THE OVULE AND EMBRYO SAC OF *FOUQUIERIA*.

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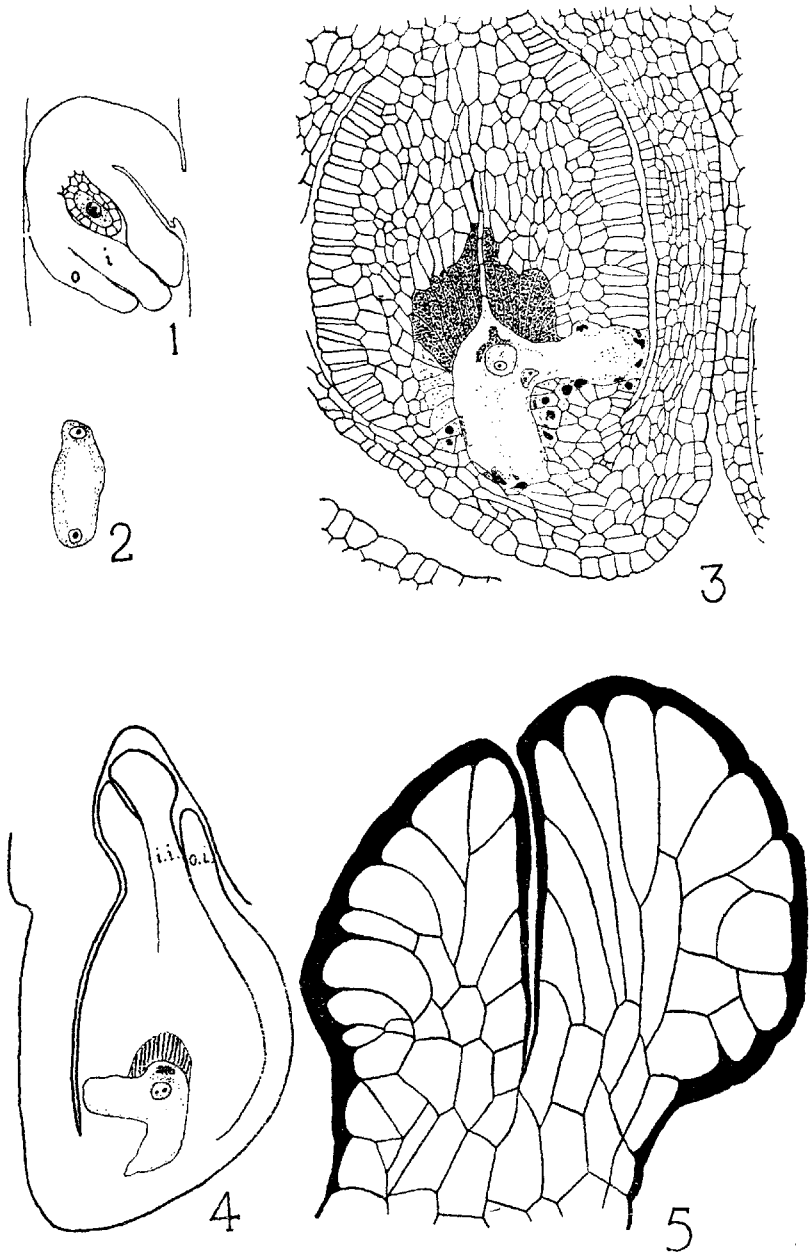
During the course of a personal discussion on the presence of a nucellar epistase in angiosperms, Dr. P. Maheshwari invited my attention to D. A. Johansen's (1936) paper on the 'Morphology and embryology of *Fouquieria*' and remarked that the author had evidently mistaken the inner integument for the nucellus. A further study of the paper revealed that the development of the embryo sac had also been wrongly described as tetrasporic. Mauritzon (1936), who studied *Fouquieria splendens* independently and without any knowledge of Johansen's work, has shown that the nucellus is very meagre in the young ovule and, as the latter grows older, disappears completely, the embryo sac being then in direct contact with the inner integument. He also shows that the development of the embryo sac is of the Normal type.

