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# Aberrant Ovules in Angiosperms: A Review of Selected Examples and New Observations on *Ornithogalum caudatum* (Liliaceae)<sup>1</sup>

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While studying the events of megasporogenesis and megagametogenesis in *Ornithogalum caudatum* Ait., two ovules were observed which were quite different from the others. These two ovules were from separate ovaries, but the aberrant condition was the same in each ovule. In both cases, the ovule consisted of a single set of integuments enclosing two side-by-side nucelli each with its own developing megaspore. Such multiple-megagametophyte ovules may represent a now-defunct developmental pathway from the early evolutionary history of angiosperm ovules.

INDEX DESCRIPTORS: Aberrant ovules, binucellate ovule, multiple megagametophytes

The discovery of two binucellate ovules in *Ornithogalum caudatum* stimulated a literature search for unusual or otherwise interesting conditions surrounding megasporogenesis and megagametogenesis in an attempt to determine what, if any, significance there may be in a multiple-megagametophyte condition.

A broad spectrum of anomalies was encountered in the literature such as multiple megagametophytes, multiple fertilizations, extra cells within a megagametophyte, reversed polarity of megagametophytes, ovule abortion as part of a normal developmental sequence, and megagametophytes developing from pollen grains. Not all of the aberrant conditions encountered during the literature search pertain to the development of multiple-megagametophyte ovules directly, but they have been included in the following literature review as a matter of general interest and curiosity.

Differentiation of several megaspore mother cells (MMC) within a given ovule is a common event in many plants, but usually only one MMC attains fruition. The remainder either degenerate or cease to differentiate at some premature stage. However, this is not always the case, and by far the most commonly occurring aberrant condition is the formation of multiple megagametophytes within a single nucellus.

In most instances multiple (usually 2) megagametophytes per nucellus are sporadic enough in their occurrence to be considered aberrant, e.g., *Delphinium* (Mottier, 1895), *Gossypium* (Gore, 1932), some Leguminosae (Martin and Watt, 1934), *Lilium* (Fourcroy, 1949), *Ornithogalum* (Czapik, 1972; Tilton, 1978), *Malcomia* (Prasad, 1975), and *Persea* (Sedgley, 1976). The occurrence of 3 mature megagametophytes within a given nucellus is indeed rare, only having been reported for 1 count in *Paeonia* (Cave et al., 1961) and 2 counts in *Ulmus* (Lester and Lee, 1974). *Paeonia* and *Ulmus* also produce two-megagametophyte ovules, and in both taxa both megagametophytes may be fertilized.

The cells prevenient to MMC's are usually hypodermal in origin, the archesporial cell being derived from a nucellar cell immediately under the nucellar epidermis. In *Oncidium*, however, Afzelius (1916) reported that nucellar epidermal cells may function as MMCs, and in *Solanum* (Bhaduri, 1932) and *Limnanthes* (Fagerlind, 1939), it has been reported that integumentary cells may function in this capacity. Following meiosis, the resulting 4 megaspores are found more often than not in a linear tetrad. They also commonly form a T or a L. In an unusual case, Capoor (1937) reported finding one instance of the megaspores in *Urginea* being in a decussate arrangement.

Megaspores are short-lived and either degenerate or undergo mitosis to become the megagametophyte. Megagametophytes and embryos frequently form haustoria from a variety of tissues, but haustorial formation by megaspores is unusual. In *Galium* and *Sedum* (Fagerlind, 1937), and *Potentilla* (Rutishauser, 1945), only the functional megaspore produces haustoria while in *Rosularia* (Mauritzon, 1933) they may be produced by all four megaspores.

Aposporic megagametophytes have been reported for *Ornithogalum gussonei* by Žabińska (1972), and Czapik (1972) reported the fusion of two *O. umbellatum* ovules but gave no particulars. Twin nucelli have been noted to occur in *Moringa* (Puri, 1934), *Ornithopus* (Wojciechowska, 1972), *Ornithogalum nutans* and *O. nanum* (Karagozova and Van Khankh, 1972), and *Persea* (Tomer and Gottreich, 1976). The fusion of mature twin megagametophytes by way of the breakdown of their adjoining walls has been reported for *Elatine* (Frisendahl, 1927) and two species of *Reseda* (Oskijuk, 1937). Such fusion resulted in a megagametophyte with two eggs, four synergids, four polar nuclei, and six antipodals. Mauritzon (1933) reported a similar complement of cells in some megagametophytes of *Crassula* and *Umbilicus*, but explained their occurrence as the result of a fourth mitotic division.

