THE DEVELOPMENT OF THE EMBRYO SAC IN THE FOUQUIERIACEAE

by

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ABSTRACT

Flowers of Fouquieria splendens Englem., Fouquieria macdougalii Nash, and Idria columnaris Kell. were collected and slides were made of the ovary for a study of the anatomy of the ovule and embryo sac.

Of the three species Fouquieria splendens were studied most intensively. The embryo sac was found to develop by the monosporic scheme, in which a tetrad of four megaspores is formed. Three of the megaspores disintegrate and one gives rise to the embryo sac, which has a "normal" development resulting in eight nuclei. The three antipodal cells soon separate from the remainder of the megagametophyte and disintegrate. The synergids also appear to disintegrate as the embryo sac matures. One of the important and interesting characteristics of the mature embryo sac of Fouquieria splendens was the presence of a haustorium.

The available material of Fouquieria macdougalii and Idria columnaris was examined. Comparison revealed that the three species were similar in most respects. Unfortunately the material of Idria was not sufficiently mature to determine whether a haustorium is also one of its characteristics.

INTRODUCTION

This paper deals with the embryo sac development and the anatomy of the ovule of three species in the family, Fouquieriaceae. The study was undertaken because of the disagreement in the literature about the embryo sac development of Fouquieria splendens.

Although Gray Herbarium Card Index lists thirteen species in the family, the number has been revised by many people. Nash (1903), in his revision, has listed two genera, Fouquieria (comprised of six species) and Idria (consisting of only one species). Humphrey (1935) states Fouquieria is composed of eight species and Idria contains only one, whereas Benson (1957) lists only the genus Fouquieria, consisting of three or eight species. Shreve and Wiggins (1964) lists two genera, Idria and Fouquieria.. In the region that they covered, they found four species of Fouquieria, as well as Idria columnaris. The taxonomy of the family is confused. However, all three species that this paper discusses are listed as separate species in all major sources.

The first of the three species to be discussed is Fouquieria splendens Englem. described in Wislizenus' account of his Memoir of a Tour to Northern Mexico, in 1848. It is the common ocotillo in

the Tucson area, and is known by a variety of names, including candlewood, coachwhip, vine-cactus and Jacob's staff. The plant has a variety of uses, including building material for huts, fences, and walking sticks. The flowers and seed pods have been eaten, and a sweet beverage has been extracted. It has even been used as a source of a cough medicine called "coahila" (O'Gorman, 1961). Fouquieria splendens is probably the best known of the three species because of its wide distribution and being the only species native to the United States. Humphrey (1935) states that it grows

> in the United States in southern California, extreme southern Nevada, the southern halves of Arizona and New Mexico, and the southwestern corner of Texas. On the mainland of Mexico its range is imperfectly known, but it is found as far south as the 26th parallel. In Lower California it occures at least as far south as a point just north of the 28th parallel.

This circumscription is in concurrence with the recent publication of Shreve and Wiggins (1964), except for a region in the northwestern corner of Arizona, where Fouquieria splendens is also found.

The second species examined is Fouquieria macdougalii Nash, described in the Bulletin of the Torrey Botanical Club (1903). It also has acquired a variety of names, including "palo verde", chunari, jaboncillo, torote verde, and torotillo, and is found between the 27th and the 30th parallel in the "Lower Sonoran Zone from the vicinity of Carbó, Sonora, southward into Sinaloa" (Shreve and

Wiggins, 1964). It was mentioned by O'Gorman (1961) that the bark of this species is a good substitute for soap.

Idria columnaris, Kell. is described in Hesperian in 1860 (Shreve and Wiggins, 1964). It is commonly known as "cirio", or the "boojum tree" and as an exotic plant which is often cultivated in botanical gardens. Idria, a monotypic genus, is native to an area just above the 27th parallel to the 30th parallel in Lower California, and is also found on the coast of Sonora just below Libertad (Shreve and Wiggins, 1964).

Excellent maps of the distribution of all three species can be found in the publication of Shreve and Wiggins (1964).

