

ANATROPY AND ONTOGENY OF THE BITEGMIC OVULE IN *CHROZOPHORA* A. H. L. JUSSIEU (EUPHORBIACEAE)

J. BOR and R. N. KAPIL

Hugo de Vries-Laboratorium, Universiteit van Amsterdam and Department of Botany,
University of Delhi, Delhi-110007, India

SUMMARY

A study of the initial ontogeny and curvature of the ovule in *Chrozophora obliqua* and some other euphorbiaceous taxa explains why the outer integument develops asymmetrically in bitegmic anatropous ovules. The almost simultaneous occurrence of periclinal divisions in the dermatogen of the outer integumentary primordium and funicle and the synchronous elongation of both funicle (viz. the raphe) and outer integument (antiraphe) strongly support the idea that this integument and the raphe are derivatives of the funicle. The primordium of the inner integument, on the other hand, appears to be an independent rim-like outgrowth of the nucellar base. Therefore, inner and outer integuments are not homologous appendages from an ontogenetic point of view and the concept of 'congenital fusion' must be discarded as an explanation. It has also been proposed that the dividing line of nucellus and funicle is situated between the attachment zones of the inner and the outer integument. Accordingly, the term "nucellus" is to be defined as that part of the ovule which is completely surrounded by the inner integument.

Both the integuments are initiated by periclinal divisions of a subdermal initial and further divisions result in the vertical growth of the primordia. The outer integument becomes multi-layered as a result of characteristic radial divisions in the subdermal layer, and a vascular bundle differentiates at its periphery. The large, curved nucellar beak is principally of dermal origin. A hypostase differentiates below the embryo sac during prefertilization stages, whereas the development of a nucellar podium takes place only after fertilization. The caruncle consists mainly of an aerenchymatous tissue.

The diagnostic value of a number of distinctive ovular features in Euphorbiaceae has been discussed; the general occurrence of a nucellar beak and especially a thick, subdermally derived and vascularised inner integument in the taxa constituting the subfamily Crotonoideae s.s. seem to indicate that this is a homogeneous group.

1. INTRODUCTION

The embryology of *Chrozophora* was recorded earlier by one of us in three representatives of this genus (KAPIL 1956a, b); however, not much attention was given to the study of the ovular ontogeny. As the initial ontogenetic processes show a striking similarity and follow certain patterns, at least within the subfamilies Acalyphoideae, Crotonoideae and Euphorbioideae (cf. WEB-

STER 1975), it is likely that such ontogenetic features, when used as taxonomic characters, will throw some light on phylogenetic relationships¹.

Besides, we have also re-evaluated the concept of anatropy, as related to the initial development and delineation of funicle, nucellus, and integuments. The anatropous, bitegmatic ovule is the most common type found among angiosperms, but the origin of anatropy has not been satisfactorily explained, as the majority of ovular studies are based on stages in which the integuments have already appeared (STRASBURGER 1872, 1879 and WARMING's extensive paper of 1878 are among the few exceptions). This has resulted in a number of traditionally accepted, but controversial, morphological interpretations which are briefly summarized below (see also under "Discussion").

Although MIRBEL (1829) was the first to introduce the term "*ovulum anatropum*", SCHLEIDEN (1837) gave an authoritative definition of the curvature which has been accepted by many morphologists: "*Dieses Ende der Axe [funicle]² erleidet nun häufig eine Krümmung, so dass seine Spitze [nucellus]² auf sich selbst zurück gebogen wird... und mit dem gerade bleibenden Theil (raphe) verwächst*". BAILLON (1876, pp. 167–8) related the development of the anatropous ovule to the form of the ovular primordium ("*mamelon primitif*") which, immediately after its inception, can either be erect or somewhat curved. In the first instance the nucellus is inverted completely in relation to the funicle during, and after, the appearance of the circular swelling which represents the inner integument ("*ovules anatropes réfléchis*", e.g., Ranunculaceae). In the second group (e.g. Euphorbiaceae) Baillon suggests that the anatropy is caused by a unilateral development of the different ovular portions. Other authors (STRASBURGER 1872, 1879; WARMING 1878; GOEBEL 1923; NETOLITZKY 1926) uphold the latter viewpoint, especially with regard to the outer integument. More recently Bocquet and Bersier emphasized that: "*The very early bending of the ovule beneath the chalaza is the basic phenomenon which is characteristic for anatropy*" (BOCQUET 1959; BERSIER 1960; BOCQUET & BERSIER 1960).