Tomer and Gottreich (1976) noted several unusual conditions for *Persea*, i.e., egg apparatus without a filiform apparatus, additional nuclei — from few to twenty — within the central cell, and the occurrence of two egg apparatus within one ovule. Some megagametophytes of *Crepis* (Gerassimova, 1933) and *Nicotiana* (Goodspeed, 1947) contained a few extra nuclei while in both *Hartmannia* (Johansen, 1929) and *Jussieva* (Khan, 1942) instances have been reported of egg apparatus missing one synergid. Several cases of four-celled egg apparatus have been reported for *Moringa* (Puri, 1934), and one aberrant megagametophyte of *Acer* had an egg apparatus consisting of three eggs and two synergids (Haskell and Postlethwait, 1971).

Cooper (1943) demonstrated in several species of *Lilium* and in one of *Nicotiana* that a synergid was stimulated to divide resulting in haploid-diploid twins. The haploid individuals usually deteriorated at an early stage, but some did develop more fully. In *Cypripedium*, Pace (1907) claimed that the force of pollen tube entry into the megagametophyte dislodged one synergid and caused that synergid to take part in triple fusion. Wojciechowska (1972) found some *Ornithopus* ovules without a megagametophyte as did Mogensen (1975a,b) in *Quercus*. Mogensen (1975a) also found four different categories of abortive ovules in *Quercus*, abortion of all but one ovule per acorn being the usual developmental sequence. Simons (1974) claims ovule abortion in *Malus* is the result of poorly developed placentae which are unable to support functional ovules.

Multiple fertilizations of one ovule are reported for *Persea* (Sedgley, 1976), and it is postulated in the same report that the number of pollen tubes reaching the ovary is closely related to the number of

<sup>1</sup>This paper represents a portion of the author's doctoral dissertation. Microscopy was conducted under the direction of Dr. Harry T. Horner, Jr., Director, Bessey Hall Microscopy Facility, Iowa State University, Ames.

megagametophytes in the ovule, there being only one ovule per ovary in *Persea*. While only one pollen tube is able to reach the ovary in normal single-megagametophyte, single-ovule individuals, two pollen tubes were found in the micropyle of 18% of the two-megagametophyte single-ovule individuals. According to Sedgley (1976), of the approximately 66 pollen grains that germinate on the stigma, half form swollen tips and go no further than the stigma base, and the remaining tubes go no further than half to three-fourths of the way down the style. Only 1-2 tubes are able to reach the ovary, depending in part on the number of megagametophytes present. Fulvio and Cave (1964) reported seeing two pollen tubes reach the megagametophyte of *Blandfordia*.

Some megagametophytes of *Poa* (Håkansson, 1943) may have two sets of antipodals and no egg apparatus while some of *Allium* (Modilewski, 1928) have two egg apparatus and no antipodals. Examples of reversed polarity where the egg apparatus is in the chalazal end of the megagametophyte and vice versa for the antipodals include *Atamosco* (Pace, 1913), *Fuchsia* (Täckholm, 1915), *Saccharum* (Dutt and Subba Rao, 1933), and *Heptapleurum* (Gopinath, 1943) along with some others.

In *Asperula*, Lloyd (1899) stated that it is common to find completely developed megagametophytes in the normal position in addition to the chalaza and even the funiculus, while among some Loranthaceae (Rauch, 1936; Schaeppi and Steindl, 1942; Singh, 1950) the megagametophytes may protrude into the ovary and up into the style, some almost reaching the stigma.

The transformation of stamen filament tissue to ovule tissue has been reported to occur in *Nicotiana* (Bhat and Krishnamurthy, 1956; Krishnamurthy and Rao, 1960) and *Solanum* (Sirohi et al., 1964; Pullo and Slusarkiewicz, 1975). An even more interesting and unusual event is the development of a megagametophyte within a pollen grain. This phenomenon has been reported several times for several varieties of *Hyacinthus orientalis* (Némec, 1989; Mol, 1923; Stow, 1930, 1934; Naithani, 1937). The transformation from male to female gametophyte is apparently initiated by the artificial environmental conditions used in greenhouses to induce early flowering in this species. A similar transformation has been reported in one instance for *Ornithogalum nutans* (Geitler, 1941).

## MATERIALS AND METHODS

Plants of *Ornithogalum caudatum* Ait. were grown in the Department of Botany and Plant Pathology greenhouse at Iowa State University, Ames. Tissues from gynoeceia ranging in age from buds of the third floral plastochron up through mature seeds were studied. Samples were collected as needed between November, 1974 and June, 1977.