LITERATURE REVIEW

Shreve and Wiggins (1964) have the most recent and best description available of the Fouquieriaceae used in this investigation. The following comparison has been taken from the information presented in their descriptions.

The morphology of Idria columnaris is so distinctive it could not possibly be confused with the two other species, Fouquieria splendens or Fouquieria macdougalii. Idria, as can be seen in Figure 1, has the appearance of an upside-down carrot, with several short, lateral branches. It is the tallest of the three species in discussion — about 20 meters tall at maturity. Its flowers are not only much smaller than the other two species, but its panicle inflorescence at the end of the peduncle has many subsessile flowers grouped together. The panicles are from 2 to 6 decimeters long. One panicle does not have all the various stages of development, thereby differing from the other two species.

Fouquieria macdougalii is a tree, 8 meters tall at maturity, which, unlike Idria, has a short trunk 3 decimeters thick and about a meter tall, as indicated in Figure 2. It has many compound branches, giving it a bushy appearance. The inflorescence is a corymbose panicle about 1.0 to 1.5 decimeters in length. Unlike

Idria, the flowers are born singly on long slender pedicels, 5 to 30 millimeters long. They are not as compact as Idria, and are bright red in color. This species has the longest corolla of the three species. It ranges from 2.0 to 2.5 centimeters in length. It is possible to find on one panicle a range of development of the embryo sac from the megaspore mother cell to the complete embryo sac.

Fouquieria splendens is a shrub about 6 meters high at maturity. It is readily distinguishable because it has "several simple branches arising from a woody crown, but without a common aerial trunk" (Shreve and Wiggins, 1964). This can be seen in Figures 3 and 4. Its bright red flowers are somewhat crowded on racemes, which are 5 to 25 centimeters long. The length of the corolla — about 1.5 to 2 centimeters — is intermediate in relationship to the other two species previously discussed. Here it is possible to find a complete range of embryo sac development on one panicle.

Each of the species occurs on a characteristic physiographic area. Fouquieria splendens is found on the bajada, where the soil is primarily gravelly. Marks (1950) describes a bajada as a region with the following characteristics:

1. a balance between erosion and deposition
2. composed of transported or residual materials
3. texturally the soils are gravelly

4. cementation of the subsoil is almost universal.

He also states that from his investigations of Fouquieria splendens, he found the plant did not grow on a soil with a particular pH, but the soil held an "average of 5.3 inches of water in the first four feet." Idria grows in an area where granite rock out-crops (Humphrey, 1935), whereas Fouquieria macdougalii grows on the "desert flats and gentle slopes" (Shreve and Wiggins, 1964).

F. W. Went (1949) states that germination of Fouquieria splendens occurred only in August and September, further that he found it only occurring "in the immediate vicinity of old shrubs". Fouquieria splendens flowers throughout the year following rains, if the temperature is favorable. In the Tucson vicinity, one is most likely to find the most abundant flowering during May after the winter rains. This is in agreement with Darrow's findings (1943) on the floral development of Fouquieria splendens. He found that ocotillo produced flowers whenever storm periods were widely separated. He also noted that the plants did not lose their foliage until soil moisture was not available. Darrow measured both the vegetative and floral growth of Fouquieria splendens and correlated them. He found that branch production and length of the branch were greatly affected by the amount of precipitation available. After the branch grows to about 10 to 15 feet, it ceases growth. He estimated the mature age at 150 to 200 years. These ages were determined from statistical

analyses of his data. Although Darrow states that growth rings were impossible to see, Scott (1932) said they were obvious. Darrow (1943) found that the older branches produced both axillary and terminal inflorescences. He found that the development of the flowers was less affected by the climate than the development of the vegetative parts.

Scott (1932) published an article in which she described the vegetative anatomy of Fouquieria splendens. From her investigations she concluded that the reticulate pattern of the cork on the stem is caused by the alternation of regions consisting only of fibrous cork cells and non-fibrous cork cells, both containing much suberin. Since she found the underlying tissue acting as a "reserve for water, oils and sugar", she concluded that these cells were at least partially responsible for the ability to develop leaves and foliage rapidly.

