* $2n=16$ for *F. peninsularis* (=*F. diguetii*) and $2n$=approximately 16 for *F. burragei.* His count for *F. splendens* was made from meiotic material "not in the most satisfactory condition" and ovary cells and stem tips provided somatic divisions for counts in the other species. His reports indicate a basic number of $x=8$ which is not substantiated by this and other reports and perhaps is best disregarded as suggested by Raven et al. (1965).

The first reliable chromosome count was presented by Raven et al. (1965) reporting $n=12_{11}$ for a California population of *F. splendens* ssp. *splendens.* Spellenberg (in Löve, 1970) reported a chromosome number of $n=12$ for *F. splendens* ssp. *splendens* in Coahuila and $2n=24$ for *F. ochoterenae* in Puebla. M. S. Cave observed $n=36$ in pollen mother cells of *F. columnaris* (personal communication).

Chromosome counts of six additional species are presented for the first time in Table 3. Mitotic divisions were observed from root tips of seeds collected from cultivated plants (*F. macdougalii, F. diguetii*) or from rooted cuttings (*F. fasciculata, F. purpusii, F. leonilae*) or from field-collected seeds (*F. shrevei, F. burragei, F. splendens* ssp. *campanulata*). Root-tip material was pretreated in 0.004 M 8-oxyquininol, fixed in 3:1 absolute alcohol: acetic acid and stained with aceto-orcein.

The aforementioned chromosomal counts and those reported below indicate a basic number of $x=12$, and a cytological history involving tetraploidy, past hybridization and development of hexaploids. Chromosome numbers are now reported for all species in the family except *F. formosa* (Table 3). Of these, seven are diploid ($2n=24$), one tetraploid ($2n=48$) and two hexaploid ($2n=72$). When polyploidy is involved, cytological information is very useful in indicating direction of evolution (see section on classification).

INTERSPECIFIC RELATIONSHIPS AND CLASSIFICATION

NUMERICAL TAXONOMY.—Relationships within the Fouquieriaceae are somewhat difficult to assess due to the scattered distribution and conspicuous nature of certain characteristics. As an aid in understanding possible phylogenetic relationships a numerical taxonomic study was undertaken with J. W. Carmichael, University of Alberta, Canada, to determine phenetic relationships within the family.

Table 3. *Chromosome numbers of Fouquieriaceae.*

TAXON	CHROMOSOME NUMBERS	LOCALITY
Fouquieria leonilae	$2n=24$	Mexico, Guerrero: Canon del Zopilote, *Henrickson 2164* (RSA).
Fouquieria ochoterenae	$2n=24$	Mexico, Puebla: Near Acatlan on Hwy 190, *Spellenberg 2015* (NMC) (in Löve, 1970).
Fouquieria macdougalii	$2n=24$	Mexico, Sonora: 52 mi S of Santa Ana, Verity *s.n.* LA botanic garden #64.005. *Henrickson 7090* (RSA).
Fouquieria diguetii	$2n=48$	Mexico, Sonora: 5 mi N of Guaymas, Verity *s.n.* LA botanic garden #64.004. *Henrickson 7091* (RSA).
Fouquieria burragei	$2n=72$	Mexico, Baja California del Sur: Near Pichilinque, 18 km N of La Paz, *Henrickson 5450* (RSA).
Fouquieria splendens ssp. *splendens*	$n=12$	United States, California: San Diego Co., Road to Borrego Springs, 3 mi from Hwy. 78. *Kyhos* (*62-62*), no voucher (Raven et al., 1965).
	$n=12$	Mexico, Coahuila: N of Saltillo, *Spellenberg 2016* (NMC) (in Löve, 1970).
Fouquieria splendens ssp. *campanulata* var. *albiflora*	$2n=24$	Mexico, Durango: 4 mi N of Rodeo, along Hwy 45, *Henrickson 3175* (RSA).
	$2n=24$	Mexico: Durango: 7 mi S of Rodeo along Hwy 45, *Henrickson 3174* (RSA).
Fouquieria splendens ssp. *breviflora*	$2n=24$	Mexico, San Luis Potosí: 21 mi S of Matehuala along Hwy 57, *Henrickson 3174* (RSA).
Fouquieria fasciculata	$2n=24$	Mexico, Hidalgo: Laguna Metztitlan, *Henrickson 2068* (RSA).
Fouquieria purpusii	$2n=24$	Mexico, Puebla: 23 (air) miles SSE of Tehuacan, at Cerro Petlanco, *Henrickson 2142* (RSA).
Fouquieria columnaris	$n=36$	Mexico, Baja California del Norte: 15 mi SE of El Rosario, *D. Hutt s.n.* (UC) (count by M. S. Cave, personal communication).
Fouquieria shrevei	$2n=24$	Mexico, Coahuila: S of Laguna del Rey, *Henrickson 3124* (RSA).

A total of 14 Operational Taxonomic Units (OTU's) was used in this study including ten taxa of specific rank, three subspecies constituting an eleventh species and a second population series of *F. formosa* which has not been taxonomically recognized. The OTU's are listed in Fig. 12. Morphological diversity within the family is high and 71 characteristics were scored for each OTU, following the guidelines of Sokal and Sneath (1963). Of these, 31 involved ecological-vegetative attributes and 40 reproductive (inflorescence, flower, fruit and seed) attributes. Care was taken not to represent gross characteristics more than once. Therefore the complex of characteristics associated with xylem succulence is represented by only a single attribute. When quantitative series were used, e.g., vessel-element length, pollen diameter, etc., character states were based on natural breaks in the series. Number of states used for each attribute ranged from 2 to 5. Characters used and number of states recognized (in parentheses) are as follows: 1, mature height (3); 2, growth habit (3); 3, vegetation association (3); 4, soil association (2); 5, young stem diameter (3); 6, epidermis persistence (2); 7, young stem pubescence (2); 8, extent of decurrent ridges (2); 9, decurrent ridge persistence (2); 10, decurrent ridge outline (3); 11, stem phyllotaxy (2); 12, periderm persistence (2); 13, mature thickness of periderm fibrous layers (2); 14, phellem cell length (2); 15, phellem cell shape (2); 16, composition of periderm fibrous-suberized layers (2); 17, periderm sclereids, presence (2); 18, bark (phloem through periderm) thickness (2); 19, cortical sclereid nest thickness (3); 20, initial sclereid nest presence (young stems) (2); 21, presence of short-shoot spur branches (2); 22, long-shoot leaf blade length (2); 23, short-shoot leaf shape (4); 24, presence of leaf pubescence (2); 25, ventral leaf surface sheen (2); 26, presence primary phloem fibers (2); 27, average vessel element length (3); 28, presence of vestured vessel pits (2); 29, lignification of xylem parenchyma (2); 30, extent of water-storage tissues (2); 31, presence of primary thickening meristem (2); 32, inflorescence type (3); 33, average inflorescence length (3); 4, thickness of inflorescence rachis (2); 35, direction of inflorescence maturation (2); 36, inflorescence position (2); 37, inflorescence bract size (2); 38, presence of inflorescence pubescence (2); 39, corolla lobe position (4); 40, corolla length (4); 41, corolla tube-limb ratio (4); 42, corolla tube straightness (2); 43, corolla color (5); 44, presence of trichomes inside corolla (2); 45, corolla thickness (2); 46, corolla lobe shape (3); 47, corolla lobe basal outline (3); 48, corolla lobe apical outline (3); 49, sepal trace number (2); 50, sepal length (3); 51, sepal apex outline (3); 52, level of style branching (2); 53, extent of style exsertion (2); 54, style-stamen relative length (3); 55, ovule number (2); 56, stamen number (2); 57, presence of filament appendages (2); 58, anther color (2); 59, extent of basal filament vesturement (3); 60, anther tip outline (3); 61, extent of stamen exsertion (2); 62, polar diameter of pollen (3); 63, pollen lumina size (3); 64, pollen sexine muri thickness (2); 65, pollen muri composition (2); 66, capsule length (2); 67, capsule outline (2); 68, seed color (2); 69, arrangement of seed trichomes (2); 70, seed trichome distal thickness (3); 71, cotyledon length (2).

Relative difference between states of two OTU's for a single attribute was taken as the difference between observed values divided by the observed range over all the OTU's. The relative difference between the OTU's based on a number of attributes was taken as the weighted arithmetic average of their relative distances on each attribute (Carmichael and Sneath, 1969). As this particular program presented relative differences for construction of taxometric maps, relative similarities were extrapolated.

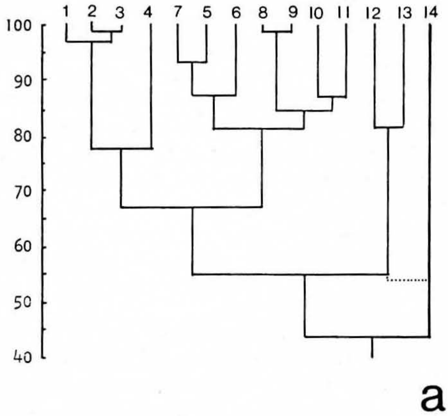
Data on relative similarities (relative closeness) of (1) all 71 attributes, (2) the 31 vegetative and (3) the 40 reproductive attributes were arranged in diagonal half matrices (Fig. 11) and rearranged placing OTU's with high similarity near the diagonal. This was used to construct average link dendrograms (Fig. 11). Average link dendrograms present a quantitative hierarchial ordering in which pairs of OTU's combined at levels directly representing their similarity while groups of OTU's are united at levels representing the average similarity between constituents of the two groups.

The dendrograms based on (1) ecological-vegetative, (2) reproductive, and (3) total attributes effectively illustrate close relationships of pairs or small groups of OTU's. Two population series of *F. formosa* (OTU's 8, 9) show a high degree of similarity in each dendrogram. In contrast, the three subspecies of *F. splendens* (OTU's 1, 2, 3) are very similar vegetatively but differ more in reproductive characteristics. *Fouquieria fasciculata* and *F. purpusii* (OTU's 12, 13), on the other hand, are more similar in reproductive than vegetative features while *F. ochoterenae* and *F. leonilae* (OTU's 10, 11) have about equal similarity in vegetative and reproductive attributes. The three Sonoran Desert taxa, *F. macdougalii, F. diguetii,* and *F. burragei* (OTU's 5, 6, 7) show interesting relationships: *Fouquieria diguetii* shows greater similarity with *F. burragei* in vegetative features but is more similar to *F. macdougalii* in reproductive attributes. The close phenetic similarities noted above concur with those independently derived through intuitive thought processes (although the latter method does not allow quantitative expression of similarities).

Similarities indicated between consecutively larger groups of OTU's are much less accurate. The conventions used to construct average link dendrograms provide for linkage of groups of OTU's with the highest average similarity (derived by averaging the similarities of constituent OTU's). While the level of combination of OTU's 1–4 and 5–7 present no problems, other combinations give either limited or deceptive information. The coefficients of similarity between OTU's 5–10 are very close; in the dendrogram showing reproductive attributes (Fig. 11b) they range from 68 to 69 percent similarity and all seven are combined at one level. At lower levels of similarity, dendrograms can be misleading. *Fouquieria fasciculata* and *F. purpusii* (OTU's 12, 13) have closest similarities with *F. columnaris* (OTU 14) as shown in dendrograms for reproductive and total attributes (Fig. 11 b, c). Their next highest association is with OTU's 5, 6, 7 at a level only a few units below but they are combined with OTU's 5, 6, 7 at an average level for OTU 1 through 11 at a much lower level. The similarity of OTU's 12, 13 with OTU's 5, 6, 7 is indicated with a dotted line in Fig. 11b. In contrast, regarding ecological-vegetative attributes, *F. fasciculata* and *F. purpusii* (OTU's 12, 13) have a highest average similarity with OTU's 1–11, but have a combined similarity with OTU 14 (*F. columnaris*)

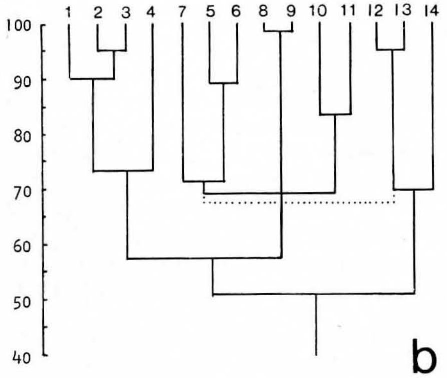
ECOLOGICAL-VEGETATIVE ATTRIBUTES (1-31)

2	98												
3	98	96											
4	77	79	75										
5	78	76	76	80									
6	69	66	66	71	86								
7	72	74	69	78	93	88							
8	59	57	61	62	81	87	79						
9	61	60	63	64	83	89	82	98					
10	62	60	64	75	84	79	77	86	84				
11	63	60	65	70	80	84	77	84	82	87			
12	53	55	55	59	54	55	52	54	56	62	63		
13	56	54	58	58	58	53	51	52	54	60	55	82	
14	39	37	37	36	48	48	40	42	45	40	46	58	50
	1	2	3	4	5	6	7	8	9	10	11	12	13



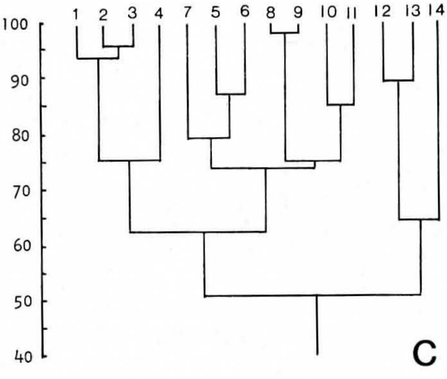
REPRODUCTIVE ATTRIBUTES (32-71)

2	90												
3	91	95											
4	67	77	76										
5	62	58	59	52									
6	63	59	61	60	89								
7	69	73	72	70	75	67							
8	56	56	57	55	70	64	73						
9	57	57	58	54	71	66	74	98					
10	50	52	53	59	69	70	66	71	72				
11	58	51	56	55	68	76	61	66	67	83			
12	58	61	57	61	67	65	68	54	55	58	58		
13	55	61	57	61	64	66	68	51	52	58	58	94	
14	49	50	48	45	59	68	61	37	39	48	46	69	68
	1	2	3	4	5	6	7	8	9	10	11	12	13



ALL ATTRIBUTES (1-71)

2	93												
3	94	96											
4	71	78	76										
5	69	65	66	63									
6	65	62	63	65	87								
7	70	73	71	73	83	76							
8	57	56	59	58	74	74	75						
9	59	58	61	58	76	76	77	98					
10	55	55	58	66	75	74	74	77	77				
11	60	55	59	61	73	79	68	73	73	85			
12	56	59	56	60	62	61	62	54	56	60	60		
13	56	58	57	60	61	60	61	51	53	59	57	89	
14	45	45	44	42	54	54	52	39	41	45	46	65	61
	1	2	3	4	5	6	7	8	9	10	11	12	13



at a slightly lower level (as shown with a dotted line in Fig. 11a). The similarities implied at consecutively lower levels of the dendrograms cannot necessarily be considered an accurate reflection of phenetic relationships. The linear ordering of OTU's in the dendrograms is also somewhat misleading. *Fouquieria burragei* (OTU 7) is about equally similar to OTU's 1–4 and 8–11, but this is not indicated.

An alternative method for displaying phenetic relationships between OTU's by taxometric maps (Fig. 12) has been developed by Carmichael and Sneath (1969). Taxometric maps incorporate the complement of relative similarity—relative distance (distance = 1 - similarity). Close similarity (e.g., 94 percent) is expressed by a short distance (six proximity units) and corresponding larger differences by proportionately longer distances. Taxometric maps present in two dimensions a basic multidimensional display in which distance of each OTU from others is expressed independently. It avoids averaging of similarities between groups of OTU's and the arranging of OTU's in a linear sequence as in dendrograms.

The conventions for construction of taxometric maps is as follows (Carmichael and Sneath, 1969). The OTU's are represented by dots (Fig. 12). The most central OTU (i.e., closest to all other OTU's) is placed in the center of the map. The next-most-central OTU is placed in any direction from the first at a scale distance representing relative distance (e.g., one proximity unit = 2 mm). The two dots are connected by a straight line. The position of the next-most-central OTU is determined by triangulation and is placed in either direction from the first two at the proper distance. Triangulation is used for placing successive next-closest OTU's. Distance between distantly related items will be distorted but can be represented nonetheless. Stretched distances are represented by solid straight lines of the proper length connected to the OTU's by dashed continuations. Squeezed distances are represented by bent lines of proper length. This procedure preserves the closest inter-OTU distance while distances between distantly related items are distorted. Their actual distances can be indicated by the aforementioned conventions for stretched and compressed relations which reveal the nature and amount of distortion and therefore do not mislead one as much as a statistically compressed model (i.e., a dendrogram). Data used to construct two-dimensional taxometric maps have been used to construct three-dimensional models with wire representing distance and cork balls the OTU's. This allows actual display of multidimensional OTU relationships, supposedly without distortion.

It is significant that about the same pattern of phenetic similarity is expressed independently by both floral and vegetative features. This increases the credibility of phenetic relationships indicated. The data dis-

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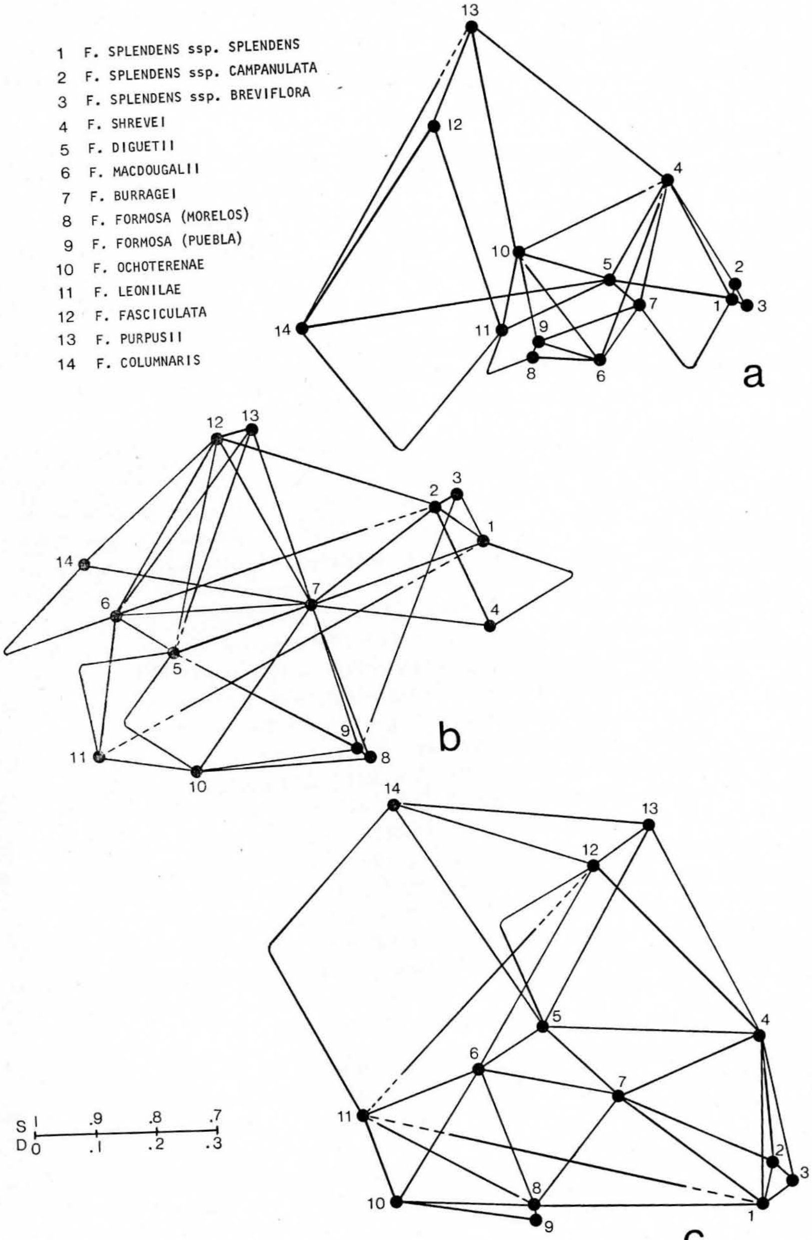
Fig. 11. Diagonal half-matrix or proximity tables and average-link dendrograms for 14 OTU's indicated in Fig. 11 for: a, ecological-vegetative attributes (1–31); b, reproductive attributes (32–71); and c, all attributes (1–71). Dotted lines in dendrograms a and c indicate next closest similarities of OTU's 12–13 with OTU's 5–7 and 14 respectively.


1 F. SPLENDENS ssp. SPLENDENS
2 F. SPLENDENS ssp. CAMPANULATA
3 F. SPLENDENS ssp. BREVIFLORA
4 F. SHREVEI
5 F. DIGUETII
6 F. MACDOUGALII
7 F. BURRAGEI
8 F. FORMOSA (MORELOS)
9 F. FORMOSA (PUEBLA)
10 F. OCHOTERENAE
11 F. LEONILAE
12 F. FASCICULATA
13 F. PURPUSII
14 F. COLUMNARIS
a
b
c
S 1 .9 .8 .7
D 0 .1 .2 .3

played in Figs. 11 and 12 indicate that four groups of taxa can be distinguished within the family. Two of these groups are composed of woody species OTU's 1–4 and OTU's 5–11, while two groups have succulent growth habits and are represented by OTU's 12, 13 and OTU 14. Combining information of phenetic relationships with anatomical and cytological data allows one to construct the following putatively phylogenetic system of relationship.

The basic group consists of OTU's 5 through 11. Of these, *Fouquieria leonilae* and *F. ochoterenae* (OTU's 10, 11) have the greatest number of basic characteristics that reasonably can be considered primitive in the family; e.g., both are diploid ($2n=24$), they have dorsi-ventral leaves, initial single traces to each sepal, ten stamens, and 6(–12) ovules per ovary. They are possibly remnants of the basic line of the family.

Derived from this basic line are three species forming a polyploid series — *F. macdougalii* ($2n=24$), *F. diguetii* ($2n=48$) and *F. burragei* ($2n=72$) (OTU's 6, 5, 7). All three species occur in northern desert regions and are characterized by shrubby, small-tree habits, isolateral leaves, paniculate inflorescences. Of these, *F. macdougalii* and *F. diguetii* have very similar red tubular, decandrous flowers and inflorescences and the latter species may have arisen directly from *F. macdougalii* stock. *Fouquieria burragei* is vegetatively similar to *F. diguetii* but is very distinctive in floral characteristics, having short salverform, rose-pink to white corollas, 14–23 stamens and narrow elongate paniculate inflorescences. *Fouquieria burragei* obviously is of amphiploid origin. The close similarity with *F. diguetii* ($2n=48$) indicates that it may be one parent. The other parent would be a diploid species with numerous stamens, elongate inflorescences and possibly short flowers (*F. splendens*?).

Fouquieria formosa (OTU's 8, 9) appears to represent a separate line derived from *F. leonilae-F. ochoterenae* stock with which it has many characteristics in common. It is characterized by racemose inflorescences, dorsiventral leaves, 10–20 stamens, and red curved corollas. All of the above (OTU's 5–11) have shrubby or small tree growth habits.

A distinct line derived from the first group consists of *F. splendens* and *F. shrevei*, both diploids ($2n=24$) (OTU's 1–4). They are characterized by distinctive woody candelabraform or "ocotillo" habit and have distinctive seed membrane hair structure, 12–23 stamens, isolateral leaves, etc. The first two features occur only in these two species. These species are quite distinct from one another but their close relationship is made obvious by their sharing of unique characteristics.

Fig. 12. Taxometric maps indicating relative proximity of 14 OTU's of Fouquieriaceae (indicated in upper left) using: a, ecological-vegetative attributes (1–31); b, reproductive attributes (32–77); and c, all attributes (1–72). Increased distance between OTU's indicates increased phenetic dissimilarity. For explanation of conventions see text or Carmichael and Sneath, 1969. Scale: S=similarity units; D=distance units when range is 0–1.

The remaining species are characterized by massive proliferation of xylem parenchyma which forms much enlarged succulent central trunks (Fig. 1 d–i). They also have separate decurrent ridges on stems, determinate inflorescences and whitish decandrous flowers. This series is divided into two distinct groups. *Fouquieria fasciculata* and *F. purpusii* ($2n=24$) (OTU's 12, 13) are characterized by persistent epidermis and small white flowers in similar determinate corymbose inflorescences. They are phenetically intermediate between the basic woody groups (OTU's 1–4; 5–11) and the remaining taxon *F. columnaris* (OTU 14), a hexaploid ($2n=72$) which is very distinctive in both floral and vegetative features. That the origin of *F. columnaris* involves amphiploidy is difficult to dispute. It may have arisen through past hybridization between or within the lineage now represented by *F. purpusii* and *F. fasciculata*.

The four groups of taxa discussed above, however, are not equally distinct from one another. The two groups with succulent growth habits can be distinguished from one another and from the woody species by a number of distinct vegetative and reproductive characteristics. In contrast, the two woody groups are less distinct from one another. *Fouquieria burragei*, for example, shows about equal similarity to members of both woody groups (Fig. 12).

It is important to emphasize that of the 11 extant species, seven are restricted endemics, possibly declining species. The roles other taxa, already extinct, have played in the evolution of the family—particularly in amphiploidy—is unknown.

CLASSIFICATION.—In the past, species of the family have been classified in two genera, *Fouquieria* and the monotypic *Idria* (Nash, 1903; Standley, 1920-1926; Shreve and Wiggins, 1964; Henrickson, 1967, 1969a). This scheme was developed before much was known about vegetative and floral structures of the succulent species, *F. fasciculata* and *F. purpusii*, which have certain characteristics intermediate between the two genera. In the previous section, the family was shown to consist of four groups of species. This should be reflected in the system of classification. This can be accomplished by erecting (1) four genera, (2) three genera, combining all the woody species into one genus, while recognizing the others as separate genera, (3) two genera, segregating the woody and succulent species or (4) one genus with divisions made at the subgeneric and/or sectional level. Of the four possible systems, the erection of four genera (1) and combination of the succulent species into one genus (3) are difficult to defend. The former would overemphasize differences and the latter would combine the two distinct succulent groups into an unnaturally broad genus. A more tenable system would consist of three genera (one woody and two succulent) or one genus of three subgenera (with the woody species divided into two sections). Both proposals are defensible. In the former the three genera would be *Fouquieria* (type: *F. formosa*) for the woody species, *Bronnia* (type: *B. spinosa*=*F. fasciculata*) for two succulent species and *Idria* (type: *Idria columnaris*) for the third. In the latter choice of systems, all would be combined under *Fouquieria* as three subgenera: *Fouquieria, Bronnia* and *Idria.*

It is important to note at this time that the basic structure of reproductive features (floral, fruit, and seed) and many external and internal stem and root characteristics are uniform throughout the family. Several of these characteristics are restricted to the family. In contrast, distinctive characteristics useful in distinguishing major groups within the family are few. They include features of stem succulence, inflorescence maturation, style length and a few stem characteristics. A number of other genera with relatively uniform floral structures contain species differing greatly in vegetative features, for example, woody perennial shrubs and annual herbaceous species commonly occur within a genus. Similar variation from woody to succulent species characterize *Euphorbia, Senecio, Pachypodium, Pelargonium, Japtropha* as well as *Ipomoea, Phytolacca, Coreopsis, Lobelia,* etc. On the other hand, families like Cactaceae and Aizoaceae have been divided into numerous constituent genera differing slightly.

As the Fouquieriaceae is a small family, uniform in most basic reproductive as well as stem characteristics, I feel relationships of taxa would most accurately be reflected by placing all species into one genus and distinguishing groups of species at the subgeneric and sectional level. This classification has been followed in this paper and is formally presented below.

FOUQUIERIACEAE A. P. de Candolle, Prod. 3: 349. Mar., 1828 (as Fouquieraceae) nom. conserv.

FOUQUIERIA Humboldt, Bonpland et Kunth, Nov. Gen. Sp. 6: 81. 1823.

