

## INTEGUMENTARY STUDIES IN THE POLYCARPICAEE

### II. MAGNOLIA STELLATA AND MAGNOLIA VIRGINIANA

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#### SUMMARY

The histogenetic development of the integuments of two representatives of the Magnoliaceae, *Magnolia stellata* and *M. virginiana*, was studied. The mode of development is the same in these two species. The two integuments have a different form of initiation: The inner integument (i.i.) is wholly of dermal derivation, whereas the primordium of the outer integument (o.i.) is formed as the result of cell divisions in the first subdermal cell layer. There is no apical initial or apical growth in either integument. The initials of the i.i. form rows of cells by repeated periclinal cell divisions, which rows develop independently in mutual juxtaposition to form a ring-shaped wall, the whole structure remaining meristematic. The i.i. is mainly three-layered, the o.i. is (in the younger stages at least) four-layered. The micropyle is formed by both integuments. The i.i. only becomes thicker by "secondary" cell divisions in the micropylar region. After fertilization appreciable changes take place in the o.i., the innermost cell layer forming the sclerotesta and the outer layers the vascularized sarcotesta.

#### 1. INTRODUCTION

The family of the Magnoliaceae figures largely in various phylogenetic theories, and its alleged primitive status in particular has induced many phytomorphologists to study this taxon intensively. As far as the embryological characters of the ovule are concerned, the investigations were mainly restricted to the development of the archesporium, to features of the gametogenesis, to the development of the endosperm, and to the embryogenesis. According to DAVIS (1966) the magnoliaceous ovule is anatropous, bitegmic, and crassinucellate, the micropyle being formed by the i.i. and the o.i. together. Our insight into the relations with other families of the *Polycarpiceae*, such as *Schisandraceae*, *Illiciaceae*, *Degeneriaceae*, *Annonaceae* and *Winteraceae* could be improved by comparing the various embryological features. However, reports concerning the integument and the testa are scarce and not sufficiently detailed. The few publications dealing with integument development already indicate quite clearly that there are appreciable differences in the histogenesis of the integuments between different families of the Angiosperms (compare WARMING 1913, ROTH 1957, BOESEWINKEL & BOUMAN 1967, BOUMAN 1971 a, b). The multi-layered integuments of the *Liliiflorae* (BOUMAN 1971 a) and some *Polycarpiceae* (e.g., present paper), for instance, are formed in a fundamentally different way, although their ultimate (mature) stages are very similar (HUBER 1969).

There are strong indications of the constancy of the histogenetic features of integument initiation and of other embryological characters within a taxon. The possible contribution of a greater knowledge of these histogenetic processes to taxonomic and phylogenetic inquiry has been the principal stimulus of the present study. Owing to the small number of relevant publications, as yet no generalizations can be drawn up. Line drawings illustrating embryological papers sometimes provide certain indications, but as a rule they are too inadequate to permit the drawing of more definite conclusions concerning the histogenetic development of the integuments. The descriptions of integuments and of their mode of growth are, generally speaking, too incomplete to be useful: mostly only the ultimate number of cell layers is recorded.

The first report concerning the genus *Magnolia* is from ASA GRAY (1858), who gave an accurate description of the development of the ovule into a young seed. He described the whole development of the ovule, but the histogenetic details of the later stages only, more particularly the changes in the structure of the integuments after fertilization of the ovule. Gray noted that the hard sclerotesta is formed "by the innermost layer of young cells lining the primine (i.e., the o.i.)".

MANEVAL (1914) found that in *Magnolia virginiana* the i.i. is initiated earlier than the o.i. He referred to Gray whose results he confirmed.

KAPIL & BHANDARI (1964) reported that in the mature seed of *Magnolia stellata* and of *M. obovata* the i.i. is 3 to 4 cell layers thick and the o.i. 8 to 10 cell layers. They also state that the i.i. is of dermal and the o.i. of subdermal origin.

HAYASHI (1964), who studied *Magnolia liliiflora* and *Michelia fuscata*, says: "the inner integument arises as a rim-like outgrowth from the surface of the nucellus and the development of the primordium of the outer integument follows".