Humphrey (1935), in his detailed account of the stem anatomy of Idria, states that Fouquieria splendens has a stem anatomy which resembles the branch of Idria. He also states that both contain water storage cells which appear alike, and have a similar leaf anatomy. His final conclusion is that the trunks are homologous, but the forks of Idria may correspond to the branches of Fouquieria splendens, and

that the branches of Idria may be homologous to the "undeveloped shoots in the thorn axils of Fouquieria splendens." In 1931, Humphrey published a detailed account of the thorn formation in Fouquieria splendens. In this paper he is at variance with Scott (1932), and states that the thorns are "an outgrowth of the cortex and epidermis" (Humphrey, 1931), rather than derived from the petiole, as is frequently assumed.

Although three articles have been published which are concerned with the embryo sac development of members of the Fouquieriaceae, none of these deal with the species Fouquieria macdougalii or Idria columnaris.

Johansen (1936) and Mauritzon (1936) both published articles about the development of the embryo sac of the Fouquieriaceae. Apparently neither was aware of the fact that the other was working on the same problem. There is much disagreement between their conclusions concerning the embryo sac development of Fouquieria splendens. Johansen expanded his investigation to include Fouquieria peninsularis Nash and Fouquieria burragei Rose, whereas Mauritzon limited his investigations to Fouquieria splendens.

Johansen (1936) described the ovary as one-celled, containing "three parietal septiform placentas, which occasionally so fill

the cavity as to make it seem triloculate". He also states that the ovules were antropous and varied in number from two to five. He found no evidence of a vascular supply in the funiculus. Two integuments eventually surrounded the embryo sac, but the inner integument, which developed first, was swollen at the micropyle end and was never completely surrounded by the outer integumant. Khan (1943) states that Johansen's description of the integuments is accurate, but that later in Johansen's paper, when he wrote about the massive nucellus, he had confused the large inner integument for the nucellus. Johansen did not offer an explanation of the origin of the wings on the seed, but merely states that they developed from the epidermis of the seed coat and pushed over the inner and outer integuments. The description of the origin of the wings is rather ambiguous in both articles.

Although Johansen believed that the tapetum formed the so-called "epistase" - referring to thick-walled, heavily-stained cells surrounding the narrow micropyle - Khan (1943) states that Johansen had again mistaken the inner integument for part of the nucellus; the "opistase" was actually a part of the inner integument.

Both the nucellus and the megagmetophyte develop rapidly. The megaspore mother cell is formed from the hypodermal archesporium,

while the one- to two-layered nucellus is developing (Johansen, 1936). From this point on, the authors do not agree. According to Mauritzon, the result from the divisions of the megaspore mother cell is a triad. The two nuclei near the microphyle are contained in one cell; the nucleus just under these two forms a second cell. Eventually, these three nuclei disintegrate, leaving only the third cell containing the megaspore nucleus, which gives rise to the embryo sac. Johansen found no evidence of a tetrad or triad; thus, he concluded that the development is tetrasporic. Khan's (1943) explanation is that Johansen had mistaken the two-nucleate stage of miotic division for the first division of meiosis. Khan's reasoning is that the large vacoule present in Johansen's illustration is evidence that it cannot possibly be the two-nucleated stage. He quotes Mahashewari (1941); "The two- and four-nucleate stages of a monosporic embryo sac always show a large central vacuole, while this is hardly ever the case in the tetrasporic embryo sacs, where such a large vacuole is seen only after the four-nucleate stage is over."

Johansen goes on to describe embryo sac development in the three species he examined. He states that he found only one embryo sac with eight nuclei. Many contained only six. From these containing six, he found the following two cases. In the first case, the embryo sac contained two synergids, two antipodals, and two polar

nuclei; the second type consisted of two synergids, two antipodals, one polar nucleus, and one egg. He explained this strange phenomenon as the failure of all nuclei to divide at the four-cell stage. He states that he never found one of the antipodals acting as a polar nucleus.