Typifications and generic synonymy are given under infrageneric headings.

Shrubs to small trees of arid regions, 2–8(–23) m tall, with much reduced to erect, woody or succulent trunks, bearing simple to ramifying, outwardly arching to horizontal, spinose, heteroblastic branches. Periderm translucent, often exfoliating in thin sheets or restricted to decurrent ridges and associated with persistent epidermis. Stem cortex with peripheral aggregations of sclereids and assimilatory tissue and inner starch- and anastomosingly arranged water-storage tissue. Young branches glabrous to rarely canescent, 2.5–5(–40) mm in diameter, with nodes in 2/5 to 8/21 phyllotaxy; nodal spines 2–45 mm long, subtended by tapering, continuous decurrent ridges separated by distinct or shallow furrows, or recurrent ridges widely separated. Long-shoot leaves with elliptical blades, long petioles, abaxial petiole forming into rigid spine. Short-shoot leaves in axillary fascicules of 2–6(–10), linear to broadly obovate, acute to emarginate at apex, cuneate at base; shortly petiolate to nearly sessile; leaves glabrous or slightly pubescent below, entire, isolateral or dorsi-ventral. Inflorescence indeterminate or determinate, terminal to axillary, spicate, racemose to paniculate or corymbosely paniculate; flowers subtended by three caducous bracts. Sepals 5, separate, strongly imbricate in a 2/5 phyllotaxy, lance-ovate to broadly orbicular, acute to emarginate at apex, cuneate to cordate at base, with broad scarious margins and thick cuticle; outer two slightly smaller, more lance-ovate than inner three. Corolla sympetalous, cylindrical to salverform, tube ampliate, with 5 imbricate, oblong-ovate incurved to reflexed lobes, white, cream-yellow to scarlet red or dark maroon-red. Androecium hypogynous; stamens 10 or more and varying from (10–)14–17(–23), unevenly exserted; filaments slightly adnate to corolla base, broadened and with unicellular hairs at base extending over ovary, occasionally with basal ligulate spur, upper filament cylindrical, glabrous; anther tetrasporangiate, introrse, dehiscent along two lines, oblong-lanceolate, acuminate at apex, two-lobed at base. Gynoecium superior, ovary tricarpellate, with septiform parietal but basially axile placentation, ovules anatropous, bitegmic, 6–20; style three-branched usually in upper half, stigmas terminal. Fruit a loculicidal dehiscent capsule, lance-ovate in outline, with parenchymatous, columnar axile placentae; seeds 6–15, oblong elliptical, with flattened membranous margins of unicellular trichomes; endosperm scanty, proteinaceous; embryo 3–9 mm long, cotyledons oblong to elliptical, flat; hypocotyl short, flat to cylindrical. Chromosome number $x=12$ ($n=12, 24, 36$).

1. FOUQUIERIA subgen. FOUQUIERIA. TYPE: *F. formosa* H. B. K., Nov. Gen. Sp. 6: 81. 1823.

Plants woody throughout; periderm exfoliating in thin sheets; decurrent ridges nearly continuous on young stems; corolla red or if white with more than 10 stamens; style exserted.

1a. FOUQUIERIA sect. FOUQUIERIA. TYPE: *F. formosa* H. B. K.
Philetaeria Liebmann. Dansk Vidensk. Selsk. Skrivt., ser. 5, 2: 283. 1851.

Basal trunks 4–60 dm high; stems moderately branched throughout, nodes in 2/5–3/8 phyllotactic pattern; corolla glabrous within; seed membrane trichomes flattened distally, with anastomosing thickenings.

1b. FOUQUIERIA sect. **Ocotilla** Henrickson, sect. nov.
Trunci basalis 2–4 cm alti, ramos multos rectos tenues ferentes cum furcis supra in aetate; nodis plerumque in 5/13 phyllotaxe; corolla intra basale pubescentia; trichomis membranae semenis cylindraceis, cum 3 densationibus parietis in spiris.

Basal trunks 2–4 dm high, bearing many straight, slender branches which ramify only with age, node mostly in 5/13 phyllotactic arrangement; corolla pubescent near base within; seed membrane trichomes cylindrical, with three spiraling thickenings.

TYPE: *F. splendens* Engelm. in Wisliz., Mem. Tour North. Mexico 98, 1848.

2. FOUQUIERIA subgen. **Bronnia** (H. B. K.) Henrickson, stat. et comb. nov.
Bronnia H. B. K., Nov. Gen. Sp. 6: 83, 1823 (pro gen.). TYPE: *B. spinosa* H. B. K. l.c. [=*F. fasciculata* (Roem. et Schult.) Nash].
Fouquieria sect. *Bronnia* (H. B. K.) Niedz. in Engl. et Prantl, Natürl. Pflanzenfam. 3(6): 294. 1895.

Plants with basal trunks or central stems enlarged and succulent within; epidermis persistent over much of stem; decurrent ridges initially separated; corolla white; stamens 10, 5 long (alternate), 5 short, exserted; style exserted.

3. FOUQUIERIA subgen. **Idria** (Kellogg) Henrickson, stat. et comb. nov. *Idria* Kellogg, Hesperian 4: 101, pl. 1860. (pro gen.). TYPE: *I. columnaris* Kellogg, l.c.

Plants with large tapering central trunk, succulent to apex; periderm thin, not exfoliating; decurrent ridges initially separated, in 8/21 phyllotactic arrangement; corolla cream-yellow; stamens 10, exserted; style included.

KEY TO THE TAXA OF FOUQUIERIACEAE

A. Trunks woody throughout, with solid xylem; decurrent ridges nearly continuous on young stems; corollas reddish or at least so in bud; central axis of inflorescence indeterminate.

Subgenus *Fouquieria*

B. Plants with one or more definite trunks, stems branched above; corolla tubes glabrous within; stamens 10 or 12–23; filaments without adaxial spurs near base; inflorescence spicate, racemose to paniculate; nodes in 2/5–3/8 phyllotaxy.

Section *Fouquieria*

C. Stamens 10; corolla lobes erect to ascending at maturity.

D. Inflorescence spicate to racemose; leaves dorsi-ventral.

E. Young stems thin, 2.5–3.5 mm in diameter, shallowly furrowed; inflorescence spicate, slightly racemose at base, 13–30 cm long; corollas strong red, tube 22–36 mm long, lobes flaring outward; Guerrero.

1. *F. leonilae*

EE. Young stems thick, 5–6 mm in diameter, deeply furrowed; inflorescence racemose, 5–10 mm long, with short pedicels; corollas dark maroon-red, tube 9–13 mm long, lobes erect; Puebla, Oaxaca.

2. *F. ochoterenae*

DD. Inflorescence paniculate; leaves isolateral.

F. Panicles corymbose, often as broad as long; pedicels thin, 0.2–0.6 mm thick, (3–)5–30 mm long.

3. *F. macdougalii*

FF. Panicles conical, longer than broad; pedicels 0.6–0.8 mm thick, 2–6(–13) long.

4. *F. diguetii*

CC. Stamens 12–23; corolla lobes reflexed at maturity.

G. Inflorescence narrowly paniculate, (6–)12–35 cm long; corolla rose-pink with white below; tube 6–10 mm long; southern Baja California.

5. *F. burragei*

GG. Inflorescence spicate, 1.5–10 cm long; corolla orange-red to red; tube 17–27 mm long, slightly curved; mainland Mexico.

6. *F. formosa*

BB. Plants with short trunks bearing many upright, ascending, strict, usually unbranched stems; corolla tubes slightly pubescent within near base; stamens 12–20; filaments with adaxial basal spur extending over ovary or if this is lacking, flowers sessile; inflorescence narrowly paniculate or lacking and flowers sessile on stem; nodes in 5/13 phyllotaxy.

Section *Ocotilla*

C. Flowers in narrow terminal panicles, 1–30 cm long; filaments with small basal adaxial spur extending over ovary; corolla tubular, ampliate towards throat, lobes tightly reflexed, coiled; petals red, orange-red, pink to cream-white; leaves grey-green with slight, scarious margins.

7. *F. splendens*

D. Corolla red to dark or light orange-red.

E. Corolla tube (6.5–)11–18(–22) mm long; inflorescence narrowly paniculate, averaging 9–22 cm in length in Sonoran, 5–11 cm long in Chihuahuan desert; peduncles and pedicles of lower inflorescence 6–11(–25) mm long; California, Baja California, to Texas, Coahuila, northern San Luis Potosi.

7a. *F. splendens* ssp. *splendens*

EE. Corolla tube 6–10 mm long; inflorescence conically paniculate, averaging 10–23 cm in length; peduncles and pedicels of lower inflorescence (5–)10–70 mm long; southern San Luis Potosi, Tamaulipas, Hidalgo, Queretaro.

7c. *F. splendens* ssp. *breviflora*

DD. Corolla purple-pink to white, without tinge of orange at maturity. Corolla tube 5–9 mm long; Durango.

E. Corolla strong purple-pink to pink.

7b1. *F. splendens* ssp. *campanulata* var. *campanulata*

EE. Corolla cream-white.

7b2. *F. splendens* ssp. *campanulata* var. *albiflora*

CC. Flowers sessile, 1(–3) per node along upper stems; filaments without spur; corolla salviform, lobes reflexed; petals reddish in bud, white at maturity; leaves dark green, with broad conspicuous scarious margins.

8. *F. shrevei*

AA. Trunks succulent at base or throughout, with highly parenchymatous xylem; decurrent ridges widely spaced on young stems; corollas white to cream-yellow; central axis of inflorescence determinate.

B. Corollas white; lobes erect; stigmas exserted; flowers borne on corymbose panicles, 3–9 cm long; trunks shiny, green, with persistent epidermis, woody at tip, succulent and enlarged below.

Subgenus *Bronnia*

C. Central trunks enlarged only at base, abruptly narrowing above; leaves spatulate-oblanceolate, young stems with decurrent ridges 13–32 mm long; Hidalgo.

9. *F. fasciculata*

CC. Central trunks enlarged almost to apex, conically tapering; leaves linear, young stems with decurrent ridges 7–14 mm long; Puebla, Oaxaca.

10. *F. purpusii*

BB. Corollas cream-yellow; lobes incurved; stigmas included; flowers borne in terminal panicles 13–40(–60) cm long; trunks dull green to yellow, with thin periderm, succulent throughout, with horizontal, spinose, woody branches; Baja California del Norte, Coastal Sonora.

Subgenus *Idria*

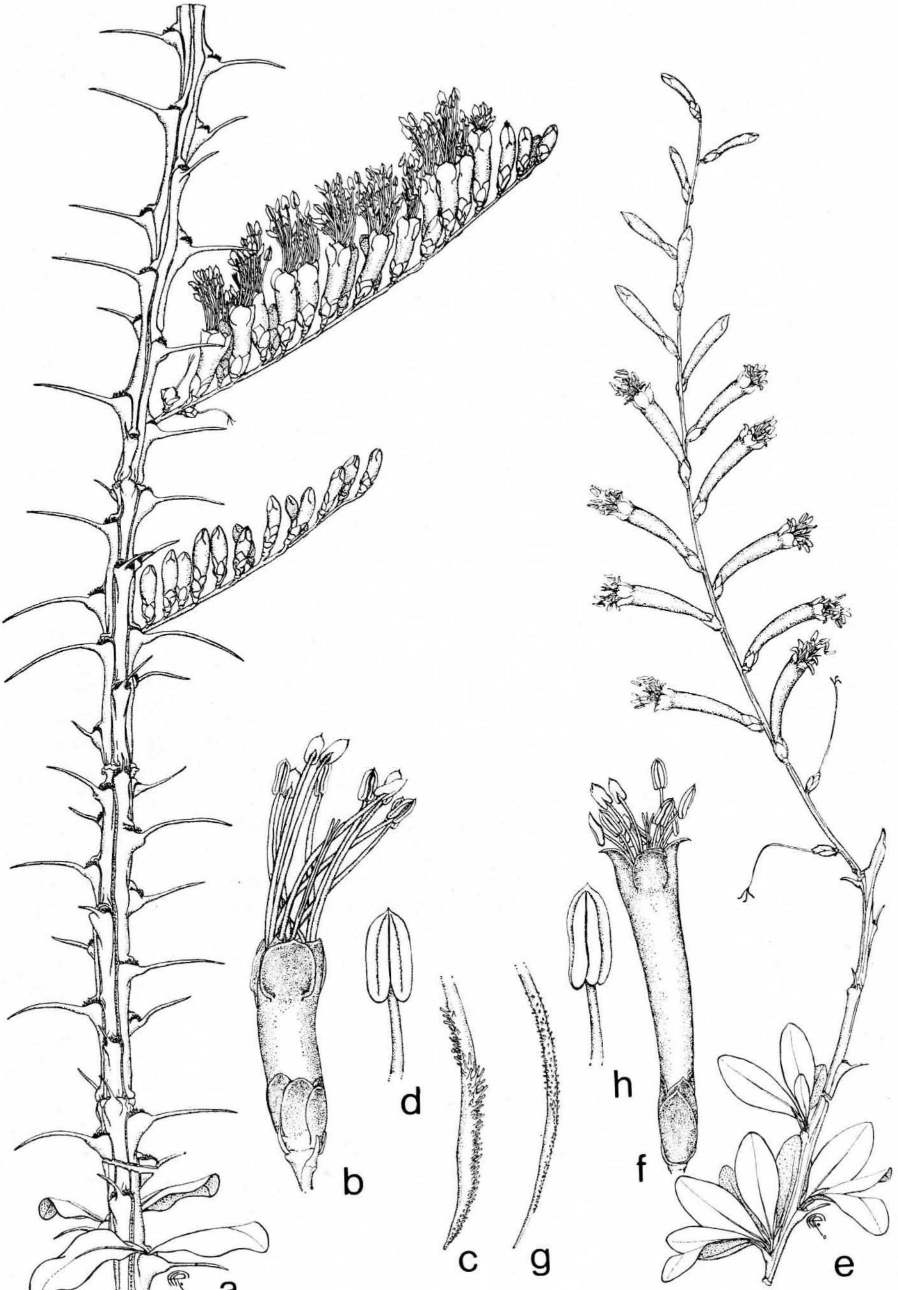
One species.

11. *F. columnaris*

1. **FOUQUIERIA LEONILAE** F. Miranda, Bol. Soc. Bot. México 26: 127, pl. 128. 1961. TYPE: MEXICO. GUERRERO: Cañon del Zopilote, cerca de Venta Vieja (Carretera Mexico-Acapulco) en selva baja decidua de latera de barranca lateral al Cañon, 19 Jan., 1960, *F. Miranda 9273* (HOLOTYPE: MEXU! fls.; ISOTYPE: US!; PARATYPE: 30 Aug., 1960, *Miranda 9282*, MEXU!, duplicate US! lvs.).

Small, sparsely-branched trees, 2–4(–7) m high with 1–3(–5) trunks to 2–3(–4) m high, 4–20(–30) cm in diameter. Periderm light-bronze, thin, smooth, exfoliating in thin sheets, translucent, larger stems often green due to cortical chlorenchyma. Young branches thin, delicate, 2.5–3.5 mm in diameter, very slightly furrowed; decurrent ridges maroon-red, turning silver-grey and falling from stems 3–4 cm in diameter, 9.5–13 cm long, tapering to the fifth node below. Spines 5–11 mm long, slender, slightly curved, in a 2/5 phyllotaxy. Long-shoot leaves, 20–25(–35) mm long with petioles 7–12 mm long, blades 14–25 mm long, 5–10 mm wide, narrowly elliptical, acute at apex, narrowly cuneate at base. Short-shoot leaves in fascicles of 3–6, (25–)30–42 mm long, 9.5–15(–20) mm wide, oblanceolate, to elliptical or broadly elliptical, acute to rounded at apex, cuneate at base, with petioles to 8 mm long; leaves dorsi-ventral, dark green above, grey-green below, with slightly scarious, entire margins. Inflorescence spicate, occasionally slightly racemose toward the base, with pedicels to 0.5 mm long, terminal to subterminal, erect to ascending, 13–30 cm long; rachis slender, 1–2 mm in diameter, dark maroon; floral bracts dark red-maroon, ovate-subulate, caducous, 2–4 mm long, 1–2.5 mm wide. Sepals maroon-purple, greenish at base, with broad white scarious margins, outer two 4.5–6 mm long, 3–4 mm wide, inner three 5–8 mm long, 3–5 mm wide, broadly ovate to elliptical, acute to rounded at apiculate apex often with margins infolding, rounded to cuneate at broad base. Corolla tubular-funnelform, dark red, greenish under sepals, 27–36(–42) mm long, tube 22–36 mm long widening towards throat, ascending, slightly curved outward, diameter 4–4.5 (5 pressed) mm at throat, 2.5–3 mm at base, corolla limbs flaring, 4.5–6 mm long, 3.5–4 mm wide, broadly ovate with narrow white, scarious, infolding margins, acute and apiculate at tip, cuneate at broad base. Stamens 10(–11) exserted, of unequal length; filaments red, yellow to white in lower half, 30–34(–43) mm long, lower 10 mm very slightly broadened with scattered, short, stubby hairs to 0.2 mm long; anthers red, 4–4.5 mm long, 1.5 mm wide, narrowly oblong, cuspidate at tip, cordate at base. Ovary 1–1.5 mm high, with 6 ovules; style dark red, yellow to white below, 28–43(–45) mm long, 3-lobed 2–6 mm from tip. Capsules tan, tinged with purple, lanceolate to narrowly ovate in outline, 17–22 mm long, 6–8 mm wide; seeds 3–6, whitish-tan, 13–16 mm long, 6–8 mm wide, with membranes 4.5 and 2 mm long at ends and sides respectively; membrane hairs 60–120 μ thick near tip with perpendicular thickenings; embryo 6–8 mm long, cotyledons elliptical, 5–6.5 mm long, 2.5–3.5 mm wide.

Fouquieria leonilae is known only from Cañon del Zopilote south of the Rio Balsas (Rio Mexcala) in the state of Guerrero (Fig. 14) where it is common from 500 to 1100 m on rocky hillsides on outcroppings of a whitish,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possibly gypseous or calcareous soil. It is associated with deciduous species of *Bursera, Cordia, Pseudosmodingium, Haematoxylon, Hibiscus, Cephalocereus,* and *Hechtia* in an arid tropical scrub vegetation. This region averages 700–800 mm annual precipitation concentrated from June through October. This species flowers during the dry season from December through March.

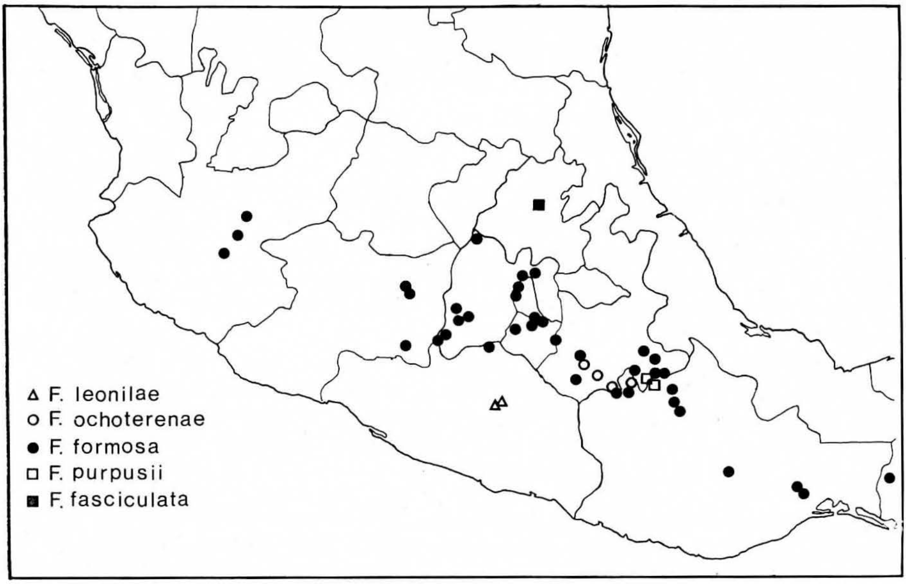

Fig. 14. Distribution of *Fouquieria leonilae, F. ochoterenae, F. formosa, F. purpusii* and *F. fasciculata* in Central Mexico.

The species is very distinctive and vegetatively can be distinguished by its sparsely branched small tree habit consisting of one or more definite trunks covered with a smooth papery, bronze periderm and the very slender, delicate, slight-spined young stems which are initially dark maroon but turn silver grey prior to developing the characteristic papery periderm. The

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Fig. 13. a–d. *Fouquieria ochoterenae.*—a. Terminal stem bearing axillary racemose inflorescence of erect flowers. Decurrent ridges are truncated at base and separated by deep furrows. Short-shoot leaves, not present during flowering season are thick and rigid.—b. Mature flower showing exserted stamens. Note position of style and basal bracts subtending flower.—c–d. Stamen.—c. Basal filament (radial view) showing extent of trichomes.—d. Anther, adaxial surface. (*Henrickson 4320*).—e–h. *Fouquieria leonilae.*—e. Terminal stem with slender elongate spicate inflorescence. Note curvature of corolla and characteristic slender stems. Leaves, shown below are not present in flowering season.—f. Mature flower. Note position of stigmas among anthers.—g–h. Stamen.—g. Basal filament (radial view) showing short sparse pubescence.—h. Anther, adaxial side. (*Henrickson 2164*).—a, e ×0.5; b, f ×1.5; c–d, g–h ×4.

delicate, long, spicate inflorescences and dark-red decandrous flowers (Fig. 13) are also distinctive. This species is most closely related to *F. ochoterenae* which occurs in a very similar vegetation zone in Puebla and Oaxaca. Their similarities and differences are discussed under the latter species.

Although no pollinator activity was observed during two trips to Cañon del Zopilote, floral structures suggest pollination by hummingbirds. The red tubular flowers are odorless, strongly nectariferous and are produced in delicate terminal inflorescences which would seemingly exclude heavier perching birds. The species is sufficiently common and floriferous to support a population of hummingbirds which are recorded throughout Guerrero (Friedman et al., 1950).

Chromosome number: $2n=24$.

Etymology: Named for Dra. Leonila Vazquez, entomologist at the Instituto de Biologia de la Universidad Nacional de Mexico.

Representative specimens: MEXICO: GUERRERO: 35 km NNW of Chilpancingo, 3–5 km on road from Casa Verde to Xochipala, *McVaugh 22185* (MICH); 1 km S of Venta Vieja, Cañon del Zopilote, *Henrickson 2164-8* (RSA); 2 km SW of Venta Vieja, Cañon del Zopilote, *Henrickson 4326* (RSA).

2. FOUQUIERIA OCHOTERENAE F. Miranda, Anales Inst. Biol. Univ. Nac. México 13: 458, pl. 459, 1942. TYPE: MEXICO. PUEBLA: Lateras yesos por encima de Amatitlan, cerca Matamoros, 25 Jul., 1942, *F. Miranda 2093* (LECTOTYPE: MEXU! lvs.; PARATYPE: 26 Dec., 1942, *Miranda 2575*, MEXU!, duplicates GH, F! fls.).

Small trees 4–8 m high with 1–2 trunks, 1–2 m high to 10–20(–30) cm in diameter; upper stems widely divergent, with a dichotomous-like branching pattern; trunks and larger stems covered with thin, translucent, dark-bronze periderm interrupted by persistent, grey, decurrent ridges arranged in five gradually spiralling series. Young branches thickish, 5–6 mm in diameter, deeply furrowed; decurrent ridges dark maroon, turning light grey with age, long persistent, 36–57 mm long, extending to fifth node below, slightly protruding at truncate base. Spines 4–30 mm long, thick, slightly curved, in a 2/5 phyllotaxy. Long-shoot leaves 35–50 mm long, with petioles 12–18 mm long, blades 23–33 mm long, 14–18 mm wide, broadly obovate, rounded at tip, cuneate at base. Short-shoot leaves in fascicles of 1–3, (24–)30–53(–80) mm long, (12–)17–27 mm wide, broadly obovate-elliptic to broadly obovate, obtuse to rounded, often retuse at apex, broadly cuneate at base, with petioles 2–5 mm long; leaves dorsi-ventral, dark green above, grey-green below, leathery, with white to reddish scarious, often undulate margins, central vein very marked towards base. Inflorescence racemose, subterminal, borne along upper branches, 5.5–9.5 cm long with stout, dark red-maroon rachis 1–2(–3) mm diameter at base; pedicles, 2–5 mm long, bearing three, maroon-red oblong to subulate caducous, medial bracts to 4 mm long, 1 mm wide, lateral bracts 1–1.5 mm long. Sepals dark red-maroon, occasionally with green below, with broad white, scarious margins; outer two sepals 3–4.5 mm wide, 3.2–5 mm long, inner three 4–5 mm wide, 5–6 mm long, broadly ovate to orbiculate, rounded to emarginate, occasionally apiculate at apex, cordate at broad thickened base. Corolla tubular, dark red-maroon, curved upward, 14–19 mm long, tube 9–13 mm long, expanding towards throat, diameter 5–6 (7 pressed) mm at throat, 3–4 mm at base; limbs upright, appressed against filaments, 5.5–6.6 mm long, 5–5.5 mm wide, broadly ovate to broadly elliptical with scarious margins, rounded but apiculate at apex, truncate at broad base. Stamens 10, exserted, of unequal length; filaments dark red above, whitish to yellowish below, 22–30 mm long; lower 7–8 mm slightly broadened laterally with short unicellular hairs which increase from 0.1 to 0.3 mm in length from lower abaxial surface laterally to upper adaxial surface above ovary, upper filament cylindrical, glabrous. Anthers dark red, 3.5–4 mm long, 2 mm wide, elliptic to slightly ovate in outline, apiculate at tip, cordate at base. Ovary 1.2 mm high, with 6(–12) ovules; style dark red, 25–30 mm long, branching 4–5(–8) mm from tip into (2–)3 branches. Capsules tan, often tinged with dark red, 18–22 mm long, 5–7 mm wide, lanceolate to narrowly ovate in outline; seeds 3–6, whitish tan, 10–12 mm long, 6 mm wide with membranes 3 and 2 mm long at ends and sides respectively; membrane hairs 50–120 μ wide distally with perpendicular thickenings; embryo 6 mm long, cotyledons oblong-elliptical, 4.5 mm long, 2.5 mm wide.

Fouquieria ochoterenae is known only from southwestern Puebla and adjacent Oaxaca where it occurs in the deciduous arid tropical scrub vegetation from 1250 to 1500 m elevation (Fig. 14). At the type locality, near Amatitlan, Puebla, Miranda (1942a) notes the species occupies the more arid slopes with shallow soil and becomes a dominant species on outcroppings of selenite, fibrous gypsum and limestone, where it occurs with *Bursera, Pseudosmodingium, Ceiba, Actinocheita, Acacia, Mimosa, Manihot,* and *Hechtia.* Rainfall over its range averages 600–750 mm a year concentrated from May through October (Miranda, 1942a, 1943). The species flowers in the dry season from November to April.

The species can easily be distinguished by both vegetative and floral features (Fig. 13). Mature plants have one to two dominant trunks which bear widely divergent stems with a restricted but dichotomous-like branching pattern. This dichotomous pattern results from production of divergent pairs of long-shoot stems from or near the stem tips. Lateral branching from older stems is infrequent. Young stems are thick, deeply furrowed and have stout spines. The decurrent ridges are short, truncated at the base and are persistent on older stems and trunks in five gradually spiraling rows. The erect, red-maroon, decandrous flowers are produced on short racemose inflorescences all along the upper branches up to 2.5 cm diameter. Inflorescences are not restricted to a terminal or subterminal position. The close proximity of the inflorescences to the thick stems allows exploitation of the flowers by various perching birds. In the Petlalcingo region, the yellow grosbeak (*Pheucticus chrysopeplus*) (Miller, 1957) was observed feeding on the flowers while perching on the adjacent stems in such a way that long exserted anthers contacted the face above the beak. Doves have also been observed feeding on the flowers and evidence of carpenter bee nectar robbing is occasionally observed.