BHANDARI (1967) confirmed Gray's description of the origin of the sarcotesta.

The present paper aims at a more detailed description of the initiation and histogenesis of the integuments in *Magnolia*.

## 2. MATERIALS AND METHODS

Material of *Magnolia stellata* (Sieb. & Zucc.) Blackburn and of *M. virginiana* L., collected in the Botanical Garden, University of Amsterdam, was fixed in Craff III, IV, or V, and embedded in paraffin wax or in Ralwax (because older stages of development of *M. virginiana* could not be satisfactorily sectioned in paraffin wax). Sections  $7\mu$  thick were cut and stained with Safranin according to Johanson and counterstained with Astra Blue. Camera lucida drawings were made of selected sections: since not perfectly median longitudinal sections of an ovule may give cause to misinterpretation, only the best sections selected from a total of 488 slides were used. Integument development in *Magnolia virginiana* could be followed to the stage of seed maturity, but in *M. stellata* only up to the stage of closure of the micropyle after fertilization owing to incomplete seed setting. Presumably the Dutch climate is too cold for *M. stellata* to produce mature seeds, whereas in *M. virginiana* mature seeds develop quite regularly. As far as

can be ascertained, the ultimate integument development is the same in the two species studied.

### 3. HISTOGENETIC ANALYSIS

#### 3.1. Generalities

According to LEINFELLNER (1967) the carpel of *Magnolia* belongs to the peltate type. The only indication is the presence of a ventral-median vascular trace. The vascular innervation of the ovules is supplied by branches of this trace (*v.m.* in *fig. 1*), which is a derivative of the inner ring of vascular bundles in the floral axis. In each pistil two ovules develop at the same level. *Fig. 1* shows a part of a section through a flower perpendicular to the floral axis showing the ovules in juxtaposition. The bending of the ovule to become anatropous occurs in a "horizontal" plane, i.e., in a plane perpendicular to the floral axis. A transverse section through the flower, accordingly, provides the required longitudinal section through the ovules (compare *fig. 1*). The curvature of the ovule is brought about by a somewhat faster growth at one side of the ovule primordium (*fig. 2*). The i.i. appears a short time before the o.i. and initiates first at the concave side of the ovule from where it extends laterally to form ultimately a circular raised wall around the nucellus primordium.

The subdermal cells of the ovule primordium divide periclinally and thus make the nucellus grow (*fig. 3a*). One of these cells, distinguished by its larger size, becomes the archesporium cell which in turn divides into a macrospore mother cell and a parietal cell, etc.

The i.i., in contrast to the o.i., is entirely of dermal origin, but at the base of the i.i. also some periclinal divisions occur in the subdermal tissue, so that this part (the chalazal zone) becomes slightly broader (*fig. 3*). The o.i. is initiated by the periclinal divisional activity of these subdermal cells. From this stage onward the rate of growth of the two integuments remains about the same.

Whilst the ovule is bending, the o.i. overgrows the distal part of the ovule as a cap (see *fig. 2*). When the curvation is completed the micropyle lies near the funicle (*fig. 2d*). On the chalazal side of the ovule a large mass of parenchymatic tissue develops (*fig. 3c*, the area left white). This, like other developmental features, is clearly associated with a future function in seed dispersal. At maturity this parenchymatic tissue forms a part of the fleshy sarcotesta with oil cells which is bright orange on the outside. The innermost cell layer of the o.i. forms a protective sclerotesta around the enclosed parts of the seed containing the endosperm and the embryo.

The funicular vascular strand bifurcates near the chalaza, one of its branches ending in a dendroid ramification in the hypostase where the vascular elements become surrounded by tannin-containing tissue deeply staining with Safranin, and the other branch soon bifurcating once more into strands innervating the o.i. (*fig. 5*).