Buds and flowers were dissected in 1% glutaraldehyde and placed immediately into 2% glutaraldehyde in 0.05M sodium cacodylate buffer (pH 8.0) 1 h at room temperature followed by fresh 2% glutaraldehyde (same buffer) at 4°C overnight. Overnight fixation was followed by four 15 min buffer rinses, dehydration by a graded ETOH series, and overnight infiltration with Luft's epon (Luft, 1961) via a graded prop-

ylene oxide series.

Two  $\mu$ m sections were cut with dry glass knives and placed in serial order on dry glass slides. Sections were viewed with phase optics and selected for staining. Each section selected was floated on a drop of glass-distilled water and heated gently over a spirit lamp to expand it. After the water evaporated, the slide again was heated carefully over a spirit lamp to adhere the section to the slide.

Sections were stained with either aniline blue black (Fisher, 1968) or methylene blue-azure II (Humphrey and Pittman, 1974) and counterstained with basic fuchsin (Humphrey and Pittman, 1974). Following staining, slides were rinsed with D.D.H<sub>2</sub>O, air dried at room temperature, and immersed overnight in xylene. Coverslips were mounted with Piccolyte.

## OBSERVATIONS

An anomalous condition in which twin nucelli enclosed within one pair of integuments was noted in two ovules of *Ornithogalum caudatum* (Fig. 1). Each ovule was from a different ovary. Both nucelli of both ovules contained a developing megagametophyte, and both megagametophytes of each ovule were synchronized at the same developmental stage (Figs. 1, 2, 7, 9 and 11). At the time of fixation, they were in the dyad stage between meiosis I and II.

Measured across their chalaza, the binucellate ovules were approximately one-third again as wide as normal ovules, but there is no difference in length (Fig. 7). Each of the twin nucelli is just slightly narrower and shorter than normal, but the common chalaza is more massive (Fig. 7). The binucellate ovules appear normal in all other respects, including general shape and appearance, starch content, and degeneration of nucellar cells around the developing megagametophyte (Figs. 1-12).

## DISCUSSION

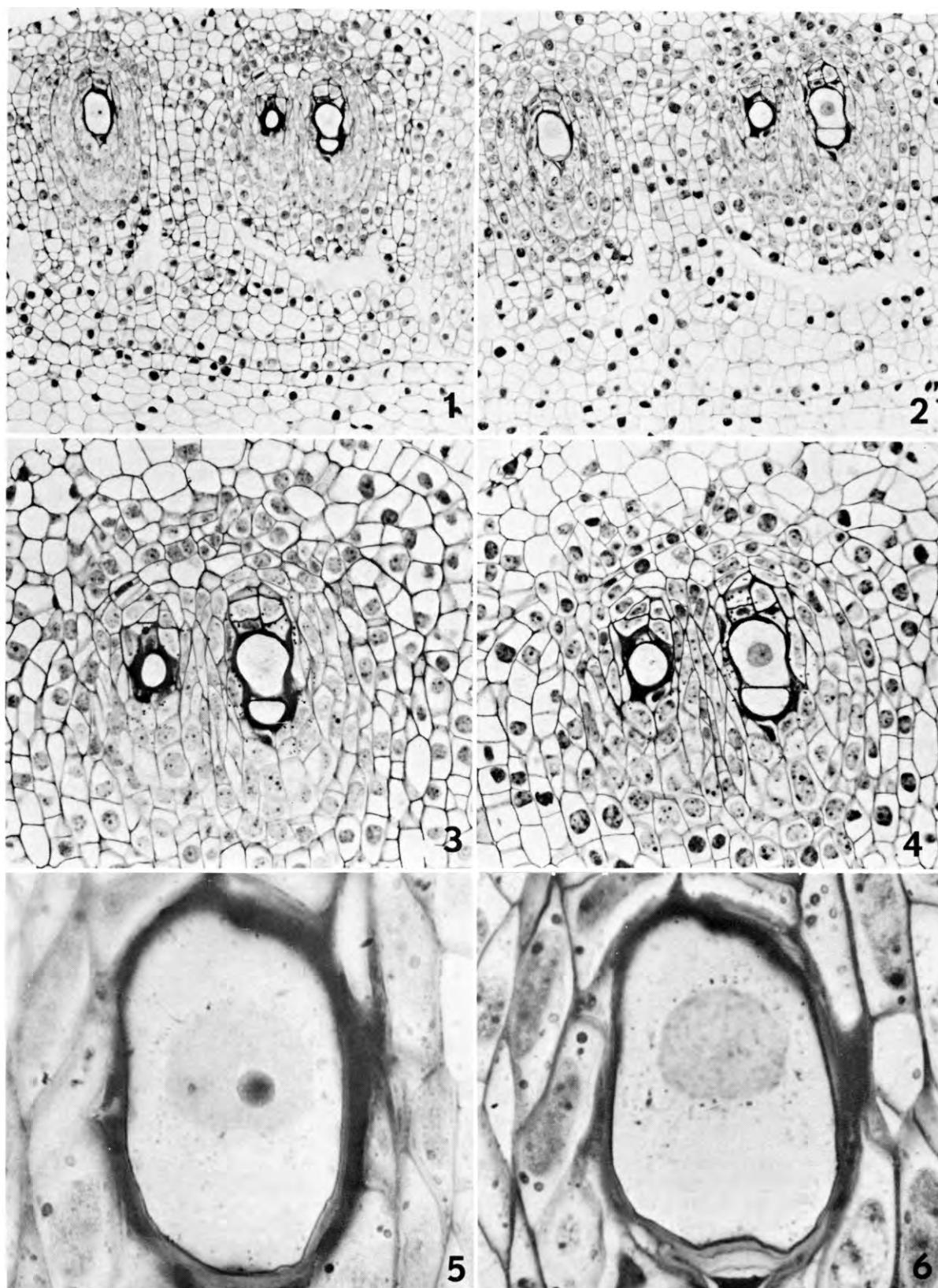
As noted in the Introduction, a wide variety of aberrant conditions have been reported to occur in the ovules of many plants. These abnormalities result from internal and/or external forces which ultimately induce changes in the genetic and/or biochemical and physiological sequence of events which leads to normal development. However, evolutionary changes necessarily preclude developmental sequences of extant organisms, in their normal state, from being the same as were those of their ancestors. A change must have occurred somewhere.