Fouquieria ochoterenae is most closely related to *F. leonilae* with which it shares the following characteristics: dorsi-ventral leaves, small tree habit, flowers with dark red corollas, ten stamens, borne on narrow racemose to spicate inflorescences, initial one-trace sepal vascularization and a reduced number of ovules (six, occasionally to 12 per ovary). The latter two characters occur only in these two species. Their distinguishing characteristics are associated with longer, more delicate features of *F. leonilae* as contrasted to thicker, shorter features of stems and flowers of *F. ochoterenae.*

Fouquieria ochoterenae was first collected in leaf (*Miranda 2093,* 25 Jul., 1942) and later recollected from the same area in flower (*Miranda 2575,* 26 Dec., 1942). Miranda designated both specimens as types (syntypes) and both specimens are mounted on one sheet at MEXU. I here designate *Miranda 2093* (lvs.) as lectotype and *Miranda 2575* (fls.) as paratype. Miranda's (1942b) illustration has the inflorescence positioned incorrectly. The flowers extend towards, not away from the stem.

Chromosome number: $2n=24$ (Spellenberg in Löve, 1970).

Vernacular name: "Rabo de Iguana" (Miranda, 1942b).

Etymology: Named after Dr. Isaac Ochoterena, eminent Mexican biologist.

Representative specimens: MEXICO: PUEBLA: 24 km S of Izucar de Matamoros, *Henrickson 2096-7* (RSA); 12 mi S of Acatlan, *Wiggins 13253* (DC); 15 and 18 km S of Acatlan, *Henrickson 2118-9, 4320* (RSA). OAXACA: 57 km SW of Tehuacan (possibly cultivated), *Henrickson 2126* (RSA).

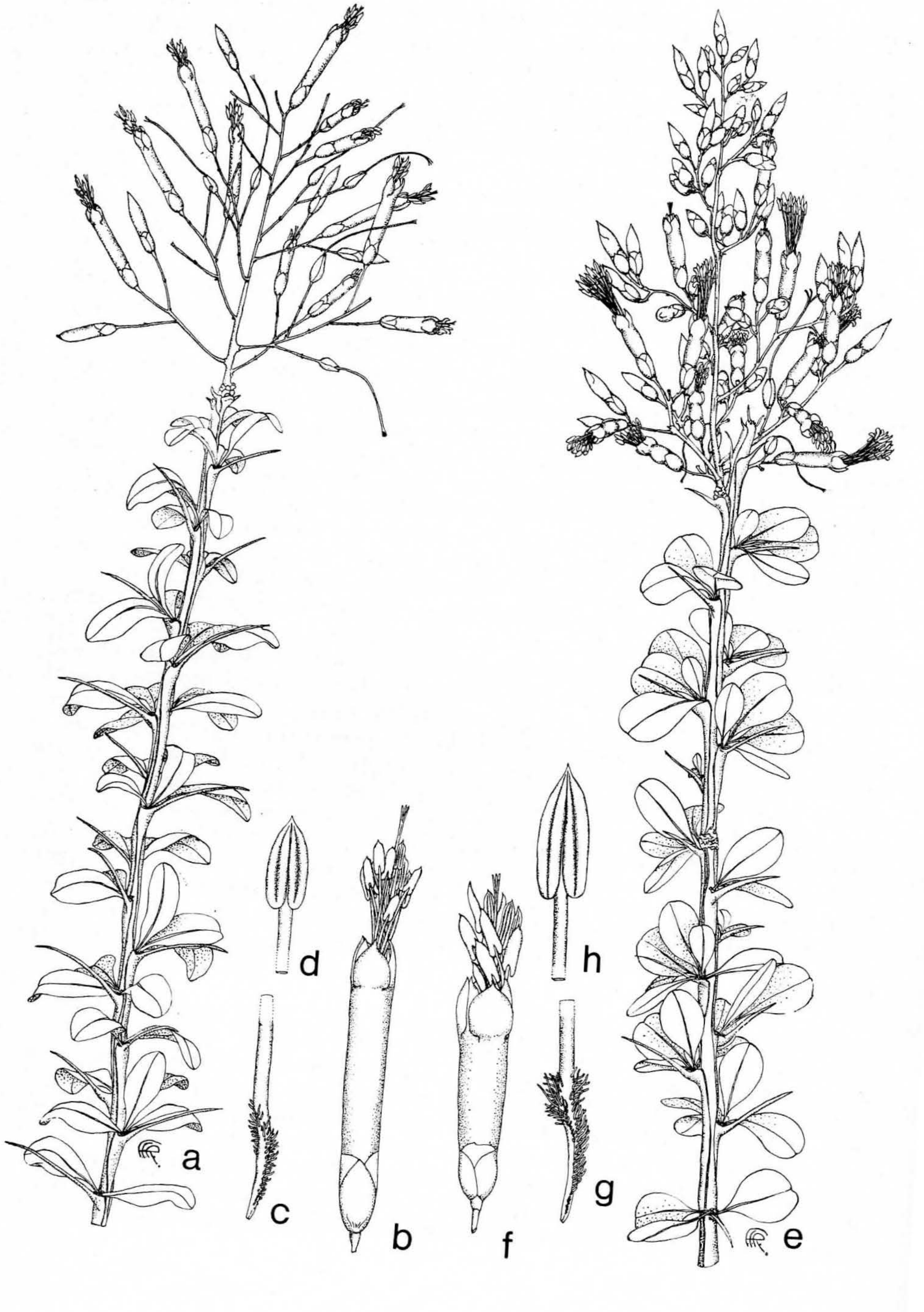
3. FOUQUIERIA MACDOUGALII Nash, Bull. Torrey Bot. Club 30: 454, 1903. TYPE: MEXICO. SONORA: From living plants collected at Torres, Mexico in 1902 by MacDougal (no. 28) which flowered in the conservatories of the New York Botanical Garden in June, 1903. (HOLOTYPE: was at NY, not extant; LECTOTYPE here designated: SONORA: Alamos, *E. Palmer 306,* 28 Mar.–8 Apr., 1890, NY! fls.; duplicates ARIZ, CAS, GH, MEXU, MICH, US!).

Fouquieria jaboncillo Loes., Freddes Repert. Spec. Nov. Regni Veg. 9: 356, 1911. TYPE: MEXICO. SINALOA: Bei Topolobampo, auf der Hacienda Correrepe und in den Waldern zwichen Fuerte und Choix. Dec. 19—*Endlich 701 a, b.* (Syntypes were at B, no longer extant, NEOTYPE here designated: SINALOA: ca. 20 mi NE of Los Mochis toward El Fuerte, *Henrickson 1632,* 20 Jun., 1964, RSA!).

Echeveria paniculata Sesse & Mocino ex DC. Prod. 3: 350, 1828 "as syn."

Small trees 2–6(–11) m high with 1–4(–5) basal trunks to 1–2 m high, 15–40 cm in diameter, stems divergent, much branched above, often pendulous at tips. Periderm light bronze, thin, smooth, translucent, with underlying chlorenchyma conspicuous, exfoliating in thin sheets. Young branches 3–3.2 mm in diameter, very slightly furrowed; decurrent ridges dark maroon to brown, turning light grey with age, 42–65 mm long, tapering to fifth node below, falling from stems 4–5 cm in diameter. Spines 4–35(–42) mm long, slender, in 2/5–3/8 phyllotaxy. Long-shoot leaves 30–55(–70) mm long, with petioles 10–30 mm long and blades 14–25(–40) mm long, 5–10(–21) mm wide, narrowly elliptical to elliptical, with acute apex, abruptly narrowing to petiole. Short-shoot leaves in fascicles of 2–5, 12–30(–60) mm long, 7–14(–18) mm wide, with petioles 3–7(–18) mm long, broadly obovate to lanceolate or elliptic, acute to rounded or slightly retuse at apex, broadly to narrowly cuneate at base; leaves isolateral, dark green above, light green below, slightly to moderately pilose near midrib or pilose throughout lower surface in young leaves, midrib prominent below near base, entire. Inflorescence corymbosely paniculate, occasionally racemose above or throughout when small, (1.5–)3–8(–20) cm long, usually as broad or more so, terminal to subterminal; rachis pink-red, delicate, 0.8–1.5(–2) mm thick near base; pedicels (3–)10–17(–32) mm long, 0.2–0.6 mm thick, expanding abruptly at flower base; peduncles (0–)8–40(–70) mm long, 0.4 mm wide; floral bracts caducous, subulate, to 3 mm long, medial bract at swollen peduncle-pedicel junction, lateral two along pedicel below flower. Sepals pink-red to green with broad white scarious margins, 4.5–6.5 mm long, 4.2–5 mm wide, broadly ovate to orbicular, infolded, rounded, often apiculate at apex, rounded to truncate at broad base, outer two usually longer than the broader inner three. Corolla tubular, bright red to scarlet, whitish to greenish under sepals, 18–26 mm long; tube cylindrical, slightly enlarging towards throat, 13–21 mm long, diameter 3.8–4.2 mm at throat, 2–3 mm at base; limbs erect, 4–5 mm long, 3–5 mm wide, broadly ovate to broadly elliptical, acute, often apiculate at apex, truncate to slightly cordate at broad base, with scarious margins commonly infolding near tips. Stamens 10, long exserted, filaments 26–36 mm long, bright red, whitish at base, lower 6–7 mm broadened laterally, with hairs increasing from 0.5 to 1 mm from basal abaxial portion laterally to adaxial side above ovary, upper filament cylindrical, glabrous; anthers red, 3–4 mm long, 1 mm wide, elliptical, apiculate at apex, strongly cordate at base, occasionally with small hairs between anther sacs in bud. Ovary 1.5 mm high, with 16–18 ovules; style 25–45 mm long, red, 3-branched 1–3 mm from tip; stigmas stationed above anthers. Capsule tan, often tinged with red, broadly lanceolate in outline, 16–29 mm long, 5–7 mm wide; seeds 6–13(–15), tannish-yellow to beige, 12–15 mm long, 5–6 mm wide, with membranes 3–4 and 1.5–3 mm long at ends and sides respectively, membrane hairs 60–110 μ broad near tips, with perpendicular thickenings; embryo 6–8 mm long; cotyledons elliptical, 4–5 mm long, 2–2.6 mm wide.

Fouquieria macdougalii ranges from sea level to about 600(–800) m elevation from the Sonoran Desert of Central Sonora southward to the tropical deciduous forest along the Sierra Madre Occidental of southeast Sonora and adjacent Chihuahua and to the thorn forest of south-central Sinaloa (Fig. 16). Average annual precipitation varies from 155 to 400 mm in the desert and coastal regions and from 400 to 900 mm in the Sierra Madre foothills. Rainfall occurs mainly in late summer from July through October. Flowering follows rains but may occur at any time throughout the year. This species occupies alluvial rocky flats and slopes on granitic and to a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lesser extent volcanic based soils. It also grows on open lava beds (Shreve, 1951) and coastal sandy playas as near Topolobampo, Sinaloa. In the tropical deciduous forest the soils are much richer, often loamy. Shreve (1951) notes the northern range is limited by the plant's susceptibility to frost damage and it is there restricted to south-facing slopes bordering valleys above the influence of temperature inversion.

Fouquieria macdougalii is a dominant small tree in the Southern Plains of the Sonoran Desert where it is associated with species of *Cercidium, Olneya, Prosopis, Acacia, Bursera, Jatropha, Lemaireocereus, Lophocereus,* and *Ipomoea.* In the foothills of the Sierra Madre it is less frequent but grows much larger and occurs with many of the above as well as with *Haematoxylon, Caesalpinia, Karwinskia, Ceiba, Lysiloma, Erythrina, Pachycereus,* and *Cassia.* It is sympatric with *F. splendens* in northern Sonora and *F. diguetii* near Guaymas.

The species is distinguished by its small tree habit with slender, divaricate, often terminally pendulous branches, its open, nearly rounded corymbose panicles with delicate peduncles and pedicels and the bright red, narrow, cylindrical, decandrous flowers with erect corolla lobes (Fig. 15). It is most similar to *F. diguetii.* Similarities and differences are discussed with the latter species.

Fouquieria macdougalii ranges over a broad precipitation spectrum which increases from the arid desert and coastal regions towards the Sierra Madre. The wide variation in precipitation is reflected by mature plant height, which ranges from 2–5 m in arid zones to 8–11 m in moist regions. Inflorescence size is also generally affected by moisture conditions; however, a direct correlation is not always present. Data on inflorescence size variation are presented in Fig. 17 in which inflorescence length (measured from available specimens) is compared with the general range of the annual rainfall (Hastings and Humphrey, 1969 a, b; Vivó and Gómez, 1946) for seven regions comprising the total range. As rainfall increases from northeast to southeast Sonora there is an associated, though moderate, increase in mean inflorescence length. In contrast, populations along the northwest coast of Sinaloa near Topolobampo have significantly shorter inflorescences when compared to similar arid regions in Sonora. The other Sinaloan regions also tend to have shorter inflorescences in spite of high precipitation. Whether the relatively shortened inflorescences found in Sinaloa are the result of some other environmental factor or have a genetic basis is not known. The

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Fig. 15. a–d. *Fouquieria macdougalii.*—a. Terminal stem bearing characteristic broad paniculate inflorescence with delicate peduncles and pedicels.—b. Mature flower showing erect corolla lobes and terminal position of style.—c–d. Stamen.—c. Filament base (radial view) showing extent of trichomes.—d. Anther, adaxial surface. (Stem: *Muller 3645*; Inflorescence: *Palmer 306*).—e–h. *Fouquieria diguetii.*—e. Terminal stem with paniculate inflorescence. Note comparative thickness of pedicels and peduncles.—f. Young flower showing initial emergence of style and stamens.—g–h. Stamen.—g. Filament base (radial view) showing extent of trichomes.—h. Anther, adaxial surface. (Stem, *Barr 61-105*).—a, d ×0.5; b, f ×1.5; c–d, g–h ×4.

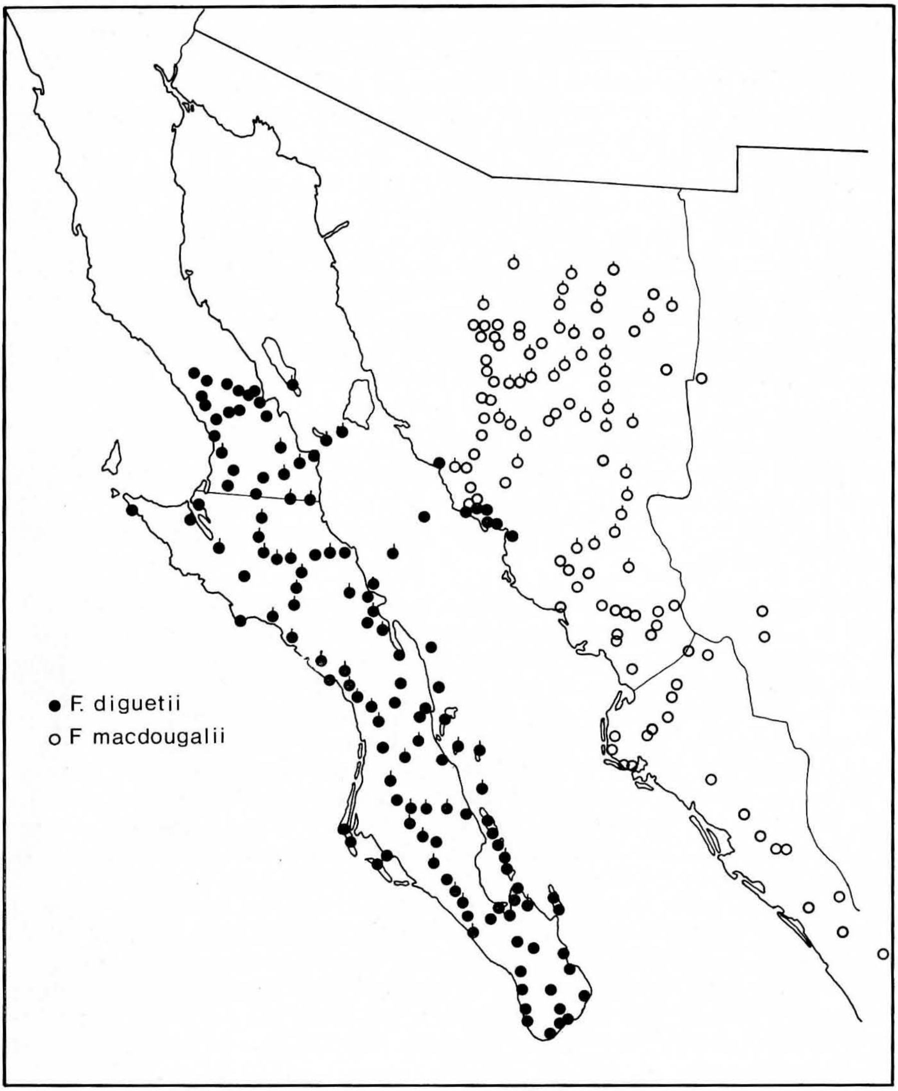


Fig. 16. Distribution of *Fouquieria diguetii* and *F. macdougalii* in northwestern Mexico. Circles with upward projections indicate field sightings recorded by Hastings et al., 1972.

coastal populations near Topolobampo tend to flower throughout the dry season, producing very reduced, often racemose, inflorescences. A similar inflorescence reduction occurs in coastal populations of the related *F. diguetii.* As the Sonoran and Sinaloan populations are basically the same except for inflorescence characteristics, the populations are not nomenclaturally distinguished. In 1911 Loesener described specimens collected by Endlich from northern Sinaloa (Topolobampo and Choix) as *F. jaboncillo.* He, however, erroneously related it to Nash's *F. fasciculata* rather than *F. macdougalii* which indicates he was not intentionally distinguishing the short-inflorescence forms from others.

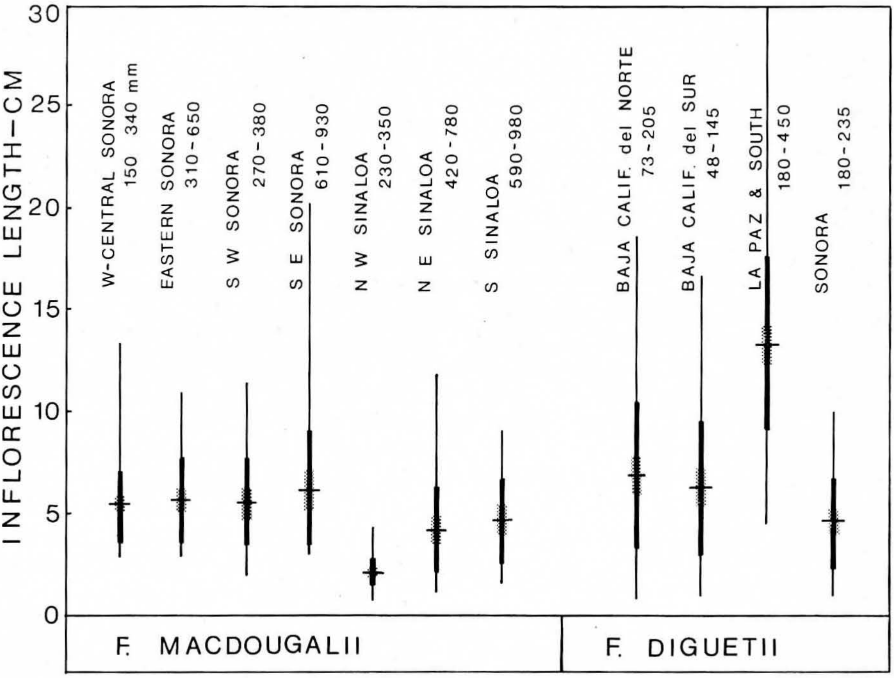


Fig. 17. Variation of inflorescence length (in cm) from separate sections of range of *Fouquieria macdougalii* and *F. diguetii.* Range in average annual precipitation (in mm) for each area is indicated under location to allow comparison of precipitation with inflorescence length. Data on inflorescence length taken from available herbarium specimens. Horizontal bar indicates mean, range is shown by thin vertical line, standard deviation by bold line, standard error by broad checkered line ($n=28$ to 115). Precipitation data from Hastings and Humphrey 1969a, b.

Visitations to the flower by hummingbirds have been observed in Sonora (near Hermosillo) and Sinaloa (near San Blas) and they appear to be the principal pollinators. The stigma is stationed above the anthers which presumably would favor outcrossing over self-pollination. Evidence of carpenter bee robbing was observed occasionally.

Chromosome number: $2n=24$.

Vernacular names: Sonora, Sinaloa, "Chunari," "Chinari," "Chunuli," "Torotillo," "Torote jaboncillo"; Sinaloa, "Palo verde," "Jaboncillo," "Torote verde" (fide Gentry, 1942; Standley, 1925).

Etymology: named after Daniel Trembly Macdougal whose living specimen of this species flowered at the New York Botanical Garden and eventually caused Nash to revise the family.

Representative specimens: MEXICO. CHIHUAHUA: Rio Bonito, *LeSueur 1157* (TEX, F); 1 mi S of Batopilas, *Palmer 228* (GH). SONORA: 23.6 mi S of Benjamin Hill, *Hastings & Turner 64.6* (ARIZ, DS, SD); 10 mi N of Carbo, *Wiggins 7259* (DS, MICH, US); between Noria and Carbo, *Ferris 8762* (DS, NY, POM, US); Rayon, *Thurber 952* (GH, NY, MO); Granados, *Hartman 266* (GH, US); ca. 5 mi N of Moctezuma, *S. White 398* (ARIZ, GH, MICH); El Rio Bonito, near El Nopalera, Munic. Nacore Chico, *Muller 3645* (F, GH, MICH, MO, UC); 4 mi W of San Pedro de las Cuevas towards Matape, *Wiggins & Rollins 455* (ARIZ, DS, GH, MICH, MO, UC, US); vicinity of Hermosillo, *Rose, Standley & Russel 12475* (GH, NY, US); 40 mi S of Hermosillo, *Abrams 13351* (DS); 18 mi N of Guaymas, *Kimnach 235* (US); San Pedro Bay, *T. Craig 699* (POM); 19 mi NW of Queriego on rd to Cajeme, *Wiggins 6455* (MICH, POM, UC, US); 15 mi W of Alamos, *Henrickson 2447* (RSA); Alamos, *Palmer 306* (ARIZ, CAS, GH, MEXU, MICH, NY, US); San Bernardo, Rio Mayo, *Gentry 1322* (ARIZ, F, MO, UC); 60 km S of Navojoa, *Henrickson 1623* (RSA). SINALOA: El Posole, near Ahome, *Ortega 5583* (DS, MEXU, POM, US); Topolobampo, *Rose, Standley & Russel 13327* (NY, US); 20 mi NNE of Los Mochis, *Henrickson 1628–1633* (RSA); San Blas, *Rose, Standley & Russel 13207* (GH, NY, US); El Fuerte, *Rose, Standley & Russel 13505* (NY, US); 9 mi N of Guamuchil, *Walker 105* (TEX); 0.2 mi N of Terreros, ca. 45 mi N of Culiacan, *Breedlove 1515* (DS, MICH); Culican, *Palmer 1804* (F, GH, NY, US); Conitaca, Munic. Cosala, *Montes 812* (MEXU, US); San Ignacio, *Montes 686* (US).

4. FOUQUIERIA DIGUETII (van Tiegh.) I. M. Johnston, Contr. Gray Herb. 75: 30, 1925.

Bronnia digueti van Tiegh., J. Bot. (Morot) 13: 297, 1899. TYPE: MEXICO. BASSE-CALIFORNIE: (near La Paz) 1897, *Diguet s.n.* (LECTOTYPE here designated: P! fl.; ISOTYPE P! ft.).

Bronnia thiebauti van Tiegh., loc. cit. TYPE: MEXICO. SONORA: ile d' Ardilla, Guaymas, Jun., 1866, *Thiebaut 41* (HOLOTYPE: P! fl.).

Fouquieria peninsularis Nash, Bull. Torrey Bot. Club 30: 445, 1903. TYPE: MEXICO. LOWER CALIFORNIA: La Paz, 11 Dec., 1847, *Maj. W. Rich s.n.* (HOLOTYPE: NY! fl, ft.).

Bronnia spinosa auct. non. H. B. K.; Benth., Voy. Suplh. 1: 16. 1844.

Shrubs to small trees (1–)2–4(–8) m high; small plants with short stocky basal trunk to 2 dm high, to 3 dm in diameter bearing several crooked, moderately branched, ascending main stems with numerous divergent young stems above, occasionally smaller plants with a more candelabraform-like habit but with noticeably crooked stems; larger plants with 1–5 basal stems to 1 m high, 2 dm in diameter, moderately branched above, upper stems erect or horizontal to pendulous at periphery of crown; periderm dark bronze, thin, exfoliating in thin plates and interrupted by persistent grey, corky, decurrent leaf bases. Young branches (3–)5–6.5 mm in diameter, very slightly furrowed; decurrent ridges maroon, glaucous, turning grey with age, glabrous or rarely canescent, long persistent, 45–60 mm long, tapering and obliquely truncate at fifth node below. Spines (5–)10–25 mm long, slender, in 3/8 or 2/5 phyllotaxy. Long-shoot leaves 16–44 mm long, with petioles 9–23 mm long, blades 7–22 mm long, 5–15 mm wide, ovate, acute to rounded, occasionally apiculate at apex, cuneate, rarely nearly rounded at base. Short-shoot leaves in fascicules of 2–5, 12–26(–35) mm long, 8–12(–28) mm wide, with petioles 1.5–6 mm long, broadly obovate to ovate, occasionally elliptical, rounded to slightly emarginate at apex, broadly to narrowly cuneate at base; leaves glabrous, occasionally pilose below or on both sides when young, isolateral, grey-green, entire, sometimes scariously margined. Inflorescence paniculate to racemose when reduced, terminal to subterminal, conical, (1–)6–15(–30) cm long, 2–5(–13) cm broad near base; rachis pink-red, tan in fruit, 1.5–4 mm in diameter at base, glabrous, rarely pilose; pedicels thickish, (0.4–)0.6–0.8(–1.2) mm in diameter, 2–6(–13) mm long, expanding below flowers; peduncles (2–)10–35(–65) mm long, 0.7–1.2(–20) mm in diameter; floral bracts caducous, medial bract 3–4 mm long, elliptical, acute to acuminate at apex, rounded at broad base; lateral bracts smaller, along pedicel below flower. Sepals mottled red-pink with white scarious margins, occasionally greenish, (4.5–)6–7 mm long, (4–)4.5–6 mm wide, broadly obovate to orbicular, rounded to apiculate, or occasionally emarginate at apex, truncate to cordate at broad base, outer two shorter than inner, more orbiculate sepals. Corolla tubular, strongly red, whitish to green under sepals, waxy, relatively thick in texture, (16–) 20–25 mm long; tube cylindrical, slightly expanding towards throat, 16–18 mm long, diameter 4–5 mm at throat, 2–3 mm at base; limbs erect, 5–7 mm long, 4–6 mm wide, broadly ovate to broadly elliptical with broad scarious, infolding margins, obtuse to rarely truncate and apiculate at apex, cordate at broad base. Stamens 10, exserted, filaments 27–34 mm long, strong red, whitish at base, lower 5–7 mm broadened laterally, arching over ovary, with hairs increasing from 0.5 to 1.5 mm long from mid-abaxial side laterally to adaxial side above ovary, upper filament glabrous; anthers yellow to red, 5–6.2 mm long, 1.5 mm wide, oblong-lanceolate in outline, apiculate at apex, cordate at base. Ovary green, with 16–20 ovules; style (26–)30-36 mm long, strong red, 3-branched (3–)4–5 mm from tips; stigmas stationed above anthers. Capsules tan, lanceolate in outline, 19–27 mm long, 5–7.5 mm wide; seeds 8–15, yellowish tan, 12–15 mm long, with membranes 3.5–5 and 1 2–2 mm long on ends and sides respectively, membrane hairs 40–125 μ thick at ends with perpendicular anastomosing thickenings; embryo 7 mm long, cotyledons elliptical-ovate, 5 mm long, 2 mm wide.

