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INTRODUCTION

The family Fouquieriaceae, which consists of small trees and shrubs restricted to arid parts of Mexico and the southwestern United States, includes two genera, *Fouquieria* with eleven known species and the monotypic *Idria*. Langman (1964) has offered a useful bibliography of papers dealing with various aspects of the family.

Little is known regarding the phylogenetic relationships of the Fouquieriaceae, and its placement in systematic treatments has varied considerably. Initially, Humboldt, Bonpland and Kunth (1823) and Kunth (1824) placed *Fouquieria* in the Portulacaceae. De Candolle in his *Prodromus* (1828) elevated the genus to the family Fouquieriaceae which he associated with the Portulacaceae, but he mentioned similarities with the Crassulaceae, Turneraceae and Loasaceae. Endlicher (1836–1840) and Walpers (1852–1853), treated the group as a subfamily of the Frankeniaceae. Spach (1836) placed the family near the Tamaricaceae, following Bartling's (1830) suggestion. Bentham and Hooker (1862) treated the group as a tribe Fouquiereae of the Tamaricaceae. Engler and Prantl (1895) in the first edition of the *Natürlichen Pflanzenfamilien* treated the group as a subfamily Fouquierioideae of the Tamaricaceae. However, in a supplement, Engler (1897) elevated the group to family status, Fouquieriaceae, near the Tamaricaceae, a treatment accepted by Hallier (1912) and more recently by Hutchinson (1950), Takhtajan (1954), Cronquist (1957), and others. Bessey (1915) placed the Fouquieriaceae within his Ebenales. Engler (1925) concurred with the opinion of Bessey as did Benson (1957). In a revision of the family, Nash (1903) urged polemoniaceous affinities. Engler and Gilg (1924), in the tenth edition of the *Syllabus der Pflanzenfamilien,* moved the Fouquieriaceae to the Tubiflorae beside Polemoniaceae. This treatment was also followed in the eleventh and twelfth editions of the *Syllabus der Pflanzenfamilien* (Engler and Diels, 1936: Melchior, 1964) but with reservations. Curiously, the type species of the Fouquieriaceae, *Fouquieria fasciculata,* was first included by

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Roemer and Schultes (1819) within *Cantua,* a primitive genus of the Polemoniaceae.

In this paper the pollen morphology of the species of the Fouquieriaceae is described and compared with other families considered closely related in various phylogenetic treatments. The only published account of the pollen of this family is that of Erdtman (1952), who gives brief descriptions of pollen of four species. One of these, *Fouquieria spinosa,* is a synonym of *F. diguetii.*

MATERIALS AND METHODS

In this study, a critical analysis was made of sixty-six collections representing the eleven known species of the Fouquieriaceae. Personal collections as well as loans and gifts from various institutions and individuals provided the pollen samples. Pollen preserved in formalin-acetic acid—70 percent ethyl alcohol (Johansen, 1940) was available for all species and other samples were obtained from dried herbarium collections. Collections studied for each species are cited following the descriptions of the pollen. Abbreviations designating the herbaria possessing the vouchers are in accordance with the system of Lanjouw and Stafleu (1964). Collections accompanied by preserved material are so designated.

In order to analyse carefully the fine structure of the pollen grains, material was processed in several ways to rule out misinterpretations based on preparation or staining artifacts. All samples of dried pollen were successfully expanded in 50 percent alcohol solution at room temperature, as it was found that heating often overexpanded the grains. Each pollen sample then was divided into four portions and treated as follows: (1) Two portions were cleared in 2.5 percent NaOH at room temperature for 2–3 days and washed in distilled water. One portion then was stained in 1 percent aqueous solution of safranin O, mounted in distilled water, and sealed with a beeswax-paraffin mixture (Berglund et al., 1959) or commercial fingernail polish. The other portion was stained in a 50 percent ethyl alcohol solution containing 1 percent safranin O, destained in absolute alcohol, transferred to xylene, and mounted in canada balsam for permanent slides. The water-mounted preparations allowed for better resolution and more critical analysis of the fine structure of the pollen grains. The descriptions of pollen are derived mainly from these preparations, as are the photographs. (2) The third portion was dehydrated in an ethyl alcohol series and mounted in a mixture of safranin O and glycerine jelly (Johansen, 1940). This method allows study of the intine and is preferable for measurements of some pollen grains. (3) The fourth portion was washed in distilled water, stained in a 1 percent aqueous solution of ruthenium red, and mounted in distilled water in accordance with the technique of Bailey (1960). Ruthenium red is a selective stain for compounds of the intine and provides clear definition of the latter. These preparations were also used in some cases for the determination of pollen grain size.

Thin sections of pollen grains were prepared of several species according to standard paraffin techniques (Johansen, 1940). Sections 2μ or less in thickness proved very valuable for analysis of sexine construction.

A collection of *Fouquieria splendens* Engelm. *[Henrickson 2459]* was studied

electronmicroscopically. Fresh pollen grains were fixed in a 5 percent phosphate buffered gluteraldehyde solution and post-fixed in a 5 percent phosphate buffered osmium tetroxide solution (Pease, 1964). Following alcoholic and propylene oxide dehydration, they were imbedded in a mixture of Araldite and Epon (Mollenhouer, 1965). Thin sections were cut using glass knives in a Porter-Blum microtome MT-1. Observations and electronmicrographs were made with a Philips E. M. 75 and a Siemen's Elmiskop 1 A.

All measurements involving light microscopy were made with the aid of an ocular micrometer. Measurements of relative thickness of sexine and nexine were determined from optical sections of whole mounts, whereas measurements of equatorial and polar diameters utilized non-cleared grains. An ocular micrometer was also used for the measurements of the sexine configuration at the mesocolpial areas and at the poles. Study of the fine structure of the sexine was aided by phase contrast microscopy and electron microscopy.

Palynological terminology follows that of Erdtman (1952, 1960).

ACKNOWLEDGMENTS

POLLENMORPHOLOGICAL FEATURES

SIZE.—The average size of the pollen grains of the family ranges from 28 μ to more than 65 μ in equatorial diameter and from 23 μ to ca 50 μ in polar diameter. Measurements are based on fully expanded grains mounted both in water and glycerine jelly and include the natural protrusion of the intine at the germ pores. The measurements obtained from the glycerine jelly preparations are about 3 percent larger than those from the water mounts; this probably due in part to the heating required in the preparation of the former and the nature of the medium.

In all species, variation in size exists within a sample and among samples, particularly those species with larger grains. Size variation among single collections of a species generally is less than 10 percent of the average diameter.

Variation in size of pollen grains between species correlates directly with variation in flower length, which ranges from 1.1 cm to 3.5 cm in the family. Flower size in turn correlates directly with anther size, etc. Figure 1 graphically correlates the pollen grain size with flower size. The latter is expressed as the

sum of the length of the corolla and the width at the corolla throat.

SHAPE.—Fully expanded pollen grains are suboblate in shape (Fig. 4 f). Dried pollen is fusiform in shape (perprolate) with the apertures sunken and forming grooves (Fig. 5 d). Occasionally the dry grains are suboblate as in expanded grains. Harmomegathic changes accompanying water intake gradually changes the shape from perprolate to suboblate. Insufficient expansion, as in material
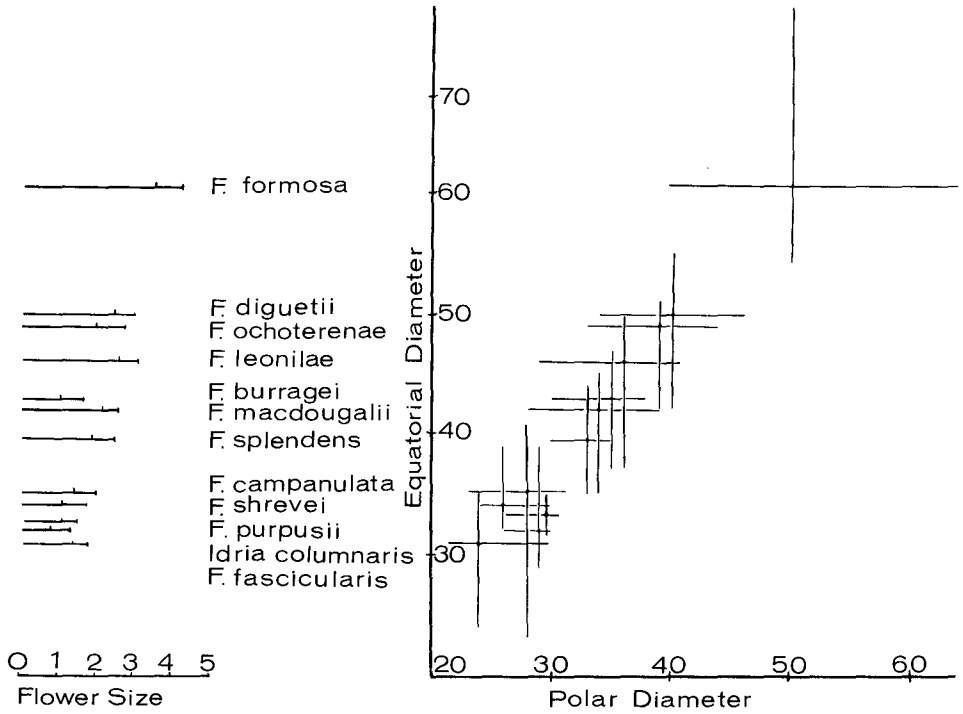
Fig. 1. Diagrammatic representation of pollen dimensions in comparison to flower size. *Right:* Pollen diameters showing means and ranges. Polar diameter as abscissa and equatorial diameter as ordinate (in microns). *Left:* Average flower size shown as sum of corolla length and width at corolla throat (in mm) represented by left and right segments respectively. The positive correlation between flower size and pollen size is apparent.

treated by acetolysis results in intermediate shapes. Erdtman (1952) referred to the grain as suboblate to prolate, probably on this account.