At maturity the fruit of *Magnolia virginiana* dehisces along a dorsal groove (*dg* in *fig. 1*), which does not coincide with the closed suture of the carpel mar-

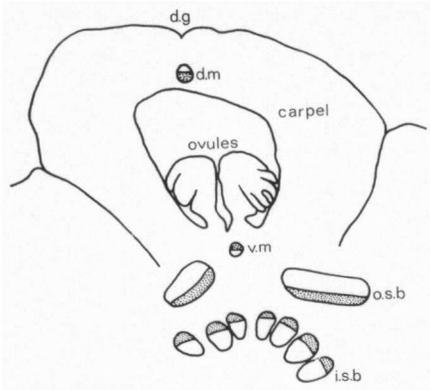


Fig. 1. Transverse section through the carpel at the level of insertion of the ovules (d.g. = dorsal groove). One of the inner ring of stelar bundles (*i.s.b.*) has moved outward and enters the pistil base between two bundles of the outer cortical system (*o.s.b.*), subsequently to divide into the ventral-median (*v.m.*) and the dorsal-median (*d.m.*). The *v.m.* sends off branches to the ovules. The two bundles *o.s.b.* also split off branches which enter the carpel and run along the margin of the conduplicate part of the pistil.

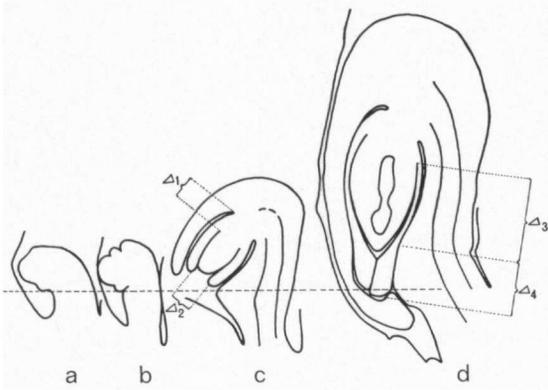


Fig. 2. Longitudinal sections of ovules in different stages of development drawn in outline; *a* represents the stage of initiation of the *i.i.*, *b* the phase in which the *o.i.* is initiated, *c* the further development of the ovule, and *d* a young seed.

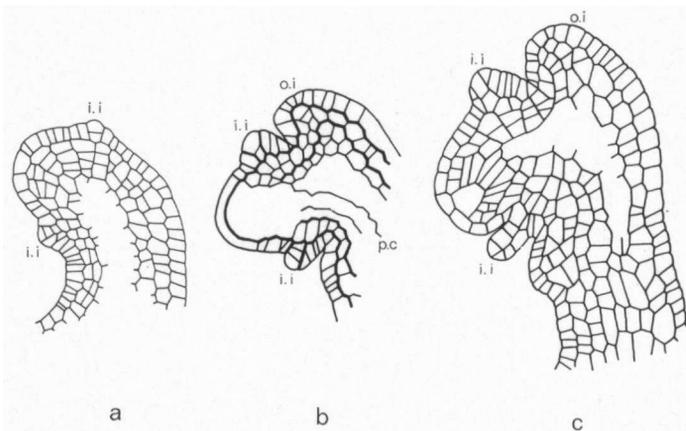


Fig. 3. Successive developmental stages of an ovule: *i.i.* = inner integument, *o.i.* = outer integument, *p.c.* = procambial strand.

gins. The brightly coloured seeds protrude from the desiccated fruit valves. We did not observe seeds hanging on thread-like funicular remains as repeatedly reported in the literature. Upon a light touch the whole infructescence drops off, because the stalk becomes separated from the supporting branch by a preformed zone of abscission. Only part of the ovules develop into seeds, so that in the majority of the follicles only one seed matures, and in some two seeds or none at all.

