BLUMEA 28 (1982) 53 - 60

NOTE ON THE STRUCTURE OF DEVELOPING SEEDS OF KNEMA AND HORSFIELDIA (MYRISTICACEAE)

W. A. VAN HEEL

Rijksherbarium, Leiden, Netherlands.

SUMMARY

The structure of the seed is based on the massive development of the ovule immediately above the insertion of the outer integument. This may be called endochalazal development, as suggested by F. Bouman (Pers. comm.).

For the understanding of the structure of a seed, the knowledge of the development of the ovule is necessary. This statement certainly fits the Myristicaceae, because the change in the relative position of the ovule parts during development is considerable. In contrast with the anatomy of mature seeds of Myristicaceae, the structure of developing seeds has been investigated insufficiently. Moreover the few extant publications on development deal with *Myristica* only, except the book of Corner (1976) which is also on *Knema* and *Horsfieldia*. Fortunately it appears from Corner's contribution that there are no fundamental differences in seed structure between the three genera. The derivation of the testa and its hard layer, the development of the inner integument of the ovule and its final location in the seed, the position of the inner one of the two vascular bundle systems, the origin of the aril and its vascular bundles, and the origin of the ruminations, have been the subjects of discussion.

The opinions may be briefly summarized. As regards the main process marking the development from ovule to seed, authors can be divided into two groups as follows.

Group I.

Voigt (1885): 'the growth of the ovule takes place mainly below the insertion of the inner integument. On the ripe seed the inner integument is a tiny tip'. Hallström (1895): The insertion of the inner integument is half way up the micropyle. However, some other data of Hallström are contradictory. Periasamy (1962): 'there is a massive chalazal development'.

Nair (1972): 'after fertilization a chalazal meristem pushes the inner integument toward the apex. The inner seed coat is chalazal tissue'.

Group II.

Sastri (1954): 'the boundary of nucellus and inner integument becomes vague in older ovules'. Mohana Rao (1974): 'there is no pronounced basipetal growth of the chalaza, and no pushing off of the inner integument to the micropylar part. As a consequence this author describes the inner zone of the seed coat as derived from the inner integument. Roth & Lindorf (1974): 'the original condition of the two integuments is maintained. The inner epidermis of the inner integument is not sharply demarcated in the mature stage'. Corner (1976): 'there is no pachychalaza (enlargement of the nucellar base)'. Accordingly Corner distinguishes a testa and a tegmen on the ripe seed in all three genera.