Integuments are supposed to originate at the base of the nucellar primordium (NETOLITZKY 1926, p. 31) or below the nucellus, i.e., in the chalazal or distal funicular region (see SCHLEIDEN 1837, p. 307; STRASBURGER 1879, p. 35; GOEBEL 1923, p. 1734; WARMING & POTTER 1932, p. 242). The inner integument arises as a ring-like swelling, whereas the outer integument is usually only conspicuous on the side opposite the funicle (convex side of the ovule, i.s.), and... "*is suppressed on the side next to the funicle...*" (MCLEAN & IVIMEY-COOK 1956, p. 1391; see also GOEBEL 1923, pp. 1723, 1734). Or: "*...fusion of the outer integument and the funicle is congenital and histological evidence of this union is lacking*" (EAMES 1961, p. 259; see also SCHLEIDEN 1839, p. 35; PURI 1970 p. 3; FAHN 1974, p. 534 etc.).

¹ In the subfamily Phyllanthoideae not only the structure of the seeds is very different (CORNER 1976), but also the initial ontogenetic processes display a dissimilarity, for instance, as regards the origin of the inner integument (which is dermal in *Antidesma*, *Bischofia*, *Phyllanthus* and *Securinega*).

² Parentheses ours.

STRASBURGER (1872, p. 416) described this remarkable phenomenon as: "... er [outer integument]² greift zu beiden Seiten um die Samenknospe und schliesst an das Gewebe des Funiculus an...", and many later authors followed him.

2. MATERIALS AND METHODS

Our observations are based on slides of *Chrozophora obliqua* and *C. rottleri* made earlier for a study of their life cycle (see KAPIL 1956a, b). The illustrations (except fig. 5) are original, and were necessitated by a better understanding of the ontogeny of the euphorbiaceous ovule.

3. EARLY OVULE DEVELOPMENT

Initial Ontogeny – The three ovular primordia arise on the apical flanks of the floral axis and consist of a number of characteristic layers, referred to as dermatogen (1_1), subdermatogen (1_2) and central core (1_3), respectively (fig. 1A, B). They begin to curve immediately after inception due to a higher mitotic activity in the peripheral cell layers at the basal, abaxial side of the primordium (abaxial growth). As soon as the archesporial cell divides to form primary sporogenous and parietal cells, the apical dermal cells also begin to divide periclinally (fig. 1C). Simultaneous mitotic activity in subdermatogen and dermatogen is thus responsible for the prominent apical growth of the nucellus.

The inner integument becomes visible as a circular swelling around the base of the nucellus, just above the curved ovular region (i.e., funicle: figs. 1D, 2B). Concurrently, the outer integument appears as an elevation at the convex side of the ovule. Both integuments are initiated by periclinal divisions of a subdermal initial which push up the dermatogen. The latter layer exhibits an increased anticlinal mitosis, mainly on the outer convex side, and leading to the vertical growth of the integumentary primordia.

In the outer integument, especially, the apical dermal cells divide several times periclinally as well. In addition, a number of dermal cells of the inner funicular region, just next to the primordium of the inner integument, also starts dividing periclinally (fig. 1E; cf. BOR & KAPIL 1975, fig. 3C). This suggests that not only the inner, but also the outer integument is initiated by a ring-shaped meristem, spreading laterally from the convex side of the ovule to the inner side of the funicle. However, as the meristematic activity is much more pronounced on the convex side of the ovule, the outer integument develops from the distal funicular region as a crescent-shaped sheath.