3.2. The inner integument

The i.i. is entirely of dermal origin. The subdermal tissue at most forms a slight outward bulge (*figs. 3 and 4*). In a median section the first indications of integument initiation are usually confined to three cells (*a, b, c*) which show periclinal divisions. There is some variation in the number and in the orientation of the walls formed during these divisions (compare *figs. 7a, b, c, and fig. 8*). The outer two cells of the integument primordium do not divide quite periclinally as a rule, but by means of a more oblique wall which is always oriented in such a way that a daughter cell is formed obliquely leaning up against the central initial. The resulting cellular arrangement is highly characteristic (*figs. 7b and 8b*). Such slanting cell walls are produced in larger numbers on the abaxial side of the primordium than on the opposite side (*figs. 3c, 4a and b, 7c*). The

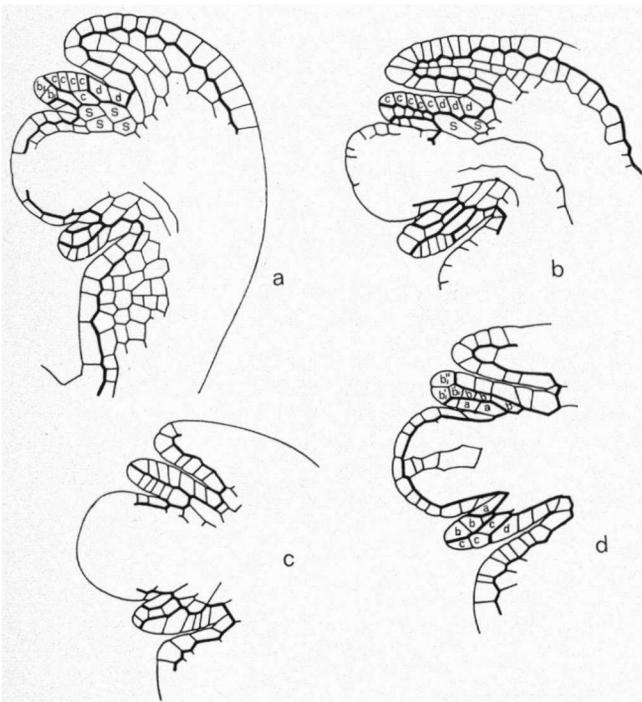


Fig. 4. Various cell patterns in the growing integuments.

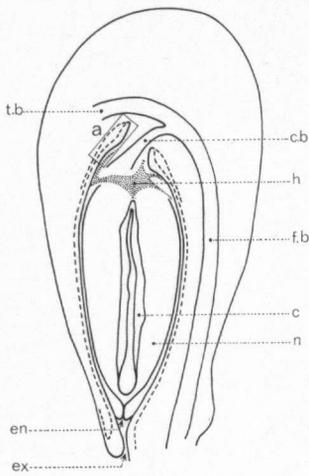


Fig. 5. Diagrammatic median section through a young seed: *f.b.* = funicular bundle, *t.b.* = tegumentary bundle, *c.b.* = chalazal bundle, *h* = hypostase, *c* = embryo sac with endosperm, *n* = nucellar tissue, *en* = endostome, *ex* = exostome. (The dotted area represents the tannin-containing tissue).

rate of cell division is therefore, relatively, greater on the one side, so that the integument is pressed against the nucellus.

On the adaxial side of the primordium the first periclinal wall formed is usually more transversely oriented (see, e.g., *fig. 8b*).

The initially very narrow zone of the ovule primordium lying between the bases of the i.i. and o.i. ( $\Delta_1$  in *fig. 2*) gradually increases in size. This is accompanied by a typical mitotic activity (of the cells marked *d* and *s* in *figs. 4a* and *4b*, for instance). The tissue in this area forms the hypostase.

The various configurations of the integument primordium can be recognised in the more advanced stages of development. The pattern shown in *fig. 4b*, for instance, can be traced back from *fig. 7b*. The cells *a*, *b* and *c* of the integument primordium thus correspond with the three rows of cells of the basal part ( $\Delta_3$  in *fig. 2*). In this case the conclusion may be drawn that the three initials *a*, *b* and *c* have each formed a row of cells by periclinal divisions. This simple description does not always hold, as can be deduced from *fig. 4a*. The cells exhibit a certain amount of opportunism in the determination of their ultimate destination. Although the integument is for the greater part three-layered, it appears two- or four-layered in some sections. *Fig. 8a* demonstrates how a four-layered pattern can be initiated, but a two-layered condition (as in *fig. 4c*) can only originate from an initiation by means of two periclinally divid-

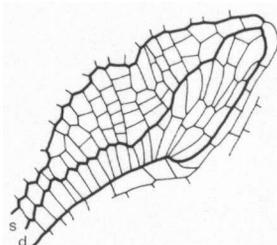


Fig. 6. Detail of the inner two layers of the o.i. (cut out *a* in *fig. 5*) during the formation of the sclerotesta. The cells of the dermal layer become extended and divide periclinally. Around the hilum the subdermal cells divide periclinally.