APERTURES.—The pollen grains are tricolporate. In expanded grains colpi are elliptical, acuminate, acute or slightly rounded at the tip. Germ pores are rectangular or squarish (Fig. 4 b–c), rounded in highly expanded grains. The nexine covering the colpi is uniform in thickness except at the germ pores, where it thins gradually and flares outward. No nexine thickening is present around the germ pores or along the colpi as in many other colporate pollen grains.

Exine flakes, which are fragments of the exine covering, are frequently present in the germ pores in all species (Fig. 3 b).

Aberrant apertural types were observed infrequently. Grains with six apertures, only four of which have protruding germ pores have been observed in several species (Fig. 4 a). Only two such grains are formed from a tetrad of
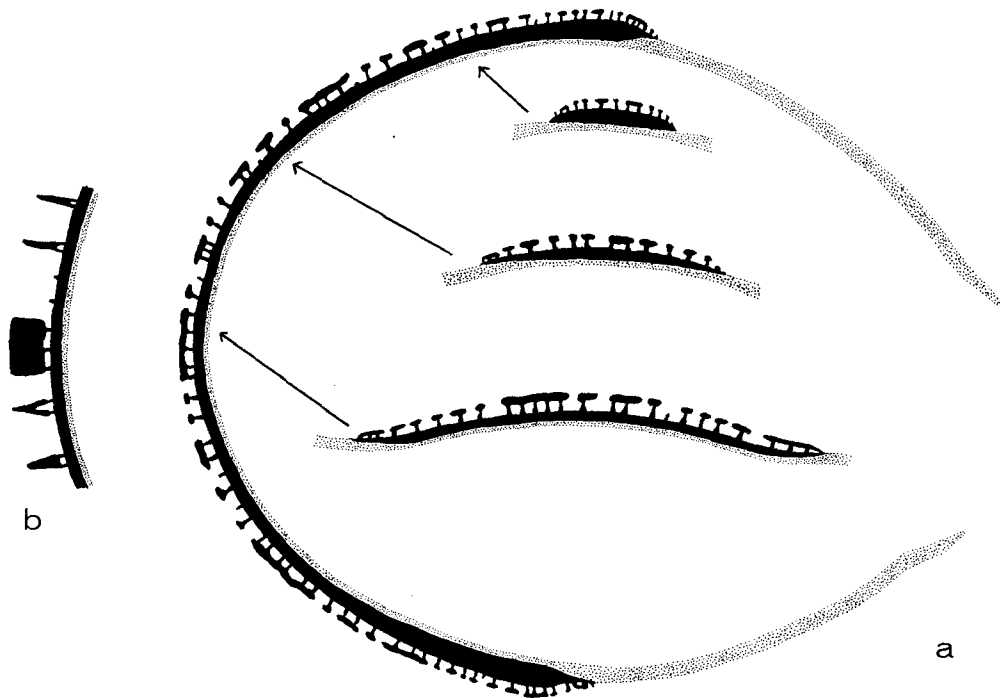

Fig. 2. Schematic representation of the ultrastructure of the exine of pollen of the Fouquieriaceae.—a. Longitudinal section of pollen grain of *Fouquieria* through mesocolpia and germ pore (right), and transection of mesocolpia at points indicated by arrows. Variation in thickness of less electron-dense nexine 2 layer (stippled) and more electron-dense nexine 1 layer and sculptured sexine (black) is shown. Nexine 2 layer beneath mesocolpia is thin and constant in thickness but thickens near colpi margins and constitutes aperture membrane exclusively. Nexine 1 layer thickens towards poles in center of mesocolpia as sexine thins towards poles and along colpi margins.—b. Section of exine of *Idria columnaris* through mesocolpia showing thickened ectosexine characteristic of the genus. (Nexine 2 layer stippled, nexine 1 layer and sexine black).

microspores and each grain contains two microspores. In *Fouquieria burragei* [*Henrickson and Christman 2173*], in addition to typical tricolporate pollen grains, an array of aberrant pollen types was found. Many grains were tricolporate with a normal proximal polar configuration but with apertures extending horizontally to the polar axis at the distal pole. These apertures delimit a
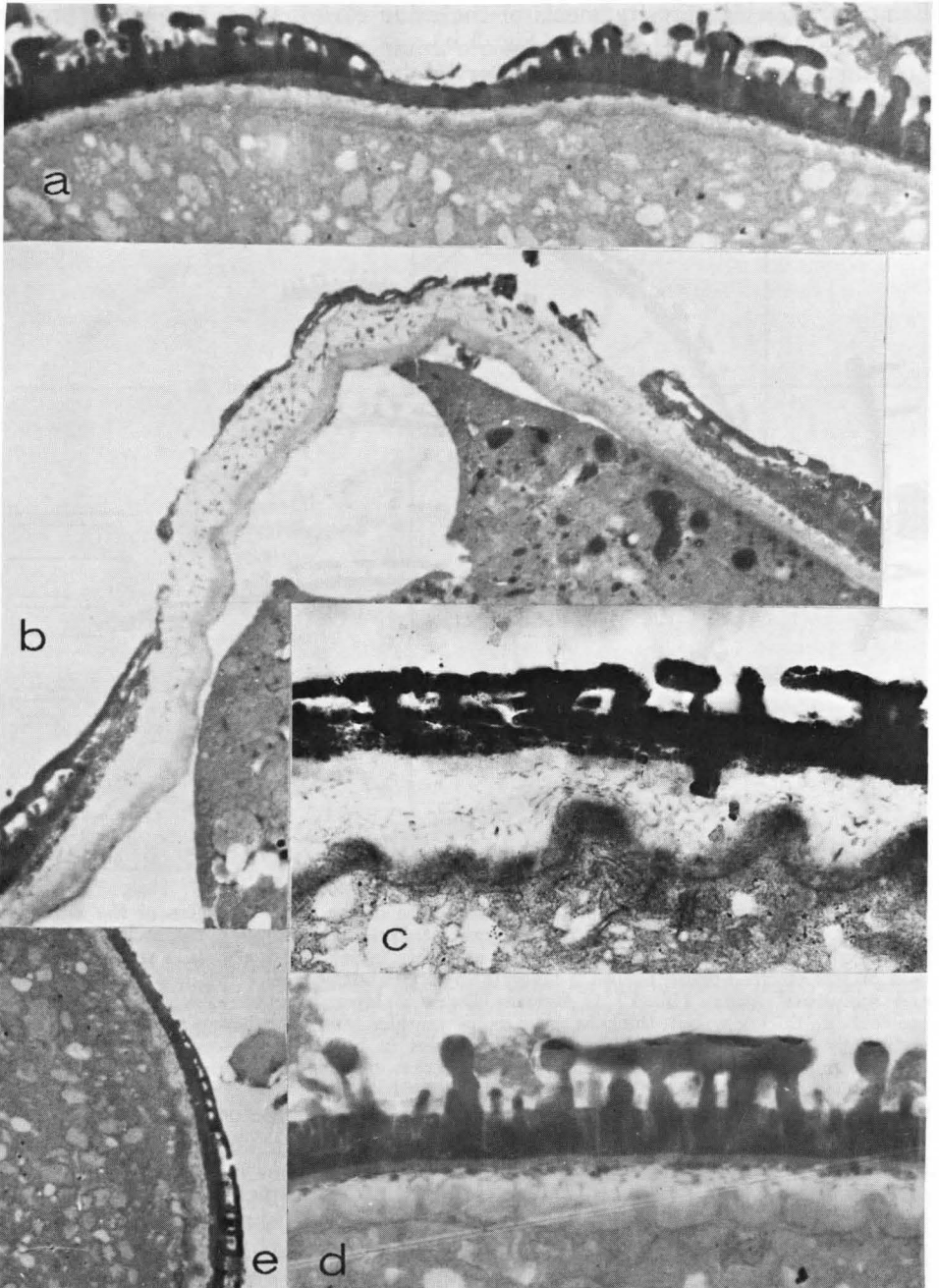
triangular segment of exine at the distal pole (Fig. 5 a). Triangular segments are present on both poles in some grains, whereas other grains have rounded or squarish polar segments delimited by circular apertures. The medial band may have one, two, three or no connecting apertures passing between the polar segments (Fig. 5 b–c). These grains often lack germ pores.

In a collection of *Fouquieria splendens [Henrickson 2459]* grains having two interconnecting apertures and two germ pores that formed a continuous band parallel to the polar axis of the grain were observed. These bands delimited two saddle-shaped segments of exine. Grains with this configuration also were observed rarely in collections of other species.

EXINE.—The exine between the colpi (the mesocolpial area) consists of a sculptured sexine and a continuous basal nexine as described by Erdtman (1952). The sexine of the Fouquieriaceae consists of columnar bacula (the endosexine) supporting a reticulating superstructure, the tegillum (the ectosexine). The sexinous ridges, or muri, form lumina which vary in size and arrangement and account for the intraspecific differences in the pollen grains. The reticulate pattern, size and sexine height varies on a pollen grain and between species. The nexine thickness varies in the mesocolpial areas and is thickest at the poles. It is of a constant thickness over the apertures.