Anatropy – In order to comprehend the anatropous curvature of the ovule, successive developmental stages have been represented in serial order (fig. 2). The position of the megaspore has been considered to be inalterable, since its basal nucellar region, i.e., the zone of attachment of the inner integument

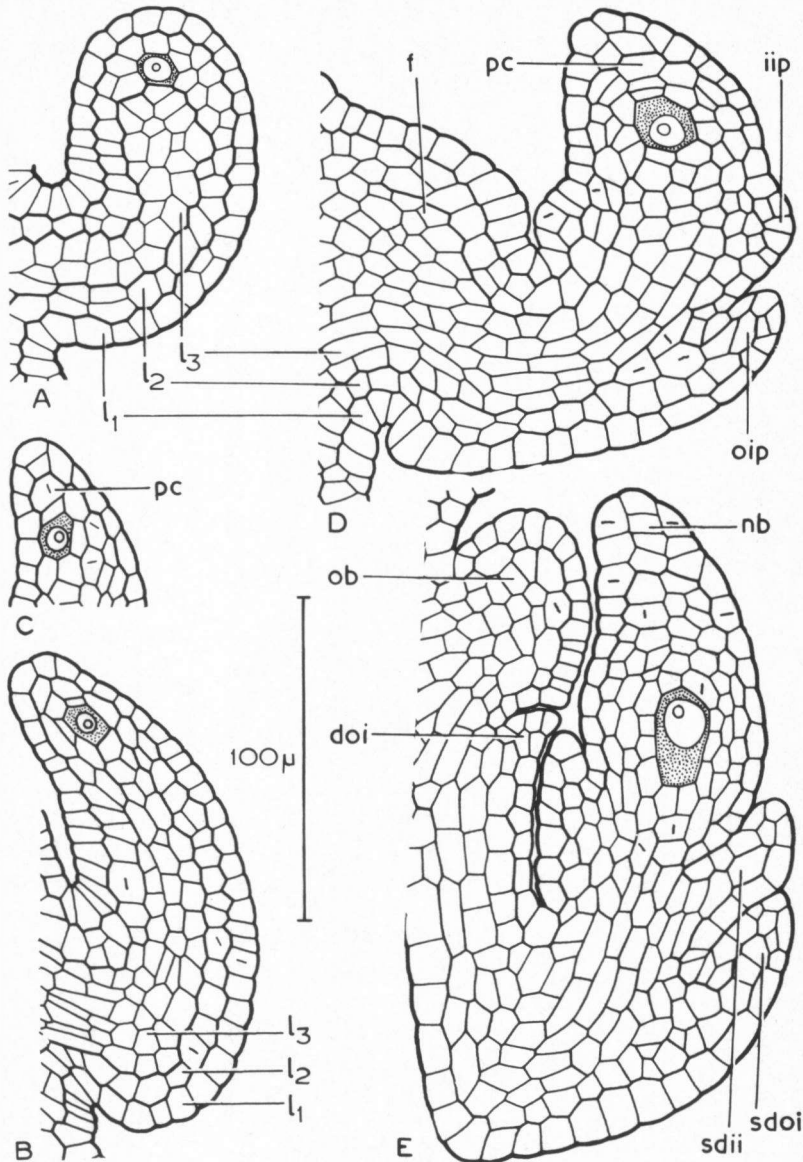


Fig. 1 A-E – Development of young ovule (*doi*, dermal initials of outer integument; *iip*, primordium of inner integument; l_1 , dermatogen; l_2 , subdermatogen; l_3 , central core; *nb*, nucellar beak; *ob*, obturator; *oip*, primordium of outer integument; *pc*, parietal cells; *sdii*, subdermal initial of inner integument; *sdoi*, subdermal initial of outer integument).

A: *Chrozophora obliqua*, l.s. ovular primordium.

B, C: *C. rottleri*, same.

D, E: *C. obliqua*, l.s. young ovule, initiation of integuments.

Three zones are separated by a thicker line: dermatogen, subdermatogen and central core are distinguishable in figures A-D.