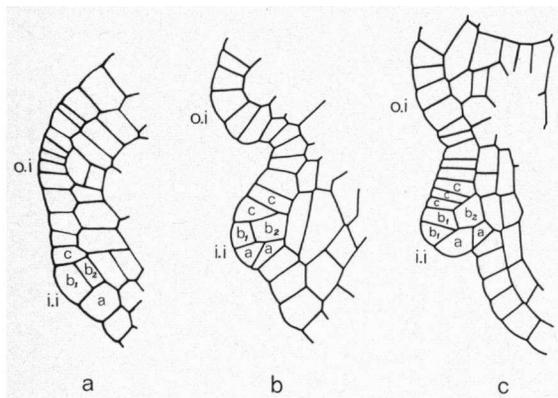


Fig. 7. Successive stages of initiation of the i.i.; o.i. = outer integument. Daughter cells of the same initials ("cell families") are indicated by the same letter.

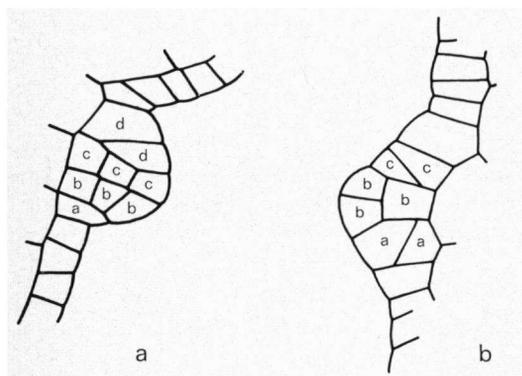


Fig. 8. Initiation of the inner integument.

ed cells. Also from *fig. 4d* one can easily reconstruct that a two-layered structure develops by the failure of cell *a* to divide. In all these cases the growth is homogeneous, all cells remaining meristematic. Growth by means of an apical cell, as described for *Capsella* by ROTH (1957), does not occur.

The cells marked *b*<sub>1</sub> in the figures have a great share in the formation of the micropylar region. The newly formed cell wall in this cell is, properly speaking, anticlinal again, and this is rather characteristic. Already at this stage of development in the primordium a basal portion ( $\Delta_3$  in *fig. 2d*, cells *b* in *fig. 4d*) and a micropylar part ( $\Delta_4$  in *fig. 2d*) can be distinguished. The basal portion encloses the nucellus as a cup and must increase in girth appreciably as the nucellus grows larger, whereas the distal region tends to become narrower in connection with the formation of the endostomium ( $\Delta_2$  in *fig. 2c*). The position of the cells *b*<sub>1</sub> of *fig. 4a* is reflected in the later stages of the histogenesis of the micropylar region (compare *fig. 4d* & *9a*). The cell *b*<sub>1</sub>' of *fig. 4d* has undergone several mitotic divisions to produce the cell pattern shown in *fig. 9a*. The situation of the cells *b*<sub>1</sub>' in this figure is typical. *Fig. 9b* shows that the inner cell layers contribute towards the formation of the micropylar portion of the i.i. by dividing periclinally. The cellular pattern of the closed micropyle is rather irregular (*fig. 9c*);