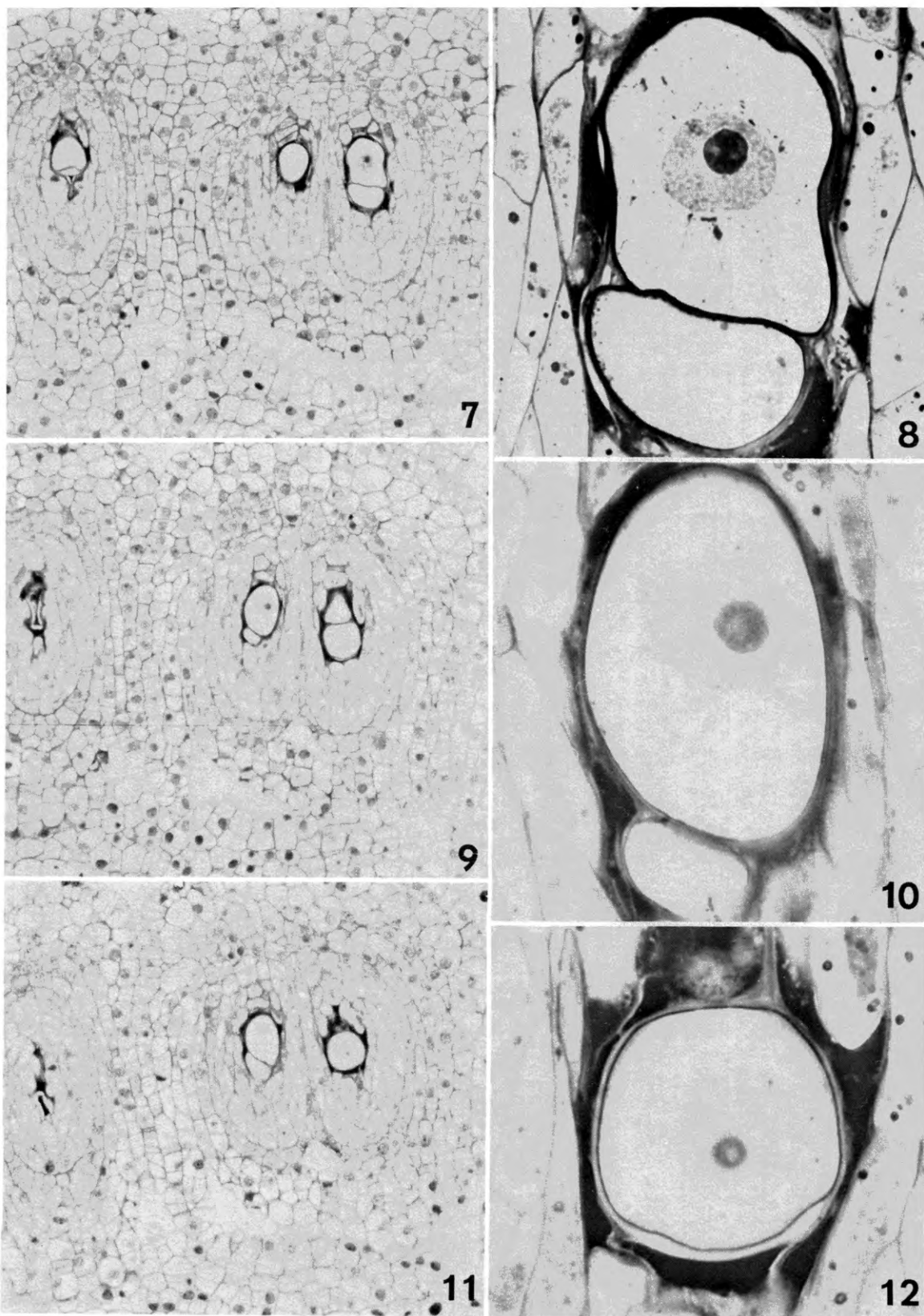
Development of more than one megaspore into a functional megagametophyte within a given ovule might possibly have been a normal condition in the evolutionary history of angiosperm ovules. The maturation of all four megaspores in some primitive plants tends credence to this hypothesis. The occasional occurrence of multiple-megagametophyte ovules in extant angiosperm taxa thus may represent an expression of that now-defunct developmental pathway.