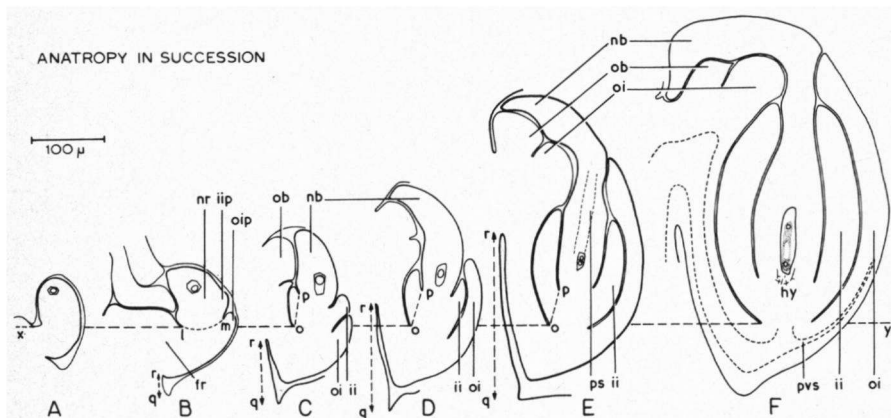


Fig. 2 A-F – *C. obliqua*, diagrams of six successive developmental stages showing anatropy and growth of ovule (fr, funicular region; hy, hypostase; ii, inner integument; iip, primordium of inner integument; l-m, dividing line of nucellus and funicle; nb, nucellar beak; nr, nucellar region; ob, obturator; oi, outer integument; oip, primordium of outer integument; o-p, attachment zone of inner integument; ps, parietal strand; pvs, provascular strand; q-r, basal axial region of locule).

A-E: L.s. ovules during megasporogenesis.

F: Same, 2-nucleate embryo sac stage.

The apical growth of the ovule takes place mainly in the region located above the axis X-Y.

(fig. 2, o-p), grows hardly during early ovular ontogeny. The strong initial curvature of the funicular region and the unilateral origin of the outer integument characterise anatropy at first. As the inversion proceeds, the central axial region below the zone of attachment of the ovule (fig. 2, q-r) elongates rapidly by intercalary growth so that this attachment zone is carried upward (cf. LANDES, 1946). Simultaneously, the funicle elongates appreciably and the funicular, outer integumentary "bulge" (fig. 1E: doi) is also carried upward. It should be noted, however, that this dermal zone is situated at approximately the same level as the distal region of the outer integument. That is to say, the growth of both the outer integument ('antiraphe', CORNER 1976) and the funicle (viz., raphe) is so neatly synchronised that together they form the continuous outer envelope of the anatropous ovule. Anatropy, thus, originates from the simultaneous functioning of several localised meristems: apical, abaxial and intercalary meristems.

4. ADVANCED ONTOGENY

Nucellus – Continuous divisions of the parietal and apical dermal cells result in the formation of a long, curved nucellar beak (fig. 3). The longitudinal rows of parietally and dermally derived cells remain distinguishable from one another, as the cytoplasm of the central parietal tissue stains more densely. Consequently, one can observe that the parietal layers are limited to the straight part of the nucellar beak, whereas the larger curved region is exclusively dermal in