Mauritzon mentions only eight-nucleate embryo sacs. His drawing shows a seven-nucleate sac in which the two polar nuclei have fused.

According to Johansen's investigations, Fouquieria burragei and Fouquieria peninsularis presented a totally different type of dvelopment after the four-nucleate stage. In these two plants he found the two synergids were formed from a division of one of the nuclei at the micropyle end. The remaining three nuclei did not divide, but rather two were destined to act as polar nuclei while the other nucleus near the micropyle became an egg. He concluded this because: 1) he saw no evidence of antipodals; 2) the endospera appeared triplcid. He describes the synergids in the young mature embryo sac as having an irregular organization with no defined vacuoles, no indentations, and no filiform apparatus.

Johansen (1936) and Mauritzon (1936) describe the development of a similar haustorial projection in the later stages of the embryo

sac. Johansen found this feature in the three species he investigated. He states that in all but one case the polar nucleus, which was usually binucleolate, was never found far into the haustorial arm; it was usually found near, but not in, the arm. As the haustorium grows, it destroys the cells in its path until it has reached the "epidermal cells of the nucellus" (Johansen, 1936). He explains the haustorium as having an essential nutritive function since he found no evidence of a vascular supply in the raphe. Khan (1943) reports the presence of the haustorium, but he feels Johansen has mistaken the nucellus for the inner integument, thus it destroys the inner integument - not the nucellus. Although Khan does not discuss the possible function of the haustorium, he does describe the presence of a vascular supply in the raphe of Fouquieria splendens.

Johansen observed that fertilization is porogamous. As the pollen tube grows down an extremely narrow channel between the elongated cells of the inner integument, the surrounding material disintegrates. He states that the egg cell is so small at times that it equals the size of the polar nucleus. By the time fertilization has occurred, the synergids have disintegrated and the fused polar nuclei have moved to a position just adjacent to the egg, which has migrated toward the micropyle. The zygote rests while the endosperm grows. Eventually, the former is pushed into the space between the lips of

the inner integument. After the large, thin-walled endosperm cells have nearly completed development, the zygote begins growth. As the endosperm develops, it absorbs the contents of the cells surrounding the embryo sac, and it progressively pushes the zygote further towards the obalazal end of the sac. Finally the zygote is completely surrounded by the endosperm.

Figure 1

Figure 2

Figure 3

Figure 4

METHODS AND MATERIALS

Location

Only plants of Fouquieria splendens, Fouquieria macdougalii, and Idria columnaris were available in Tucson during a two-year period. Fouquieria splendens is the only species native to the Tucson area. The flowers were collected from various localities within a fifty-mile radius of Tucson. Collection sites included Bear Canyon, the city of Tucson, and Benson, Arizona. It was found in flower between April and November. The flowers of Idria columnaris were collected on a number of dates during June and July from the University of Arizona cactus garden. The flowers of Fouquieria macdougalii were collected at the Arizona-Sonora Desert Museum during November, 1964.

Collection

The greatest collection problem is to obtain material with the megaspore mother cell in stages of meiosis and the embryo sac showing mitotic figures. The best technique for the "Fouquierias" was dividing a young inflorescence into equal parts from older to younger buds, labeling and separating the segments. Idria required a different technique. Because it has an inflorescence which does not have a wide range of stages, it was best to collect on consecutive days.

Killing and Fixing

It was essential to strip from the buds the non-essential floral parts, stamens, and the basal part of the peduncle. Next, the stigma was trimmed, thus leaving only the ovary and a portion of the receptacle. This is a tedious and difficult task because of the small flowers. Dissecting the flowers enabled the killing-fixing solution and the embedding solutions to penetrate rapidly and thoroughly.

Three killing-fixing solutions were employed. Carnoy's and Navashin's were not satisfactory, because they made the material tough and brittle, thus interferring with sectioning. Formalin-aceto-alcohol proved best, but it was necessary to submerge the material immediately to reduce plasmolysis.

It was found desirable to leave the material in the killing-fixing solutions for at least five days to insure good penetration of the cells. The ovaries were then run through the tertiary-butyl-alcohol series (Johansen, 1940).