ULTRASTRUCTURE OF EXINE.—The electron microscopic studies add greatly to the understanding of the structure of the exine. As shown in Figure 3 d, the nexine, in the sense mentioned above, is a two-layered structure consisting of an electron-dense upper layer which is continuous with the sexine and a thin, less electron-dense lower layer. With discovery of nexine layering, Erdtman (1960) modified his former terminology. He designated the outer nexine layer, that continuous with the sexine, as the nexine 1 layer and the inner less electron-dense layer, the nexine 2 layer. No nexine 3 layer in the sense of Erdtman was observed in the grains studied electronmicroscopically.

The distinction between nexine layers was first established by Faegri (1956) on the basis of differential staining with basic fuchsin. The sexine and outer

Fig. 3. Electronmicrographs of *Fouquieria splendens [Henrickson 2459 (RSA)]*.—a. Section through aperture membrane and adjacent mesocolpia near tip of aperture membrane, showing relatively abrupt decrease in thickness of sexine and nexine 1 layer and gradual increase in lower nexine 2 layer at aperture margins. The aperture membrane consists of nexine 1 exclusively. ca ×17,100.—b. Section through germ pore of grain, showing gradual thickening of outer intine layer and constant thickness of more electron-dense inner cellulose-containing layer. Note scattered electron-dense bodies in outer intine layer and fragments of exine over germ pore. Sexine, nexine 1 and nexine 2 layers gradually decrease in thickness at germ pore margins. Holes in protoplasm of grain are interpreted as artifacts. ca ×14,600.—c. Section near aperture membrane showing the characteristic layered intine with its uneven lower surface, the outer layer with its characteristic electron-dense bodies, and the inner more electron-dense intine layer. The latter probably contains cellulose. A thin even more electron-dense layer which is continuous inside the intine may be an artifact. Sexine and nexine 1 layer becoming thin as the nexine 2 layer thickens towards aperture margin (to the left). ca × 24,500.—d. Section of mesocolpial exine and intine showing the double layered intine with its characteristic uneven lower surface, the thin nexine 2 layer, the thicker nexine 1 layer and the sculptured sexine. Note origin of bacula of sexine deep in nexine 1 layer, small channels in nexine 1 layer perpendicular to spore surface, narrowing of bacula beneath tegillum, presence of intermural ornaments, and oils associated with sexine. ca ×31,000.—e. Section showing gradual transition of apertural and mesocolpial nexine layers. ×7,300.
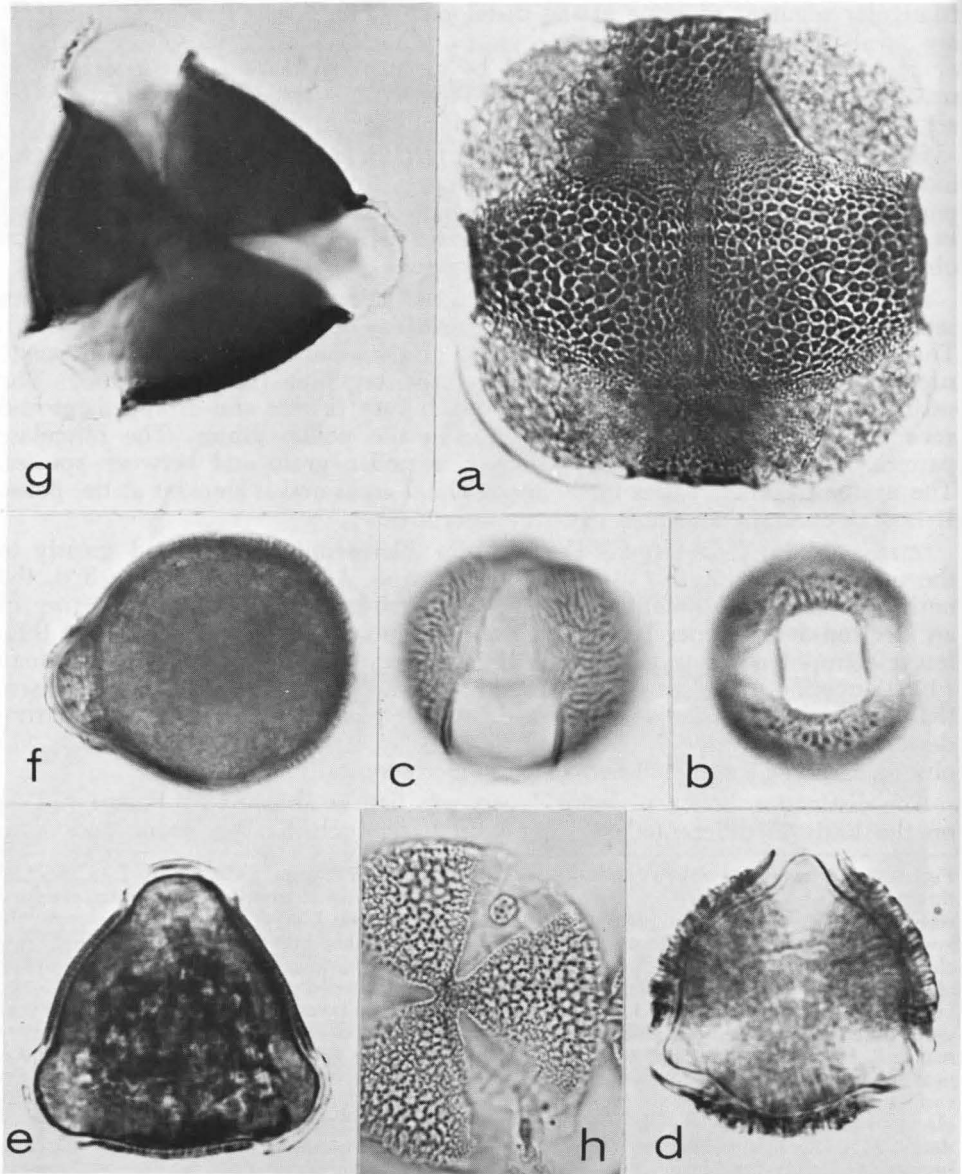
Fig. 4. Photographs of cleared and noncleared grains.—a. *Fouquieria diguetii*. A 6-aperturate grain with four germ pores *[Rutherford 447].*—b–c. *Fouquieria macdougalii*. The germ pores and associated aperture membranes are shown *[Henrickson 1630].*—d. *Idria columnaris*. Polar view showing thickened exine *[Henrickson 2173].*—e. *Fouquieria campanulata*. Polar view showing double layered intine *[Henrickson 1735].*—f. *Fouquieria splendens*. Equatorial view

nexine layers take the stain and the inner layer of the nexine does not. Faegri's terminology emphasizes the staining properties of the exine. His *ektexine* is that part of the exine which stains with basic fuchsin. It consists of three parts, (1) the outer *tectum* supported by (2) the column-like *columellae* that often form (3) a basal *foot layer* over the non-staining layer, the *endexine*. Faegri's foot layer and endexine are the nexine 1 and nexine 2 layers of Erdtman (1960). Pollen grains of several species of Fouquieriaceae were stained with basic fuchsin. Observations from such differential staining supported the electron microscopic observations.

As can be observed in Fig. 3 d, small channels parallel to the columnar bacula are present in the nexine 1 layer. These are similar to those observed by Skvarla and Larson (1966) in the tectum and foot layers of *Zea mays*. The bacula may be constant in diameter or may decrease in diameter immediately below the tegillum. The extent and significance of the nexine 1 and nexine 2 layers are discussed below.

NEXINE.—The nexine thickens from the equatorial mesocolpial areas toward the poles and is thickest at the poles (Fig. 2). The polar nexine may be twice as thick as the nexine at the adjacent aperture membrane tips. The nexine thickening is due to an increased thickness of the more electron-dense nexine 1 layer while the less electron-dense nexine 2 layer remains constant in thickness at the pole and throughout the mesocolpial area. The nexine of the aperture membrane and the equatorial mesocolpial areas are of the same thickness; however, along the aperture margins the nexine 1 layer thins gradually as the nexine 2 layer thickens and forms the aperture membrane (Fig. 2 a). Figures 3 a–e show the transition occurring at the aperture margin. Flakes of the more electron-dense nexine 1 and sexine layers on the aperture membrane may form granulate aperture membranes. Structural differences of the nexine 1 and nexine 2 layers facilitate changes in volume due to desiccation.

SEXINE.—Variation in sexine configuration and structure is present in a pollen grain, within a species and between species. The sexine is thickest in the mid-mesocolpial areas and is thinnest along the colpi and poles (Fig. 6 f). The size of the reticulate pattern correlates directly with the sexine thickness and is smallest at the poles and aperture margins. This positive correlation also exists between species, with the finely reticulated species having relatively thin sexines. In *Fouquieria formosa*, a species with fine reticulations, the sexine is about one-half the thickness of the nexine in the equatorial mesocolpial areas, whereas in species having pollen with larger reticulation patterns, the sexine is as thick as the nexine. In certain species, the reticulation pattern may diminish and form a scrobiculate pattern along the apertures and at the poles. A scrobiculate pattern dominates some grains of *Fouquieria formosa*. Areolate and pilate configurations were observed along the colpar margins and poles in a

showing layered intine. From ruthenium red preparation *[Henrickson 1830].—g. Fouquieria macdougalii.* Shown is the cellulose constitutent of the inner layer of intine as it protrudes at germ pores in cleared grains *[Henrickson 1624].—h. Porana ricasoliana,* Convolvulaceae *[Britton and Britton 9900* (NYBG)*],* showing a sculpturing pattern similar to Fouquieriaceae, with simplibaculate muri and reticulation pattern which diminishes in size toward poles and colpi margins. All ×1,000.

few species. The presence of areolate and pilate configurations indicates an ontogenetic development similar to reticulate patterns.