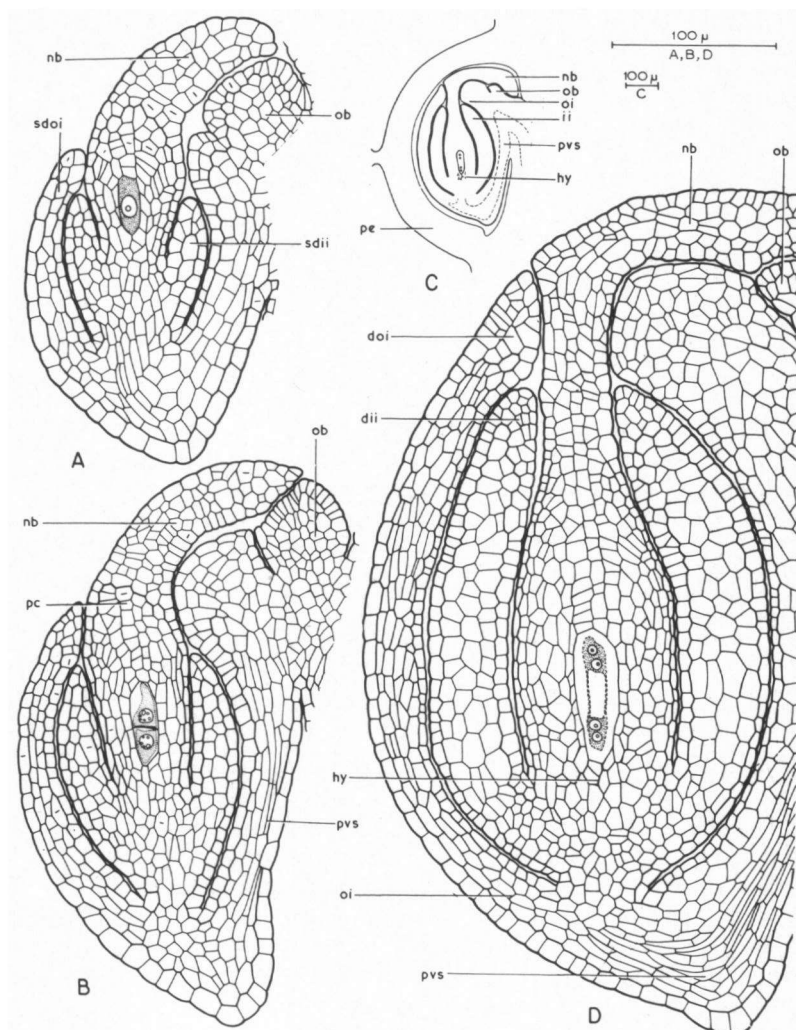


Fig. 3 A-D – *C. obliqua*, development of ovule (*dii*, dermal rim of inner integument; *doi*, dermal rim of outer integument; *hy*, hypostase; *ii*, inner integument; *nb*, nucellar beak; *ob*, obturator; *oi*, outer integument; *pc*, parietal cells; *pvs*, provascular strand; *sdii*, subdermal initial of inner integument; *sdoi*, subdermal initial of outer integument).

A, B: L.s. ovule during stages of megasporogenesis. The dermal and subdermal tissues of nucellar beak and integuments are separated by a thicker line.

C, D: L.s. ovule at 4-nucleate embryo sac stage.

origin. The subdermal cells, which initially divide anticlinally, start dividing in a radial plane as well (see fig. 4 H-K).

The initiation of the obturator, which takes place during early megasporogenesis, is basically the same as described earlier in *Euphorbia* and *Codiaeum*

(BOR & BOUMAN 1974). The development of the obturator and nucellar beak are closely correlated processes (cf. SCHWEIGER 1905). The obturator does not increase much in size after its inception and is carried upward by the growing ovule (figs. 2, 4A, F). On the other hand, the nucellar beak elongates considerably, curves sharply, and establishes a close contact with the obturator. During fertilization the tissues of both these organs become so closely pressed together that it is difficult to recognize them as individual entities. The dermal cells of the obturator elongate radially and sometimes divide transversely; the subdermal obturator tissue is characterised by the presence of druses which are also abundant in the ovarian tissue (fig. 4 L).

The central and basal nucellar regions are composed of radial rows of cells rich in amyloplasts (fig. 4 J, K). Some cells, located directly below the embryo sac, develop wall thickenings during gametogenesis. This tissue is referred to as the hypostase which reaches its maximum size at fertilization (fig. 4A, E, F, K; cf. LANDES 1946). During post-fertilization the tissue situated below the hypostase exhibits a secondary meristematic activity and forms a characteristic podium. The podium is at its base completely surrounded by the ramifications of the raphe bundle, consisting of well-developed, annular and spiral tracheids (fig. 4G). The bundle is collateral. Although the central nucellar tissue is resorbed during seed maturation, remnants of the nucellar beak, hypostase, and podium persist in the ripe seeds.

Inner Integument – The initial upgrowth of the inner tegumentary rim is mainly governed by two meristematic activities: (1) periclinal³ divisions of the apical subdermal initials and (2) anticlinal divisions of the dermal layer whose growth rate is higher on the outer side of the integument (figs. 1E, 3). In later stages subdermal cells start dividing in various planes, but an increased mitotic activity in the apical portion of the inner epidermis results in the formation of radial rows of dermal cells (seen in t.s., fig. 4I), which appears to be a characteristic feature of the euphorbiaceous integuments.

During fertilization, both epidermal layers of the inner integument become conspicuous and rich in cytoplasm (fig. 4F). According as the maturation of the seed proceeds the cells of the subdermal layers enlarge and become highly vacuolated; they contain abundant amyloplasts. The cells of the outer epidermis elongate radially and become sclerotic and obliquely oriented. The cell walls of the inner epidermal layer, on the other hand, develop fibrous thickenings but do not elongate in a radial plane, as was observed, for instance, in *Euphorbia geniculata* (figs. 4G, 5).