Sectioning

In sectioning, the most difficult problem is obtaining medial sections of the embryo sac. The funiculi are twisted, thus

the ovules are oriented in the ovary at random. For this reason, much of the interpretation had to be a reconstruction of the sections. For best results, the ovary was aligned longitudinally to the blade.

Although the "Fouquierias" were relatively easy to section, Idria presented many problems. The flowers are smaller and difficult to manipulate unless some portion of the stem is attached. The stem is hard - so much so that it is nearly impossible to obtain good sections, especially in older material. Not only is the stem hard, but the buds also contain thick suberized cell walls. This presents staining problems which will be discussed later. Cooling the microtome blade and tilting it at a greater angle - about 45 degrees - than customary assisted in overcoming the difficulties mentioned previously.

Although an 8 to 12 micron range was attempted, the best results were obtained from sections cut at 10 microns.

Mounting

Haupt's adhesive was used (Johansen, 1940). A few drops of 4% formalin solution containing safranin stain was applied on top of the adhesive. Then the ribbons were flattened on a hot plate. The formalin dries quickly and a few drops of safranin stain were very advantageous because this enabled one to determine which slides were

useful. The safranin stain did not interfere with later staining. It was found best to drain the excess formalin from the slide and not return the slide to the hot plate, but leave it exposed to the light so that a photochemical reaction between the gelatin and the formalin could take place.

Staining

Three staining techniques were tried. These were safranin-fast green-orange G., and two variations of Heidenhain's Iron Hamatoxylin. Safranin-fast green-orange G. was used only on Fouquieria splendens and Idria columnaris, but proved so unsatisfactory that it was not attempted on Fouquieria macdougalii. The material absorbed safranin, thereby making the embryo sac invisible.

A shorter variation of Heidenhain's Iron Hematoxylin staining procedure was also discarded in favor of Heidenhain's Iron Hematoxylin (Johansen, 1940). It was found most satisfactory to use the minimum time periods, except when rinsing in water - in which case several careful rinses were essential to avoid contamination of the stain. For best results, the sections were de-stained until a light-brown coloration was apparent. This took at least twenty minutes. The slides in the coplin jars were submerged in a pan of cold running water for at least one hour. Following this, the slides were trans-

ferred through the alcohol-xylol series. They remained in the first xylol solution for five minutes. Then, they were placed in a coplin jar containing the final solution of pure xylol and remained there for five more minutes before mounting.

OBSERVATIONS

Integuments

The embryo sac and nucellus are enclosed by an inner as well as an outer integument. The inner integument, which develops first, is swollen, particularly at the micropyle end, and extends beyond the outer integument. As it grows, the elongated swollen end, which has the appearance of two lips in a medial longitudinal section, meets, leaving only a very narrow micropyle. By the time the complete embryo sac is formed, the swollen end of the inner integument has grown so that it is pushing against the placenta.

Another important characteristic of the anatomy of the three ovules, shown in Figures 10, 11 and 12, is the elongated cells originating from the inner integument and arising around the embryo sac and alongside the micropyle. It might also be noted in Figure 11 that only Fouquieria macdougalii contains very heavily stained block-like cells around the embryo sac.

Megagametophyte

Figure 5 is a camera lucida drawing from a demial section of an ovule in the megaspore mother cell stage. It clearly shows the two integuments and the megaspore mother cell. At this stage, the

nucellus is a prominent structure, composed of one or two cell layers which are in conjunction with the embryo sac. The megaspore mother cell is ovoid - measuring 0.02 mm in width - with a distinct spherical nucleus which fills about one-fourth of the cell. The chromosomes are obvious and black, but are very small and difficult to count. Various stages of prophase were present, but none of the other stages of moiosis were found. The cytoplasm is dense and contains no distinct vacoules. At this stage the ovary measured 9 mm in length; the particular ovule in Figure 5 was 1.5 mm long, whereas a cross-section of another ovule containing another megaspore mother cell measured 1.1 mm across, thus indicating that the ovules were nearly spherical at this time.