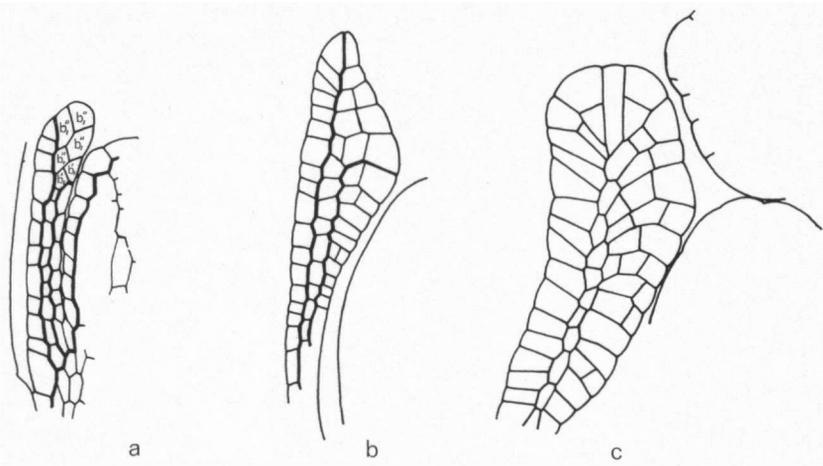


Fig. 9. Successive developmental stages of the micropylar part of the integument.

the various cell families are not clearly distinguishable. The longitudinal extension of the basal part of the i.i. comes about by intercalary growth. Sometimes its growth proceeds at a faster rate than the growth of the nucellus, so that a small gap appears between the i.i. and the nucellus. This changes after fertilisation has taken place.

The rapid increase in volume of the ovule during seed setting seems to stretch the outer layer of the i.i. passively, so that its cells become extended and flattened. The other cell layers grow along actively and the shape of the cells does not change appreciably (*fig. 10*).

Also during the final stages of seed setting the i.i. usually remains three-layered. No vascular strands develop. The i.i. does not contribute substantially to the formation of the testa; it "*persists as a papery layer*" (BHANDARI 1967).

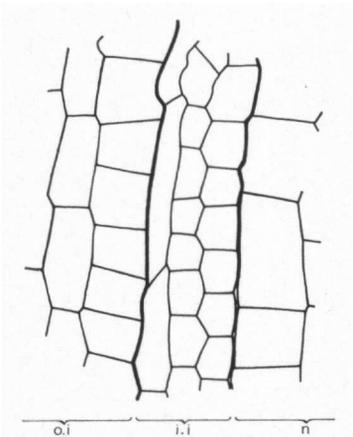


Fig. 10. Longitudinal section of the i.i. of a young seed. *n* = nucellus.

3.3. The outer integument

The o.i. originates on the convex side of the ovule primordium. At the place of its initiation the cells of the dermal layer start dividing anticlinally (fig. 7a). The subdermal tissue below these cells forms a bulge by periclinal divisions. When viewed under a dissecting microscope, the o.i. appears in this stage of development as a ring-shaped wall interrupted at the concave side where a separate outward bulge is formed (see fig. 11). It is not quite clear if these two parts, i.e., the bulge on the inner side and the horseshoe-shaped wall on the dorsal side, are initiated separately or as a ring-shaped meristem. Both parts of the young o.i. are visible in a median section of the ovule (see figs. 2, 3 and 4). During the process of bending of the ovule the dorsal part of the o.i. overgrows the nucellus as a cap. The histogenesis proceeds qualitatively in the same way in the two parts, viz., by periclinal divisions in the subdermal cell layers which produce parallel rows of cells (fig. 12). Also during later developmental stages no apical cell growth occurs, all cells remaining meristematic. In fig. 13 are shown two cells in the apical part of the growing o.i. dividing almost simultaneously.

In the drawings showing the general aspects of the growing ovule (fig. 2) an appreciable elongation of the funiculus above the horizontal line can be observed. The anticlinal cell divisions responsible for this growth in length occur more frequently than the periclinal divisions of the integument initiation on the funicular side (fig. 12). The fold between the o.i. and the i.i. thus becomes deeper as a result of this growth process. The anticlinal mitotic activity is stronger on

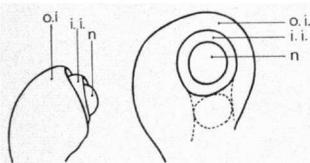


Fig. 11. Young [ovule] viewed from the micropylar side. The o.i. does not develop as a ring wall but as a cap and forms a bulge on the funicular side. n = nucellus, i.i. = inner integument.