Although Mauritzon has given a correct account of *F. splendens*, a comment on Johansen's (1936) paper is felt necessary for various reasons.

Johansen (1936, p. 95) writes: 'Each ovule is invested with an inner and an outer integument (Fig. 1). The inner integument precedes the outer in time of origin. The former furthermore grows faster and is thicker by reason of possessing a larger number of layers of cells. The elongated lips of the inner integument soon meet above the nucellus and there become considerably swollen; the nucellus is thus completely enclosed.' So far his account appears to be quite correct and agrees with his Fig. 1 (reproduced here also as Fig. 1). The nucellus clearly consists of only 1-2 layers of cells and the megaspore mother cell is situated directly below the epidermis. But there is a remarkable disagreement between this and what he writes later. On pp. 95-96 he states: 'In the nucellus, crowning the megagametophytic cavity, and apparently forming part of the tapetum, there is situated a group of thick walled vertically elongated cells (Fig. 9). . . . . The walls of these cells become suberised during the maturation of the seed, and move upward toward the micropylar end of the ovule while the surrounding nucellar cells are being destroyed to make room for the cellular endosperm. The group apparently breaks through the epidermis of the nucellus at the apex of the latter and becomes plugged between the lips of the inner integument, blocking the opening through which the pollen tube entered.' These cells, in his opinion, constitute a kind of epistase. His Fig. 9 (redrawn as Fig. 3 here) shows a mature embryo sac surrounded by a thick tissue of cells which, according to him, is the nucellus and some of whose cells are said to form the epistase (shaded in Fig. 3). On one side of the supposed nucellus is the raphe and on the other a single integument. Since the figure shows no structure between this nucellus and the raphe, one is immediately led to ask: Where is the inner integument and where are its thick lips which enclose the nucellus and become plugged by the epistase? On that side also, which is away from the raphe, there is only one integument instead of two. The inevitable conclusion is that what Johansen has taken to be the nucellus is itself the well-developed and massive inner integument. It is strange that although Johansen earlier speaks of a well-developed inner integument, its *absence* in his Figures 8 and 9 did not strike him as something problematic.

A well-developed nucellus, projecting through the micropyle is not unknown in some other angiosperms. It is so in the Malpighiaceae for instance (Stenar, 1937; Subba Rao, 1940), but here there can be no confusion as both the integuments are present in addition to the nucellus.



FIGS. 1–5. *Fouquieria*.

FIGS. 1–3. Redrawn from Johansen's Figs. 1, 2 and 9 respectively.

Fig. 1. ***F. splendens.*** Median longitudinal section of young ovule showing the megasporocyte surrounded by the inner (i) and outer (o) integuments. Fig. 2. ***F. splendens.*** Binucleate megagametophyte. ×368. Fig. 3. '***F. burragei.*** Median longitudinal section of ovule with mature pentanucleate megagametophyte. Notice the canal traversing the cap-like epistase (stippled). Redrawn from a photomicrograph.' Figs. 4–5. ***F. peninsularis.*** Fig. 4. Longitudinal section of an ovule at the mature embryo sac stage, showing the outer (o.i.) and inner (i.i.) integuments. Note the thick 'lips' of the latter and the narrow micropyle (reconstructed from several sections). ×120. **Fig. 5.** Apical portion of the inner integument magnified to show the micropyle. ×608.

Fig. 4, showing an ovule in longitudinal section, and Fig. 5, showing a portion of the same on a more magnified scale, have been drawn from a preparation of *F. peninsularis* made by Johansen himself and presented to Dr. Maheshwari. Here we find a narrow canal in the upper half of what Johansen supposes to be the nucellus. It is quite distinct and appreciably wide in the apical portion but narrows down towards the base fading out of sight near the middle. It obviously corresponds to the micropyle and, therefore, confirms the view that the supposed nucellus is the inner integument.