It is believed that the tetrad stage of all three species has been found. Unfortunately, it is not possible to distinguish the nuclei of Fouquieria macdougalii or Idria columnaris. Figure 6 clearly indicates the linear tetrad of Fouquieria splendens, each cell containing one nucleus. The three cells near the micropyle are obviously separate and disintegrating, and the fourth large megaspore nucleus is surrounded by cytoplasm in which two distinct vacucles have appeared. The material shows a prominent nucellus which shows no signs of disintegration. The elongated cells of the inner integument have formed, and the elongated portion of the same integument has closed, thus forming the extremely narrow micropyle. At this stage of development, the longitudinal section of the ovary is 10 mm. The ovule is

2.5 mm long by 2.0 wide. The megaspore nucleus is approximately 12.5 microns in diameter.

The two-nucleate sac was the next stage observed. The three megaspores at the micropyle end have disintegrated as illustrated in Figure 7, the remaining megaspore nucleus has divided to form two distinct nuclei. In the material, vacucles are difficult to determine because of an underlying layer of cells; however, from all appearances there seems to be one large vacuole present in the middle of the embryo sac. The nucellus is beginning to disintegrate. Throughout the sections, the nucellus breaks down first at the micropyle end, and remains intact at the chalazal and until the eight-nucleate is formed. The length of the ovary is the same as the tetrad section examined, but the cross-section of the ovule measures 3.5 mm by 2.5 mm, and the embryo sac is 0.9 mm long by 0.3 mm wide.

Some question might be raised as to the interpretation of the four-nucleate stage (see Figures 8A and 8B, which are camera lucida drawings of two sections of one embryo sac) because of the central position of the upper nuclei, as drawn in Figure 8B. This could possibly be a completed embryo sac with the egg cell missing. Since the cytoplasm is plasmolyzed and folded over, this might explain the displacement of the nuclei. Further, there is no evidence of the antipodals and, secondly, the synergids in the complete sac have a triangular shape; thus, it seems reasonable to assume this represents a four-nucleate

stage. Also, the sections contain nucellar material, at the chalazel end of the sac, which is not disintegrating.

Figure 9A and 9B represent a camera lucida drawing of two sections of a very nearly mature embryo sac of Fouquiera splendens. In the material, large vacoules are present throughout the cytoplasm. One is just above the egg and the other is in the middle of the sac. Figure 9A clearly contains a large egg and two polar nuclei. Figure 9B illustrates the two large and obvious synergids, which show no signs of deterioration. The egg is the largest nucleus, measuring 12.5 microns in diameter. The smallest are the polar nuclei, measuring 6.5 microns in diameter. Intermediate in size are the synergids, measuring 8.5 microns in diameter. Otherwise, the size of the ovule and its components are nearly identical to the two- and four-nucleate stages. Thus, it might be concluded that the ovule and the embryo sac develop rapidly. The anitpodals are not in the drawings (Figures 9A and 9B) because they appear to form separate cells, which then disintegrate. They form a linear chain of three cells outside the embryo sac, and later may be confused for disintegrating cells of the nucellus. They can be distinguished from nucellar cells because:

1. the nucellus is a one- to two-layered structure;
2. the nucellus is found in close conjunction with the embryo sac before the cells disintegrate, and the cells do not have as definite a separation as do the antipodals;

3. the nucellus has nearly completely disintegrated, leaving only vestiges of cells by the time the antipodals have separated.

The nearly mature sac was also found in Idria and, from the material, seems to be identical to Fouquieria splendens. Figure 12 is a section showing the egg nucleus of this stage. In the sections, the embryo sac contains two synergids, two polar nuclei, and a large egg nucleus. One large antipodal nucleus is visible in the section. However, in another section, they seem to be forming separate cells as they did in Fouquieria splendens. Further comparison is not possible because sufficient suitable stages were not available.