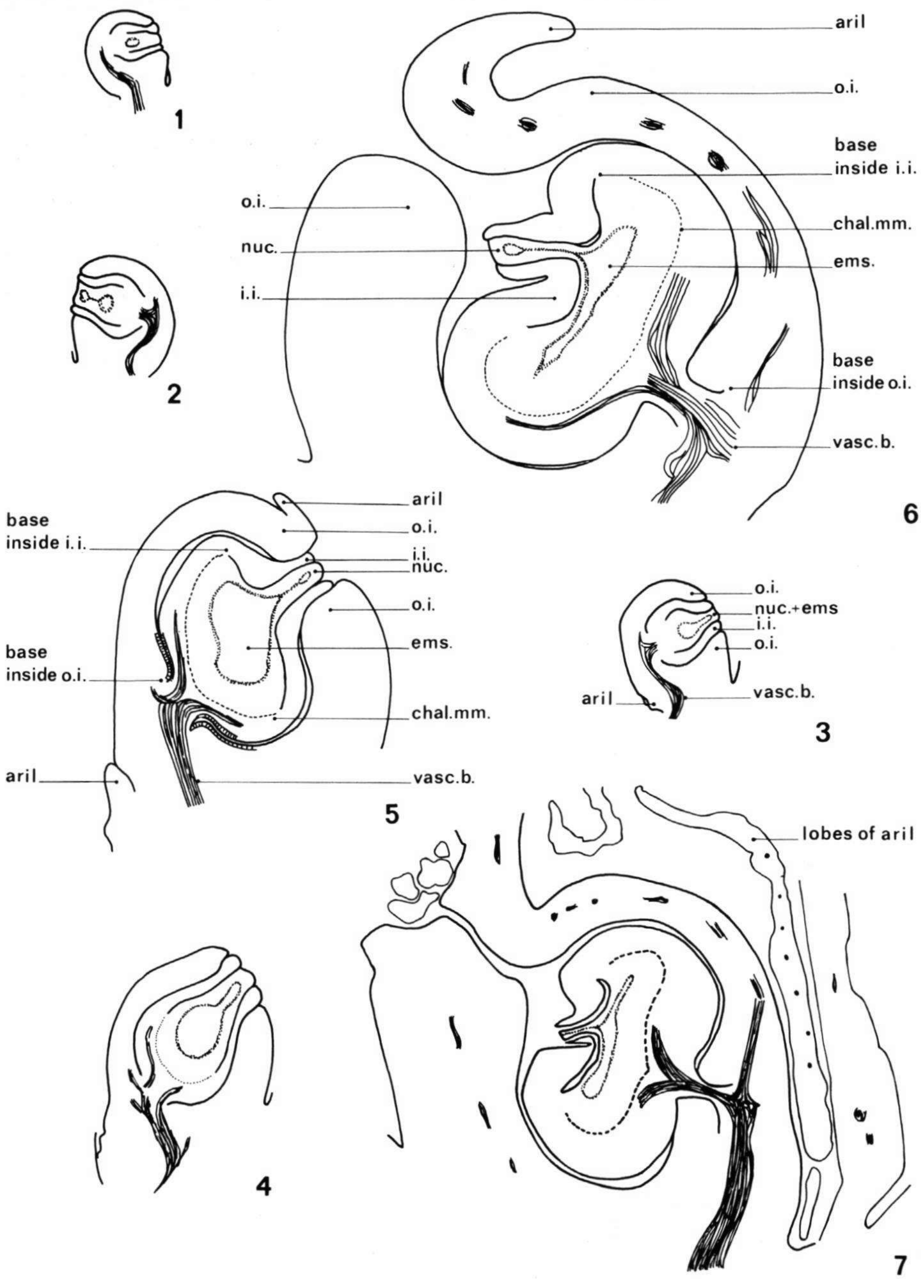
Whereas, in short, group I authors think that the seed coat is derived from the outer integument on the outside and the chalaza on the inside, group II authors think that the seed coat is entirely integumental. In this paper I will try to show that this contradistinction is not quite realistic.

All authors mention that the outer vascular bundle system belongs to the outer integument. However, the inner vascular bundle system is considered as chalazal by Voigt and Nair (group I), and as integumental by Sastri and Mohana Rao (group II). In the same manner the ruminations are reported to develop from the chalaza by Periasamy and Nair (group I), and from the tegmen or the inner integument by Mohana Rao and Roth & Lindorf (group II). Corner distinguished between basal (chalazal) and lateral (tegmic) intrusions. All authors state that the hard layer of the seed is formed by a palisade of lignified cells, which is derived from the inner epidermis of the outer integument. Corner reports also that the cells of the outer epidermis of the inner integument differentiate into groups of fibres or sclerotic cells (not in *Myristica fragrans*). The aril originates from funicular as well as from exostomal tissue, according to Voigt, Nair, Endress (1973), Mohana Rao, and Corner. The vascular bundles of the aril are connected with those of the funicle. In addition, a connection of the vascular bundles with the bundles in the distal part of the outer integument is present, according to Sastri and Endress. However, such a connection is claimed to be absent by Voigt, Nair, and Mohana Rao.

In view of a possible solution of the controversy, I collected material from several trees cultivated in the Kebun Raya at Bogor, during a visit in 1969. By making collections on the same trees at regular intervals, I obtained some stages of development which proved of interest to the above discussion. Hoewever, meristematic processes could not be followed in detail. The species considered are *Knema laurina* Warb., *K. tomentella* Warb., *Horsfieldia iryaghedi* (Gaertn.) Warb., *H. glabra* (Bl.) Warb., and *H. sylvestris* (Houtt.) Warb.