A probable cause of Johansen's misinterpretation is suggested by his Figs. 1 and 2 (reproduced as Figs. 1 and 2 respectively) and his account of the development of the embryo sac. He supposes that Fig. 2 represents a stage immediately following that in Fig. 1. Actually, however, he has missed, between these two, all the stages showing the division of the megaspore mother cell, the formation of the tetrad, and the growth of the functional megaspore. It seems clear that during this interval the nucellus is entirely used up by the growing megaspore, and the inner integument comes to lie in direct contact with the embryo sac.

It may also be added that if the nucellus has disappeared, the so-called 'epistase' must belong to the inner integument.

Coming to the development of the embryo sac, Johansen says that in *Fouquieria splendens*, *F. peninsularis*, and *F. burragei* it is tetrasporic. According to Mauritzon who investigated *F. splendens*, it is monosporic. Due to this difference in the reports of these authors, Maheshwari (1937) pointed out the need for a reinvestigation of these plants. After the megaspore mother cell stage, Mauritzon figures a row of three cells of which the uppermost is binucleate and the lowest much larger than others. The latter is obviously the functional megaspore formed as a result of the division of the megaspore mother cell. The embryo sac is consequently monosporic and there is no reason to doubt the validity of this conclusion. But there is also other evidence that goes to show that it is *not* tetrasporic as claimed by Johansen. As pointed out by Maheshwari (1941, p. 251), in the tetrasporic types a large central vacuole is usually not seen at the 2- and 4-nucleate stages but makes its appearance only when the four nuclei are preparing for the next division. Johansen's Fig. 2 (Fig. 2 here) shows this vacuole even at the 2-nucleate stage indicating that these nuclei do not represent the dyad stage but are the products of the first division of the megaspore nucleus. (See also Maheshwari, 1942, on *Euphorbia heterophylla*.)

Comparing *F. splendens* with *Myricaria germanica*, Johansen (p. 98) writes: '*F. splendens* and *M. germanica* follow an almost identical developmental scheme.' This comparison is entirely invalid not only because the embryo sac of *F. splendens* is monosporic but also because the development of the embryo sac in *Myricaria germanica* is not of the *Adoxa*-type as reported by Frisendahl (1912), on whose work Johansen bases his statement, but of the *Fritillaria*-type. As pointed out by Maheshwari (1937), Frisendahl's figures show the 1+3 arrangement of the nuclei at the four nucleate stage of the embryo sac as well as the difference in the relative sizes of the micropylar and chalazal pairs of nuclei of the 'four nucleate' stage—really the secondary four nucleate stage (see also Zabban, 1936, and Maheshwari, 1941).

Dealing with the haustorial function of the lateral arm of the mature embryo sac in *Fouquieria*, Johansen writes: 'Since there is no vascular supply in the funiculus or raphe, and there apparently exists no other method by which water and foodstuffs are transported to the ovule, the development of the haustorial arm may logically be considered the remedy of this defect.' The defect does not exist, however. The preparation of *F. peninsularis* presented by Johansen to Dr. Maheshwari shows that the raphe does possess a vascular supply and the explanation for the occurrence of the haustorium must, therefore, be sought elsewhere.

Summary.

Johansen's observations on *Fouquieria* are criticised as the result of a careful study of his own figures and of a preparation of *Fouquieria peninsularis* presented by him to Dr. Maheshwari. It is concluded that:—

1. The nucellus in *Fouquieria* is not massive as claimed by Johansen but extremely reduced and all traces of it are lost during the development of the embryo sac.
2. The ovule is provided with two integuments of which the inner is more massive and forms the micropyle. The 'epistase' of Johansen does not belong to the nucellus but to the inner integument.
3. The ovule has a normal vascular supply in the raphe.
4. The development of the embryo sac is not tetrasporic but monosporic as reported by Mauritzon (1936).

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