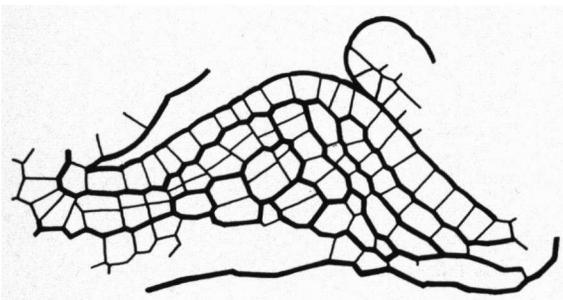


Fig. 12. Longitudinal section of o.i. at the funicular side (the "bulge").

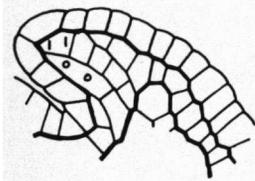


Fig. 13. Primordium of the o.i. showing mitotic activity in the subdermal layer.

the dorsal side and causes the curvature of the ovule. The dorsal part of the o.i. remains pressed against the i.i. and the nucellus because also in this region the growth rate is higher at the dorsal side of the ovule. The unequal growth rates gradually bend the ovule over into its final anatropous position.

The o.i. and the i.i. keep pace when they overgrow the developing nucellus, so that their rims remain in juxtaposition and ultimately form the micropyle. The dermal layer of the developing o.i. remains one cell thick until the level of the endostome has been attained and it remains one-layered at the antiraphe side. The exostome proper is formed by periclinal cell divisions in the dermal layer of the *lateral* sides of the o.i. and of the bulge on the funicular side. This differential apical development of the o.i. produces a T-shaped exostome partly overlying the circular to elliptic endostome which suggests in the longitudinal sections of the ovule (if not exactly median) that the o.i. protrudes much beyond the i.i. The structure thus formed at the funicular side of the micropyle has been described by KAPIL & BHANDARI (1964) as an "incipient obturator". In these later stages of development vascular bundles become differentiated in the o.i. The raphal bundle first splits off a branch to the hypostase to bifurcate more distally into two strands innervating the o.i. proper. Several small offshoots penetrate into the massive parenchymatic tissue on the chalazal side.

After fertilization has taken place considerable structural changes occur in the o.i. The cells of the inner dermal layer of the o.i. become stretched and appear very much extended in a transverse section of the ovule (*d* in *fig. 6*), but at the same time periclinal cell divisions occur which produce columns of superimposed cylindrical cells. This layer becomes sclerotic to form the hard sclerotesta. The growth in the longitudinal direction proceeds at a much faster rate around the chalaza, so that a kind of pit-like perforation of the sclerotesta is formed ("heteropyle") which surrounds the ingoing vascular bundle (*figs. 5* and *6*). The tissue surrounding the heteropyle is formed by the second cell layer (see *s* in *fig. 6*). The parenchymatic tissues of o.i. and funicle grow out to form the massive sarcotesta which is more strongly developed on the chalazal side, as we have seen (*fig. 2, fig. 5*).

#### 4. DISCUSSION

The occurrence of a single integument among the more advanced Angiosperms has suggested to many workers that the bitegmic condition is the most primitive (TAKHTAJAN 1959, 1969; EAMES 1961). The histogenesis of the integuments of *Magnolia* described in the present paper (*viz.* a 2- to 4-layered i.i. of dermal derivation and a subdermally initiated o.i.) clearly differs from the condition in *Capsella* (both integuments of dermal origin, two cell layers thick), in *Lilium* (both integuments of dermal origin, the o.i. becoming "secondarily" multi-layered), and in *Lactoris* (both integuments of dermal initiation, the i.i. "secondarily" three-layered). Apart from the number of integuments, the mode of integument initiation and the histogenesis appear to provide useful taxonomic and phylogenetic criteria. The growth of the integuments in *Capsella* is brought

about by apical cell growth or by a marginal meristem, for instance, whereas the growth of the integuments in *Magnolia* is unlocalized. This implies that the histogenesis of the integuments must be taken into account in discussions concerning the homology of integuments: are all inner integuments homologous and all outer integuments also phytomorphologically equivalent, and is the solitary integument in unitegmic taxa the homologue of the o.i., or of the i.i., or is it a fusion product of the two?