The muri are simplibaculate, duplibaculate or multibaculate depending on their width. The bacula are usually distributed along the margins of the duplibaculate muri and occasionally are variable in diameter. As shown by the electronmicroscopic studies, the bacula may constrict beneath the tegillum (Fig. 3 a–c). The ectosexine and endosexine are approximately of the same thickness in *Fouquieria* (Fig. 2 a); however, in *Idria* the ectosexine is much thicker than the endosexine (Fig. 2 b).
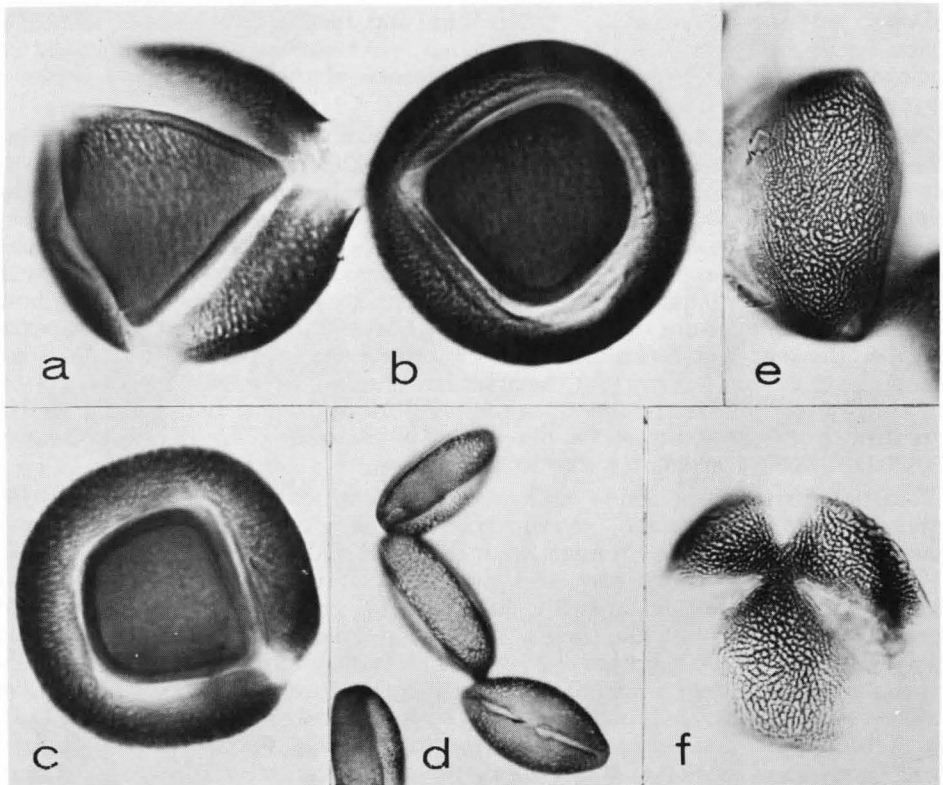
Fig. 5. Photographs of cleared and noncleared grains.—a–c. *Fouquieria burragei.* Shows aberrant aperture configurations *[Henrickson and Christman 2173].*—a. Grain with triangular segment at distal pole of otherwise normal tricolporate grain.—b. Shown here is one of the two circular apertures that delimit a circular polar segment. The grain lacks germ pores.—c. Grain similar to b, but with one aperture membrane crossing the middle exine band; again, without germ pores.—d. *Fouquieria diguetii.* Dried pollen showing typical perprolate shape and sunken apertures *[Rutherford 447].*—e–f. *Fouquieria purpusii.* The characteristic sculpturing patterns with very subtle striations are shown *[Henrickson and Christman 2153].*—d. ×300, all others ×1,000.

The lumina formed by the muri are variable in outline and size. Usually the lumina are angular, but they are rounded when scrobiculate or if the muri are notably widened at the corners between the lumina. Both angled and rounded lumina may occur in the same grain. The lumina may be constant in size (homobrochate) or variable (heterobrochate).

SEXINE SCULPTURING.—Sculpture patterns, although primarily reticulate are variable both intra- and interspecifically. The size of reticulations, measured as the number of lumina per 10 linear μ, varies considerably among the species and in collections of certain species. More diversity is found in the relative thickness of the muri and the size of the lumina. In a few species the muri vary considerably in thickness. Certain primarily simplibaculate species will have slightly thickened duplibaculate areas. Others which have duplibaculate muri forming parallel striae, between which lie simplibaculate muri, form distinctive linear configurations (Fig. 8 b) and show much variation in muri thickness. In certain grains of *Fouquieria formosa* the muri are exceptionally broad, multibaculate, and scrobiculate and are separated by series of scrobiculi (Fig. 7 d). Although the basic sculpturing pattern is randomly reticulate, most species also have some striate areas. Striations may be subtle and consist of straightened or curved muri maintaining a constant dominant direction (Fig. 8 a–b), or the muri may become more distinct as mentioned above. Striations are most common along the small reticulations bordering the apertures. These usually parallel the aperture margins, but, in some collections, striations curve inward to the mesocolpial area. The sexine pattern at the poles may be randomly reticulate or markedly striate if the muri are of distinctly unequal sizes. The striae may be continuous with the colpi margins or may originate from the mesocolpial areas. In several species, sculpturing becomes areolate, pilate, or indistinct at the poles.

INTERMURAL ORNAMENTS.—In several species with larger lumina, small rod-shaped pila were observed in the lumina. These were not always consistently present in the samples of pollen of a particular species. Intermural ornaments were present in the grains studied electronmicroscopically. They appear as bacula which have not developed a tegillate counterpart (Fig. 3 d).

OILS.—Oil-like droplets are associated with the pollen grains of all species. The yellow-gold globules stain red with Sudan IV, a stain selective for fatty and oily compounds (Johansen, 1940). These oil-like substances are also present along the inner walls of the anther sacs, and probably are derived from the tapetum. They can be observed in the electronmicrographs as darkly staining amorphous bodies (Fig. 3 d). The degree to which the oils become associated with the pollen grains varies. These associated oils probably play an important role in the adherence of the pollen to the pollinator.

INTINE.—The hydrophilic intine is layered throughout. The intine in the mesocolpial area consists of two layers, an outer less electron-dense layer and an inner more electron-dense layer which contains cellulose (Bailey, 1960). The lower cellulose-containing layer (Fig. 3 b–c) is continuous around the protoplasm of the pollen grain and is constant in thickness throughout. In cleared, expanded grains, the cellulose can be seen protruding from the germ pores (Fig. 4 g). This inner intine layer undulates greatly in the mesocolpial areas (Fig. 3 c). At the germ pore, the outer, less electron-dense layer of the intine

thickens considerably (Fig. 4 e–f). Electronmicrographs of the intine show scattered electron-dense structures throughout the outer intine (Fig. 3 b–c). At the germ pore, remnants of the sexine and nexine as well as oils are often present over the intine.

Tests were made with IK_2I-H_2SO_4 (Bailey, 1960) to establish the presence of cellulose in the intermost intine layer. Figures 3 b–c show an electron-dense layer on the inside of the inner intine layer. Whether this is a separate third layer, a portion of the inner intine layer, or an artifact of staining or sectioning has not been ascertained (Skvarla, personal communication). It appears too thin to be the visible cellulose component of the intine.

Figure 3 b shows a circular depression in the protoplasm beneath the germ pore. Thin sections were stained with aniline blue (Johansen, 1940), a specific stain for callose, to determine if these depressions were callose plugs. The tests were negative and these depressions are interpreted as artifacts. They did not occur in all germ pore sections.

CYTOLOGY.—Although the present study is not cytological in scope, liquid preserved material revealed that all pollen grains at the shedding stage were uninucleate.

SPECIES DESCRIPTIONS

The following key incorporates the more stable characters of pollen grain and reticulation size. Other characters often show too much variation to be employed. In a few cases, groups of species are not separated further due to overlapping variation found in the samples analysed. *Fouquieria burragei* and *F. splendens* have relatively distinct forms with finer reticulation patterns that are separated from the more common forms.

    A.   Sexine about twice the thickness of the nexine; reticulations fewer than 5 per 10 linear μ in the mesocolpia ....*Idria columnaris*

  AA. Sexine about same thickness as nexine or thinner; reticulations mostly more than 5 per 10 linear μ in the mesocolpia ....B.

      B. Pollen grain size less than $40 \times 30 \mu$ when fully expanded ....*Fouquieria campanulata*
                                                                  F. fasciculata
                                                                   F. purpusii
                                                                   F. shrevei

     BB. Pollen grains more than $40 \times 30 \mu$ when fully expanded ....C.