The final stage examined was the complete embryo sac containing four nuclei. This was found in both Fouquieria splendens and Fouquieria macdougalii. Figures 10 and 11 are composite drawings taken from this stage. Although it is not possible to determine whether or not fertilization has occurred, the well-developed haustorium and the four nuclei are obvious. In both figures, the egg (near the micropyle) and the polar nucleus (near the haustorium) can be seen. The synergids in Fouquieria macdougalii have disintegrated more than in Fouquieria splendens. In the material, the sytoplasm is dispersed around the edge of the embryo sac, while in the center and extending into the arm of the haustorium, a large indistinct vacuole can be found. A comparison of the ovule anatomy of these two figures and Figure 12 has been given previously in this section.

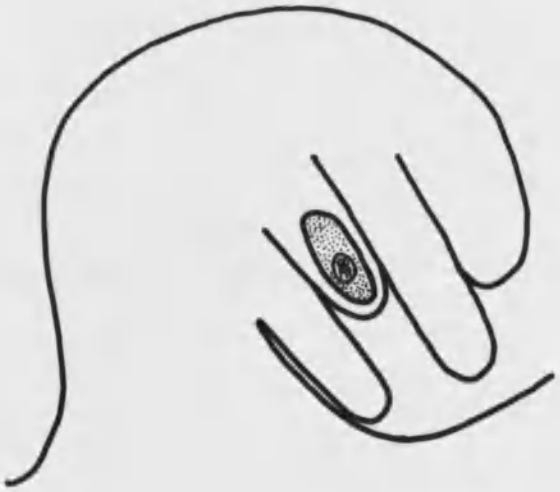

Figure 5

Figure 6

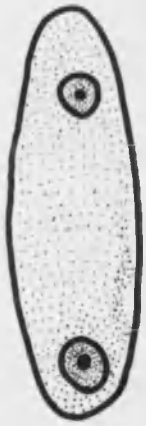

Figure 7

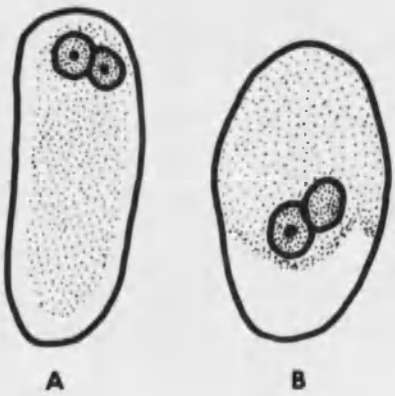

Figure 8

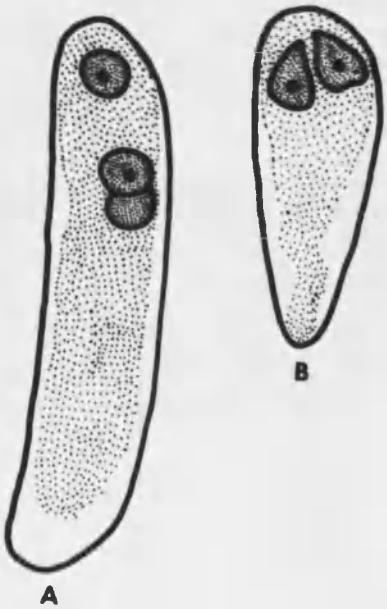

Figure 9

Figure 10

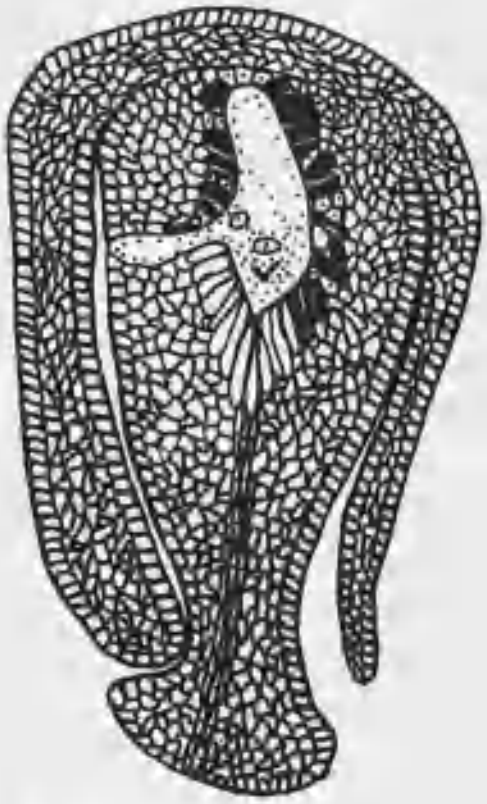

Figure 11

Figure 12

DISCUSSION

These investigations indicate that the ovule anatomy of the three species is similar. The embryo sac is surrounded by two integuments. The inner integument has the same characteristics in all three species. These characteristics are the elongated cells around the embryo sac and along the micropyle, and the development of the swollen portion of the inner integument at the end of the micropyle. The elongated cells around the embryo sac of Fouquieria macdougalii stain more heavily than similar cells in the other two species. The nucellus of all three species appears to be a similar one- to two-layered structure. The megaspore mother cell is identical in the two species of Fouquieria, but no conclusion can be drawn concerning Idria because it was not found. Although this study of the embryo sac development of Fouquieria macdougalii and Idria has by no means been completed, the stages of these two species, which were observed, correspond to similar stages in Fouquieria splendens.

One of the important feature characteristic of Fouquieria splendens and Fouquieria macdougalii is the haustorium present in the later stages of the embryo sac. It begins as a small extension off the middle of the embryo sac and enlarges until, at maturity, it has grown through the outer layer of cells of the inner integument. A