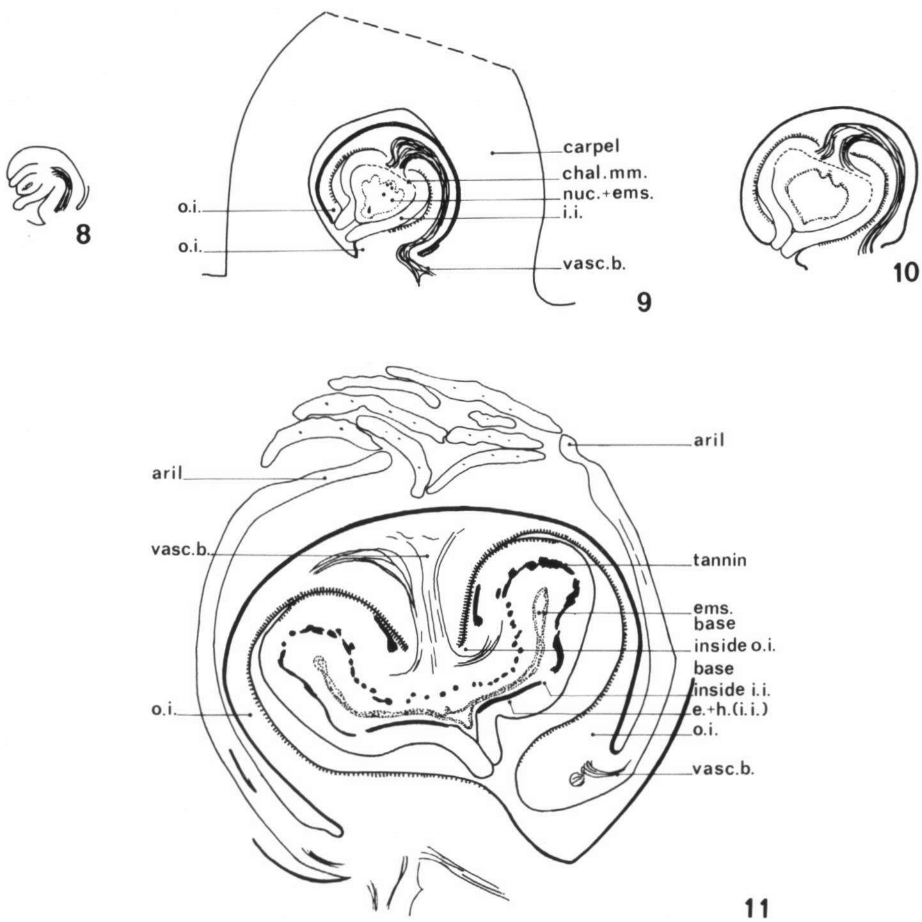
My figures 1–7 (*Horsfieldia* spp.), and 8–12 (*Knema* spp.), are arranged in order of increasing age. The oldest developmental stage given by Corner is just slightly younger than the one of my fig. 5. The enormous expansion of the embryosac is at once evident. As regards the main question it is important to realize that, while the inside base of the inner integument is shifting upwards, the outside base seems to remain where it is, down near the inside base of the outer integument.

The insertion region of the inner integument, as it were, is enlarged greatly. In *Ricinus* the development of the seed presents us with a similar process. Singh (1954) stated that here 'the active proliferation of the chalazal area is the factor responsible for most of the enlargement of the seed. Due to its activity the distance between the bases of the outer and inner margins of the inner integument increases considerably'. Exactly this leads also to the understanding of the seeds of Myristicaceae. Corner (1976) remarks that in some Euphorbiaceae, e.g. *Cleidion* and *Ricinus*, the pachychalaza affects only the