    C. Pollen grain size averaging more than $55 \times 45 \mu$ when fully expanded ....*F. formosa*

  CC. Pollen grain size smaller than $55 \times 45 \mu$ when fully expanded ....D.

      D. Reticulations averaging more than 11 per 10 μ in mesocolpia ....*F. leonilae*
                                                    F. ochoterenae
                                                          fine reticulate forms of
                                                   F. burragei
                                                   F. splendens

DD. Reticulations averaging fewer than 10 per 10
    μ in mesocolpia ....E.
E. Muri mostly simplibaculate, thin; lumina angled ......*F. splendens*
                                                   F. ochoterenae
EE. Muri with conspicuous duplibaculate, thickened seg-
ments or completely duplibaculate; lumina rounded
or angled ....F.
    F. Muri mostly duplibaculate, thickish, seldom
       striate in mesocolpia; lumina rounded ....*F. diguetii*
    FF. Muri variable in width, simplibaculate or dupli-
       baculate, often striate in mesocolpia; lumina
       angled or rounded ....*F. burragei*
                                                 F. macdougalii

FOUQUIERIA BURRAGEI Rose
(Figs. 5 a–c, 6 a–d)

Average equatorial diameter 43 μ (37–47 μ); average polar diameter 35 μ (30–37 μ); polar/equatorial ratio 0.78–0.86; suboblate; tricolporate or variously modified (see text); germ pore ca 14 μ × 17 μ, squarish to rectangular. Exine 1.5 μ; sexine 0.8 μ; nexine 0.7 μ. Exine thickness variable, 1.2–2.0 μ. Sexine sculpturing very variable. Some collections striate, finely reticulate with heavy striae oriented toward poles, others randomly reticulate with the reticulation pattern larger, having subtle striae in mesocolpia and heavy or light striae along colpi. Occasionally becoming areolate-pilate along colpi margins and at the poles. Lumina variable, ca 12 (10–18) per 10 μ in striate grains, 6 (4–8) per 10 μ in mesocolpia of more reticulate grains; 7 (4–8) per 5 μ at poles in both types. Lumina heterobrochate, rounded or angular. Muri thickness constant in striate grains, equal in width to the lumina; very variable in width in more reticulate grains, often with parallel duplibaculate muri connected by thinner simplibaculate muri, also thickened in corners between lumina. Muri simplibaculate and duplibaculate. Intermural ornaments not observed. Aperture membranes psilate to slightly granulate.

COLLECTIONS STUDIED: *Carter 4720* (RSA); *Carter 4906* (RSA); *Chambers 788* (DS); *Henrickson and Christman 2172* (RSA), preserved; *Henrickson and Christman 2173* (RSA), preserved; *Lenz 9–64* (RSA), preserved; *Lindsay 1–19–64* (SD), preserved.

FOUQUIERIA CAMPANULATA G. V. Nash
(Figs. 4 e, 6 e)

Average equatorial diameter 35 μ (25–41 μ); average polar diameter 28 μ (23–34 μ); polar/equatorial ratio 0.79–0.84; suboblate; tricolporate, rarely 6-aperturate; germ pores ca 12 μ × 13 μ, rounded to squarish. Exine ca 1.2 μ; sexine 0.55 μ; nexine 0.65 μ. Sexine sculpturing with or without subtle striations in mesocolpia, non- to heavily striated along colpi and across poles. Lumina 10 (7–14) per 10 μ in mesocolpia, 6 (5–8) per 5 μ at poles. Lumina angular, homobrochate to slightly heterobrochate. Muri thin, mostly constant in width, infrequently forming slight striations; simplibaculate. Intermural ornaments absent. Aperture membranes psilate to slightly granulate.

COLLECTIONS STUDIED: *Hawksworth and Weins 324* (COLO); *Henrickson 1735* (RSA), preserved; *Henrickson and Christman 2079* (RSA), preserved; *Matuda 37376* (MEXU); *Palmer 84* (GH) TYPE; *Parratt* (RSA), preserved; *Wiggins 13216* (DS).
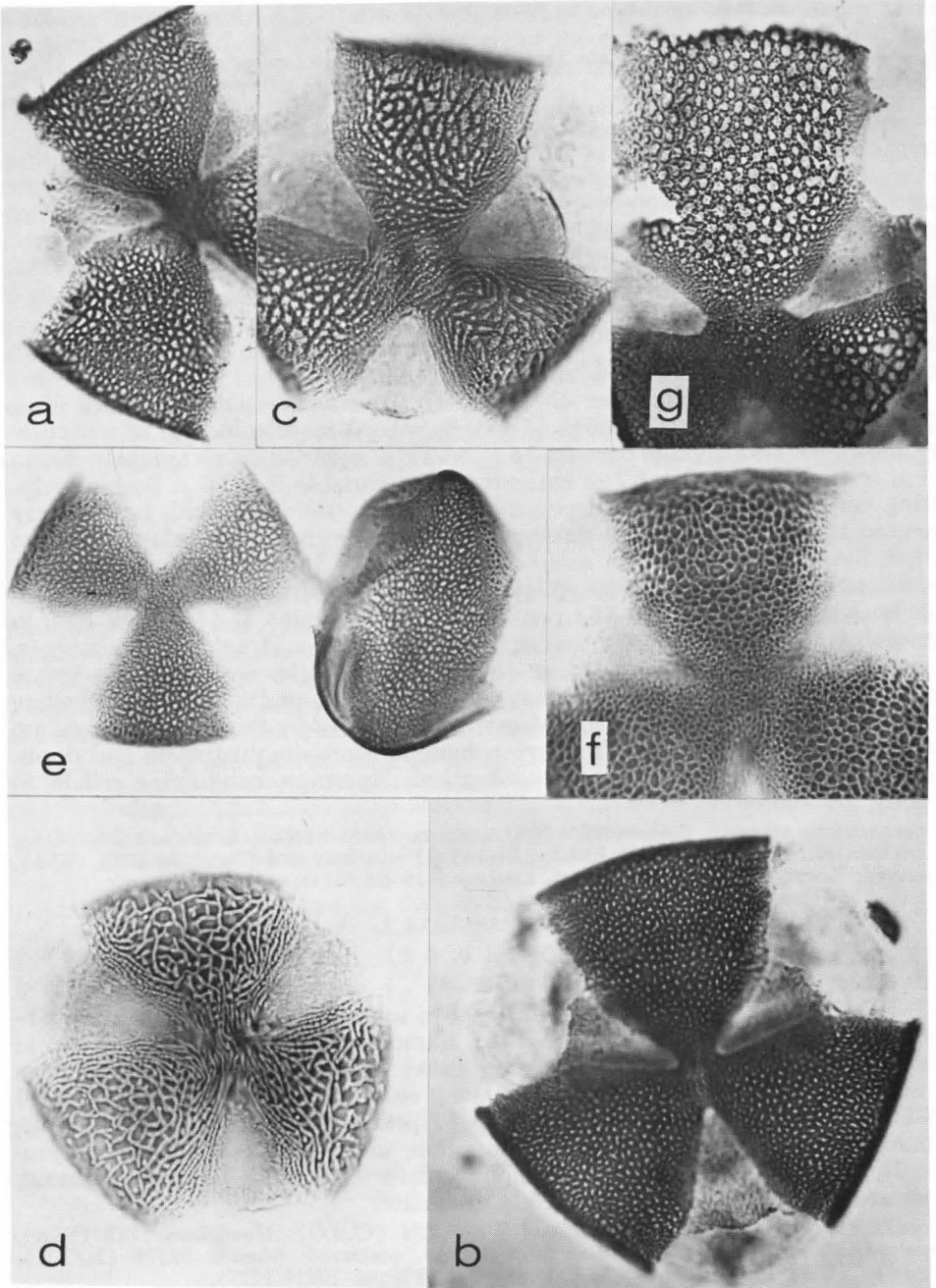
FOUQUIERIA DIGUETII (Van Tieghem) I. M. Johnston
(Figs. 4 a, 5 d, 6 f–g)

Average equatorial diameter 50 μ (42–57 μ); average polar diameter 40 μ (34–46 μ); polar/equatorial ratio 0.78–0.86; suboblate; tricolporate; infrequently 6-aperturate; germ pores ca 16 μ × 17 μ or less, squarish to rectangular; pollen grain size variable. Exine 1.6 μ; sexine 0.9 μ; nexine 0.7 μ. Sexine sculpturing mostly randomly reticulate in mesocolpia, non- or lightly striate and occasionally becoming areolate-pilate at colpi margins; finely reticulate, occasionally striate to areolate-pilate at poles. Lumina 6 (2–8) per 10 μ in mesocolpia, 7 (5–9) per 5 μ at poles. Lumina rounded, occasionally angled; strongly heterobrochate. Muri variable in thickness, occasionally scrobiculate when thick, mostly widened; duplibaculate and simplibaculate. Intermural ornaments usually present. Aperture membranes granulate. Oils prevalent.

COLLECTIONS STUDIED: *Carter 4789* (UC); *Henrickson 1569* (RSA), preserved; *Henrickson 2228* (RSA), preserved; *Rutherford 323* (RSA), preserved; *Rutherford 349* (RSA), preserved; *Rutherford 447* (RSA), preserved; *Thorne and Henrickson 32679* (RSA), preserved.

FOUQUIERIA FASCICULATA (Roemer & Schultes) G. V. Nash
(Fig. 7 a)

Average equatorial diameter 31 (26–35 μ); average polar diameter 25 μ (22–30 μ); polar/equatorial ratio 0.82–0.85; suboblate; tricolporate, rarely 6-aperturate; germ pore ca 11 μ × 12.5 μ, squarish to rectangular. Exine 1.3 μ; sexine 0.5 μ; nexine 0.8 μ. Sexine sculpturing randomly reticulate, with or without subtle striations, striate or not along apertures; polar sculpturing variable, reticulate to striate with muri forming ridges. Lumina 11 (9–14) per 10 μ in mesocolpia; 6–7 per 5 μ to undiscernable at poles. Lumina angled to rounded, heterobrochate. Muri thin, constant in width or thickening in areas between lumina; simplibaculate to rarely duplibaculate. Intermural ornaments absent. Aperture membranes psilate.

COLLECTIONS STUDIED: *Henrickson and Christman 2070* (RSA), preserved; *Matuda* (Matuda Herbarium).