Fouquieria diguetii is very common in the Sonoran Desert of Baja California from an area about 40 km N of Punta Prieta (29° 10′ N Lat.) south through the tropical deciduous forest below La Paz to Cabo San Lucas (Fig. 16). Disjunct populations also occur in Sonora near Guaymas and on many islands in the Gulf of California. It occurs mainly on broad alluvial plains and hills below 600 m elevation, but is found as high as 1200 m on Cerro de Gigantea (fide *Carter 2042*). It grows on a wide variety of soil types from rocky volcanic slopes with little soil, to rocky alluvial mesas and slopes with reddish volcanic clays to clay and sandy clay flats, to decomposed granite sand and sandy coastal playas. Average yearly precipitation ranges from a mere 70–150 mm in the Sonoran Desert of Baja California, 180–250 mm around Guaymas, Sonora, up to 450 mm in the tropical deciduous forest south of La Paz. The desert regions, which may go without rain for a year, receive sporadic winter and early spring rains, while the Cape region receives summer rains from July through September. Flowering predominates in the winter from February through May but some flowers may be produced throughout the year.

Common associates in the Sonoran Desert include species of *Bursera, Larrea, Jatropha, Encelia, Pedilanthus, Opuntia, Pachycereus pringlei* (S. Wats.) Brit. & Rose, *Lemaireocereus, Agave,* and *Yucca.* In the short tree forests of the Cape region it occurs with *Pachycereus pectin-aboriginum* (Engelm.) Brit. & Rose, *Bursera, Jatropha, Lemaireocereus, Acacia, Pithecellobium, Lysiloma, Prosopis,* and *Karwinskia.* Over portions of its range it is sympatric with *F. splendens, F. burragei* and *F. columnaris* in Baja California and *F. macdougalii* in Sonora.

Fouquieria diguetii is distinguished by its bright red, tubular decandrous flowers, conical paniculate inflorescences, isolateral leaves, shrub to small tree habit and decurrent ridges persistent on older stems (Fig. 15). It is most closely related to *F. macdougalii* of Sonora. They are similar in inflorescence, floral, leaf and long-shoot structures as well as growth habit. *Fouquieria diguetii,* however, has thicker peduncles and pedicels, shorter, thicker corollas, persistent decurrent ridges and is very distinct palynologically (Henrickson, 1967). The species also differ in chromosome number which suggests a possible derivation of *F. diguetii* ($2n=48$) from *F. macdougalii* ($2n=24$) stock. In coastal regions, *F. diguetii* is vegetatively very similar to *F. burragei.* They can easily be distinguished, however, by inflorescence and floral structures.

Considerable variation in growth habit and inflorescence length exists over the range of the species. Plants of arid Sonoran Desert range from 1–3 m in height at maturity. Smaller plants often have a candelabraform-like habit but with tortuous, moderately branched stems. In the southern tropical deciduous forest, mature plants commonly exceed 4 m in height and have one or more large trunks which branch with increasing frequency towards the top producing many erect to horizontal young stems at the crown. Inflorescence length follows a similar variation pattern. Those of the arid Sonoran Desert are 5.1(1.5–12.2) cm long, while in the more moist tropical deciduous forest they are significantly longer, 11.5(4–30.5) cm. The smallest inflorescences are produced in coastal populations which tend to flower through much of the year (Fig. 17). The length of inflorescence is dependent on moisture available at time of development. Even on an individual plant, inflorescences produced during the dry season are much shorter than those produced in the wet season. The broad environmental influences over these characteristics limit their usefulness in subspecific classification.

Leaves and young stems of this species are usually glabrous but infrequently plants have scattered unicellular trichomes on basal portions of the leaves. Inflorescences and/or young stems of these plants may also be pubescent. The pubescent plants are usually infrequent within a population and are not distinguished taxonomically.

Visitation by hummingbirds to the ascending, red, cylindrical flowers has been observed near Bahia de los Angeles and La Paz, and these animals apparently are the principal pollinators. The style is situated just above the anthers, which would apparently promote outcrossing.

Fouquieria diguetii is based on van Tieghem's *Bronnia digueti* which was published without exact locality. The type specimen has inflorescences to 22 cm long and must have been collected near La Paz where Diguet visited late in 1897.

Chromosome number: $2n=48$.

Vernacular name: "Palo Adan," "Palo de Adan."

Etymology: Named for Leon Diguet, a French explorer who traveled through Baja California near the turn of the century.

Representative specimens: MEXICO. BAJA CALIFORNIA DEL NORTE: 28.9 rd mi W of Bahia de los Angeles, *Hastings & Turner 66-197* (ARIZ, SD); 10 mi W of Bahia de los Angeles, *Wiggins & Wiggins 14798* (CAS, DS, MEXU, MICH); 1 mi N of Punta Prieta, *Wiggins 5374* (DS, GH, MICH, NY, POM, UC, US); 15 mi S of Miller's Landing, *Chambers 745* (DS, UC); 10 mi W of Mesquital, *Bratstrom s.n.* (SD); Calmalli, *Purpus 141a* (DS, US); El Arco, *Rutherford 349* (RSA); San Francisquito Bay, *Johnston 3456* (CAS, GH, UC, US). BAJA CALIFORNIA DEL SUR: S shore of "Nursery Channel," N end Scammon's Lagoon, *Wiggins 16781* (DS); Turtle Bay (Puerto San Bartolome), *Anthony 144* (CAS, DS, F, GH, NY, US); 9 mi E of San Ignacio, *Wiggins & Wiggins 18203* (CAS, DS, MEXU); Picachos de Santa Clara, *Gentry 7685* (ARIZ, DS, UC); Abreojos Point, *Rose 16242* (US, NY); head of Concepcion Bay, *Rose 16720* (NY, US); NW of Cerro de Gigantea, *Carter 2042* (DS, UC); Las Cuevitas, below Comondu, *Gentry 4461* (ARIZ, GH); Isla Carmen, *Rose 16632* (US); mouth of Cajon de Liqui (S of Loreto), *Carter 4907* (UC); 25 mi S of Mission Delores (pubescent lvs.), *Wiggins et al. 282* (DS); S end of Amortajada Bay, San Jose Island, *Moran 3762* (DS); San Francisco Island, *Moran 3735* (DS); Santa Maria Bay, *Rose 16269* (GH, NY); Estero Dalinas, *Porter 465* (CAS, DS, GH, MEXU); 2 mi N of El Pilar, *Wiggins 15449* (CAS, DS, GH, TEX, UC); 93 km N of La Paz by road, *Henrickson 4388* (RSA); El Mogote, La Paz, *Porter 349* (CAS, DS, GH, MEXU); S end Cerralvo Isl., *Moran 3595* (DS); 15.5 mi S of Todos Santos (pubescent infl.), *Porter 367* (CAS, DS, GH, MEXU); 6 mi NW of Santiago, *Constance 3170* (DS, GH, MEXU, MICH, MO, UC, US); Punta Frailes, *Dawson 1136* (F, MICH); San Jose del Cabo, *Jones 24028* (ARIZ, CAS, F, GH, MICH, MO, NY, POM, SD, UC). SONORA: Estero Tastiota, *Hastings & Turner 65-161* (ARIZ, SD); 10 mi N of Empalme, *Wiggins 6335* (DS, MICH, UC, US); 4 mi E of San Carlos Bay, *Hutchinson 2442* (MEXU, SD, UC); San Pedro Nolasco Island, *Johnston 3130* (CAS, GH, US); 4.5 mi N of Empalme towards Ortiz, *Wiggins 11635* (DS, SD); 1 km S of Peon, *Hastings et al. 61-34* (ARIZ, MEXU).

Reported from the following islands in the Gulf of California (Reid Moran, pers. comm.) Isla Angel de la Guarda, Isla San Lorenzo, Isla San Esteban, Isla San Pedro Nolasco, Isla Tortuga, Isla San Marcos, Isla San Ildefonso, Isla Coronados, Isla Carmen, Isla Danzante, Isla Montserrat, Isla Santa Catalina, Isla Santa Cruz, Isla San Diego, Isla San Jose, Isla San Francisco, Isla Partida, Isla Espirito Santo, Isla Cerralvo, Isla Margarita, Isla Magdalena.

5. FOUQUIERIA BURRAGEI Rose, J. New York Bot. Gard. 12: 267, 1911. TYPE: MEXICO. BAJA CALIFORNIA: Pichilinque Island (18 km N of

La Paz), 27 Mar., 1911, *J. N. Rose 16523* (LECTOTYPE: here designated US! fl., ft.; ISOTYPE: NY! ft.).

Shrubs 1–3 m high with 2–5 short, twisted trunks to 8 dm high, to 1.5 dm in diameter with several crooked, ascending to divergent, sparsely branched stems. Periderm dark bronze, waxy, exfoliating in thin sheets, interrupted by persistent decurrent ridges. Young branches 3–3.5 mm in diameter, very slightly furrowed; decurrent ridges dark maroon, glaucous, turning grey with age, long persistent, 29–47 mm long, tapering to fifth node below. Spines (5–)10–25(–33) mm long, slender, ascending, in a 3/8(–2/5) phyllotaxy. Long-shoot leaves 17–35(–44) mm long with petioles 10–35 mm long, blades (5–)10–18 mm long, 3–5.5 mm wide, elliptical, acute at apex, cuneate at base. Short-shoot leaves in fascicules of 2–5, (8–)12–17(–29) mm long, (4–)6–10(–13) mm wide, with petioles 1–2 mm long, broadly obovate, rounded, often emarginate or infrequently apiculate at apex; leaves isolateral, grey-green on both surfaces with entire margins. Inflorescence an elongate, narrow panicle, erect to ascending, terminal to subterminal, (6–) 12–25(–35) cm long, with short, ascending, determinate lateral peduncles 5–10(–20) mm long in lower part, 1–2 mm long in upper half, pedicels 1–3 mm long; rachis 2–3 mm thick at base, red-maroon, turning tan in fruit. Floral bracts caducous, medial bract ovate, acute, to 10 mm long, 4 mm wide, lateral bracts subulate, to 6 mm long. Sepals greenish white at sides and base, purple to pink near tips, with broad, white scarious margins, 4–5 mm long, 3–4 mm wide, the outer two more lance-ovate, the inner three ovate to orbicular, rounded and apiculate at tip, rounded to slightly cordate at broad base. Corolla salverform; rose-red to pink in bud, limbs and upper tube rose-red to light pink, lower tube yellow-white to white or white (albino) throughout at maturity, 9–13.5 mm long; tube 6–10 mm long, often slightly curved outward; diameter 3.5–4.5 mm at throat (5 pressed), 2–3 mm at base; limbs recurved 4–5 mm long, 3.5–5 mm wide, broadly ovate, rounded to truncate at apiculate tip, with upper margins inrolled to accentuate pointed apex, slightly cordate at broad base. Stamens 15–19(–23), exserted 1.2 to 2.4 times the length of floral tube; filaments 13–20 mm long, white, lower 5–9 mm slightly broadened laterally, curved over ovary, with hairs increasing from 0.5 to 1 mm long from lower abaxial side extending laterally to adaxial side above ovary to form 3–4 mm thick ring of white, pilose hairs around filament, upper filament cylindrical, glabrous; anthers yellow, often tinged with red, 3.5–5 mm long, 1.2 mm wide, oblong in outline, apiculate at tips, cordate at base. Ovary 1.5 mm high, with 12–15 ovules; style (10–)15–22 mm long, 3-branched, usually to 2–4 mm from the base, occasionally branched near middle. Capsule tan, lanceolate to narrowly ovate in outline, 12–18 mm long, 5–7 mm wide; seeds 5–10 light tan-white, 10–11 mm long, 5 mm wide with membranes 2 and 1.5 mm long at ends and sides respectively; membrane hairs 50–140 μ thick at ends, flattened, with perpendicular anastomosing thickenings; embryo 5–6 mm long, cotyledons elliptical, 4 mm long, 2 mm wide.

Fouquieria burragei is known only from widely scattered populations near the gulf coast of Baja California from Bahia Concepcion south to the vicinity of La Paz and on adjacent islands in the Gulf of California (Fig. 19). It occurs on rocky slopes with shallow sandy to volcanic clay soils, from just above sea level to 200 m elevation. This Coastal Sonoran Desert and thorn scrub region averages 100–200 mm annual precipitation which falls in sporadic showers mainly from July through January. Flowering occurs after rains. Common associates include species of *Bursera, Jatropha, Opuntia, Lysiloma, Lycium, Acacia, Lemaireocereus, Machaerocereus, Encelia, Ruellia,* and *Simmondsia.*

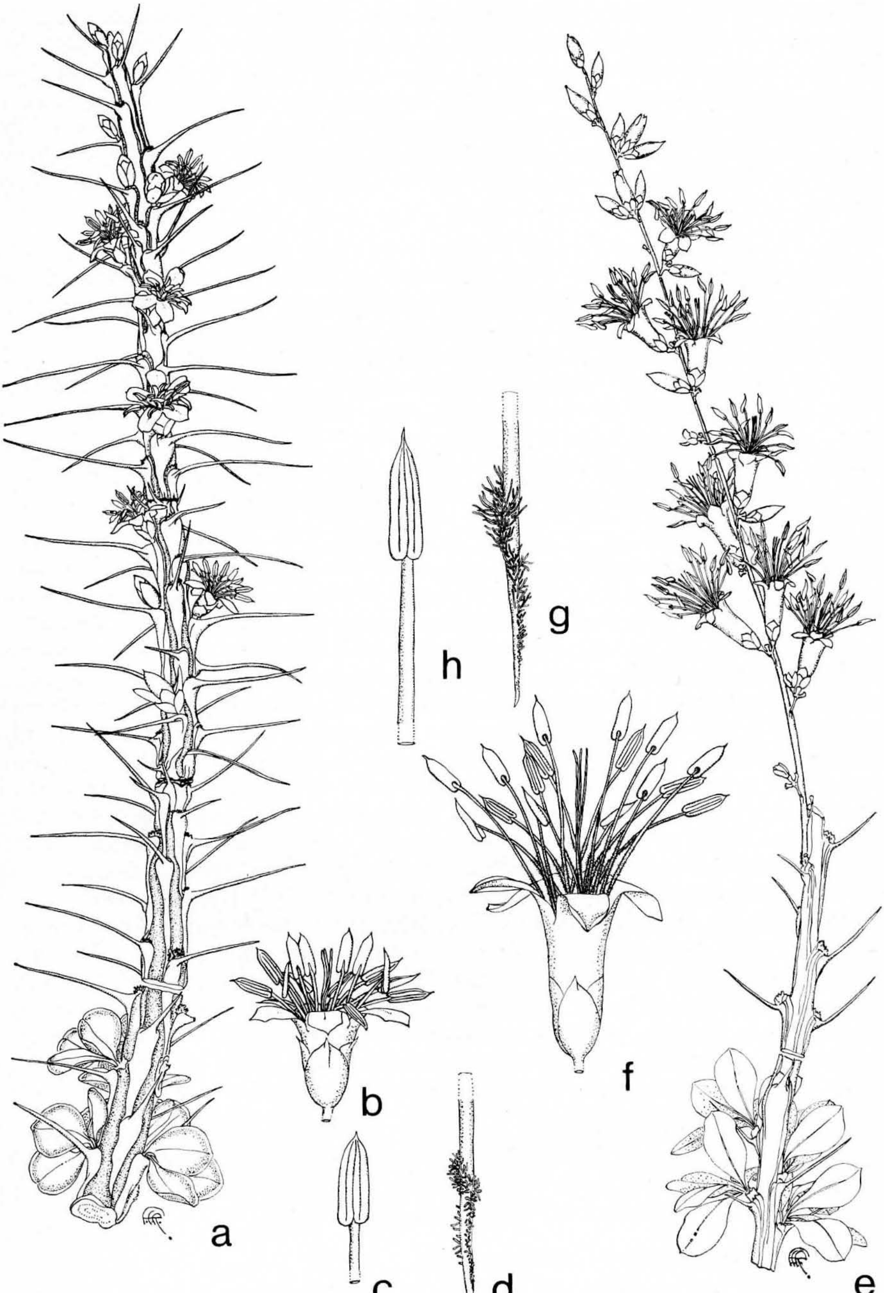
This species is very similar vegetatively to *F. diguetii* with which it is often sympatric. However, it is easily distinguished from the latter and all other species in the family by the short, rose-red to white salverform corollas, the numerous (15–23) long exserted stamens, and the elongate, narrow, upright inflorescences which are paniculate towards the base and more racemose above (Fig. 18). *Fouquieria burragei* and *F. diguetii* also differ in chromosome number (*F. burragei*, $2n=72$; *F. diguetii*, $2n=48$). This suggests a possible amphiploid derivation of *F. burragei* from hybrid stock between *F. diguetii* and some presumably now extinct diploid species having numerous stamens, possibly short, white corollas and spicate or racemose inflorescences.

The scattered populations of *F. burragei* are probably remnants of much larger population series or in some instances products of founder populations. Gene flow between these isolated populations is probably limited to nonexistent, which would allow development of interpopulation variation. Noticeable inter- and intrapopulation variation exists in several features including the degree of stamen exsertion and corolla size and color. Stamen exsertion in the mature flower ranges from 1.2–2.4 times the corolla tube length and may vary considerably between adjacent populations. Flower color is very variable and changes from bud to mature stages. In certain populations near La Paz, corollas are strong rose-red in bud but rose to pink with white tubes at anthesis. Other adjacent populations have pink corollas in bud which turn nearly white by anthesis. In contrast, populations extending along the western margin of Bahia de la Conception from about 7 miles north to about 50 miles south of Mulege are consistently white flowered (Ed Gay, personal communication). Mature flower size also varies on an individual. Corolla tubes of the proximal flowers of an inflorescence are often shorter than those of distal flowers; there is also evidence that overall flower size is directly affected by available moisture. The lack of geographical correlation, and possibility of environmental plasticity of these characters limits their use in subspecific classification.

During four trips to La Paz, in which flowering was very sporadic, no pollinator activity was observed. The short tubes, however, would allow exploitation by small insects while the long exserted stamens would perhaps allow effective pollination by hummingbirds as well.

Chromosome number: $2n=72$.

Vernacular name: "Palo de Adan" (not distinguished from *F. diguetii*).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Etymology: Named for Guy H. Burrage, commander of the U.S. Steamer "Albatross" which was used on the 1911 American Museum of Natural History organized expedition to Baja California. J. N. Rose was the botanist on the expedition.

Representative specimens: MEXICO. BAJA CALIFORNIA DEL SUR: N end of Bahia Concepción, *Gentry 1194* (MEXU); 6 mi E of Canipole, *Chambers 788* (DS, MEXU, UC); S side Cajon de Liquí (S of Loreto), *Carter 4906* (RSA, UC); Cuesta de Chuengue, 22 km S of Loreto towards Puerto Escondido, *Carter & Ferris 4720* (RSA, UC); W shore of Isla Partida, *Wiggins et al. 410* (UC, DS); Isla Gallina, off west shore of Isla Espirito Santo, *Wiggins 16, 106* (CAS); Isla Ballena, *Johnston 4074* (CAS); 18 km N of La Paz at Pichilingue, *Henrickson 2173* (RSA); 2 km N of La Paz towards Pichilingue, *Henrickson 4334* (RSA); Pichilingue Island, *M. E. Jones 27, 089* (POM).

6. FOUQUIERIA FORMOSA H. B. K., Nov. Gen. Sp. 6: 83, t. 527, 1823. TYPE: REGNO MEXICANO. 1803, *Bonpland 4411* (HOLOTYPE: P!).

Echeveria spicata Sessé et Mociño ex DC., Prod. 3: 349, 1829. *nom. nud.*

Philetaeria horrida Liebm., Dansk Vidensk. Selsk. Skrivt. ser. 5. 2: 283, pl. 285, 1851. TYPE: MEXICO. PUEBLA: Circa vallem Tehuacanensem, alt. 5–6000 ft. pr. S. Lorenzo, Venta Salada, S. Sebastian (LECTOTYPE here designated: *Liebmann 619* [S. Lorenzo] C!, duplicates, UC, US!).

Small trees to 3–8 m high with 1–2 basal trunks to 1.5–2 m high, 25–40 cm in diameter; larger stems usually dichotomously branched bearing numerous, erect to widely spreading young stems. Periderm smooth, dark bronze to yellow, exfoliating in thin papery sheets, translucent; larger stems and trunks often green from cortical chlorenchyma. Young branches (3–)4–5 mm in diameter. very slightly furrowed; decurrent ridges dark maroon, glabrous to canescent or velutinous with uniseriate hairs to 1 mm long, becoming glabrous and turning light grey with age, eventually deciduous from branches 3–4 cm in diameter, (37–)55–85 mm long, truncating against the fifth node below. Spines short, (1–)2–15(–20) mm long, ascending in 2/5 phyllotaxy. Long-shoot leaves 35–55(–62) mm long with petioles 11–21 mm long, blades 23–35(–42) mm long, 10–17 mm wide, elliptical to ovate, usually acute to obtuse, occasionally apiculate at apex, cuneate at base, petiole often much longer than spine, blade commonly pilose along midrib at base. Short-shoot leaves in fascicules of 2–5(–8), 19–40(–47) mm long, with petioles 2–4(–9) mm long, blades 17–38 mm long, 8–22 mm wide, oblanceolate, obovate to broadly obovate, obtuse, rounded to emarginate at apex, cuneate at base, commonly pubescent along midrib at base below; leaves isolateral, dark green above, lighter green below, entire. Inflorescence

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Fig. 18. a–d. *Fouquieria shrevei*.—a. Terminal stem showing sessile axillary flowers. Note short decurrent ridges, and broad scarious margins on short-shoot leaves shown below.—b. Mature flower. Flower tube often longer than one illustrated.—c–d. Stamen.—c. Filament base (radial view) showing extent of trichomes.—d. Anther, adaxial surface. (*Henrickson 3126*).—e–h. *Fouquieria burragei*.—e. Terminal stem with elongate, paniculate inflorescence. Short-shoot leaves shown below.—f. Mature flowers with short trichomes extending to upper filament (an uncommon character).—g–h. Stamen.—g. Filament base (radial view) showing distribution of trichomes.—h. Anther, adaxial surface. (*Henrickson 2173*).—a, e ×0.5; b, f ×1.5; c–d, g–h ×4.

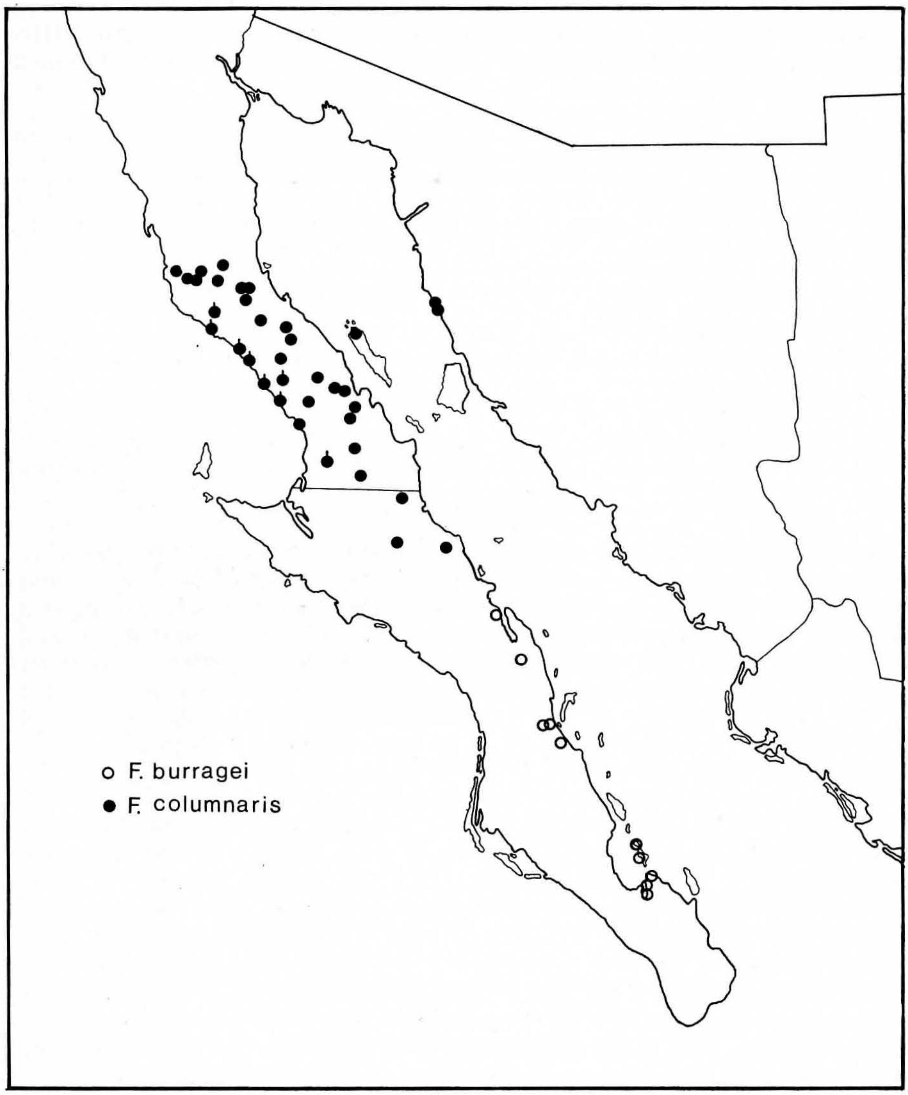


Fig. 19. Distribution of *Fouquieria burragei* and *F. columnaris* in northwestern Mexico. Solid circles with upward projections indicate field sightings recorded by Hastings et al., 1972.

spicate, 1.5–9.5 cm long, terminal to subterminal, rachis stout, 2–3 mm thick at base, reddish tan in color, often pubescent to velutinous with uniseriate hairs to 1.5 mm long, bearing flowers on protruding nodes encircled by conspicuous scars of three caducous floral bracts, medial bract 7–8 mm long, 3.5–4 mm wide, lateral bracts 4–4.5 mm long, 1.5 mm wide, bracts elliptical, acute at apex, cuneate at broad base, yellowish green to orange-red, with broad scarious margins. Sepals orange-red to red, often greenish below or throughout, with white scarious margins, outer two, 6–9 mm long, 5–6 mm wide, broadly oblong, inner three 8–10(–12) mm long, 9–10(–12) mm wide, orbicular with broad scarious margins, all with rounded to obtuse apices with distinct apicule to 0.5 mm long, rounded at broad base. Corolla salverform, scarlet to orange-red, often greenish to white near base, 24–35 mm long, with outwardly curved, slightly ampliate tube 17–27 mm long, diameter 5 (7 pressed) mm at throat, 2–3 mm at base; limbs recurved, 7–8 mm long, 5–6 mm wide, broadly ovate, rounded, with subterminal apicule at apex, cordate to truncate at broad base, with narrow white scarious margins infolding near tip. Stamens (10–)14–16(–20), long exserted; filaments 26–48 mm long, dark red to orange-red, whitish below, basal 10–14 mm slightly enlarging laterally, bearing dense uniseriate hairs to 1.5–2 mm long on adaxial surface above ovary, upper filament cylindrical, glabrous; anthers dark red, tinged with yellow, 5–6.5 mm long, 1–2 mm broad, lanceolate in outline, acuminate to cuspidate at tip, cordate at base. Ovary 2 mm high with 14–16 ovules; style red to orange-red, stout, (27–)33–45 mm long, 3(–4)-branched 5–7 mm from apex. Capsule tan, 22–37 mm long, 7–9 mm broad, lanceolate to ovate in outline; seeds (5–)10–13, tan-yellow, 15–21 mm long, 7–10 mm wide with papery membrane 5–6 and 3 mm broad at ends and sides respectively, notched at both ends, membrane hairs 100–170 μ thick at ends with anastomosing perpendicular thickenings; embryo 9 mm long, with elliptical cotyledons 8 mm long, 3.5 mm wide.