The more common condition in multiple megagametophyte ovules is the development of two or more megaspores from the same meiotic

Figs. 1-6. Binucellate ovules, both with MMC at meiotic dyad stage. Figs. 1-2. Normal ovule on left, binucellate ovule on right. Both x 168. Figs. 3-4. Dyad stage of binucellate ovule in Figs. 1 & 2. Both x 135. Fig. 5. Functional megaspore from normal (left) ovule in Fig. 1. x 1,260. Fig. 6. Functional megaspore from normal (left) ovule in Fig. 2. x 1,260.

Figs. 7-12. Serial sections through normal (left) and binucellate ovules. Fig. 7. Normal (left) and binucellate (right) ovules. x 202. Fig. 8. Megaspore dyad from right-hand nucellus of binucellate ovule. x 1,346. Fig. 9. Normal (left) and binucellate (right) ovules. x 202. Fig. 10. Chalazal megaspore of meiotic dyad from left-hand nucellus of binucellate ovule. x 1,346. Fig. 11. Normal (left) and binucellate (right) ovules. x 202. Fig. 12. Micropylar megaspore of meiotic dyad from right-hand nucellus of binucellate ovule. x 1,346.







tetrad within a given nucellus. This approximates the condition encountered in some primitive plants. The two examples of multiple-megagametophyte ovules reported here for *Ornithogalus caudatum*, and in the literature for *O. nutans* and *O. nanum* (Karagozova and Van Khankh, 1972), *Moringa* (Puri, 1934), *Ornithopus* (Wojciechowska, 1972), and *Persea* (Tomer and Gottreich, 1976), however, are different in that they have twin nucelli. This difference is significant because the multiplicity of megagametophytes in these ovules is the result of each nucellus having its own MMC and megagametophyte rather than there being one nucellus with two or more megagametophytes as in the other condition.

The occurrence of twin nucelli may be related to the evolutionary development of integuments, but this suggestion comes merely as a matter of speculation. Based on Sedgley's (1976) evidence in *Persea* that more megagametophytes attract more pollen tubes, one could speculate that some systems developed a binucellate ovule in an attempt to enhance the chances of successful fertilization, i.e., more pollen tubes per ovule, without the complications of nutrition and space considerations encountered in ovules with a single nucellus and multiple megagametophytes.

Another aberrant reproductive strategy which may give the same end result as the binucellate condition seen in *Ornithogalus candatum* is the fusion of two ovules as reported to occur in *O. umbellatum* (Czapik, 1972). By the same token, the aberrant condition in which a multiplicity of egg apparatus cells occurs within a single megagametophyte might represent a condition similar to single-nucellus, multiple-megagametophyte ovules in terms of their ability to attract pollen tubes.

On the other hand, none of the aberrant conditions, such as binucellate ovules, may have anything to do with evolutionary history or attempted reproductive strategies. Instead, they may represent only unrelated errors in the normal sequence of developmental events and have no significance. However, the occurrence of similar aberrant conditions in related as well as non-related taxa tends to support their association with evolutionary history. Binucellate and other multiple-megagametophyte ovules thus do seem to represent an expression of developmental pathways repressed by evolutionary pressures.

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