FOUQUIERIA FORMOSA H. B. & K.
(Figs. 7 b–e)

Average equatorial diameter 61 μ (55–79 μ); average polar diameter 50 μ (39–70 μ); polar/equatorial ratio 0.71–0.82; subspheroidal-suboblate; tricolporate, rarely 6-aperturate; germ pores ca 20 μ × 20 μ, squarish to rounded. Exine 1.4 μ; sexine 0.5 μ; nexine 0.9 μ. Sexine sculpturing very variable. Basic pattern finely reticulate, with subtle swirling striations, lumina 13 (9–15) per 10 μ in the mesocolpia, and with striations along colpi curving inward to mesocolpia. The poles are randomly reticulate or striate. Other grains show tendency towards

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Fig. 6. Photographs of cleared grains.—a–d. *Fouquieria burragei.*—a–b. Figures show diversity present within one flower, both from *Lindsay 1–19–64.*—c–d. Striate grains from *Lenz 9–64* and *Carter 4720* respectively, showing striae across poles.—e. *Fouquieria campanulata.* Typical sculpturing pattern with subtle striations is shown *[Henrickson 1735].*—f–g. *Fouquieria diguetii.* Figure f shows strong heterobrochate sculpturing *[Rutherford 323].*—g. Shown are typical duplibaculate thickened muri, intermural ornaments, and slightly granular apertures *[Henrickson 1569].* All ×1,000.
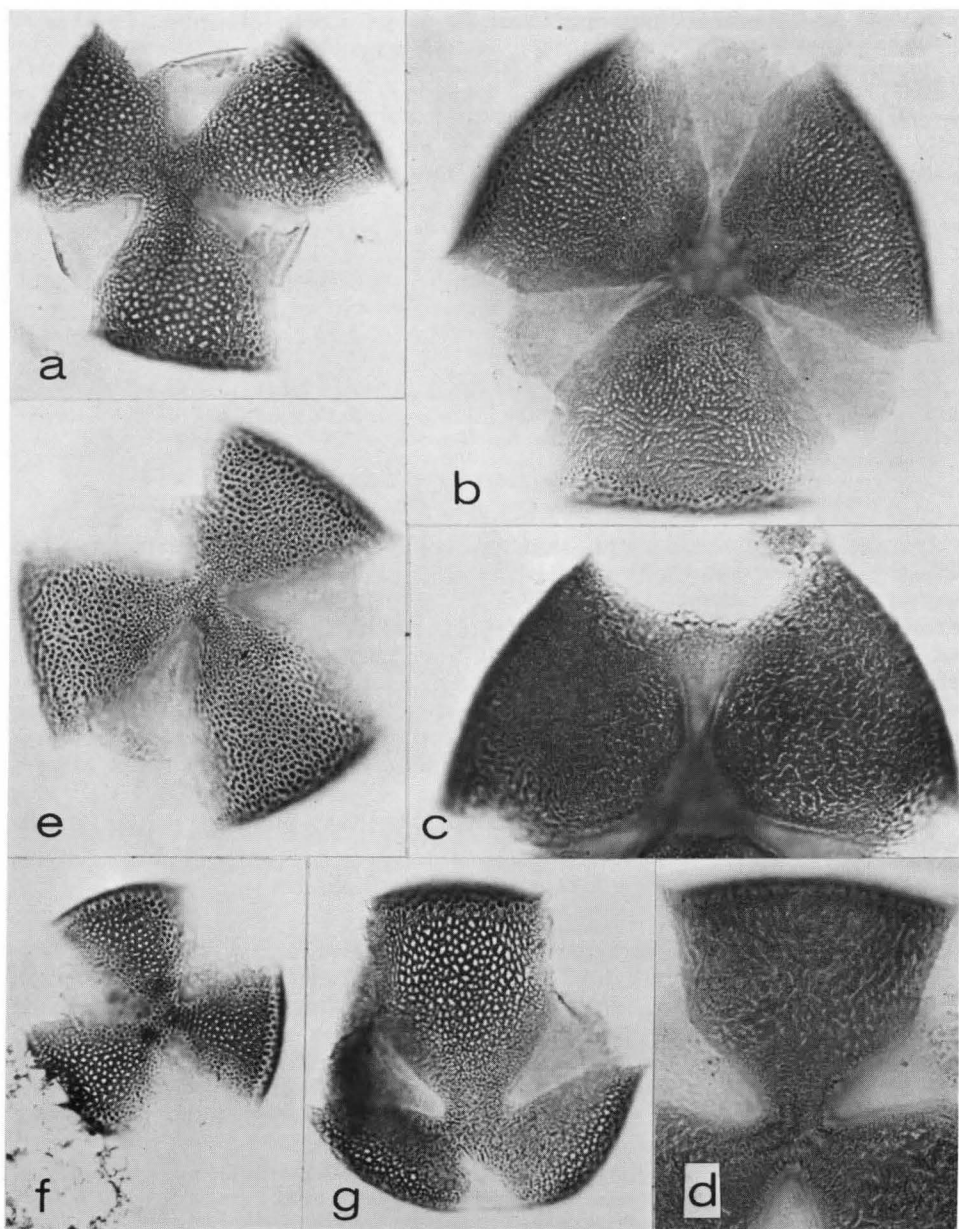
Fig. 7. Photographs of cleared pollen grains.—a. *Fouquieria fasciculata*. Shown is the typical reticulate pattern in Matuda collection.—b–d. *Fouquieria formosa*. The basic reticulate pattern as found in *Pringle 2420* is shown in b. A more derived condition with large multibaculate,

thickening of muri. Muri ultimately becoming greatly expanded to 3 μ wide and 7 μ long, multibaculate, scrobiculate. The wide muri are separated by narrow series of scrobiculi, ca 0.5 μ in diameter. Scrobiculate lumina 8 (5–12) per 10 μ in mesocolpia. Poles finely reticulate, with 6 (5–8) lumina per 5 μ, or with broad areoles separated by series of scrobiculi forming a reverse reticulation pattern, or pilate, or with muri forming fine ridges separated by series of fine lumina. Muri simplibaculate to multibaculate; lumina rounded, homobrochate to heterobrochate. Intermural ornaments absent. Aperture membranes granulate. The fine reticulate pattern forms ca 95 percent of the *Pringle 2420* collection but is represented in smaller percentages in all other pollen samples studied.

COLLECTIONS STUDIED: *Henrickson and Christman 2107* (RSA), preserved; *Henrickson and Christman 2122* (RSA), preserved; *Hinton 7070* (GH); *Matuda 19555* (GH); *Matuda 21928* (MEXU); *Moore et al 5707* (GH); *Pringle 2420* (RSA); *Wiggins 13289* (DS).

FOUQUIERIA LEONILAE F. Miranda
(Fig. 7 e)

Average equatorial diameter 46 μ (38–50 μ); average polar diameter 37 μ (30–43 μ); polar/equatorial ratio 0.78–0.83; suboblate; tricolporate; germ pore ca 12 μ $\times$ 14 μ, rectangular to squarish. Exine 1.15 μ; sexine 0.50 μ; nexine 0.65 μ. Sexine sculpturing randomly reticulate or with very subtle striations in mesocolpia; highly or lightly striate along colpi, striae parallel to colpi margin or curved inward; finely reticulate or rarely striate at poles. Lumina 10 (8–14) per 10 μ in mesocolpia; 7 (6–9) per 5 μ at poles. Lumina angled to rounded, strongly heterobrochate. Muri variable in thickness, grains with thin muri and large angled lumina or grains finely reticulate with muri of variable width. Muri simplibaculate to duplibaculate in widened areas. Intermural ornaments absent. Aperture membranes psilate.

COLLECTIONS STUDIED: *Henrickson and Christman 2164* (RSA), preserved; *Matuda* (Matuda Herbarium).

FOUQUIERIA MACDOUGALII G. V. Nash
(Figs. 4 b–c, 6 a–b, 8 a–b)

Average equatorial diameter 42 μ (35–45 μ); average polar diameter 34 μ (28–39 μ); polar/equatorial ratio 0.80–0.84; suboblate; tricolporate; germ pore ca 13 μ $\times$ 13 μ, squarish. Exine 1.7 μ; sexine 0.9 μ; nexine 0.8 μ. Sexine sculpturing reticulate with subtle or prominent striations paralleling colpi; polar reticulation fine to undiscernible, with light to prominent striations. Lumina 8 (6–10) per 10 μ in mesocolpia, 7.5 (6–9) per 5 μ at poles. Lumina rounded to angular, heterobrochate. Muri variable in thickness. When grains striate, sculpturing consisting of wide duplibaculate to multibaculate muri interconnected by thin simplibaculate to nonbaculate muri. Grains rarely very heavily striate with muri of uniform thickness and equal to width of lumina. Grains occasionally without striations. Intermural ornaments not present. Aperture membranes slightly granulate.