Fouquieria formosa occurs on rocky alluvial slopes and valleys on lateritic to calcareous soils from Lago de Chapala region of Jalisco to southeastern Oaxaca (Fig. 14). It exists in tropical deciduous forest and arid tropical scrub vegetations at elevations from 2400 to 700 m (to 100 m near Tehuantepec, Oaxaca (fide *Wiggins 13289*). Average annual precipitation ranges from about 1000 mm in Guerrero and Morelos to 300 mm in northern Oaxaca and occurs mainly from June through September. The species flowers from October through February; however, some flowering may occur throughout the year.

The species is distinguished by its small tree habit, its terminal, short, spicate inflorescences and large orange-red flowers with decurved corollas and variable (10–)14–16(–20) stamen number (Fig. 20). Its relationship lies with the dendroid fouquierias although not apparently close to any particular species.

Considerable phenotypic (inter- and intrapopulation) variation exists throughout the range of *F. formosa*. Young stems and/or inflorescences may be glabrous to velutinous with unicellular hairs to 1 mm long. Spines are almost lacking in some populations, in others they are variable in length and 4–15 mm or 10–20 mm long. Flowers vary from 27–37 mm in total length, from deep orange-red to yellow-orange in color, while stamens

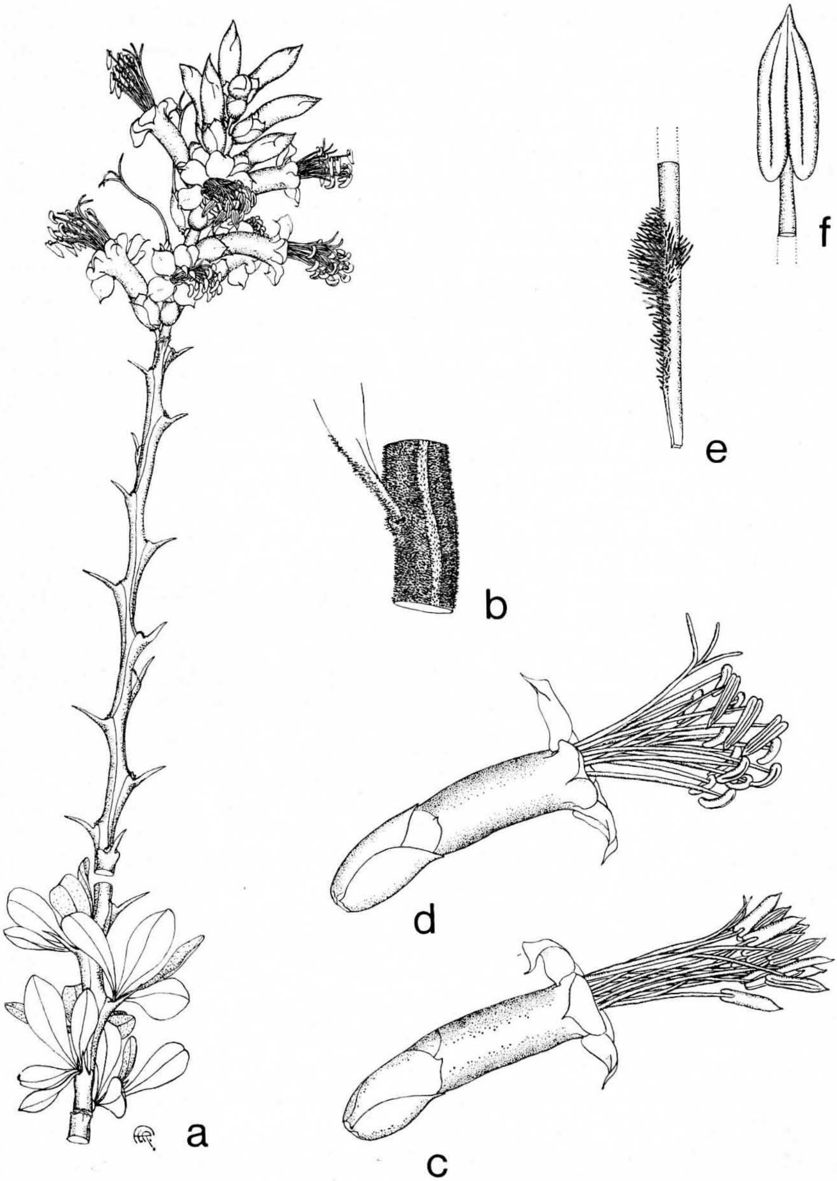


Fig. 20. *Fouquieria formosa.*—a. Terminal stem with short terminal spicate inflorescence. Note short spines, shallow furrows between decurrent ridges. Short-shoot leaves shown below.—b. Section of canescent stem without spines. Note trichomes on adaxial base of leaf.—c–d. Flowers.—c. Young flower showing initial extension of anthers.—d. Mature flower showing eventual position of anthers and upper position of style.—e–f.

number from 10 to 20. Spine length and stamen number often are not constant on an individual indicating environmental influences over their development. Stem and inflorescence vesturement as well as flower color varies greatly both within and between populations but only slightly on individual plants. Figure 21 illustrates the variation of five of these characteristics: stamen number, corolla tube and calyx length, spine length and presence or absence of stem or inflorescence vesturement over the range of the species. As corolla color was not available from dried specimens it was not used. While strong geographical correlation of these characters does not occur, certain tendencies can be noted. Individuals from the arid region of southeastern Puebla and northern Oaxaca tend to have glabrous stems, long spines and short flowers with medium to high stamen numbers, while populations from the moist highlands of Morelos and México tend to have vestured stems, short spines and medium to low stamen numbers. Geographical and environmental variation of these characteristics prevent establishment of valid subspecific taxa.

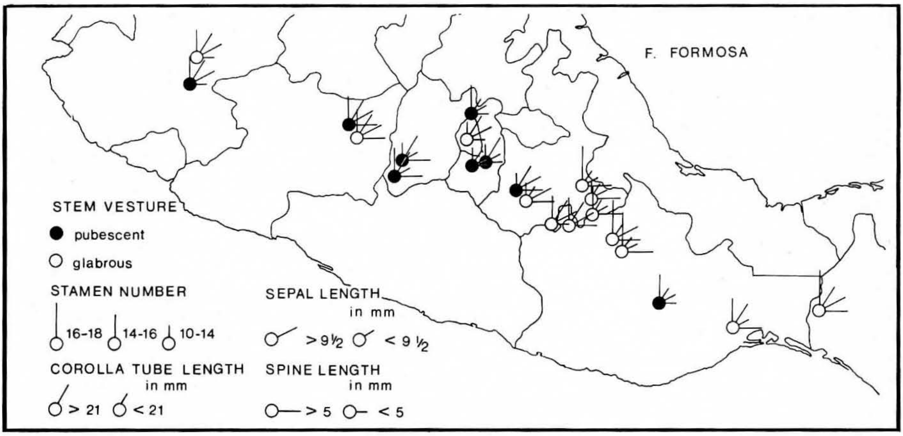


Fig. 21. Distribution of characteristics of vestured stems, stamen number, corolla, sepal and spine length throughout range of *Fouquieria formosa*.

The exact location of the type collection is not known. The holotype (P) has very small spines, canescent stems and 12 stamens per flower, features characteristic of populations in the states of México and Morelos and vicinity. Humboldt and Bonpland traveled through this region in September through October in 1803 (McVaugh, 1968).

Stamen.—e. Filament base (radial view) showing extent of trichomes mainly on abaxial surface.—f. Anther, adaxial surface. (*Henrickson 4327*).—a ×0.5; b ×1.5; c–d ×1.5; f–g ×4.

Unidentified hummingbirds have been observed visiting the tubular, orange-red flowers in southeastern Puebla and at Yautepec, Morelos, and are probably the principal pollinators. Utilization of flowers by perching birds, however, may also occur. Additionally, small transverse cuts of the corolla tube just above the sepals characteristic of the robbing habit of carpenter bees (*Xylocopa* spp.) and bumblebees (*Bombus* spp.) (Grant and Grant, 1968) are commonly observed on specimens throughout its range. As the flower tube provides a landing platform away from the exserted stamens and stigma, insect visitors probably do not affect pollination unless they collect pollen.

Vernacular names: "Palo Santo" Puebla, Morelos; "Rabo de Iguana" near Acatlan, Puebla (Miranda, 1942b); "Rosalillo," "Tlapacon" Jalisco, Puebla (Standley, 1923); "Corona de Cristo" (fide *Hinton 7070*); "Flor de Jabon," Oaxaca (fide *Carlson 2192*).

Representative specimens: MEXICO. JALISCO: Old fields and gardens near Guadalajara, *Pringle 2420* (AA, F, GH, MEXU, MO, NY, UC, US); W end Lake Chapala between Jocotepec and S. Juan Cosala, *McVaugh & Koelz 391* (MICH). MICHOACAN: 6 km S de Tzitzio, *Rezdowski 23733* (WIS); 44.5 km from El Temascal on rd to Huetamo, *Moore et al. 5707* (GH, UC);. MEXICO: Polotitlan, *Matuda 26799* (MEXU); Sierra de Guadalupe nr San Andres, *Rezdowski 21560* (DS, MICH, SMU, TEX); Vigas, Temascaltepec Dist., *Hinton 7070* (AA, ARIZ, F, NY, US); San Nicolas, Valle de Bravo, *Matuda 37373* (MEXU, F); Bejucos, Temascaltepec Dist. (some with 10 stamens), *Hinton 7536* (GH). MEXICO D. F.: Puerto de Santa Isabel, Sierra de Guadalupe, *Balls 4937* (AA, US). MORELOS: near Cuernavaca, *Rose & Rose 11100* (NY, US); Yautepec, *Henrickson 4325* (RSA); 3 mi SW of Totolapan toward Tlayacapan, *Porter 1446* (DS, MEXU). GUERRERO: Tetipac, *Miranda 25* (MEXU). PUEBLA: 24 km S of Matamoros, *Henrickson 2105* (RSA); 11 mi SW of Puebla-Oaxaca Border, *Porter 1452* (DS, GH, MEXU); Calcareous hills near Tehuacan, *Pringle 6296* (CAS, F, GH, MEXU, MICH, MO, NY, UC, US); Zapotitlan Valley, *C. E. Smith et al. 4003* (F, MEXU, US); W of Rio Salada around Petlanco, *C. E. Smith et al. 3664* (F, MEXU, US); near Coxcatlan on Cerro Ajuereado, *C. E. Smith et al. 3565* (F, MEXU, US). OAXACA: 13.1 mi beyond Teotitlan toward Tecomavaca, *Kimnach & Moran 163* (UC); Dominguillo, S of Cuicatlan, *Miranda 1020* (MEXU); Cerro de Carbonera, Matatlan, *Conzatti 1471* (US); 7.7 mi N of Tehuantepec, *Wiggins 13289* (DS, MEXU); Guengosa, Tehuantepec, *Matuda 2223* (MEXU, MICH).

7. FOUQUIERIA SPLENDENS Engelm. in Wisliz., Mem. Tour North. Mexico, 98, 1848.

Synonymy and typification given under subspecific headings.

Shrubs to small trees 2–10 m high with candelabraform habit consisting of 6–30(–100) erect to outwardly arching, spinose, wand-like stems arising from a short, broad basal trunk (7–)15–25(–40) cm in diameter, 10–20 cm high; branches strict, often ramifying at base and/or near tip and becoming distally pendulous with age. Periderm of older stems bronze to dull yellow, in thin, translucent, waxy sheets which weather away between five spiralled series of persistent, grey, decurrent leaf bases. Young branches (3–)4–5(–6.5) mm in diameter, moderately furrowed; decurrent ridges dark maroon, turning grey with age, (26–)45–55 mm long, usually tapering to eighth node below. Spines (5–)15–25(–42) mm long, straight or curved, in (3/8–)5/13 phyllotaxy in either direction. Long-shoot leaves (20–)30–50 mm long with petioles (10–)15–25 mm long, blades ascending, 10–25(–35) mm long, (3.5–) 5–10 mm wide, narrowly to broadly elliptic to oblanceolate, acute at apex, narrowly cuneate at base. Short-shoot leaves in fascicles of (2–)4–11, 17–35 mm long, (3.2–)5–11 mm wide with petioles 2–8 mm long, linear-spatulate to broadly obovate, acute, rounded to emarginate at apex, cuneate at base; leaves isolateral, blue green to grey green on both surfaces, with narrow scarious margins. Inflorescence paniculate, often racemose above, narrowly conical to cylindrical in outline, ascending to pendulous in older plants, (1–)10–20(–30) cm long, with fascicules of 1–3 pedicels, 2–13 mm long near tip, peduncles and pedicels (5–)10–30(–70) mm long at base, rachis dark purple-red to 4 mm thick at base; floral bracts caducous, dark purple to reddish or green, medial bract 4–9 mm long, 2–6 mm broad, broadly elliptical to broadly ovate, obtuse, with broad scarious margins near base, lateral two bracts smaller, elliptical occasionally subulate; flowers erect, forming crest along inflorescence. Sepals orange-red, pink to cream-white, greenish to purple-pink near base, with whitish scarious margins, 4.5–6(–9) mm long, 3.5–5.5 mm broad, outer two broadly ovate, obtuse at apex, inner three larger, more oblong to nearly reniform, obtuse to emarginate at apex, rounded to slightly cordate at broad base with broad scarious margins; corolla tubular, strong reddish orange, strong yellowish pink, strong purplish pink to cream white, often darkening with age, 10.5–28 mm long, tube 6.5–22 mm long, ampliate towards throat, diameter 3.5–6 mm wide at throat, 2–3 mm at base, tube with 2–5 mm band of unicellular hairs 2–6 mm above base within; limbs tightly reflexed, 4.5–7 mm long, 3.5–5 mm wide, broadly ovate to elliptic, rounded at broad base. Stamens (12–)14–16(–20), exserted, of unequal length; filament (8–)12–25(–34) mm long, strong reddish orange, strong purple-pink to white, often turning darker red with age, whitish at base, lower 3–7 mm slightly broadened laterally or angled with distinctive adaxial, truncated spur to 1.5 mm long projecting above ovary, with unicellular hairs from 0.2 to 1.5 mm long extending from upper abaxial sides around to and over adaxial spur, upper filament cylindrical, glabrous. Anthers yellow to tinged with orange-red to strong orange-red, often turning dark red upon drying, 4–5 mm long, lanceolate in outline, often apiculate at apex, deeply cordate at base. Ovary 1.5–2 mm high with 12–16 ovules; style orange-red, purple-pink to white, usually white below, 8.5–32 mm long, 3-branched 3.5–21 mm from tip, stigma situated among or below anthers. Capsules tan, lanceolate to ovate-lanceolate in outline, (12–)14–22 mm long, 5–7 mm in diameter; seeds 5–13, white, 7–13 mm long, 4–6 mm wide, with membranes to 5 and 2 mm wide at ends and sides respectively, membrane hairs 30–50 μ thick near tips with three spiralled occasionally anastomosing thickenings; embryo 5–7 mm long, with cotyledons elliptical-oblong to lanceolate in outline 4–5 mm long, 2–2.5 mm wide.

This species, the widest ranging in the family, is characterized by a candelabraform or "ocotillo" habit, terminal, conical, ascending paniculate inflorescences and erect tubular flowers with reflexed corolla lobes and pubescent internal corolla surfaces. Stamens number 12–20 and have small adaxial spurs at the filament base above the ovary. Nash (1903) recognized two species in this group, one with cylindrical corollas (*F. splendens*), the other with short campanulate corollas (*F. campanulata*). As shown below the populations of the Sonoran and Chihuahuan Deserts exhibit a gradual west-east variation pattern involving reduction of corolla size which makes such a distinction based on corolla size untenable. Populations with long or short orange-red corollas extending from California to Coahuila and northern San Luis Potosí are distinguished as *F. splendens* ssp. *splendens*. Nash's *F. campanulata* is an allopatric population series in Durango with purple-pink or cream-white corollas and is here distinguished as a subspecies based mainly on floral color differences. An additional subspecies with short, orange-red corollas but distinct elongate, broad inflorescences from San Luis Potosí to Hidalgo is described as new.

7a. FOUQUIERIA SPLENDENS Engelm. in Wisliz. ssp. SPLENDENS, Mem. Tour North. Mexico, 98, 1848 (as *Fouquiera*). TYPE: MEXICO. CHIHUAHUA: Santa Cruz (ca. 75 km) S of Chihuahua towards Saucillo; 29 Apr., 1847, *A. Wislizenus 261* (LECTOTYPE MO! fls.); PARATYPES: NEW MEXICO: Jornada del Muerto (ca. 98 km S of Socorro towards El Paso, Texas); 2 Aug., 1846, *A. Wislizenus 216* (MO! lvs.); COAHUILA: between Cienaga Grande and Castañuela (ca. 50–70 km W of Saltillo); 9 May, 1847, *Gregg 600* (MO! fl., ft.).

Fouquieria splendens Engelm. in Wisliz. form β *micrantha* Th. Loesener, Feddes Repert. Spec. Nov. Regni Veg. 9: 357, 1911 (as *Fouquiera*). TYPE: MEXICO. DURANGO: Chaparrales bei Alamo (ca. 40 km WSW of Cuencame), *A. Endlich 166* (HOLOTYPE): was at B, no longer extant; NEOTYPE here designated: DURANGO: 4 mi SW of Cuencame along Hy 40, 25 Apr., 1969, *Henrickson 3157* (RSA).

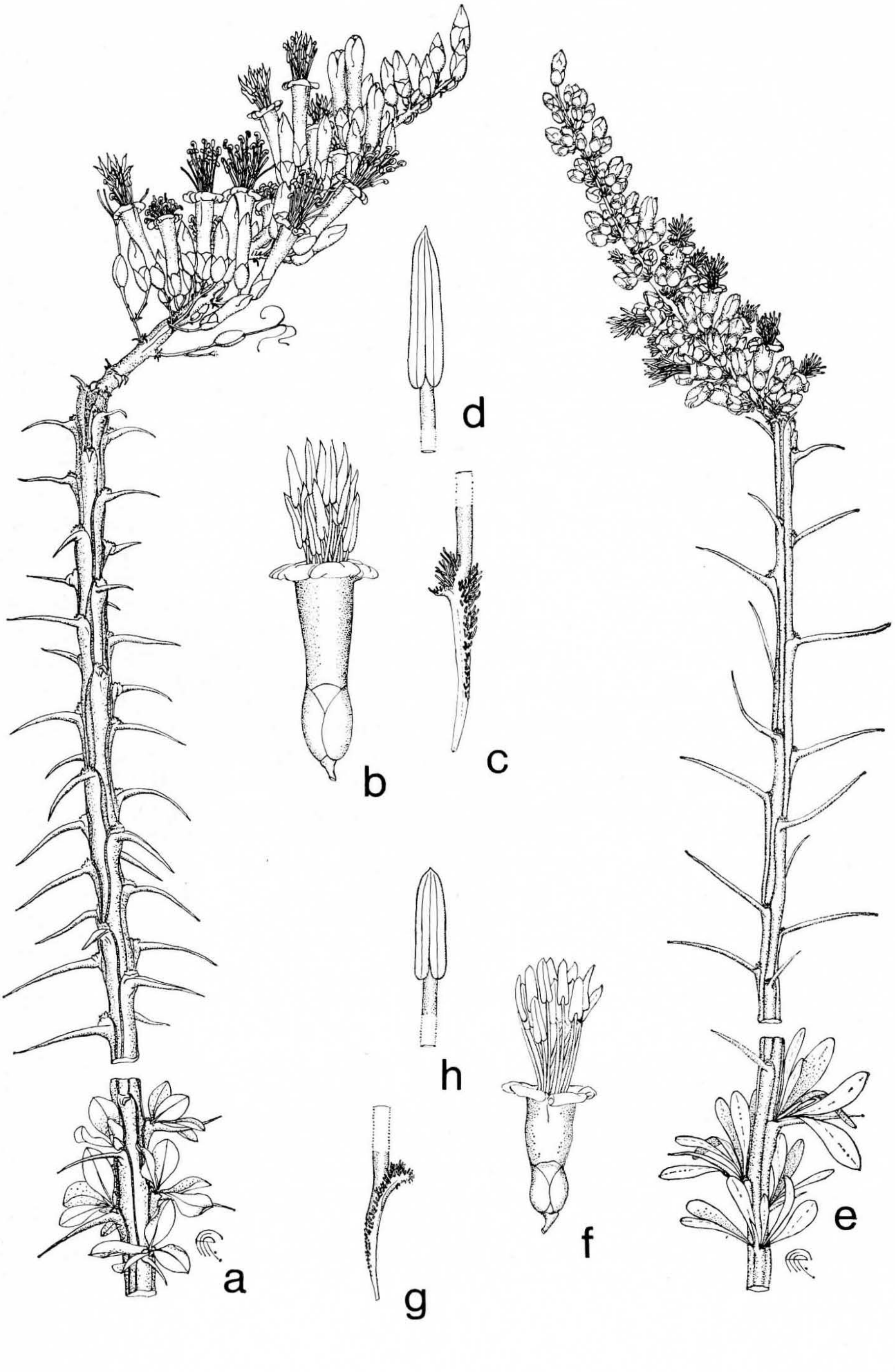
Fouquieria spinosa (HBK) Torrey in Emory, Mil. Recon. 147, pl. 8, 1848. not HBK.

Plants with 6–100 erect to ascending, occasionally distally pendulous, and branched stems, 2–12 cm in basal diameter. Short-shoot leaves in fascicules of 2–6, 10–22(–30) mm long, 4–9 mm wide, with petioles 2–8 mm long, broadly to narrowly obovate to spatulate, acute, rounded to emarginate at apex. Inflorescence broadly to narrowly conical in outline, ascending to infrequently pendulous, (2–)10–20(–30) cm long, pedicels 2–5(–13) mm long near tip, peduncles and pedicels 6–11(–25) mm long near base. Medial floral bract 6–9 mm long, 2.5–6 mm broad, lateral bracts to 7 mm long, 3 mm wide, dark maroon-red with white, scarious margins. Sepals mottled orange-red to red, greenish at base or light yellowish green throughout, occasionally pink with purple-pink near base, with whitish broad scarious margin, 4.5–6.5(–9) mm long, (3.6–)4.5–6 mm wide. Corolla strong reddish orange, less frequently strong red or strong yellowish pink, infrequently pale yellow "albino," greenish below sepals, often drying dark red, (14–) 16–22(–28) mm long, tube (6.5–)11–18(–22) mm long, slightly ampliate, diameter (3.5–)4–6(8–pressed) mm wide at throat, 2–3 mm at base; limbs strongly reflexed 4.5–6(–7) mm long, 3.5–5 mm wide, broadly oblong ovate to broadly elliptical, rounded to slightly apiculate at apex, tapering to broad base. Stamens (12–)14–18, filament strong reddish orange to red (12–) 16–20(–36) mm long, with lower 4.2–8 mm broadened, adaxial spur 0.2–1 mm long. Anthers yellow, often tinged with red, drying red, 4–6 mm long. Ovary with 12–18(–20) ovules; style strong reddish orange, red to pink, white near base, 13–32 mm long, 3-branched 11–21 mm from tip.

Fouquieria splendens ssp. *splendens* ranges from the Sonoran Desert of southern California, Arizona and southernmost Nevada south to Baja California and Sonora and in the Chihuahuan Desert and adjacent Mesquite Grassland from New Mexico, and Texas south to Zacatecas and northern San Luis Potosí (Fig. 23). In the Sonoran desert it occurs from sea level to about 700 m elevation and up to 1800 m on a few south-facing mountain slopes in Arizona. It grows most commonly on rocky slopes or outwash plains but also on fine textured soils and sand in more arid regions. Average annual rainfall which ranges from a mere 40 up to 450 mm occurs mainly in winter but also in summer in Arizona and Sonora. It is a conspicuous plant in the creosote bush scrub vegetation with species of *Larrea, Ambrosia, Cercidium, Agave, Prosopis, Olneya, Dalea,* and *Encelia* and is sympatric with *Fouquieria diguetii, F. macdougalii* and *F. columnaris.* In the Chihuahuan Desert and adjacent mesquite grassland it ranges from 1000 to 2100 m elevation again most commonly on rocky slopes and hillsides and to a lesser extent on sandy substrates. At the margins of its range it tends to be restricted to limestone outcroppings. Average annual precipitation here ranges from 200 to 450 mm and occurs mainly in the late summer from July through October. Associates include *Larrea, Flourensia, Parthenium, Acacia, Agave, Yucca, Hechtia, Prosopis, Cercidium,* and *Bouteloua.*

This wide ranging subspecies shows considerable variation in a number of floral features (Figs. 24, 25). Corolla tube length, used as a measurement of corolla size, ranges from 6 to 22 mm. Populations in Baja California and California have corolla tubes 12–22 mm long while those in southern Texas and Coahuila range from 15 to 6 mm. At extreme margins of its distribution are populations with corolla tubes 17–22 and 6–9.5 mm in length which one would initially consider as distinct taxa. But those in intermediate areas and near the type locality south of Ciudad Chihuahua, have corolla tubes 12–17 mm long, definitely intermediate between extreme populations. Analyses of geographical trends in corolla size are presented in Figs. 24 and 26 which show a gradual decrease in corolla tube length from the west to the east.

Corolla tube length, however, is variable both within an individual and within a population. On an individual inflorescence terminal flowers of lateral shoots are often longer than subterminal flowers. Corolla size also tends to reflect available moisture conditions, being slightly larger in wet seasons. But this broad variation pattern is not purely an instance of phenotypic dependency on available moisture. Occasional plants blooming in the wet summer season in Coahuila (which normally flower during the dry spring season) still have short flowers, showing genetic control over this characteristic.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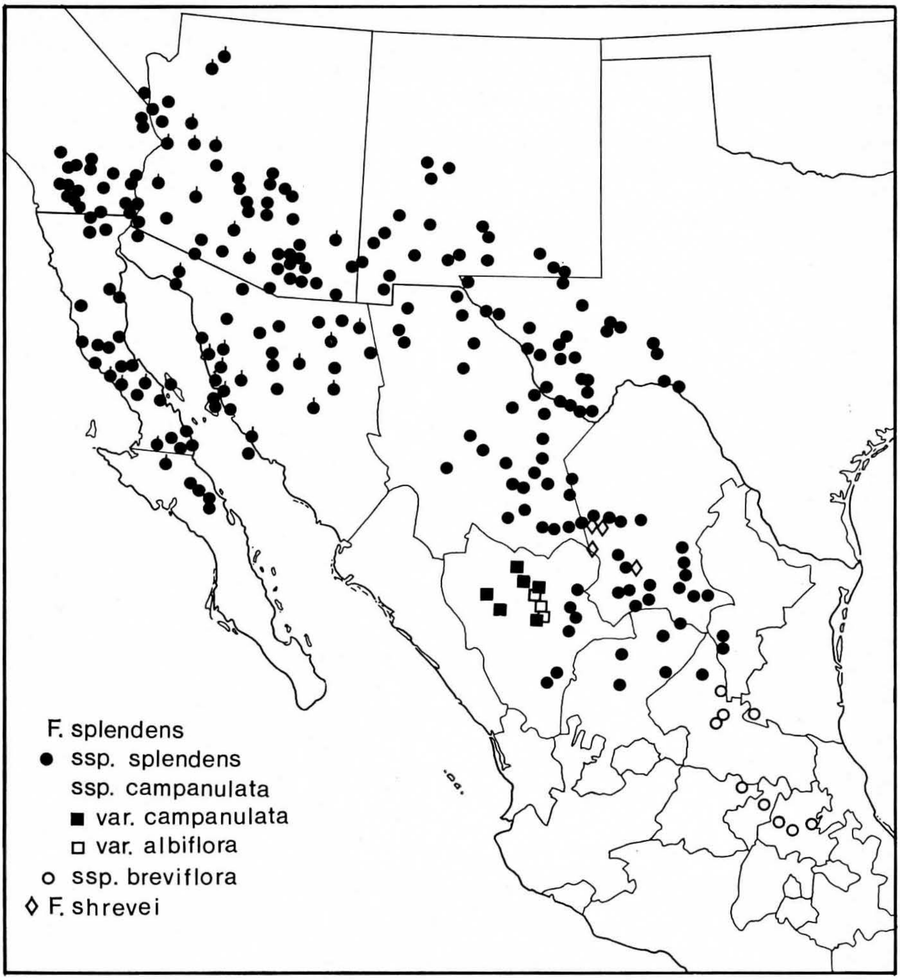

Fig. 23. Distribution of subspecies and varieties of *Fouquieria splendens* and *F. shrevei* in Mexico. Circles with upward projections indicate field sightings by Hastings et al., 1972.