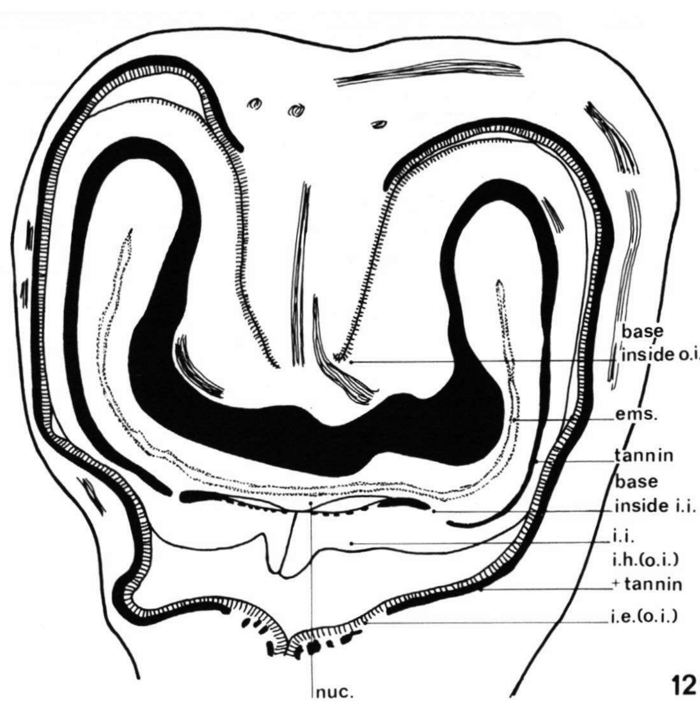


Figs. 1–7. The development of ovules into seeds in *Horsfieldia* spp. Outline drawings of microtome sections. — Fig. 1. *H. iryaghedi*; Figs. 2–3. *H. glabra*; Figs. 4–7. *H. sylvestris*. All 30 ×, except fig. 7 which is 15 ×.

tegmen. It is agreed that the region of the ovule where the integuments are inserted, is called the chalaza (Netolitsky, 1926). However, it should be realized that a sharp demarcation of chalaza, nucellus (endosperm), and integuments is not possible, not in post-initation stages anyway. A better demarcation may result from tracing the cell families at the time of initiation of the inner integument (cf. Bouman 1974). It is the region at the level of the insertion of the inner integument which proliferates very actively, preceded already by the base of the nucellus in very young ovules. In this way a new chalazal tissue is formed, in which the embryosac and the endosperm penetrates, creating the prerequisites of the large ruminated seed. Besides, the new chalazal tissue shows its own pecularities. There is a basin-shaped chalazal meristem in line with, but not contiguous to, the inside base of the inner integument. This meristem seems partly



Figs. 8–12. The development of ovules into seeds in *Knema* spp. — Fig. 8. *K. tomentella*; Figs 9–12. *K. laurina*. All 30 ×.



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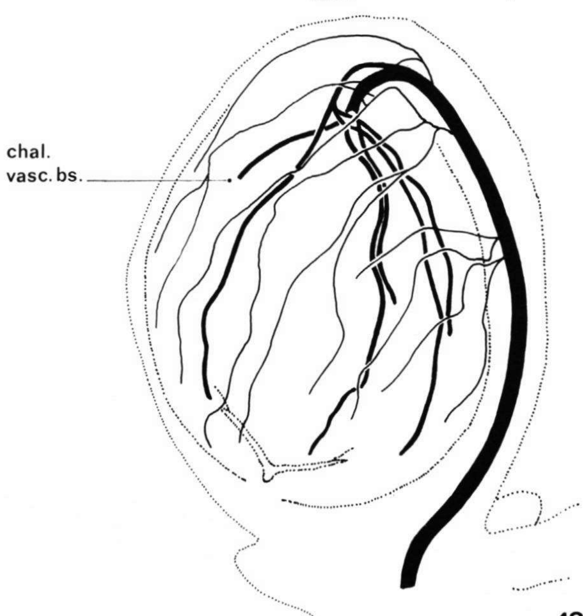

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Fig. 13 *Myristica fragrans*. The two vascular bundle systems as seen in a young seed made transparant. 15 ×.

responsible for the later active growth. Later on this region differentiates into tanniniferous cell layers, which likewise are not contiguous to the tanniniferous inner epiderm and hypoderm of the inner integument. The discontinuity is caused by a girdle of small undifferentiated cells which remains at the inside base of the inner integument. This construction may, I guess, facilitate the germination of the seed. Just below the chalazal meristem an inner vascular bundle system develops, which notably does not extend upwards further than the inside base of the inner integument. A lateral and basal extension of the new mass of tissue, which takes place around the vascular bundle entering the chalaza, is the cause of a double palisade of lignified cells. Some local thickening of the outer integument is also involved. These palisade layers represent firstly the inner epidermis of the outer integument and secondly the outer epidermis of the inner integument. However, a histogenetic study must prove the second attribution. In this way a stalked or attenuate inside ovular body is enveloped by the outer integument. The beginning of this process is shown in fig. 5. This process resembles the formation of a heteropyle, as described by Corner in Bixaceae.

The ruminations are finger-like intrusions of the chalazal part of the seed coat into the endosperm. Right at the tip of the seed a tiny region remains without such intrusions, namely along the inside surface of the inner integument. A strictly integumental concept of the seed coat could not explain why the upper part of the inside of the tegmen would not give intrusions.