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scrobiculate muri separated by series of scrobiculae is illustrated in c *[Hinton 7070]*. The characteristic polar sculpturing is shown in d *[Hinton 7070]*.—e. *Fouquieria leonilae*. Matuda collection showing heterobrochate sculpturing and thickened muri.—f–g. *Fouquieria ochoterenae*. The finer reticulation in *Miranda 2537* is shown in f. Sculpturing as in the Matuda collection is shown in g. All $\times$1,000.
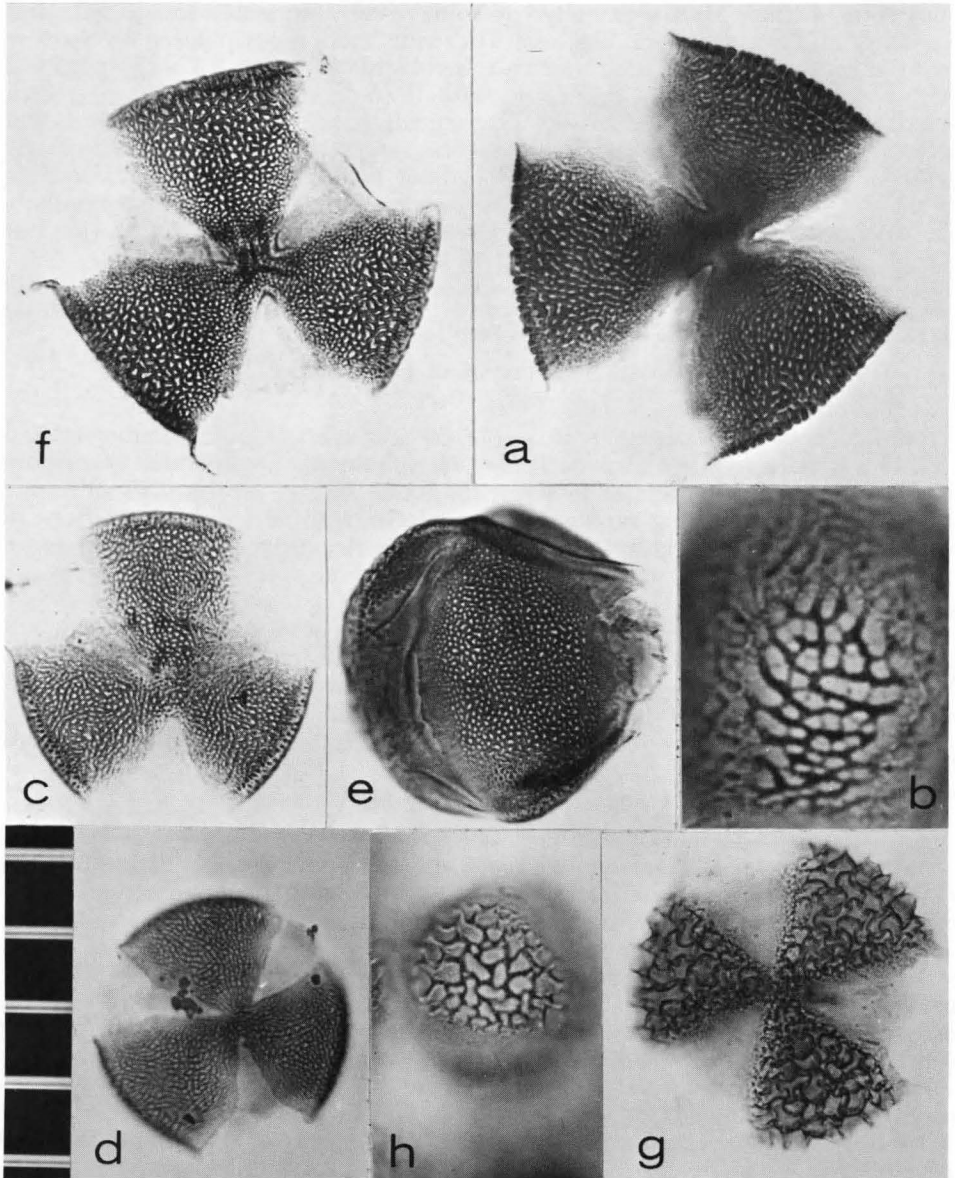
Fig. 8. Photographs of cleared grains.—a–b. *Fouquieria macdougalii.*—a. The characteristic unevenly thickened muri and striate pattern is shown.—b. This figure shows the simplibaculate to nonbaculate muri extending between broader simplibaculate to duplibaculate muri *[Henrickson 1650* and *Henrickson 2172* respectively].—c–d. *Fouquieria shrevei.* Shown are the subtle striate patterns and rather large polar reticulations *[Henrickson 1825* and *Johnston 7815*

COLLECTIONS STUDIED: *Henrickson 1560* (RSA), preserved; *Henrickson 1624* (RSA), preserved; *Henrickson 1630* (RSA), preserved; *Henrickson 1645* (RSA), preserved; *Henrickson 2172* (RSA); *Straw 2125* (RSA).

FOUQUIERIA OCHOTERENAE F. Miranda
(Figs. 7 f–g)

Average equatorial diameter 49 μ (42-51 μ); average polar diameter 39 μ (33–44 μ); polar/equatorial ratio 0.78–0.83; suboblate; tricolporate, rarely 6-aperturate; germ pore ca 15 μ ✕ 15 μ, squarish to oval. Exine 1.2 μ; sexine 0.6 μ; nexine 0.6 μ or less. Sexine sculpturing randomly reticulate or with subtle striations in mesocolpia; lightly to non-striated along colpi, striae curving inward, and sculpturing occasionally becoming areolate nearest colpi; finely reticulate to areolate-pilate at poles, occasionally muri form ridge-like patterns across poles. Lumina 9 (8–13) per 10 μ in mesocolpia; 6 (5–7) per 5 μ at poles. Lumina rounded to slightly angled, highly heterobrochate. Muri variable in width, simplibaculate to infrequently duplibaculate. Intermural ornaments absent. Aperture membranes psilate.

COLLECTIONS STUDIED: *Henrickson and Christman 2097* (RSA), preserved; *Henrickson and Christman 2118* (RSA), preserved; *Matuda* (Matuda Herbarium); *Miranda 2527* (GH).

FOUQUIERIA PURPUSII T. S. Brandegee
(Figs. 5 e–f)

Average equatorial diameter 34 μ (32–36 μ); average polar diameter 29 μ (25–31 μ); polar/equatorial ratio 0.82–0.85; suboblate; tricolporate; germ pore ca 9 μ ✕ 9 μ, squarish. Exine 1.2 μ; sexine 0.6 μ; nexine 0.6 μ. Sexine sculpturing with subtle striations in mesocolpia, with striate reticulations parallel to colpi, randomly reticulate to striate at poles. Lumina 13 (12–15) per 10 μ in mesocolpia, 7 (6–7) per 5 μ at poles. Lumina angular, slightly heterobrochate. Muri slightly variable in thickness, occasionally forming ladder-like striations; simplibaculate. Intermural ornaments absent. Aperture membranes psilate.

COLLECTIONS STUDIED: *Henrickson and Christman 2141* (RSA), preserved; *Henrickson and Christman 2153* (RSA), preserved.

FOUQUIERIA SHREVEI I. M. Johnston
(Figs. 8 c–d)

Average equatorial diameter 34 μ (32–39 μ); average polar diameter 26 μ (24–30 μ); polar/equatorial ratio 0.74–0.84; suboblate; tricolporate; germ pore ca 10 μ ✕ 13 μ, squarish to rectangular. Exine 1.3 μ; sexine 0.5 μ; nexine 0.8 μ. Sexine sculpturing reticulate with subtle striations or prominent striations with muri of unequal thickness; usually striate along colpi margins, striae parallel to colpi or curving towards center of mesocolpia. Poles with random or striate reticulations. Lumina 11 (9–14) per 10 μ at mesocolpia; 6 (5–8) per 5 μ at poles. Lumina angled, heterobrochate. Muri thin occasionally thickened, variable in more prominent striate pattern. Muri mostly simplibaculate; duplibaculate in association with striate patterns. Intermural ornaments absent. Aperture membranes slightly granular.

COLLECTIONS STUDIED: *Henrickson 1825* (RSA), preserved; *Johnston 7815* (GH) TYPE.

respectively].–e–f. *Fouquieria splendens.*–e. Finely reticulate form, *Roush 16.*–f. Typical simplibaculate form, *Jones 25650.*–g–h. *Idria columnaris.* The wavy crassitegillate muri, and the heterobrochate lumina are shown [*Rutherford 330* and *Henrickson 2173* respectively]. b, ✕2,000; all others ✕1,000. Scale: 1 unit = 10μ.

FOUQUIERIA SPLENDENS G. Engelmann
(Figs. 3 a–e, 4 f, 8 e–f)

Average equatorial diameter 39 μ (35–44 μ); average polar diameter 33 μ (30–35 μ); polar/equatorial ratio 0.82–0.87; suboblate; tricolporate; germ pores ca 0.14 μ $\times$ 14 μ, squarish. Exine 1.4 μ; sexine 0.6 μ; nexine 0.8 μ. Sexine sculpturing mostly randomly reticulate or with subtle striations in mesocolpia; frequently striate along colpi margins. Poles reticulate or subtly striate. Lumina 9 (6–11) per 10 μ in mesocolpia; 6 (5–8) per 5 μ at poles. Lumina angled, heterobrochate. Muri thin, of constant thickness, simplibaculate. Intermural ornaments absent. Aperture membranes rarely granular. *Jones 4–24–1884,* and *Roush 16* collections have finer reticulate pattern with 13 (9–16) lumina per 10 μ in mesocolpia (Fig. 8 e).

COLLECTIONS STUDIED: *Campbell 16157* (RSA); *Dunn 7924* (RSA); *Everett and Balls 21538* (RSA); *Harbison 41887* (RSA); *Henrickson 1830* (RSA), preserved; *Henrickson 2171* (RSA), preserved; *Hood 14-84K* (LA); *Jones 25650* (POM); *Jones 4-24-1884* (POM); *Parker 7245* (RSA); *Rutherford 20* (RSA), preserved; *Roush 16* (POM); *Wilson 1050* (RSA), preserved.