Fig. 22. a–d. *Fouquieria splendens* ssp. *splendens.*—a. Terminal stem bearing ascending paniculate inflorescence with upright flowers. Short-shoot leaves shown below.—b. Mature flower showing exserted, introrse stamens.—c–d. Stamen.—c. Filament base (radial view) showing characteristic adaxial ligulate spur and extent of trichomes.—d. Anther, adaxial side. (*Henrickson 4581*).—e–h. *Fouquieria splendens* ssp. *campanulata.*—e. Terminal stem with crest-like racemose inflorescence. Note comparatively narrow stem as compared to type subspecies. Narrow oblanceolate, short-shoot leaves shown at base.—f. Mature flower.—g–h. Stamen.—g. Filament base showing adaxial ligulate spur and extent of trichomes.—h. Anther, adaxial surface. (*Henrickson 3158*).—a, e ×0.5; b, f ×1.5; c–d, g–h ×4.

Variation also occurs in style-style branch ratio. Although the ratio varies somewhat within a population a general west-east trend can again be noted, as shown in Fig. 24. The styles are branched nearer the tip in populations in Baja California but nearer the base in far eastern populations.

Inflorescence length follows a similar, gradual variation pattern from west to east. Plants from the western Sonoran Desert tend to have long inflores-

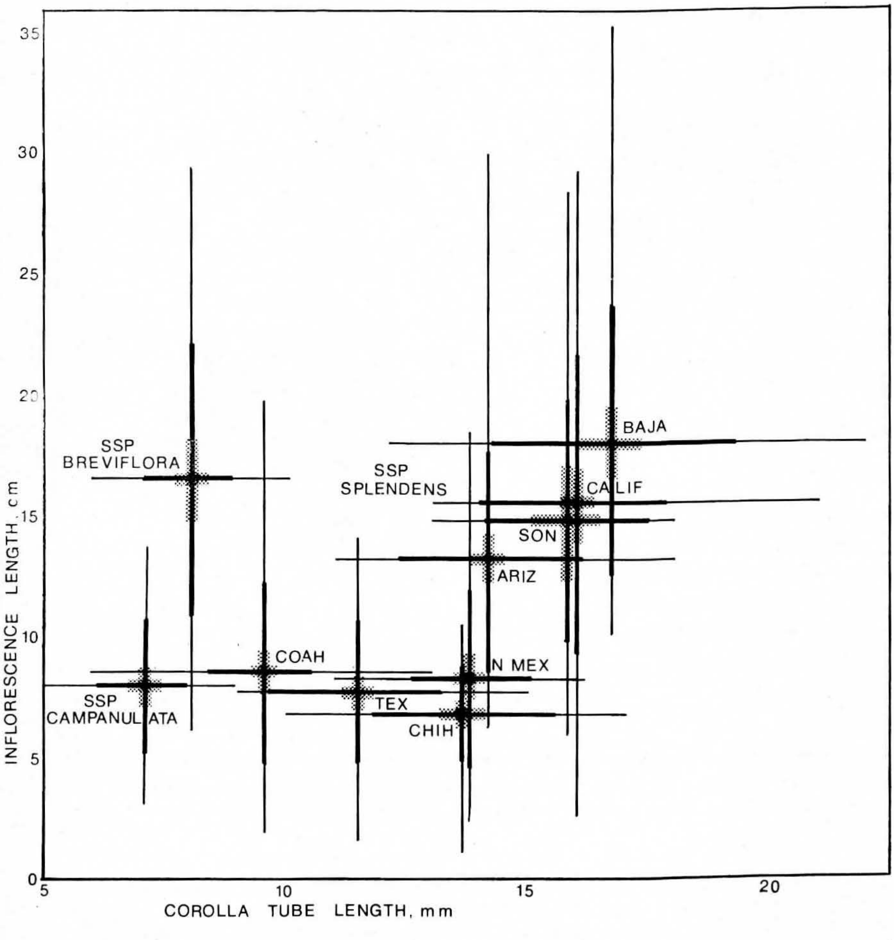

Fig. 24. Comparison of inflorescence length (in cm, ordinate) and flower size, measured as corolla tube length (in mm, abscissa) of three subspecies of *Fouquieria splendens.* Data for *Fouquieria splendens* ssp. *splendens* are presented separately for each state to illustrate gradual west-east decrease in inflorescence and corolla size from Sonoran Desert (Baja California to Arizona) to Chihuahuan Desert (New Mexico to Coahuila). Data for other two subspecies represent variation known from entire range. *Fouquieria splendens* ssp. *campanulata* (Durango) is distinguished by very short corollas (pink to

cences averaging 15–18 cm in length while those from the Chihuahuan Desert average 6–9 cm (Fig. 24). Although the average length is significantly different, the large amount of overlap limits the taxonomic value of this character.

There exists in this taxon a wide range in variation of floral and inflorescence size. This diversity, however, is by no means chaotic, but follows a pattern, with larger structures in the far west and gradually smaller struc-

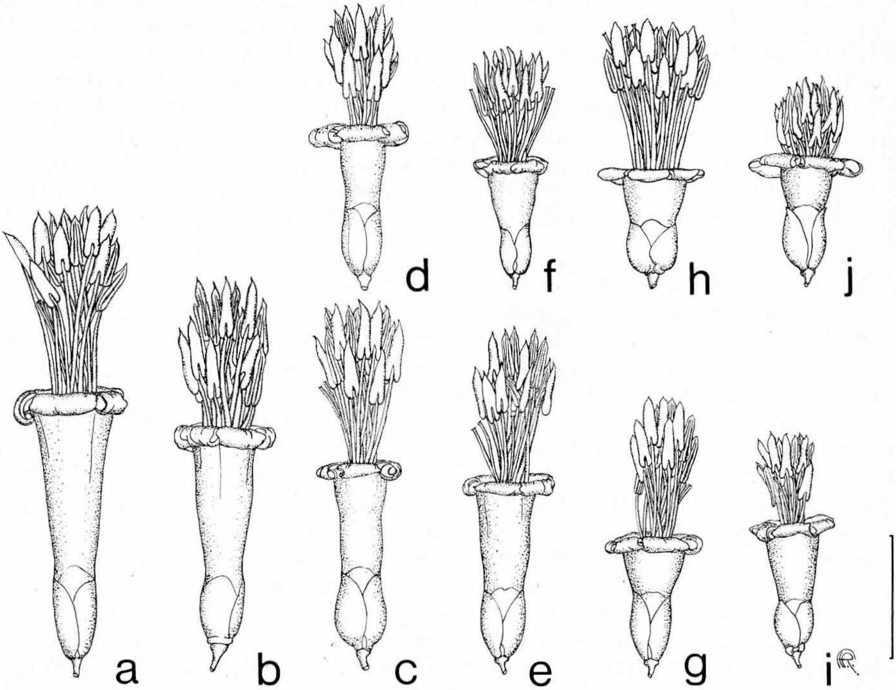

Fig. 25. Flower size variation in *Fouquieria splendens*.—a–f. *Fouquieria splendens* ssp. *splendens*.—a. San Diego, California. (*Rutherford s.n.*).—b. Near Saucillo, Chihuahua, near type locality. (*Henrickson 3199*).—c–d. Population variation, 27 mi SE of Presidio, Brewster Co., Texas.—c. (*Henrickson 3081*).—d. (*Henrickson 3082*).—e–f. Population variation, 35 mi W of Saltillo, Coahuila. (*Henrickson 3151*).—g–h. *Fouquieria splendens* ssp. *breviflora*.—g. At El Huizache, San Luis Potosí. (*Henrickson 3149*).—h. 23 km N of Ixmiquilpan, Hidalgo. (*Henrickson 2097*).—i–j. *Fouquieria splendens* ssp. *campanulata*.—j. 20 mi NW of Santiago Papasquiaro, Durango. (*Henrickson 3168*).—j. 1/2 mi N of Atotonilco, Durango. (*Henrickson 3172*).—All ×1.5. Scale unit: =1 cm.

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white in color) and short inflorescences; *Fouquieria splendens* ssp. *breviflora* (San Luis Potosí to Hidalgo) by very long inflorescences and short corollas. Data obtained from available herbarium specimens. Point of intercept marks mean, ranges represented by thin line, standard deviation by bold line, standard error by broad checkered line ($n=51$ to 113).

tures in the eastern range (Figs. 24, 26). This gradual blending of extremes through intermediate populations along a gradient in a *clinal* variation pattern makes taxonomic recognition of the diversity unrealistic.

The west to east clinal variation pattern in flower and inflorescence size appears associated with seasonal rainfall patterns. The western Sonoran Desert receives winter rains while Arizona and Sonora receive both winter and late summer rains. In contrast, the Chihuahuan Desert is characterized by summer rains. Through this range, *F. splendens* flowers in the late winter to spring from March through May. Flowering therefore occurs in the wet season in the Sonoran Desert but during the dry season in the Chihuahuan Desert where flowers are produced each spring even if precipitation the previous summer was scant. The production of flowers in the Chihuahuan Desert utilizes stored water and energy. Production of smaller flowers would conserve available energy and water resources and allow for production of a greater number of flowers, thereby increasing the reproductive potential. In the Sonoran Desert the plants are usually in leaf during the flowering season or just before, which would provide energy for larger flowers.

The flowers have a number of characteristics associated with hummingbird pollination (e.g., thick reddish, erect, elongate, tubular corollas, exserted stamens and styles, and abundant nectar). Also the winter-early spring flowering corresponds with migration periods of some species of hummingbirds. Grant and Grant (1966, 1968) have observed visitations to the flowers in California by costa, rufous and other unidentified species of hummingbirds as well as linnets and migrating western tanagers. I have observed hummingbird visitation in Texas and Coahuila. The long exserted stamens deposit the yellow pollen on the head and face around the base of the beak. The stigmas are situated among the lower anthers. Grant (1958) reports that Ocotillo in California is self-compatible and appears to be capable of self-pollination. Vector visitation therefore may not be a necessary prerequisite for seed set. The long corolla tubes limit the variety of nectar foraging visitors but pollen foraging insects could obtain abundant food and effectively transport pollen. During the spring of 1969 in Texas and Coahuila the most common visitors observed on the short-flowered ocotillo populations were carpenter bees (*Xylocopa californica arizonensis*). The carpenter bees would land on the crest of the inflorescence, lean over the side or force their heads between the short flowers and pierce the corolla tubes just above the sepals to obtain nectar. The bees repeated these actions at intervals along the inflorescence and then moved quickly to adjacent inflorescences or plants with the ventral body portions of their bodies covered with pollen. Their characteristic transverse slits on the corolla bore were common on Ocotillos in the eastern Chihuahuan Desert. Evidence of carpenter bee robbing is much less frequent on the longer flowers of western populations as the bees probably would be unable to reach the nectar producing areas from the tip of the flower where they can attain a foothold. The lower side of the inflorescence possibly would not provide an adequate foothold for efficient exploitation of nectar by robbing.

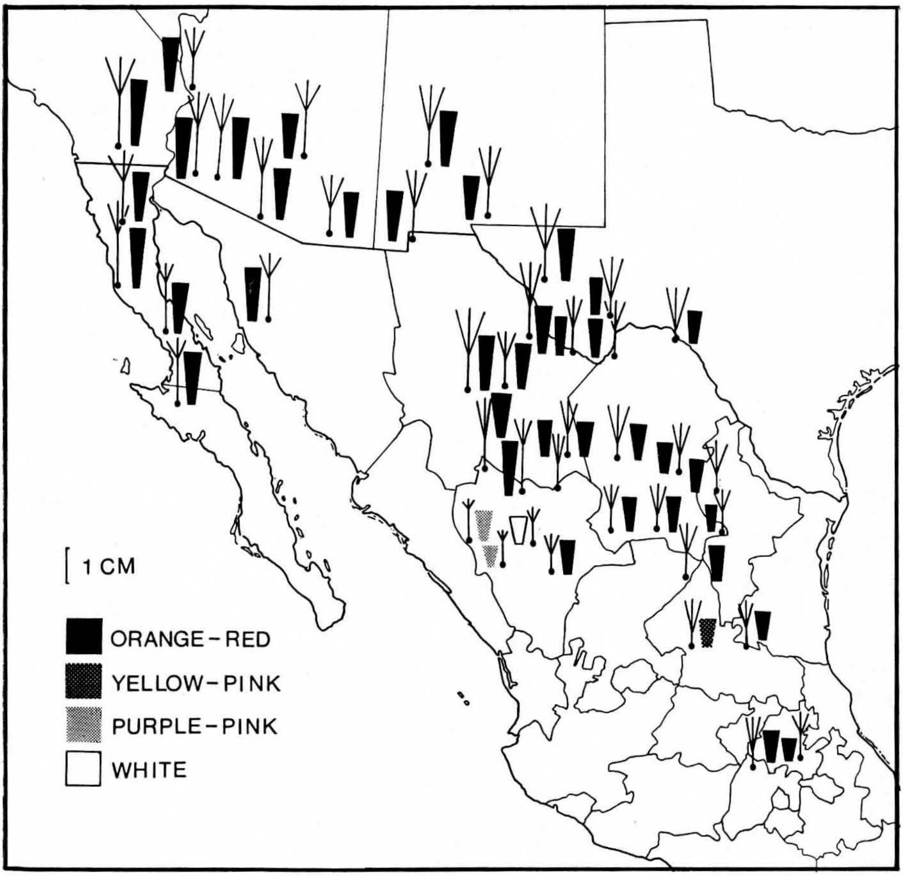


Fig. 26. Comparison of flower color (as indicated), corolla size (shown by outline of corolla tube) and style branching (as illustrated) over range of *Fouquieria splendens*. *Fouquieria splendens* ssp. *campanulata* represented by purple-pink and white corollas in western Durango; *Fouquieria splendens* ssp. *breviflora* by southernmost four populations in San Luis Potosí, Tamaulipas and Hidalgo.

It is interesting that carpenter bees appear to be effective pollen vectors while illegitimately obtaining nectar. In Southern Texas and Coahuila carpenter bees were much more frequent visitors to ocotillo than were hummingbirds. Whether the short corollas characteristic of the far eastern portion of the range formed in response to dry season flowering or if the carpenter bees may have provided a positive selective pressure for shorter corollas is unknown.

In his original description of this species Engelmann (Wislizenus, 1848) did not designate a type specimen. Wislizenus' specimen from near Saucillo, Chihuahua, is here designated as lectotype and the others are cited as paratypes. Standley (1923) and Johnston (1924) have noted the type locality as Jornada del Muerto, New Mexico, but no lectotype designation was made. Earlier in 1848 Torrey (Emory, 1848) equated Emory's specimen of this taxon to H. B. K.'s *Bronnia spinosa* (=*F. fasciculata*), but having both flowering and fruiting material and determining the two genera were not valid, offered it in a new combination under *Fouquieria.*

Chromosome number: $2n=24$ (Raven et al., 1965; Spellenberg in Löve, 1970).

Vernacular names: United States: "Ocotillo," "Candlewood," "Coachwhip," "Jacob's Staff," "Apache Whipping Stick," "Vine-cactus"; Mexico: "Ocotillo," "Albarda," "Barda."

Representative specimens: UNITED STATES. California: San Bernardino Co.: The Needles, *Jones 3831* (DS, F, NY, POM, US). Riverside Co.: Shafer Wells, *Clokey 6752* (NY, RSA, UC). San Diego Co.: Hell Hole Canyon, nr Borrego (with albinos), *Epling & Robinson s.n.* (DS, MO, NY, POM, RSA, UC). Imperial Co.: 10 mi from Niland on rd to Beal Well, *Wolf 1874* (CAS, DS, RSA, UC). Nevada: Clark Co.: 4.3 mi S of Davis Dam, *Bradley 1502* (Las Vegas). Arizona: Mojave Co.: above Pierce Ferry, Lake Mead, *Clover 6048* (MICH). Coconino Co.: high walls at mouth of Havasupi Creek, Grand Canyon, *Clover 5292* (MICH). Gila Co.: Tono Hill, *Collom 262* (MICH, MO,) NY, US). Pinal Co.: nr Florence Jct., *Ehlers et al. 6330* (MICH). Graham Co.: foothills, Graham Mts, *Kellogg s.n.* (ARIZ.) Yuma Co.: below Yuma, *Mearns 2856* (US). Pima Co.: Tucson, *Toumey 1894* (ARIZ, NY, US). Santa Cruz Co.: nr Sonoita, *Harrison 7184* (CAS, NY, UC). Cochise Co.: Hills N of Paradise, *Blumer 1254* (ARIZ, DS, F, MO, NY, US). New Mexico: Socorro Co.: 3.5 mi N of Escondido, *sin nom. 6877* (NMC). Catron Co.: Black Range, *Metcalf 891* (US). Sierra Co.: Berendo Creek, *Metcalf 891* (ARIZ, CAS, MO, NMC). Grant Co.: 8 mi NE of Bedrock, *Maguire 11546* (NY). Hidalgo Co.: Big Hatchet Mts., *Mearns 46* (DS). Luna Co.: 14 mi NE of Deming, *Henrickson 3204* (RSA). Dona Ana Co.: Mesa W of Organ Mts., *Wooton 3360* (DS, US). Otero Co.: nr Tularosa, *sin nom. s.n.* (UMC). Eddy Co.: 1 mi NW of White City, *Dole 132* (UC). Texas: El Paso Co.: El Paso, *Vasey s.n.* (F, US). Hudspeth Co.: 16¾ mi W of Sierra Blanca, *Cory 52890* (SMU). Culberson Co.: 2.5 mi W of New Mexican line, *Whitehouse 16832* (MICH, SMU). Reves Co.: Pecos ?, *Tharp 8797* (TEX). Pecos Co.: 6 mi N of Ft. Stockton, *Warnock 46773* (TEX). Jeff Davis Co.: Mt. Livermore, Davis Mts., *Hinckley 201* (NY, TEX). Presidio Co.: 11 mi NW of Presidio, *McVaugh 7956* (DS, F, MICH, SMU, TEX). Brewster Co.: 17 mi S of Government Springs, Big Bend Nat'l Park, *Whitehouse 19581* (MICH, NY, SMU); Head of Blue Creek Canyon, Chisos Mts., *Moore & Steyermark 3335* (DS, MICH, MO, NY, UC, US). Terrell Co.: 15 mi S of Sheffield, *Webster 273* (TEX, MICH). Val Verde Co.: Deep Canyons of Pecos River, nr Viaduct, *Palmer 33471* (NY, MO). MEXICO. Baja California del Norte: Signal Mt., *Mearns & Schoenfeldt 2939* (DS, US); Arroyo Mirmar, ca. 1 mi N of Aleman Mirmar, *Wiggins & Wiggins 5885* (DS, MEXU, MICH), Wash 8 mi SE of El Rosario, *Wiggins 5261* (CAS, DS, F, GH, MICH, NY, POM, UC, US); Arroyo Estalon, Isla Angel de la Guarda, *Wiggins 17005* (DS); 3¼ mi N of Punta Prieta, *Wiggins 7636* (DS, UC); San Fransquito Bay, *Johnston 3545* (CAS, GH, NY, UC, US). Baja California del Sur: Rancho Santa Cruz, Sierra Santa Lucia, SE of San Ignacio, *Moran 11773* (DS, RSA, DS); 1 mi W of ex-Mission Guadulupe, *Moran 11794* (DS, RSA, SD). Sonora: 32 mi SE of Cananea, N of Bacoachi, *Wiggins 11700* (DS, SD); 5 mi N of Moctezuma, *S. White 405* (ARIZ, GH, MEXU, MICH); 14.5 mi NW of Caborca, *Wiggins 8283* (DS, MICH, UC); Cholla Bay nr Punta Penasco, *Hutchinson 7000* (UC); Imuris, *Abrams 13189* (DS); 2 mi NW of Pto. Libertad, *Wiggins 6088* (DS); Vicinity of Hermosillo, *Rose et al. 12415* (F, NY, MO); 3 mi N of Willard's Pt. Tiburon Island, *Johnston 4258* (CAS, GH, UC); Bahia Kino, *Drouet & Richards 3529* (F). Chihuahua: 63 mi S of Ojinaga, *Henrickson 3088* (RSA); Vicinity of Chihuahua, *Palmer 91* (F, GH, MO, NY, US);

San Francisco de Borja, *Pennington 179* (TEX); 12 mi N of Saucillo, *Henrickson 3199* (RSA); 27 mi E of Hidalgo de Parral, *Henrickson 3197* (RSA); 38 mi E of Escalon, *Henrickson 3117* (RSA). COAHUILA: 42 rd mi W of Cuatrocienegas, *Henrickson 3128* (RSA); between Hipolito and Sacramento, *Wynd & Mueller 79* (GH, MO, US); 3 mi N of San Lozaro, 80 mi N of Saltillo, *Henrickson 3143* (RSA); 8 mi W of Saltillo, *Henrickson 3150* (RSA); 6 mi N of Parras, *Henrickson 3152* (RSA). NUEVO LEON: 123 rd mi S of Saltillo, *Henrickson 3146* (RSA). DURANGO: 15 mi SW of Torreon, *Henrickson 3155* (RSA); 5 mi W of Pedricenca, *Henrickson 3156* (RSA); 40–60 mi SSE of C. Durango towards Mezquital, *Maysilles 7404* (MICH). ZACATECAS: Canitas, *Rose & Hay 6328* (US); 9.2 mi W of Cedros, *Henrickson 6243* (RSA); 32.2 mi SW of Camacho, *Henrickson 6319* (RSA); 83.7 mi NE of Hwy 49 on Hwy 54, *Henrickson 6695* (RSA).

7b. FOUQUIERIA SPLENDENS Engelm. in Wisliz. ssp. **campanulata** (Nash) Henrickson, stat. & comb. nov.

Fouquieria campanulata Nash, Bull. Torrey Bot. Club 30: 457, 1903. TYPE: MEXICO. DURANGO: Santiago Papasquiaro, 1896; *E. Palmer 87*; (HOLOTYPE: NY!; ISOTYPES: GH, MO, MO, NY, US, US!).

Plants to 5 m high with 5–40 thin, erect to widely spreading branches to 2.5(–4.5) cm in diameter near base, often distally pendulous in older plants. Short-shoot leaves in fascicules of 6–11, 17–27 mm long (3.5–)5–8 mm wide with petioles to 4 mm long, linear spatulate to narrowly oblanceolate, acute to rounded at apex, cuneate and shortly petiolate at base. Inflorescence narrowly conical, ascending 6–14(–17) cm long, pedicels 1–3 mm long above, peduncles and pedicels to 8 mm long near base. Medial floral bract to 9 mm long, 3 mm wide, lateral bracts to 5 mm long, 1.5 mm wide, oblong, purplish pink to cream white. Sepals light to dark purple-pink in center, slightly greenish at base with whitish scarious margins, 4–5 mm long, 3.5–5.5 mm wide; corolla strong purple-pink to strong pink to cream white, 11.5–15.5 mm long, tube 7–10 mm long, slightly ampliate, diameter 4.5–5.5 (8 pressed) mm at throat, with 3 mm band of hairs within near base, limbs 4.5–6 mm long, 4–5 mm wide, broadly oblong to ovate. Stamens 14–18, filaments (8–)11–17 mm long, cream white to strong purple-pink, turning darker with age; lower 5–6 mm angular, with spur 1–1.5 mm long and associated hairs to 0.8 mm long; anther light yellow to tinged with red, turning darker red upon drying, 4–5 mm long. Ovary 1.5 mm high with 12–16 ovules; style purple-pink or cream white 8.5–11 mm long, 3-branched 3–4.5 mm from tip.

Fouquieria splendens ssp. *campanulata* (Fig. 22) forms extensive and dense populations along the eastern edge of the Sierra Madre Occidental west of the Chihuahuan Desert from the vicinity of Santiago Papasquiaro North to Indé and east to the Rio Nazas Basin near Rodeo (Fig. 23). It occurs in well-drained rocky (basalt to limestone) slopes in the gramma grasslands from the border of the microphyllous scrub at 1200 m to the juniper-pine woodlands at about 2000 m. The region averages 400–500 mm annual rainfall occurring mainly from July to October. Flowering occurs in the spring from March to May while the plants are leafless.

The subspecies is very similar to *F. splendens* ssp. *splendens* in growth form but has much thinner young stems (3–5 mm diameter), and mature stems rarely exceed 4.5 cm in basal diameter. The wand-like branches are erect to widely arching (Fig. 1c). Short-shoot leaves are distinctly narrower (linear-spatulate) than in the other subspecies.

This taxon is distinguished mainly by its small purple-pink to white flowers. Total corolla length ranges from 11.5 to 15.5 mm; the ampliate tubes are 7–10 mm long. Similar short corolla tubes characterize *F. splendens* ssp. *breviflora* and the easternmost populations of *F. splendens* ssp. *splendens* (Figs. 24, 26). Variation in corolla tube diameter between individuals of a population is particularly noticeable (Fig. 25). In all instances, corolla diameter correlated directly with diameter of young terminal stems, which indicates a common genetic control of peripheral development of both stem and floral meristems. The narrow flowers also have fewer stamens than the broad flowers. The styles of *F. splendens* ssp. *campanulata* are three-branched in the distal half whereas most other populations in the species except those in Baja California are branched in the middle or proximal half (Fig. 26). No examples of character intergradation between *F. splendens* ssp. *campanulata* and ssp. *splendens* are known but no specimens are available from the area of closest contact between the Rio Nazas and Cuencame.

Visitation to the flowers by unidentified hummingbirds, bumblebees (*Bombus* spp.) and carpenter bees (*Xylocopa* spp.) have been noted near the type locality. The latter two are able to obtain nectar legitimately from the shorter flowers although robbing will occur on the larger flowers.

This subspecies consists of two intergrading population systems differing in flower color. These are classified as follows:

7b–1. FOUQUIERIA SPLENDENS Engelm. in Wisliz. ssp. CAMPANULATA var. CAMPANULATA.

Sepals strong purplish pink, often greenish at base, pinkish towards tip or pinkish throughout, with yellow-white margins; petals pink to strong purple-pink, turning darker with age, greenish white under sepals; anthers yellow, tinged with red; filaments and style light pink to strong purple-pink, usually turning darker with age.

Populations known from the type locality near Santiago Papasquiaro, Tephuanes north to Indé and east to the Rio Nazas Basin have strong purple-pink corollas and pinkish sepals. These freely intergrade along the southeastern margin of their range forming mixed populations with the following white flowered taxon.

Representative specimens: MEXICO. DURANGO: 3 mi W of Santiago Papasquiaro, *Henrickson 1732–1737* (RSA); 2 mi W of Santiago Papasquiaro towards Garame, *Henrickson 3158* (RSA); 20.3 mi NW of Santiago Papasquiaro towards Tepehuantes, *Henrickson 3168* (RSA); near El Palmito Dam, *Henrickson 3187* (RSA).

7b–2. FOUQUIERIA SPLENDENS Engelm. in Wisliz. ssp. CAMPANULATA (Nash) Henrickson var. **albiflora** Henrickson, var. nov.

Fouquieriae splendente ssp. campanulatae var. campanulatae similis, sed sepalis eburneis, basale purpureo-roseis vel viridibus, petalis eburneis, antheris luteis, et filamentis et stylo albis.

Sepals yellowish white, often with purple-pink and/or green near base; petals cream white, slightly green below sepals, anthers yellow, infrequently tinged with red; filaments and style white.

TYPE: MEXICO. DURANGO: 7 mi S of Rodeo along Hwy 45, 75 air mi N of Durango, *Henrickson 3174* (HOLOTYPE: RSA!; ISOTYPES: MEXU, MICH, MO, RSA, UC!).