nucleus has always been found at the opening of the haustorium, but never in the haustorium itself. This nucleus could be one of the polar nuclei, the two polar nuclei fused, or the primary endosperm nucleus. Since a second polar nucleus was never found, it is probably one of the latter two. Maheshwari (1950) does not mention a haustorial projection as a characteristic of the "Fouquierias," but he states that Rocén found a similar occurrence in Agrostemma githago. Here too, the haustorium is associated with a nucleus, in this case the primary endosperm nucleus, which leads one to believe that the haustorium has a nutritional function and, further, that the nucleus might be responsible for its formation. The available material of Idria did not contain this late stage of development; thus, it remains a question whether or not it has a haustorium.

Considering only Fouquieria splendens, the primary point of contention is the type of embryo sac development. Johansen (1936) had described a tetrasporic scheme, whereas Mauritzon (1936) observed a monosporic scheme. Khan (1943) disagreed with Johansen and supported Mauritzon. The author's investigations differ slightly from Mauritzon, but the tetrads found in the material of Fouquieria splendens confirm a monosporic scheme of development. Mauritzon records that he observed a triad. The two nuclei nearest the micropyle are contained in one cell; the author's investigations show only a tetrad-four distinct megaspore cells.

None of the three papers published refer to the separating of the antipodals from the embryo sac. Since Mauritzon (1936) observed three antipodals in the embryo sac, perhaps he found a younger stage before they severed from the sac. In Johansen's (1936) description, he concluded that there are two antipodals in Fouquieria splendens, and that Fouquieria burragei and Fouquieria peninsularis have a five-nucleate embryo sac lacking antipodals. If the antipodals sever, as described previously, Johansen probably found later stages after their separation, when they were indistinguishable from disintegrating nucellar cells.

The investigator is also in agreement with the following other criticisms by Khan (1943) of Johansen's (1936) publication. There is a large inner integument, which gives rise to the elongated cells that surround the embryo sac and form the micropyle. The nucellus is a small one- to two-layered structure which begins disintegration early during embryo sac development. Lastly, the ovule definitely has a vascular supply in the funiculus.

Summary

1. Although the investigations of *Fouquieria macdougalii* and *Idria columnaris* were limited, all evidence found indicates that the embryo sac development and the anatomy of the ovary and its components are remarkably similar.
2. *Fouquieria splendens* has a monosporic scheme of development, in which a tetrad of megaspore cells is formed.
3. Khan's (1943) criticisms of Johansen's (1936) investigations are valid.

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