

NOTE ON THE EARLY DEVELOPMENT OF THE INTEGUMENT  
IN SOME JUGLANDACEAE

together with some general questions on the structure  
of Angiosperm ovules

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Recently a review on the Angiosperm ovule has been published by the well-known Indian botanist V. Puri (1970). In this review the author stressed the differences between Angiospermous and Gymnospermous ovules, and he refused to accept their comparability or common descent. In this respect Puri comes close to Eames (1961). Both authors tend to regard the ovules as complex emergences. Apart from the main theme, there is a striking passage in this review dealing with the Hugo de Vries Laboratory at Amsterdam. According to Puri in that laboratory facts are sacrificed for hypotheses (p. 10). In the following we would like to start with the facts concerned and present them in a more convincing way, and then ask some simple questions on the structure of the ovules in order to show just how little precise information is available. This lack of information has had the effect of producing many different hypotheses.

Boesewinkel and Bouman (1967) reinvestigated the initiation of the single integument in some Juglandaceous ovules. In a histogenetic study they showed that the development starts with subdermal and is followed by dermal periclinal divisions. They also stated that the integument arises as two halves, or valves, which are free above but become fused below especially in later stages. Unfortunately, however, they failed to give an unequivocal demonstration of this paired development by means of some good photographs. It was this lack of proof that led Puri to reject the evidence. However, it should be reported that earlier Shuhart (1932) and Leroy (1954) had published the paired initiation of the integument lobes (in *Carya spec.* and *Platycarya strobilacea* resp.), and had given photographs of microscopic slides showing cross-sections of the distal part of the nucellus flanked by two opposite tips of the young single integument. In the present paper we present two similar photographs, one of *Pterocarya fraxinifolia*, the other of *Engelhardia spicata*. In addition two other 'true to nature' photographs are given, showing two developing ovules of *Pterocarya fraxinifolia*, as they can be observed directly under a stereo dissecting microscope at low magnification, after the young pistil wall is carefully removed. There is no escape from the fact that the integument in these plants grows like two fusing lobes. The hypotheses are a different matter.

In this note we will not go into all the morphological explanations that have been advanced for the structure of the ovules. They have been reviewed by others, recently by Long (1966) and Puri (see also Meeuse, 1966). It appears that many possible explanations

— idealistic as well as phylogenetic — have been brought forward, and that the question which explanation is accepted depends largely on the inclination of each particular author. At present there seems to be no way out of this maze. However, this does not mean that there is no use for further research in this field. On the contrary, we think that better research is badly needed; that in fact the study of ovules has been neglected as compared to that of carpels. As Bouman (1971 a) put it: floral morphology was 'carpel-centred'. In this connection we would like to make some critical remarks.

The simply counting and numbering of more and more envelopes around the nucellus is probably useless for the purpose of comparison. In other words, the application of only a topographic criterion has no value for determining their homology. This is because 1) there may have been loss of integuments, 2) there may have been new formations inside existing ones, and 3) two envelopes may have 'fused', or a 'fusion' may have occurred between the nucellus and its closest envelope. All these subsidiary explanations have been advanced in literature to save the one or the other hypothesis, all without much evidence. It becomes increasingly difficult if the numbering is extended outwards, and if arils and even carpels are also taken into account. How much do we know about arilloid structures, functional devices of apparently widely different origin? The puzzle cannot be solved by '*Gestalt Typology*' or its phylogenetic image. We must first look for more evidence and evaluate everything we can find.

How can we compare anatropous with atropous ovules? What kind of fusion product is the raphe? The question has been asked by German botanists long ago but has never received an answer, nor has it led to thorough histogenetic research. Does the raphe really conform to the idea that it is the result of a fusion between funicle and integument, which occurs during the ontogeny of an anatropous ovule? Is there — on median section — always a bulge on the raphe towards the micropylar side, which conventionally represents the distal integument part that escaped fusion with the funicle? Can anything be found in Angiosperms favouring Long's interpretation of the outer integument as a chalazal overgrowth? How is such an interpretation possible in atropous ovules?

In some ovules, the integuments are initiated on the ovule primordium by subdermal in others exclusively by dermal periclinal divisions (see also Bouman, 1971 b). There are several possible explanations of this difference. For instance, thin integuments could have a dermal initiation, whereas thick integuments — that develop into thick testae — could have a subdermal origin (cf. Bouman, 1971 b). However, it could also mean that in the case of dermal origin the integument should be regarded as an elaboration of the nucellus, rather than as being homologous with syntelomic or leafy units in which case a subdermal origin should be expected. Or is the dermal origin a sign of reduction?

Recently attention has been directed towards the occurrence of ephemeral lobes terminating young integuments of ovules in some plants other than *Juglandaceae* (Van Heel, 1970, 1971). This is a phenomenon well known in recent and fossil Gymnosperms, especially in paleozoic ovules of the Pteridosperms. Is there any relation between these different cases? Generally it may be remarked that the structure of the micropyle, the endo- and the exostome has never been thoroughly studied.

There are only two papers especially dealing with the vascular bundle supply of ovules (Le Monnier, 1872, and Kühn, 1928). Moreover, some data on the vascular supply of seeds can be found in Netolitzky (1926). However, in these publications the vascular bundle patterns are not correlated with the general three-dimensional structure of the ovule and its development. Nevertheless a study of the figures of Kühn and Le Monnier is very stimulating. In a number of cases the distal portion of the outer integuments does not have median vascular bundles, which renders the whole organ anatomically bipartite.

No systematic research has been performed on the simple ecological question of a relation between the testa and the presence of vascular bundles. Do thick integuments which develop into thick testae always get many vascular bundles? Do thin integuments that do not develop into thick testae get fewer vascular bundles? Or are there no such correlations?

As a conclusion we would like to advance the opinion that the study of the Angiosperm ovules, neglected in even simple aspects of its structure, should be revitalized. It deserves great attention since the ovules are presumably the oldest organs in the flower, so that their structure can inform us about a remote past. As to the methods, the study of external features and their development should be combined with anatomy and histogeny. It should be done systematically and with due regard of ecological correlations. In the beginning the comparisons should be confined to taxonomically well known groups.

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