Extensive white-flowered populations occur in the Rio Nazas Basin from Rodeo to an area about 45 km S of Atotonilco along Mex. Hwy. 45 in scrubby grassland with *Acacia, Jatropha, Opuntia, Cnidosculus,* and *Larrea.* Extensive intergradation of the two varieties occurs in populations to the north and south of this area. The intergrading populations contain plants with strong purple-pink, white and intermediate light pink corollas. The occurrence of a wide range of intermediate flower colors indicates either a multiple gene inheritance or a series of modifying genes. This variety is based solely on flower color features. It is nomenclaturally recognized as it consists of large, pure populations at least in the center of its range.

Chromosome number: $2n=24$.

Representative specimens: MEXICO. DURANGO: Near La Cuestra (host to *Phoradendron tomentosum* ssp. *tomentosum*), *Hawksworth & Weins 324* (COLO); ½ mi N of Atotonilco 69 mi N of Durango, *Henrickson 3172* (RSA).

7c. FOUQUIERIA SPLENDENS Engelm. in Wisliz. ssp. **breviflora** Henrickson, ssp. nov.

Frutex candelabriformis vel arbor parva 2–5(–10) m alta, trunco breve, caulibus strictis, late expansis, saepe supra ramosis et horizontalibus. Foliis brachyblastorum 20–35 mm longis, oblanceolatis vel spathulatis. Paniculis late conicis vel cylindraceis, (3–)10–28 cm longis; pedicellis prope apicem (2–)4–6(–12) mm longis; pedicellis et pedunculis base (5–)10–30(–70) mm longis. Sepalis rubro-roseis vel luteo-albis, base viridibus, 4–5.5 mm longis. Petalis rubro-auranticis, 10.5–15 mm longis; tubo 6.5–10 mm longo, parum ampliato; limbis reflexis, 5–6 mm longis, 4–5 mm latis. Staminibus 15–20, exsertis; filamentis 9–18 mm longis, rubro-aurantiacis vel eburneis, antheris aurantiacis 3.5–5 mm longis. Stylo rubro-aurantiaco vel albo, 12–14 mm longo, 7–10 mm sub apice 3-ramoso.

Shrubs to small trees 2–5(–10) m tall with widely spreading branches often distally horizontal to pendulous, older plants with stems much branched above, stems 2–7(–10) cm in diameter at base. Short-shoot leaves in fascicules of 3–7, 20–35 mm long, (5–)7–10 mm wide, oblanceolate to spatulate, obtuse to rounded at apex. Inflorescence paniculate, narrowly conical to cylindrical in outline, erect to pendulous, (3–)10–28 cm long, pedicels (2–)4–6(–12) mm long near tip, peduncles and pedicels (5–)10–30(–70) mm long at base; medial floral bract to 5 mm long, 3 mm wide, lateral bract to 3 mm long, 1.5 mm wide, dull purple-red. Sepals reddish pink to yellowish white, greenish near base, margins white, scarious, 5–6 mm long, 4–5.5 mm wide. Petals strong reddish orange to strong yellowish pink and turning darker with age, whitish to greenish below sepals, 10.5–15

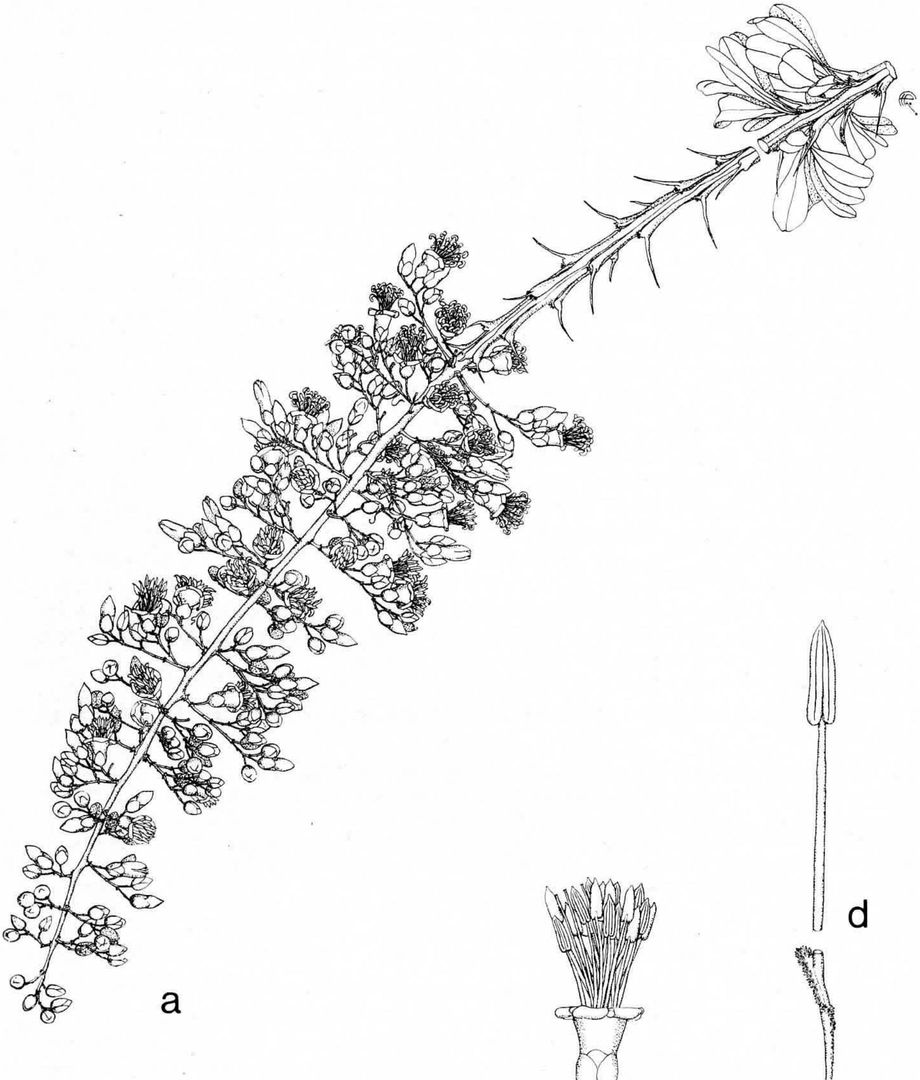


Fig. 27. *Fouquieria splendens* ssp. *breviflora*.—a. Terminal pendulous stem bearing characteristic broad, elongate paniculate inflorescence. Oblanceolate short-shoot leaves shown at base.—b. Mature flower with short corolla, elongate stamens.—c–d. Stamen.—c. Filament base showing ligulate adaxial spur and extent of trichomes.—d. Anther, adaxial surface. (*Henrickson 2079*): Holotype (RSA).—a ×0.5; b ×1.5; c–d ×4.

mm long, tube 6.5–10 mm long, slightly ampliate, diameter 4.5–5 mm wide at throat, 2–2.3 mm wide at base with 2–3 mm band of uniseriate hairs 3 mm above base within; limbs strongly reflexed, 5–6 mm long, 4–5 mm wide, broadly ovate to broadly elliptical, obtuse, rounded at broad base. Stamens 15–20, filaments strong reddish orange to cream white and turning darker orange with age, drying red, 9–18 mm long with lower 3.5–5 mm angled, adaxial spur 1 mm long with hairs to 0.7 mm long; anthers orange, drying red, 3.5–5 mm long, apiculate at apex. Ovary 1.5 mm high with 12–16 ovules; style reddish orange to white and turning darker with age, 12–14 mm long, 3-branched 7–10 mm from tip.

Type: MEXICO. Hidalgo: 23 km N of Ixmiquilpan along Hwy 85, 2 km N of Rio Tula, *Henrickson 2079* (holotype: RSA!; isotypes: ARIZ, CAS, MEXU, MICH, RSA, USN, GH!).

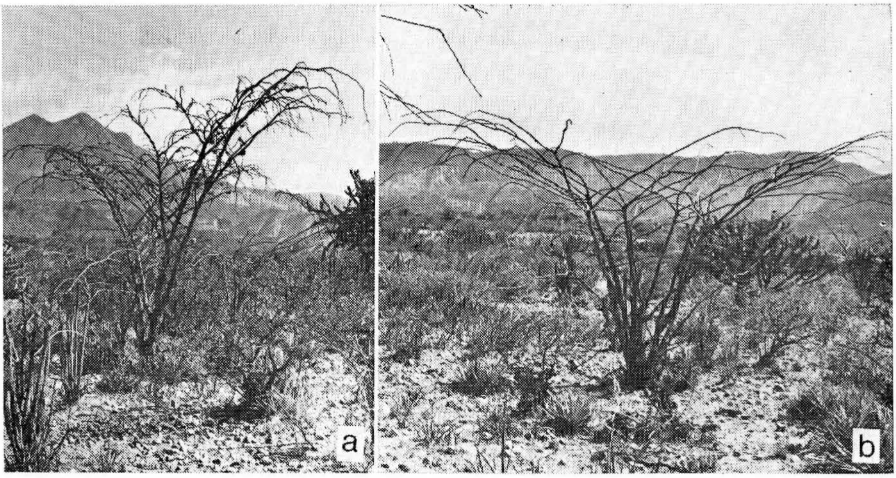


Fig. 28. Growth habit of *Fouquieria splendens* ssp. *breviflora* showing characteristic widely divergent stems. From population north of Rio Tula, 23 km north of Ixmiquilpan, Hidalgo. Plant height: a, ca. 4 m; b, ca. 6 m.

Fouquieria splendens ssp. *breviflora* (Figs. 27, 28) is known from scattered disjunct populations in low arid basins from San Luis Potosí and Tamaulipas south to Hidalgo and Querétaro (Fig. 23). It occurs on arid rocky usually south-facing slopes and hillsides from 750 to 1200 m elevation in the north and to 2100 m in the southern part of its range. It is commonly associated with species of *Yucca, Agave, Hechtia, Myrtillocactus, Opuntia, Echinocactus, Cephalocereus* and deciduous shrubs in disjunct areas of arid tropical scrub vegetation. Average annual rainfall ranges from 280 to 450 mm and is again concentrated from June through October while flowering occurs in the winter.

This subspecies is based upon character disparities which occur between populations from Coahuila south to northern San Luis Potosí and those of south central San Luis Potosí to Hidalgo. Populations in the eastern range of *F. splendens* ssp. *splendens* from around Saltillo to Matahuala have short, relatively congested inflorescences averaging 8.4 cm in length and short orange-red corollas. Populations beginning 30–50 miles south of Matahuala have much more open elongate inflorescences averaging 14.9 cm in length, yellowish pink to light orange flowers, more widely arching branches and generally larger leaves. From near Tula, Tamaulipas, and south to Hidalgo inflorescences are even larger, averaging 17.5 cm in length, and the darker orange-red corollas on the average tend to be slightly shorter. None of the distinguishing characters is unique to this subspecies. Orange-red corollas are characteristic of the type subspecies while yellowish pink corollas occur as occasional mutants. Equally short corolla tubes characterize *F. splendens* ssp. *campanulata* and some populations of the type subspecies in eastern Coahuila (Figs. 24, 25). Similar elongate inflorescences are common on plants of Baja California but they are associated with much longer flowers (Fig. 24). While the close relationship to *F. splendens* ssp. *splendens* is obvious the abruptness of character differences and apparent lack of intergrading populations support taxonomic recognition of these southern populations.

Vernacular names: "Gavia" (San Luis Potosí), "Ocotillo," "Albarda," "Barda."

Representative specimens: MEXICO. SAN LUIS POTOSI: 21 mi S of Matehuala, *Henrickson 3147* (RSA); 4 mi S of El Huizache, *Henrickson 3148* (RSA). TAMAULIPAS: 17 mi SW of Tula, *King 4461* (UC, F, NY). HIDALGO: 14 mi NW of Ixmiquilpan, *King 4204* (NY, F, UC); 5 km NW of Tasquillo, *L. Gonzalez Q. 2149* (DS); 10 km al S de Ixmiquilpan, *R. Cruz C. s.n.* (MEXU); Barranca de Meztitlan, *O. Tapia V. 24* (MEXU). QUERETARO: between Visarone, Hiquerillas, *J. Rose et al. 9765* (NY).

8. FOUQUIERIA SHREVEI I. M. Johnston, J. Arnold Arbor. 20: 238. 1939 (as *Fouquiera*). TYPE: MEXICO. COAHUILA: 26 km South of Laguna del Rey, on road to Mohovano, on gypsum-flat, 20 Sep., 1938, *I. M. Johnston 7815* (HOLOTYPE: GH!).

Shrubs 1–2.5 m high of candelabraform habit, with short trunk to 15 cm high 15 cm in diameter, bearing 15–40(–64) strict ascending to upwardly arching stems which infrequently branch near the apex or base with age. Larger stems and trunk developing thick accumulation of a "resinous" bronze-colored, translucent periderm. Young branches thick, 4–5 mm in diameter, furrowed; decurrent ridges maroon, glaucous when young, light grey with age, rigid and long persistent in a spiraled pattern (10–)15–27 mm long, tapering to fifth node below. Spines (16–)25–30(–45) mm long, often thickish, flattened above with a narrow groove along upper surface, in 5/13 phyllotaxy. Long-shoot leaves 25–40(–50) mm long with petioles 18–40 mm long and blades 8–11(–25) mm long, 4.5–6(–17) mm wide, elliptic, with acute, apiculate apex, cuneate base, occasionally much larger and obovate. Short-shoot leaves in fascicules of 1–4, 12–25(–30) mm long, 8.5–14(–18) mm wide, elliptical to broadly obovate to nearly orbicular, acute to obtuse, often apiculate or retuse at apex, broadly cuneate at base, nearly sessile to petiolate to 5 mm; leaves isolateral, dark green on both surfaces, leathery, entire, with broad conspicuous white or rarely reddish scarious margins. Flowers solitary or paired at upper nodes, sessile or shortly (1–2 mm) pedicellate, rarely in indeterminate terminal to axillary racemes 6–12 mm long of 3–12 flowers on short pedicels 3 mm long; flowers subtended by 2–5 dull reddish, subulate bracts to 6 mm long, 1 mm wide, with scarious margins. Sepals pinkish tinged with dull red, to white, green near base, (4–)5.5–8 mm long, 4–6.5 mm wide, broadly ovate, outer two often orbicular, acute to rounded and apiculate at apex, rounded at broad base, with broad scarious margins which infold towards apex to form an outwardly projecting conical point, corolla salverform, tinged with red and pink in bud, ivory-white at maturity, 12–16 mm long; tube narrow to broadly campanulate, 4.5–6.5 mm long, diameter 2–3 mm at base, 3–5 mm at throat; throat villose within with 2 mm band of uniseriate hairs to 0.6 mm long; limbs reflexed, 6–9 mm long, 4.5–6 mm wide, oblong-elliptic, obtuse and apiculate at tip, broadly rounded to slightly cordate at broad base, with scarious margins which roll back along margins and inward at tip to form distinct conical apicule. Stamens 15–17(–20), exserted, of unequal length; filaments 7.5–14 mm long, ivory-white, lower 4–5 mm angular, slightly curved over ovary, bearing uniseriate hairs to 0.8 mm long at upper abaxial sides continuing around to adaxial side over ovary, upper filament cylindrical, glabrous; anthers yellow, tinged with red, often turning red upon drying, 3–4 mm long, 1 mm wide, oblong-lanceolate, apiculate at tip, cordate at base. Ovary 1.5 mm high with 13–16 ovules; style (7–)10–14 mm long, white, 3(–4)-branched 4–7 mm from tip; capsules tan, often tinged with red, broadly ovate in outline 9–16 mm long, 5–7 mm wide; seeds 3–6(–10), white, 7–12 mm long, 5–6 mm wide with membranes to 4.2 and 1.5 mm wide at ends and sides respectively; membrane hairs 30–50 μ thick near tip with 2–3 spiralling and occasionally anastomosing thickenings; embryo 3–3.5 mm long, cotyledons ovate 2–2.5 mm long, 1.5–2 mm wide.

Fouquieria shrevei (Fig. 18) is known only from a few scattered gypsum outcroppings in the Bolson de Mapimi region of the Chihuahuan Desert in western Coahuila (Fig. 23). The Bolson region consists of low, warm basins from 1000 to 1200 m elevation which average 150–250 mm annual rainfall concentrated from July through October. The relatively low rainfall, hot climate and gypseous soil (hydrated calcium sulfate) combine to produce a severe and restrictive environment. The species is associated with only a few gypsophilous species of *Selinocarpus*, *Petalonyx*, *Flaveria*, *Dicranocarpus*, *Drymaria*, *Nerisyrenia*, and *Nama*. (Johnston, 1941), as well as *Larrea*, *Acacia*, and *Atriplex*, which continue into the adjacent *Larrea-Flourensia* scrub.

Fouquieria shrevei is often neighboringly sympatric with *F. splendens* which occurs on adjacent nongypseous (comonly limestone) soils. The two species have very similar "ocotillo" or candelabraform habits and may be easily confused at a distance. They can, however, be distinguished by several vegetative characteristics. *Fouquieria shrevei* forms large accumulations of a dark-bronze "resinous" periderm on older stems, and has broad, obovate, dark green short-shoot leaves with conspicuous scarious margins, whereas *F. splendens* has a yellowish green thin, waxy periderm, more oblanceolate, grey-green leaves with very thin scarious margins. The two species are very distinctive in floral and inflorescence features.

Fouquieria shrevei flowers in the spring from March to May when the plants are usually without leaves. The flowers, which are solitary or in pairs at the nodes of the upper 20–40 cm of the stem, are pink to reddish in bud but have pure white, short, salverform corollas at maturity. The type collection was made in late September when the plants were in leaf, and the flowers were borne in congested indeterminate racemes to 12 mm long. Such inflorescences are *not* produced during the spring flowering season when the plants are leafless, and were not observed during two field searches in July, 1964, and September, 1971, when the plants were in leaf. Such inflorescences are apparently very rarely produced and occur only when the plants are in leaf and growth resources are plentiful. One such inflorescence had reduced spines at the base and was a modified terminal long-shoot.

Pollinator visitations to the flowers have not been observed, but the light corolla color, short tube length and exserted stamens would suggest effective exploitation by a wide array of large insects.

The species is most closely related to *F. splendens*. They both have 12–20 stamens, isolateral leaves, a candelabraform habit, trichomes on the inner corolla surface and spirally thickened hairs on the seed coat. The last three characteristics are found only in these two species.

Chromosome number: $2n=24$.

Vernacular names: "Ocotillo," "albarda" (not distinguished from *F. splendens*).

Etymology: Named after Forrest Shreve, desert ecologist, who accompanied I. M. Johnston when the species was discovered.

Representative specimens: MEXICO. COAHUILA: S of Laguna de Leche, *Johnston 8613* (GH, MEXU); between La Vibora and Matrimonio Vieja, *Johnston 9343* (GH); 21 mi E of El Rey, *Henrickson 3126* (RSA); 5 km S of Los Americanos, *G. Borja B-250* (MEXU, MICH); 2 mi N of Laguna del Rey, *Henrickson 3120* (RSA); 10 mi S of Laguna del Rey, *Henrickson 1821* (RSA); 26 mi S of Estanque, near Mohovano (Topotype), *Shreve 8836* (US, ARIZ); 3 mi NE of Las Delicias jct. along Hwy 30, 40 mi NW of San Pedro, *Henrickson 6025* (RSA); 1 mi N of Las Delicias between springs, *Henrickson 6038* (RSA).

9. FOUQUIERIA FASCICULATA (Willd. ex Roem. et Schult.) Nash, Bull. Torrey Bot. Club 30: 452, 1903.

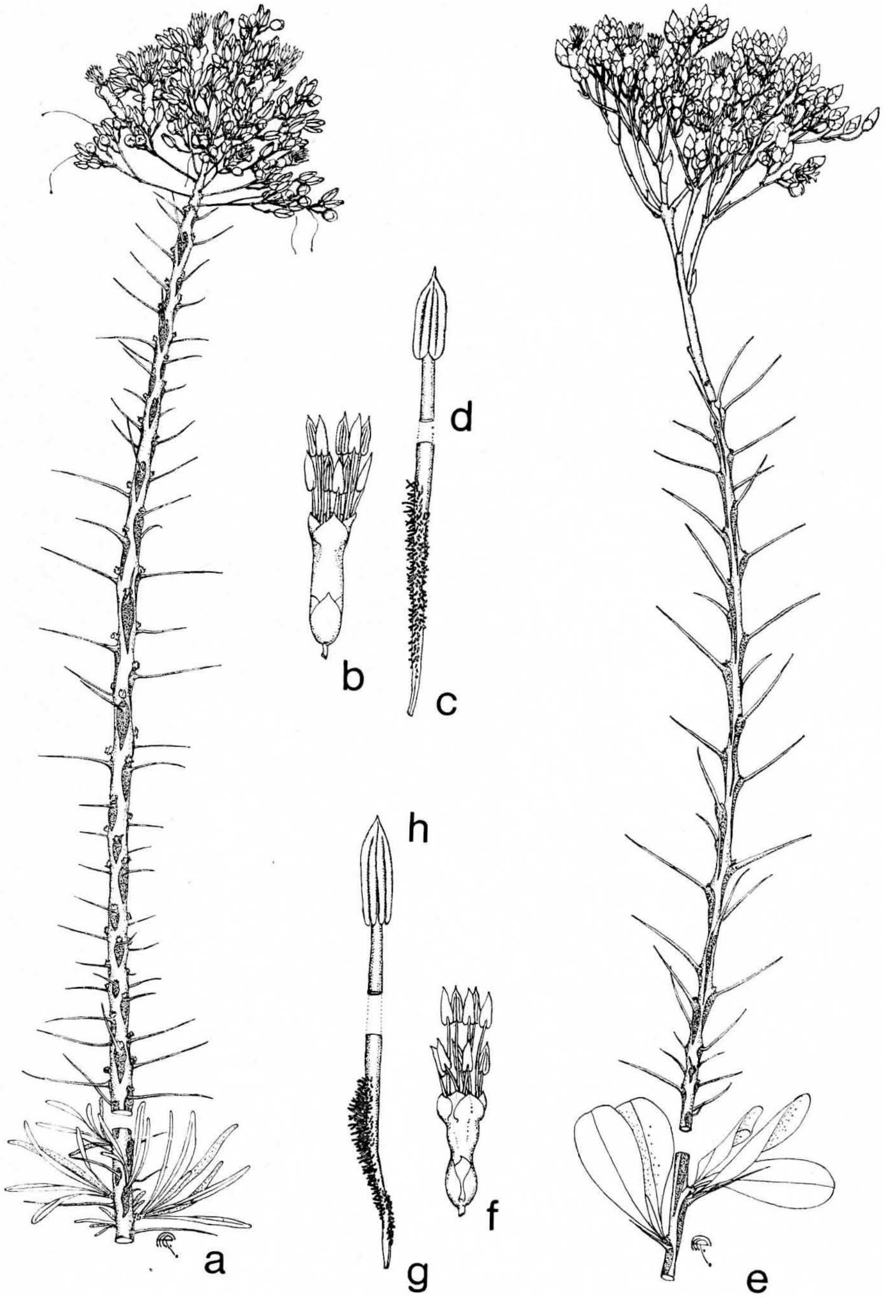
Cantua fasciculata Willd. ex Roem. et Schult., Syst. Veg. 4: 369, 1819. TYPE: AMERICA MERIDION; *Humboldt s.n.* (HOLOTYPE: B! ft.)

Fouquieria spinosa H. B. K., Nov. Gen. Sp. 3: 452, 1820. *nom. nud.*

Bronnia spinosa H. B. K., Nov. Gen. Sp. 6: 84, t. 528, 1823. TYPE: NOVA HISPANIA: Crescit rarissime prope speluncam Puente de la Madre de Dios, alt. 880 hex. (Between Atotonilco el Grande and Actopan, Hidalgo, May 1803.) *Humboldt and Bonpland 4125.* (HOLOTYPE: P! ft.; ISOTYPE: P! ft.)

Cantua spinosa (Willd. ex Roem. et Schult.) H. B. K., Nov. Gen. Sp. 6: 84, 1823. *pro syn.*

Shrubs to small trees 2–5 m high with 1–3 greatly expanded basal trunks to 25–60 cm in diameter which narrow abruptly above, continuing as 1-several woody, moderately-branched stems; expanded basal trunk succulent within due to proliferation of nonlignified xylem parenchyma; trunks and larger stems shiny green, with persistent epidermis, smooth except for horizontal wedges of hard, grey periderm which form under and replace decurrent leaf bases. Young long shoots 3–4 mm in diameter, not furrowed; decurrent ridges dark maroon, turning grey with age, 13–32 mm long, widely spaced, narrowly oblanceolate in outline, tapering down stem. Spines (10–) 15–25(–30) mm long, slender, ascending, in 3/8 phyllotaxy; elongated short-shoot spurs to 10 mm long form at nodes in older stems. Long-shoot leaves 25–55 mm long, with petioles 12–20 mm long, blades 21–35 mm long, 7–17 mm wide, oblanceolate to elliptic, acute at apex, cuneate at base, with a prominent midrib below. Short-shoot leaves in fascicules of 2–7, 16–40(–65) mm long, 8–15(–23) mm wide with petioles 3–10 mm long, broadly spatulate to oblanceolate, acute, rounded to slightly emarginate at apex, cuneate at base; leaves dorsi-ventral, dark green above, lighter green below, entire. Inflorescence corymbosely paniculate, round, dense, 4–9 cm long, 4–12 cm wide, terminal to subterminal, all branches determinate, rachis green, 2.5–3 mm thick near base, with pedicels 2–10 mm long, 0.6 mm in diameter, peduncles to 25 mm long, 1.2 mm in diameter; floral bracts narrowly subulate, 1.5–2(–10 and leaflike) mm long, lateral two scattered along pedicel. Sepals yellowish white, green at base, 3.5–4 mm long, 2.3–5 mm wide, the outer two smaller, elliptical-ovate, the inner three broadly ovate to orbicular with scarious margins, obtuse to rounded and apiculate at apex, rounded to slightly cordate at broad base. Corolla tubular, ivory white, 10.2–11 mm long, tube 7–8 mm long, slightly expanding to middle, narrowing to 2.7 mm in width at throat, glabrous within; limbs erect, 3–3.5 mm long, broadly ovate to orbiculate, margins uneven, infolding, more so in upper half, obtuse to acuminate at apex, cordate at broad base. Stamens 10, exserted, alternate 5 longer than opposite 5; filaments 7–11 mm long, white, basal 4–6 mm slightly expanded laterally with short hairs to 0.7 mm long extending from abaxial mid-portion laterally to adaxial surface above ovary, upper filament cylindrical, glabrous; anthers light yellow, 4 mm long, 1 mm wide, narrowly lanceolate in outline, with caudate apex, cordate base. Ovary green, 1 mm high, with 11–13 ovules; style 9.5–10.5 mm long, white, 3-branched, 1.5–2 mm from tip, stigmas situated among anthers. Capsules tan-brown, lance-ovate in outline, 9–12 mm long, 3.5–4 mm wide, seeds 3–6, tannish white, 7–9 mm long, 3–4 mm wide with membranes 2 and 1.5 mm wide at ends and sides respectively; membrane hairs to 50–150 μ wide near tips with or without slight perpendicular to anastomosing thickenings; embryo 4.5 mm long; cotyledons elliptical 3.5 mm long, 1 mm wide.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Fouquieria fasciculata (Fig. 29) is known only from southern Hidalgo in the Barrancas west of the Sierra Madre Oriental north of Actopan and Atotonilco el Grande (Fig. 14). Several collections are recorded from Barranca Tolantongo and vicinity near Chalmita and Lago de Metztitlan where it occurs on rocky slopes with shallow calcareous and apparently gypseous soils (Miranda, 1950). It occurs from 1200 to 1600 m elevation in pockets of arid tropical scrub vegetation dominated by numerous cacti (*Cephalocereus, Lemaireocereus, Echinocereus, Ferocactus, Mammillaria*) (Kimnach, 1965) as well as by *Bursera, Prosopis, Celtis, Escheveria, Agave* and epiphytic tillandsias. Annual precipitation averages 500–600 mm, concentrated from May through September. Flowering occurs in the dry season from December through March.