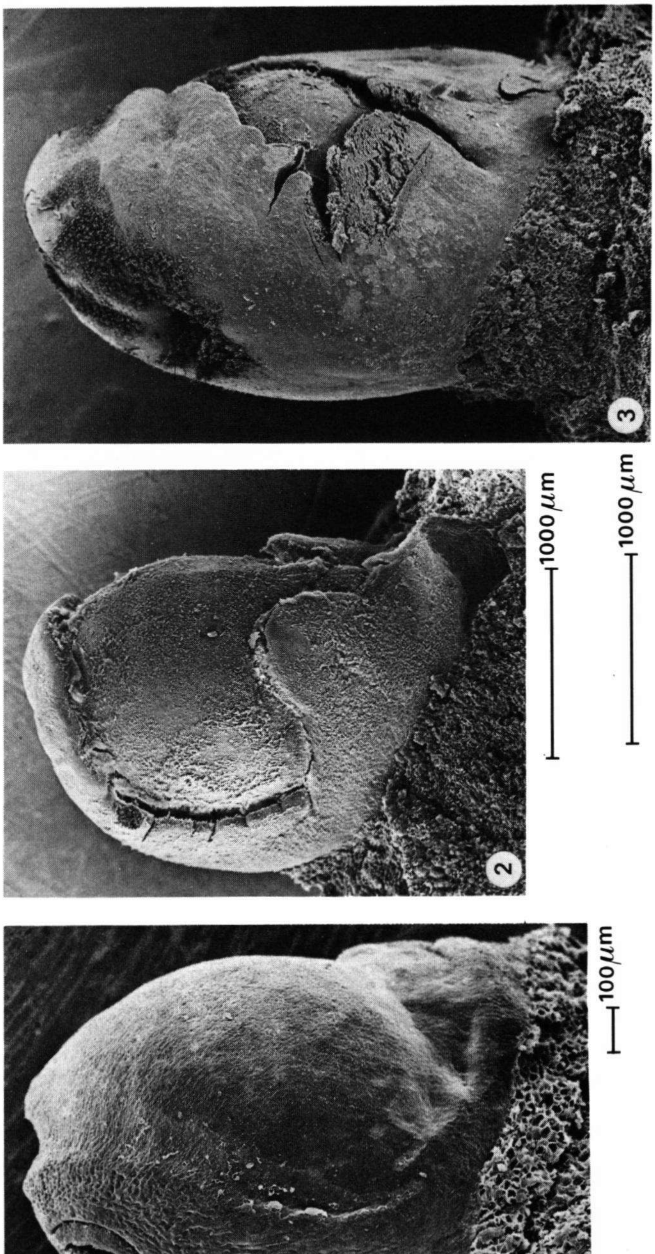
As explained above, the inner vascular bundle system runs into the chalazal part of the seed coat, not extending beyond the inside base of the inner integument. A strictly integumental concept of the seed coat would imply that a vascular bundle system – the inner one – runs into an inner integument. However, inner integuments of Angiosperms do not have vascular bundles, except in some Euphorbiaceae (Bor & Bouman, 1974).

Chalazal development of seeds can be related with the formation of ruminated seeds (Periasamy, 1962). Near to the Myristicaceae families involved are the Annonaceae, Eupomatiaceae, Degeneriaceae, Austrobaileyaceae, and Hernandiaceae. For Austrobaileyaceae (Endress 1980), and Hernandiaceae (van Heel 1971) it is known that the inner integument plays no role in seed development.

In *Horsfieldia* ovules occur which are hemi-anatropous. These ovules show more clearly than the fully anatropous ovules of *Myristica* that the aril develops from the base of the ovule as well as from the regions of the exostome, as one continuous thickening of the testa and its subsequent lobed outgrowth. Scanning photos 1–3 show increasingly older stages of development. The vascular bundles of the aril may also connect with those of the distal region of the outer integument (figs. 7 and 11). Possibly this connection is a late one.

ACKNOWLEDGEMENT

My sincere thanks are due to the Director of the Kebun Raya, Bogor, Indonesia, who gave me the opportunity to work there for a period in 1969. This visit was subsidized by the 'Stichting voor Wetenschappelijk Onderzoek van de Tropen' (WOTRO), the 'Maatschappij voor Wetenschappelijk Onderzoek in de Tropen (Treub Maatschappij), the 'Greshoff's Rumphius Fonds', and the 'Van Leersumfonds'.



Photos 1–3. The development of the aril in *Horsfieldia sylvestris*.

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