IDRIA COLUMNARIS Kellogg
(Figs. 4 d, 8 g–h)

Average equatorial diameter 32 μ (29–39 μ); average polar diameter 29 μ (26–34 μ); polar/equatorial ratio 0.78–0.88; suboblate; tricolporate, rarely 6-aperturate; germ pores ca 11 μ $\times$ 11 μ, squarish. Exine 2.7 μ; sexine 1.85 μ; nexine 0.85 μ. Sexine sculpturing randomly foveolate; foveolae large, reticulation size diminishing towards poles and aperture margins, becoming areolate in some. Lumina 3.5 (3–5) per 10 μ in mesocolpia, 4 (2–6) per 5 μ at poles. Lumina rounded, strongly heterobrochate. Muri with extended ectosexine, twice height of endosexine, tapering distally or not, wavy as seen in surface view, duplibaculate or infrequently simplibaculate; when wide at base, muri may enclose conical cavities. Intermural ornaments present in certain collections. Aperture membranes slightly granular.

COLLECTIONS STUDIED: *Benson 10385* (POM); *Henrickson 1273* (RSA), preserved; *Henrickson 2338* (RSA), preserved; *Henrickson 2346* (RSA), preserved; *Moron 11890* (SD), preserved; *Rutherford 330* (RSA), preserved.

DISCUSSION

HARMOMEGATHY.—The significance of the structural differences of the nexine 1 and nexine 2 layers becomes evident when considering their roles in harmomegathic changes of the pollen grains. The nexine 1 layer, continuous with the sexine, consists of the more electron-dense, homogeneous sporopollenine. This layer appears to be more rigid structurally than the less electron-dense, non-homogeneous sporopollenine of the nexine 2 layer constituting the aperture membrane. The relative flexibility of the aperture membranes provides a means for volume reduction caused by desiccation. The grains are suboblate in shape when moist as in the anthers before dehiscence. Upon drying, they become more perprolate (Fig. 5 d) as their volume is reduced. The less rigid nexine 2 layer of the aperture membrane folds inward and forms grooves (the grains becoming fossaperturate). This virtually seals off the germ pores, while the more rigid mesocolpial exine gradually becomes perprolate. The variable rigidity of the mesocolpial exine resulting from the increased thickness of the nexine layer

towards the poles and the shape of the apertures account for the characteristic perprolate shape. The suboblate shape is regained prior to germination. As thus interpreted, the layered structure of the nexine proves to be of considerable adaptive value with regards to pollen grain harmomegathy.

TAXONOMIC CONCLUSIONS.—Dissimilarities in pollen structure support segregation of *Idria* from *Fouquieria*. Pollen grains of the two genera are basically similar in form and structure but they differ in mode of sexine construction. *Fouquieria* has ectosexine and endosexine of nearly the same thickness, but *Idria* has a much thicker ectosexine (Fig. 2 b). *Idria* shares many other characteristics, such as foveolate lumina and intermural ornaments, with one or more species of *Fouquieria*. The basic construction of the exine, the shape of the pollen grains, and the shape and morphology of the apertures are virtually identical in the two genera.

In 1911, Loesner described a species of *Fouquieria* from Sinaloa, Mexico, *Fouquieria jaboncillo*. Palynologically and morphologically this proves to be a minor ecological variant of *F. macdougalii* probably not warranting taxonomic distinction. The pollen grains of Loesener's taxon show striate patterns similar to those of *F. macdougalii*.

Interspecific relationships as ascertained by analysis of gross morphological characters are not always reflected in the pollen morphology. Reticulation pattern more often reflects relationships to size or sexine thickness of the pollen grains rather than to phylogenetic relationships. The pollen does, however, aid in distinguishing *F. diguetii* from *F. macdougalii* and *F. splendens* when other morphological criteria fail as in fragmentary herbarium specimens.

RANGE OF VARIATION.—Exine sculpturing within a species of the Fouquieriaceae is quite variable. Variation occurs not only between collections of a species but also within a pollen sample. The occurrence of striations results in instable sexine patterns. The least constant characters involve reticulation size, width of muri, and degree of striation dominance. A particular pattern may occur in only a few grains of one collection whereas it may occur on many grains in other collections of a species. The sexine sculpturing was most variable in *F. formosa* and *F. burragei* where collections strongly varied in exine patterning (see species descriptions). Because of this variation, care was taken in preparing the descriptions especially when only a few samples had been analyzed for a species.

Analysis of numerous populations has shown that inconstancy of sculpturing pattern is characteristic of most species of the Fouquieriaceae. This suggests that limited sampling would yield incomplete and inaccurate results which further study might prove worthless. One naturally wonders whether species of the Fouquieriaceae are unusually variable or whether too few samples are typically studied in species of angiosperms at large. One suspects that too often, species descriptions encompass only a portion of the variability present.

The more stable characteristics available for distinguishing species include the size of pollen grains and in most cases with basic simplibaculate–duplibaculate characteristics of the muri. Size of pollen grains parallels flower size remarkably and both range greatly within the family. The basic muri patterns do appear uniform in closely related species, e. g. *F. splendens* and *F. campanulata*.

BASIC PLAN, RELATIONSHIPS.—Pollen grains of the Fouquieriaceae are basically tricolporate, suboblate and reticulate—a combination of characters common to many dicotyledonous families. Distinctive features of the grains include: (1), greater nexine thickening towards the poles; (2), diminishing reticulations at the poles and along the colpi margins; (3), variable reticulation patterns; (4), absence of thickening of nexine around apertures, and (5), no evidence of oroid germ pore structure. Because these particular features occur either singly or together in many families of dicotyledons, they cannot always be used as indicators of relationship. On the basis of gross morphological comparisons, the Fouquieriaceae has been treated by various phylogenists in three major groups, the Tamaricales, Ebenales, and Polemoniales. With regard to pollen morphology, each of these groups has similarities to the Fouquieriaceae. The Tamaricaceae have tricolpate pollen; the apertures lack germ pores but rupture lengthwise during germination. The pollen grains are reticulate and there is no change in reticulation size at the poles. Erdtman (1963) states that the Fouquieriaceae constitutes an aberrant element with the Tamaricales and is probably better placed in another order. The Ebenales is characterized by tricolporate pollen; the germ pore structure is oroid and frequently the nexine is thicker along the colpi. The latter feature is foreign to the Fouquieriaceae, but not universal within the Ebenales. The Polemoniaceae, regarded as more closely related to the Fouquieriaceae than the Convolvulaceae or Solanaceae, has quite different apertures (porate or forate). The Convolvulaceae is eurypalynous, with 3–4 colpate, rugate, rupate or polyforate pollen (Erdtman, 1952). Some colpate grains greatly resemble those of the Fouquieriaceae in their sculpturing. For example, *Porana ricasoliana* has a reticulate, tegillate sculpturing which diminishes in size along the apertures and at the poles (Fig. 4 h). However, other species of *Porana* have pilate sculpturing. These similarities are best interpreted as parallelisms. The Solanaceae has various pollen types, 3–5 colpate, 3–5 colporate, colporoidate to nonaperturate. Layered intines were observed in the pollen grains from each of the orders mentioned above.

Saad (1961) noted in the genus *Linum*, that there are tricolpate, pantocolpate and pantoporate pollen grains whereas colporate grains were found in other genera of the family. The diversity of apertural types within the Linaceae is similar to that between the Fouquieriaceae and the Polemoniales. In a tentative outline of trends of phylogenetic development of exine stratification, Saad (1961b) illustrates how the sexine sculpturing of a primitive polemoniaceous genus (*Cobaea*) can be derived from a type similar to that of the Fouquieriaceae.

In considering possible relationships, questions arise concerning the origin of the germ pore. Since there is no evidence of oroid structure at the germ pore in the Fouquieriaceae, can one say that their pollens were derived from colpate types as in the Convolvulaceae? Or did ancestors of the Fouquieriaceae have rather different pollen grains? Pollen of families supposedly not related to the Fouquieriaceae show some marked similarities (e.g. Crossosomataceae, Hydrophyllaceae, etc.). Differentiation with respect to pollen morphology may have been exceptional in the group of families to which the Fouquieriaceae is related. Therefore, we may expect that information from fields other than palynology will be more decisive in delimiting the precise relationships of the Fouquieriaceae.

SUMMARY

The pollen morphology of 66 collections representing 11 species of the Fouquieriaceae was critically analyzed in an effort to establish the inter- and infraspecific variation in size and sexine sculpturing and the structural morphology of the exine and intine. The average polar diameter of the various species ranges from 25 to 50 μ. This size variation correlates directly with flower size. The pollen is tricolporate, without evidence of oroid thickenings near the squarish germ pores. Sexine sculpturing is reticulate, and the reticulations diminish in size along the aperture margins and the poles there they may become pilate to areolate. Striations are frequent along the colpi margins, less so in the mesocolpial areas. The striations account for the wide variation in sculpturing characteristic of the family. The sexine is tegillate, mostly simplibaculate to duplibaculate. The lumina are angled to rounded, hetero- to homobrochate. In *Fouquieria* the bacula and tegillum are of similar thickness, whereas in *Idria* sexine is crassitegillate. As observed electronmicroscopically, the nexine is two-layered. The inner less electron-dense layer is thin in the mesocolpial area and thickens along the aperture margins to constitute the aperture membranes exclusively. The outer nexine layer, which has the same electron density as the sexine, thickens towards the poles and thins at the aperture membranes. The structural differences and localization of the nexine layers account for the change in shape accompanying harmomegathy. The intine is also two-layered. The inner layer is constant in thickness and contains cellulose. The outer layer thickens at the germ pores. Comparisons were made of the pollen of the Fouquieriaceae with that of possibly related orders—the Tamaricales, Ebenales and Polemoniales. These comparisons favor relationships with the Polemoniales although not conclusively.

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