The species is distinguished by its greatly expanded succulent basal trunks (Henrickson, 1969c), persistent epidermis and small decandrous white flowers produced in dense corymbose panicles. Young plants have a shrubby habit with numerous branches extending from one or more expanded bases. Older individuals have fewer central stems which abruptly expand to an enlarged, basal, barrel-like water-storage organ (Fig. 1).

The flowers have a delicate sweet fragrance and produce a noticeable sweetened nectar. During two brief periods of observation near Lago de Metztitlan, Hidalgo, flowers were visited by hummingbirds, large bumblebees (*Bombus* sp.) and an assortment of other insects which crawl over the dense, flattened, corymbose inflorescence. Nectar could be obtained from the short flowers by any insect with mouthparts 5–7 mm long.

Fouquieria fasciculata is very similar to *F. purpusii* of southeastern Puebla. Their similarities and differences are discussed with the latter species.

The nomenclatural history of this taxon is involved with problems developing from the separation of Humboldt and Bonpland's American botanical collections after their return to Europe in 1804 (McVaugh, 1968). One set of their collections was presented to K. L. Willdenow in 1805 for study. The remaining collections were held at Paris where C. S. Kunth was retained to study and describe them after Willdenow's death in 1812. The results of Kunth's work were published in the well known *Nova Genera et Species Plantarum* (1816–1825). Kunth, however, did not have full access to Willdenow's collection in Berlin. During this period, Roemer and Schultes

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Fig. 29. a–d. *Fouquieria purpusii.*—a. Terminal stem with rounded corymbose inflorescence. Note short, separated decurrent ridges. Linear short-shoot leaves shown at base.—b. Mature flower with erect corolla lobes. Stamens initially conform to pattern of 5 (alternate) long and 5 (opposite) short filaments.—c–d. Stamens.—c. Filament base showing distribution of trichomes.—d. Anther, adaxial surface. (*Henrickson 2142*).—e–h. *Fouquieria fasciculata.*—e. Terminal stem with flattened corymbose inflorescences. Note comparatively longer decurrent ridges. Broad oblanceolate short-shoot leaves shown at base.—f. Mature flower. Stamens initially are arranged in 5 long (alternate) and 5 shorter (opposite) pattern.—g–h. Stamen.—g. Filament base showing extent of trichomes.—h. Anther, adaxial surface. (*Henrickson 2071*).—a, e ×0.5; b, f ×1.5; c–d, g–h ×4.

were allowed access to Willdenow's collections and published in their *Systema Vegetabilium* (1819) several names and brief descriptions which were provided by Willdenow, including that of *Cantua fasciculata* (Syst. Veg. 4: 369). Their description was taken verbatim from Willdenow's handwritten label which is presently attached to the folder containing the holotype at Berlin (B) (Piepko, pers. comm.). Kunth, in 1820 (Nov. Gen. Sp. 3: 452), equated this combination to his proposed *Fouquieria spinosa* which was eventually published as *Bronnia spinosa* (Nov. Gen. Sp. 6: 83, 1823). Nash (1903) while not understanding the role of Willdenow, made the combination *Fouquieria fasciculata* (R. & S.) Nash. All nomenclatural combinations pertaining to this taxon are therefore based on Humboldt and Bonpland's 1803 collection from "Puente de Madre de Dios" in Hidalgo. Recently, Standley (1920–1926) in his *Trees and Shrubs of Mexico,* confused this taxon with *Fouquieria campanulata* Nash.

Chromosome number: $2n=24$.

Vernacular name: "Arbol de Barril."

Representative specimens: MEXICO. HIDALGO: Barranca Tolantongo, *Paray 3860* (MEXU); cerca de Chalmita, N de Cardonae, *Miranda 4026* (MEXU); cerca de San Cristobal, Meztquititlan, *Matuda 37289* (MEXU); ca. 37 (air) mi NNW of Pachuca, above Lago de Metztitlan, *Henrickson 2068-72, 2077, 4331* (RSA).

10. FOUQUIERIA PURPUSII T. S. Brandegee, Univ. Calif. Publ. Bot. 3: 386, 1909. TYPE: MEXICO. OAXACA: Rocky slopes of Cerro de Coscomate (in Sierra de Mixteca near San Luis Tultitlanapa, 2200–2300 m), Aug., 1907, *C. A. Purpus 3376* (HOLOTYPE: UC!, ft.; ISOTYPES: F, GH, MO, NY, US!).

Shrubs to small trees 1–5 m high with 1–4(–6) conical, tapering enlarged trunks to 20–60 cm in basal diameter, bearing numerous, slender, horizontally spinose branches; expanded trunks succulent within, due to proliferation of nonlignified xylem parenchyma; larger stems and trunk green with persistent epidermis, smooth, shiny except for horizontally elongated wedges of rigid, grey periderm which form under and replace decurrent leaf bases. Young long shoots 3–4.5 mm in diameter, not furrowed; decurrent ridges dark maroon, turning grey with age, 7–14 mm long, widely spaced, oblanceolate in outline, tapering down the stem. Spines (10–)17–28 mm long, slender, ascending, in 3/8 phyllotaxy; elongated short-shoot spurs to 18 mm long, 3–4 mm in diameter develop at nodes in older stems. Long-shoot leaves 35–50 mm long, with petioles 17–30 mm long, blade 15–23 mm long, 2.5–6 mm wide, elliptical-linear, acute to obtuse at apex, narrowly cuneate at base. Short-shoot leaves in fascicles of 5–9, 17–33 mm long, 2.5–4 mm wide with petioles 2–7 mm long, linear to narrowly oblanceolate, rounded-obtuse to acute at apex, narrowly cuneate at base; leaves dorsi-ventral, dark green above, lighter green below, entire. Inflorescence corymbose paniculate, rounded, dense, (2–)3.5–6 cm long and wide, terminal to subterminal, with all branches determinate, pedicels 2–9 mm long, 0.6 mm thick, bracts narrowly subulate, 1.5–2 mm long lateral two scattered along pedicel. Sepals yellow-white, light green at base, 4.2–6 mm long, 1.7–2.3 mm wide, outer two oblong without scarious margins, inner three usually more elliptical with uneven scarious margins which expand near base, acuminate at apex, rounded to truncate at broad base; corolla tubular, ivory-white, 11–13 mm long, tube 7.5–9 mm long slightly expanding in middle, narrowing to 3.6 mm width at throat, with few scattered hairs within; limbs 3.4–4.5 mm long, erect, orbicular, with uneven, infolding scarious margins, obtuse and apiculate at tip, distinctly cordate at broad base. Stamens 10, exserted; filaments 14–17 mm long, white, with lower 6–8 mm slightly enlarged and arched over ovary, bearing unicellular hairs to 1 mm long extending from abaxial base laterally to adaxial surface above ovary, upper filament cylindrical, glabrous; anthers light yellow, 4-4.5 mm long, 1–1.4 mm wide, lanceolate in outline, distinctly caudate at tip, cordate at base; ovary green, 1.2–1.5 mm high. Ovules 12–15; style 11–16 mm long, white, 3-branched 1.7–2 mm from tip, stigmas situated among anthers. Capsule tan-brown, lance-ovate in outline, 10–12(–15) mm long, 3.5–4 mm wide; seeds 3–7, reddish tan, 7–9 mm long, 2–3 mm wide with membranes to 1 and .5 mm wide at ends and sides respectively; membrane hairs 25–100 μ wide at tips, with single lateral thickening; embryo 5 mm long, cotyledons elliptical, 3.5 mm long, 1.6 mm wide.

Fouquieria purpusii (Fig. 20) is known only from a few localities in southern Puebla and northern Oaxaca (Fig. 14) where it exists in an arid tropical scrub vegetation on exposed rocky limestone outcroppings and open basaltic slopes (Smith, 1965) from 1000 up to 2300 m (Schneck, 1921) elevation. This region averages 450–600 mm rainfall concentrated from June through October. Flowering occurs during the dry season from February to April. Common associates in the deciduous scrub include species of *Bursera, Juliania, Jatropha, Cnidosculus, Plumeria, Pithecellobium,* and *Leucaena* as well as *Cephalocereus, Opuntia, Mammillaria, Agave, Brahea,* and *Fouquieria formosa.*

This species has a very distinctive growth form (Fig. 1f) characterized by one or more enlarged conical, central trunks containing large quantities of nonlignified xylem parenchyma and meandering strands of tracheary tissue (Henrickson, 1969c). The trunks and larger stems have a shiny dark green outer surface with a persistent epidermis and are marked with the often massive transversely oriented ridges of hard sclerified cork which initially forms under the decurrent leaf bases. The upper portions of the main trunks bear horizontal to ascending spinose branches which bear the small white decandrous flowers in terminal to subterminal determinate corymbose panicles (Fig. 29).

Fouquieria purpusii is very similar to *F. fasciculata* which occurs in notably similar vegetation in Hidalgo. Both species have enlarged trunks containing parenchymatous xylem water-storage tissue with persistent epidermis and corymbose panicles with nearly identical flowers. In *Fouquieria fasciculata,* however, the water-storage tissue is restricted to the base of the central stems, the leaves are elliptic and the inflorescences are larger, while in *F. purpusii* the water-storage tissue extends far up the central stems to produce a tapering growth form (Fig. 1 d–g) and the leaves are linear. The latter species also develops prominent short-shoot spurs and has shorter decurrent ridges on the young stems.

During two visits to a population along the Oaxaca-Puebla border SSE of Tehuacan no pollinator activity was observed. The erect white flowers have a delicate sweet odor, are nectariferous and sufficiently short to allow exploitation of nectar and/or pollen by a number of insects.

Chromosome number: $2n=24$.

Etymology: Named after its discoverer, J. A. Purpus, a German botanist who collected widely in Southern Mexico.

Representative specimens: MEXICO. PUEBLA: W of Rio Salada, on and around Petlanco, *C. E. Smith et al. 3669* (F, MEXU, US, NY); ca. 23 (air) mi SSE of Tehuacan at Oaxaca-Puebla border at Cerro Petlanco, *Henrickson 2140–2152, 4296* (RSA). OAXACA: 14–15 mi W of San Antonio, Dist. de Teotitlan, *Gentry 22476* (MEXU, ARIZ).

11. FOUQUIERIA COLUMNARIS (Kellogg) Kellogg ex Curran, Bull. Calif. Acad. Sci. 1(3): 133, 1885.

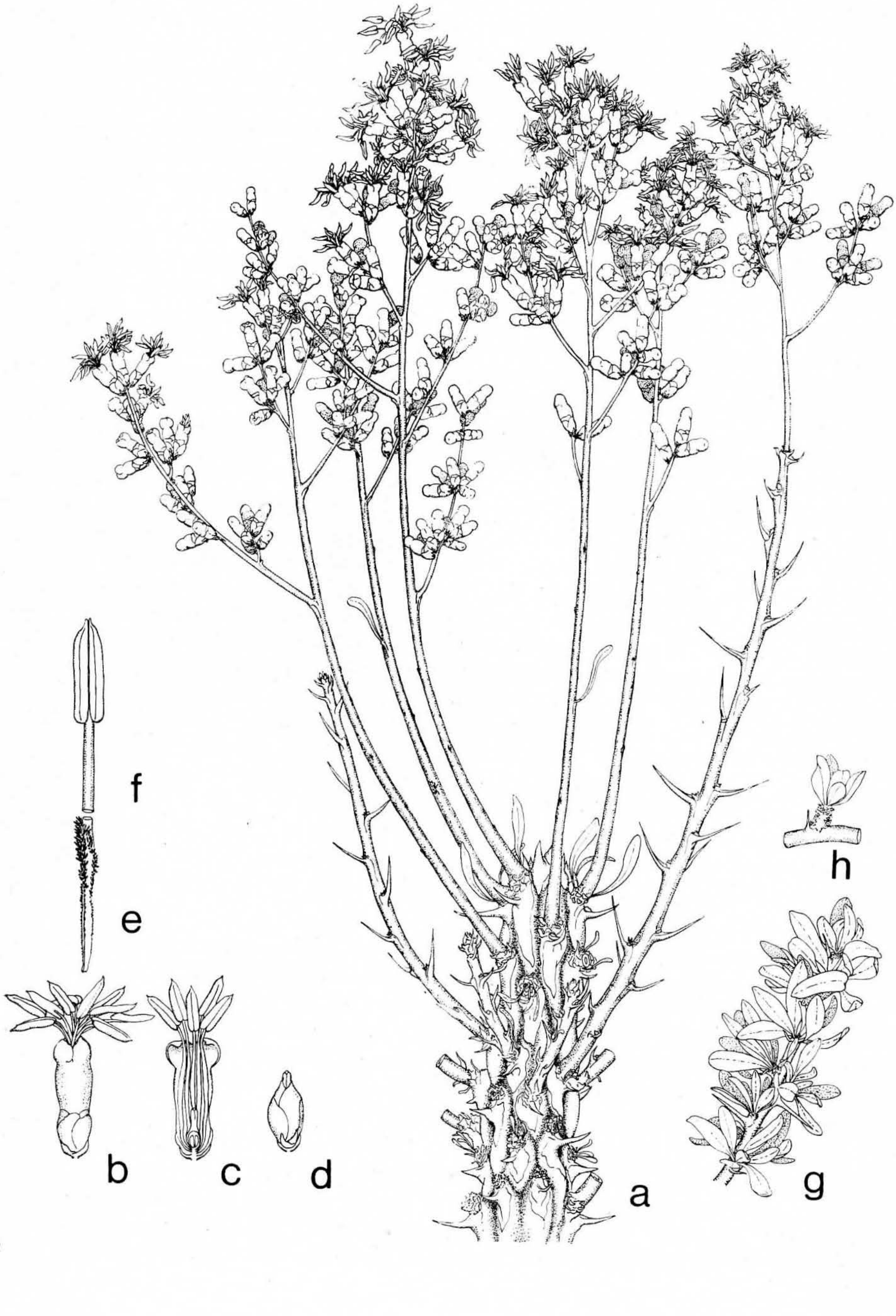
Idria columnaria Kellogg, Hesperian 4: 101 pl., 1860 (Proc. Calif. Acad. Nat. Sci. 2: 34, 1862). TYPE: MEXICO. LOWER CALIFORNIA: Bay of Sebastian, point east of Cedros Island, *J. A. Veatch s.n.* (HOLOTYPE: was at CAS, no longer extant; LECTOTYPE: GH!).

Fouquieria gigantea Orcutt, West. Amer. Sci. 2(16): 48, 1886 (as *Fouquiera*). TYPE: MEXICO. LOWER CALIFORNIA: Rosario to San Fernando near the 31st degree N lat., 4 May, 1886, *C. R. Orcutt 1353* (LECTOTYPE: GH!).

Columniform, upwardly tapering trees 1–16(–23) m tall, expanding from base to maximum diameter of 20–40(–64) cm, 20–70 cm above base and gradually tapering towards apex; central axis single or variously branched; cortex parenchymatous, much thickened with peripheral layer of sclereid nests; xylem with outer anastomosing solid cylinder and extensive inner parenchymatous core. Periderm thin, smooth, dull-green to light yellow. Central axis elongating in increments 15–45 cm in length, 2–4 cm in diameter, bearing lateral nodes in a tight 8/21 phyllotaxy; central axis long-shoot leaves 22–40 mm long with petioles 5–15 mm long, blade 10–28 mm long, 3–12 mm wide, elliptical to spatulate, obtuse at apex, cuneate at base, much thickened; petiolar spine of central axis 5–25 mm long, very stout, conical, curved upward, with broad conical decurrent base 10–23 mm long, widely spaced, tapering downward, eventually dehiscent. Lateral nodes of central axis forming either: (1) slender horizontal spinose long-shoots, or (2) short-shoot spurs, or (3) inflorescences. Young lateral long-shoot branches 2–3 mm in diameter, without furrows, woody, bearing slender spines (4–)16–30 mm long with yellow-tan discontinuous narrow, decurrent ridges 10–20 mm long in a 2/5–3/8–5/13 phyllotaxy. Lateral long-shoot leaves (19–)35–57 mm long with petioles 13–25 mm long, blades 6–32 mm long, 3–8 mm wide, broadly to narrowly elliptical, obtuse to acute at apex, cuneate at base. Short-shoot leaves of lateral branches in fascicules of 2–6, 10–20(–40) mm long, 4–7(–19) mm wide, with short petioles to 4 mm long, elliptical to obovate, obtuse to emarginate at apex, cuneate at base; all leaves isolateral, grey-green on both surfaces, entire; short-shoot spur branches developing at nodes of lateral branches to 1.5 cm long, 3 mm in diameter. Lateral branches persistent and secondarily branching, deciduous (in older plants) or not produced and replaced by 1–5 short-shoot spur branches to 50 mm long, 5 mm diameter which produce fascicules of leaves similar to short-shoot leaves of lateral branches; short-shoot spur branches infrequently reinitiate long-shoot growth. Inflorescence elongate, determinate panicles, produced in upper stem of current year's growth or rarely from shoots along entire trunk, 13–40(–60) cm long, rachis yellowish, 3–6 mm in diameter at base, lower branches 2–10(–24) cm long, upper branches progressively shorter, with small, spatulate, leaf-like bracts to 15 mm long, 2 mm wide and associated short deltoid spines to 2 mm long subtending each major branch; upper peduncle with broadly subulate bracts, 1–4 mm long; flowers crowded in upper 1/3–1/4 of inflorescence, on short pedicels or sessile on peduncle, each flower subtended by 3(–5) subulate bracts to 1 mm long. Sepals cream-yellow, 3–4 mm long, 3.5–5 mm wide, outer two orbicular with rounded apex, scarious margins, inner three broadly orbicular with broad scarious margins, rounded to deeply emarginate at tip. Petals cream-yellow, 6–7 mm long, tube 4–4.5 mm long, 3.7–4.2 mm wide at throat, limbs 2–3 mm long, 3–3.5 mm wide, orbicular, rounded and strongly incurved around apex, cordate at broad base, inflexed, appressed to filaments. Stamens 10(–12), exserted; filaments 9–11.5 mm long, lower 4.5–5 mm slightly broadened, with numerous hairs to 0.5 mm long extending from lower abaxial surface around margins to adaxial surface above ovary, upper filament cylindrical, glabrous; anthers yellowish, 3.5–4.5 mm long, 1.5 mm wide, oblong-lanceolate in outline, apiculate at apex, cordate at base. Ovary 1.5 mm high, with 13–15 ovules; style 2–2.5 mm long, 3-lobed 0.5 mm from tip, style branches and stigmas included within corolla tube. Capsules, yellowish tan, oblong-lanceolate in outline, 11–17 mm long, 3 mm in diameter; seeds 3–10, brownish tan, 10–15 mm long, 2.5–3.5 mm wide, with thin membranes 3 mm and 0.8–1.2 mm broad at one end and sides respectively; membrane hairs 40–100 μ broad, smooth or with narrow perpendicular anastomosing thickenings. Embryo 6–9 mm long, cotyledons oblong 5–6 mm long, 1.2–1.5 mm wide.

Fouquieria columnaris is restricted to the arid Sonoran Desert between El Rosario and Santa Rosalia in Baja California, on Isla Angel de la Guarda in the Gulf of California and in a small area south of Puerto Libertad on coastal mainland Sonora (Fig. 19). This arid region averages about 73–140 mm annual precipitation mainly from January to April and in lesser amounts in August through September. Rainfall is highly irregular and years may pass without heavy rainfall.

The species occurs from sea level to 1450 m elevation on deep to shallow, volcanic loams or clays to decomposed granite soils. It appears to prefer rocky, well-drained soils on hillsides, mesas and alluvial plains. Common associates include *Yucca valida* Brandegee, *Pachycormus, Pachycereus pringlei, Agave, Lophocereus, Jatropha, Larrea, Ambrosia, Opuntia, Pedi-*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lanthus, Olneya, Prosopis, Cercidium, as well as *Fouquieria splendens* and *F. diguetii.*

Fouquieria columnaris (Figs. 1 h, i; 30) is by far the most distinctive and bizarre species of the family. It is characterized by the following features: (1) a tall upwardly tapering, straight or variously branched or forked central axis consisting of a thin periderm, a thick cortex region and an anastomosing xylem cylinder surrounding a massive accumulation of water storing xylem parenchyma (Fig. 1i); (2) a series of slender, spinose horizontally oriented long-shoot stems, or short-shoot spur branches arranged in a spiralled pattern on the central trunk; (3) isolateral leaves; (4) elongate paniculate inflorescences produced near the apex of the central trunk; and (5) short, cream-yellow, decandrous flowers with inflexed corolla lobes, and included 3-lobed styles. The central axis of the plant is homologous to a single stem of other species (Humphrey, 1935). It bears spines, decurrent ridges and has a cortical water-storage network but is greatly broadened at the tip by a primary thickening meristem (Henrickson, 1968). The lateral slender long-shoot branches, however, lack the cortical water-storage network, a feature unique to the family.

The thickened central axis has an initial 8/21 phyllotactic nodal pattern which is retained as opposing left- and right-handed helices on the main trunk. In most instances nodes are arranged in five helices of low pitch in one direction encircling the stem every 11 nodes and in eight series of higher pitch in the other direction completing one circle every 21 nodes. In other plants there are eight helices in one direction and 13 in the other, both encircling the stem every 21 nodes.

The species is most similar to *F. fasciculata* and *F. purpusii* of south central Mexico as they share in a similar mode of parenchymatization of the xylem. The stems of the latter two species, however, are initially woody and the succulent xylem develops only in the lower portion of the main stem (Henrickson, 1969b). In contrast, the central axis of *F. columnaris* is highly parenchymatized from its initiation by action of a primary thickening meristem. Both groups also have widely spaced decurrent leaf bases, small decandrous flowers. They differ, however, in most other characters. Cytological data indicate an amphiploid origin of *F. columnaris* ($n=36$). *Fouquieria purpusii* ($2n=24$) or *F. fasciculata* ($2n=24$) or related stock could be considered a potential ancestor.

Fig. 30. *Fouquieria columnaris.*—a. Terminal portion of main stem bearing inflorescences and lateral stems from nodes. Note decurrent ridges, spines on succulent main stem. Inflorescences usually produced directly from main axis, but rarely from tip of lateral stems (upper right).—b. Mature flower showing infolded petal lobes, ten exserted stamens.—c. Section of mature flower showing position of included styles.—d. Flower after petals and stamens fall away showing slight exsertion of style lobes above sepal.—e–f. Stamen.—e. Basal filament (radial view) showing extent of trichomes.—f. Anther, adaxial side.—g. Lateral stem showing fascicules of short-shoot leaves.—h. Same, showing small short-shoot spur bearing fascicules of leaves. (*Henrickson 2334*).—a ×0.5; b–c ×1.5; d ×2; e–f ×4; g–h ×0.5.

The species flowers in August and September regardless of rainfall. The short, cream-yellow corollas have limbs inflexed around the filaments of the exserted stamens while the stigma is included. The flowers have a strong, sweet, honeycomb fragrance and produce a noticeably sweetened nectar. Visitations by 15 species of bees representing 11 genera in the Andrenidae, Halictidae, Megachilidae, and Apidae have been reported by Humphrey and Werner (1969) from populations in Baja California del Norte and Sonora. The bees pry open the inflexed corolla limbs to obtain the nectar and contact the protected stigma.

Fouquieria columnaris was first described by Kellogg from specimens collected by J. A. Veatch in Baja California somewhere "on the margin of the Bay of Sebastian Viscaino at a point east of Cedros Island." The type description of the species was published twice, in two nearly identical articles, one in the *Proceedings of the California Academy of Natural Sciences*, Vol. 2, 1858–1862 (the Academy proceedings for November 20, 1859) and in a San Francisco monthly periodical *Hesperian*, May, 1860. The exact date of publication of the description in the Proceedings of the California Academy is not known and it is therefore not possible to determine which article has priority of publication. It is presumed that the proceedings were published after 1962, and therefore the *Hesperian* (1960) article has priority.

In an attempt to catalog and determine synonymy for the plants in the California Academy Herbarium described by Kellogg and others, Curran (1885) published the combination *Fouquieria columnaris* Kellogg indicating the type specimen was so annotated in the herbarium. Whether Kellogg actually annotated the specimen is not known, as the holotype specimen was destroyed in the earthquake and fire of 1906. An isotype at Gray Herbarium (now lectotype) is also annotated *Fouquieria columnaris* but not in Kellogg's handwriting.

Chromosome number: $n=36$.

Vernacular names: "Cirio," "Boojum Tree" (coined by Godfry Sykes from Lewis Carrol's "Hunting of the Snark"), "Idria."

Representative specimens: MEXICO. BAJA CALIFORNIA DEL NORTE: 8 mi from El Rosario towards El Marmol, *Wiggins 4332* (ARIZ, CAS, DS, NY, UC); summit of Cerro San Juan de Dios, *Moran 11442* (DS, SD); 5 mi N of Santa Catarina Landing, *Huey s.n.* (SD); ca. 12 mi SE of San Agustin, *Henrickson 2334* (RSA); 40–50 mi S of San Agustin, *Gentry 4019* (ARIZ, DS, MO, UC); Valley Salorito, *Moran 11890* (ARIZ, DS, MEXU, SD, UC); between Punta Prieta and San Borjas, *Gander 9602* (CAS, SD); Rosalia Bay, *Anthony s.n.* (CAS, DS, F, MO, UC); Calmali, *Martinez s.n.* (MEXU); 4 mi SE of Refugio Bay, Isla Angel de la Guarda, *Moran 10470* (DS, UC). BAJA CALIFORNIA DEL SUR: Cerro San Juan, *Moran 11585* (DS, SD, UC); 1/2 mi N of Rancho de la Higuera, Sierra San Francisco, *Moran 11737* (SD, DS); S slope, summit of Cerro la Chana, *Moran 12800* (SD); E slope of Volcan las Tres Virgenes, *Moran 11675* (ARIZ, DS, SD, UC). SONORA: 8 mi S of Libertad, *Wiggins 6071* (DS, UC); E end bay of Puerto Libertad, *Graham 3808* (DS).

SUMMARY

This taxonomic revision treats the Fouquieriaceae DC. as consisting of one genus *Fouquieria* H. B. K. with 11 species in three subgenera: (1)

Subgenus *Fouquieria* with two sections, *Fouquieria* (Type: *F. formosa* H. B. K.) also including *F. leonilae* F. Miranda, *F. ochoterenae* F. Miranda, *F. macdougalii* Nash, *F. diguetii* (Van Tieghem) I. M. Johnston, and *F. burragei* Rose; section *Ocotilla* Henrickson, sect. nov. (Type: *F. splendens* Engelm. in Wisliz. ssp. *splendens*) also including *F. splendens* ssp. *campanulata* (Nash) Henrickson, ssp. nov., *F. splendens* ssp. *campanulata* var. *albiflora* Henrickson, var. nov., *F. splendens* ssp. *breviflora* Henrickson, ssp. nov., and *F. shrevei* I. M. Johnston; (2) Subgenus *Bronnia* (H. B. K.) Henrickson, stat. & comb. nov. [Type: *B. spinosa* H. B. K.=*F. fasciculata* (Willd. ex Roem. et Schult.) Nash] and including *F. purpusii* T. S. Brandegee; (3) Subgenus *Idria* (Kellogg) Henrickson, stat. & comb. nov. [Type: *I. columnaris* Kellogg=*F. columnaris* (Kellogg) Kellogg ex Curran]. The taxonomic treatment presents keys, synonymies, descriptions, typifications, range maps, citation of representative specimens and discussions of character variation and habitats.

Information of ecological habitats, growth habits, stem, leaf, floral, and fruit anatomy/pollination relationships and chromosome cytology is presented or summarized. Much of this data is used in a taxometric analysis of the family to determine phenetic relationships which are displayed in both dendrograms and taxometric maps and serve as a guide for the taxonomic treatment.

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