According to TAKHTAJAN (1969) "*the basic primitive type of seed coat (testa) in the Angiosperms (is) the Magnolia-type with its strongly developed peripheral layer of parenchyma cells*". He continues as follows: "*Endozoochory, possibly reptilian, was probably characteristic of the earliest Angiosperms*", and clearly assumes a relation between seed structure and seed dispersal. It is noteworthy in this connection to mention VAN DER PIJL'S (1969) opinion concerning the angiospermous seeds with a sarcotesta: "*Of course one could also explain all these cases of a sarcotesta as adaptive convergence, without assuming genetical links with Gymnosperms. However, in my opinion the common roots emerging from basic stock are clear. The cases treated in this chapter belong to: Magnoliaceae, Annonaceae, Winteraceae, Degeneriaceae, Dilleniaceae, Paeoniaceae, Berberidaceae, Flacourtiaceae, Euphorbiaceae, Meliaceae, Sapindaceae, Leguminosae, Sterculiaceae, Violaceae and Bixaceae. Further examples are provided by Liliaceae, and Palmae (Lepidocaryoideae). A reversal of a hard testa with specialized palissade tissue to a parenchymatous testa seems improbable*". According to A. D. J. Meeuse (priv. comm.), Takhtajan's and Van der Pijl's ideas are too one-sided: anemochory occurs in, e.g., *Welwitschia*, and the "sarcotesta" reported in seventeen divergent families is not necessarily always the same structure in a strictly phytomorphological sense (the sarcotesta is not necessarily homologous throughout these taxa). The differences in integument development, considered to be of at least some morphological and semophyletic significance by the present authors, is rather suggestive of a greater diversity and overconfident generalizations concerning seed coat morphology are to be received with diffidence.

The almost universally made distinction between integument(s) and seed coat needs some discussion. In an ontogenetic sense these are two names for the same organ, the younger stage being called integument, the older one testa. In a functional and ecological sense they are very different, however. Both have some protective function, it is true, but the soft integument is not by far equal to a sclerotesta in this respect, the function of the integument being the conduction of the pollen tube. After seed setting, however, the seed coat (or a part of it) often has some function in seed dispersal (e.g., in *Magnolia*) and the necessary provisions are made. The often very profound changes in the testa during its maturation, as described here for *Magnolia*, are connected with the ultimate function. However, in different angiospermous taxa seed dispersal is effectuated in a number of basically different ways, and the testa development differs accordingly. It is to be expected that seeds with the same dispersal mechanism show a greater uniformity in testa development, whereas seeds with a different

ecology exhibit differences especially during the advanced stages of seed coat development even if the taxa are closely related. The seed and testa of *Schisandra* differ appreciably from those of *Magnolia*, for instance, but as far as can be gleaned from descriptions and illustrations the mode of initiation and ovule development up to the stage of anthesis are very similar to the ovular histogenesis in *Magnolia* (YOSHIDA 1962; HAYASHI 1963; KAPIL & JALAN 1964). Generalizations based on the ultimate structure are obviously misleading, certainly as regards the early development of the ovular organs.

Text and illustration of embryological papers relating to *Magnoliaceae* point to a uniform type of integument development within this family with the possible exception of *Michelia*. The available data are inadequate, however, and they still require verification by means of detailed histogenetic studies.

#### ACKNOWLEDGEMENT

The assistance and critical advice received from Professor A. D. J. Meeuse, who is also responsible for the English translation of the manuscript, is gratefully acknowledged. We also wish to express our thanks to Mr. J. Vuijk for his help in making the illustrations ready for the press.

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