Outer Integument – The derivatives of the subapical initials soon start dividing radially, so that the basal region of the young outer integument is markedly broader than its distal region (fig. 3A). These divisions are quire charac-

³ The use of this terminology is somewhat confusing in this context: the integumentary primordia originate by "periclinal" divisions of a subdermal initial. In more advanced stages, however, such divisions should be referred to as "anticlinal" since the integument begins to grow vertically in order to cover the nucellus as a sheath.

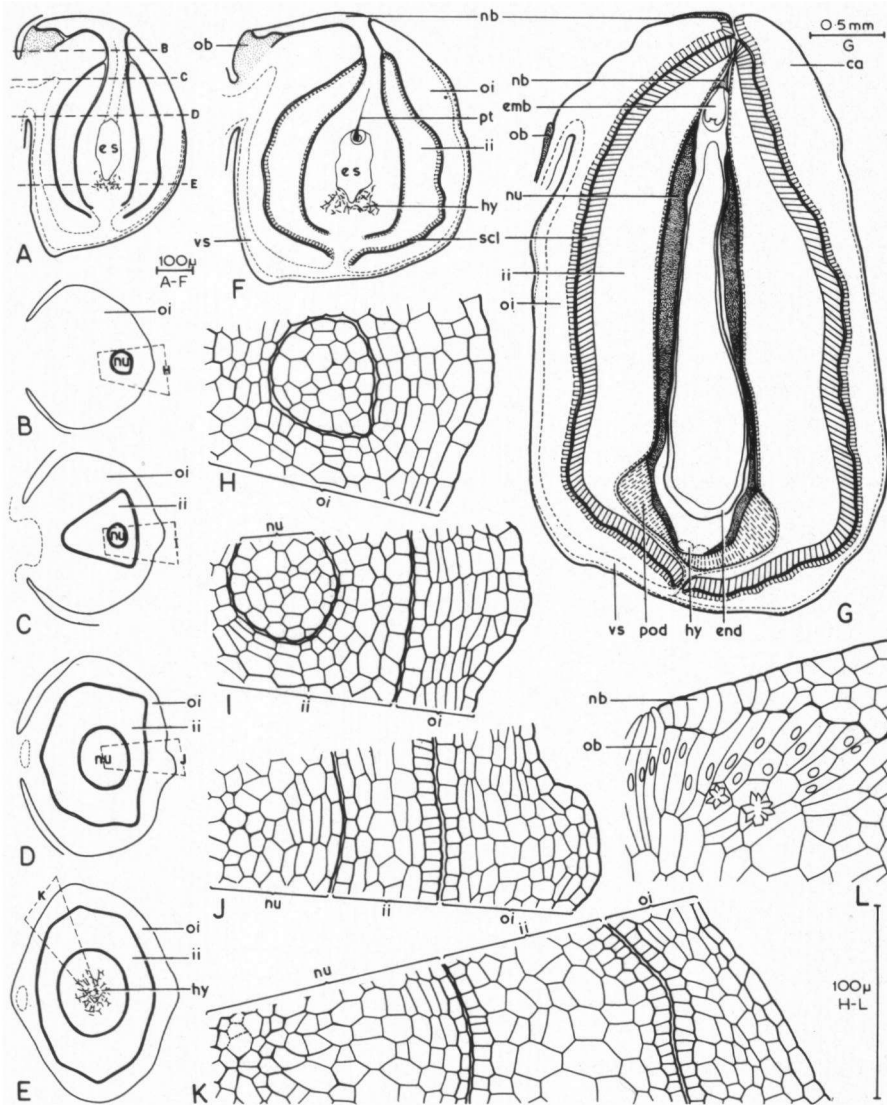


Fig. 4 A-L – *C. obliqua*, development of seed (*ca*, caruncle; *emb*, embryo; *end*, endosperm; *es*, embryo sac; *hy*, hypostase; *ii*, inner integument; *nb*, nucellar beak; *nu*, nucellus; *ob*, obturator; *oi*, outer integument; *pod*, podium; *pt*, pollen tube; *scl*, sclerotic layer; *vs*, vascular supply).

A: L.s. ovule at mature embryo sac stage.

B-E: T.s. mature ovule at levels B-E marked in figure A.

F: L.s. ovule at fertilization stage.

G: L.s. young seed, heart-shaped embryo stage.

H-K: Enlargement of regions H-K respectively, marked in figures B-E.

L: L.s. obturator and distal region of nucellar beak, fertilization stage.

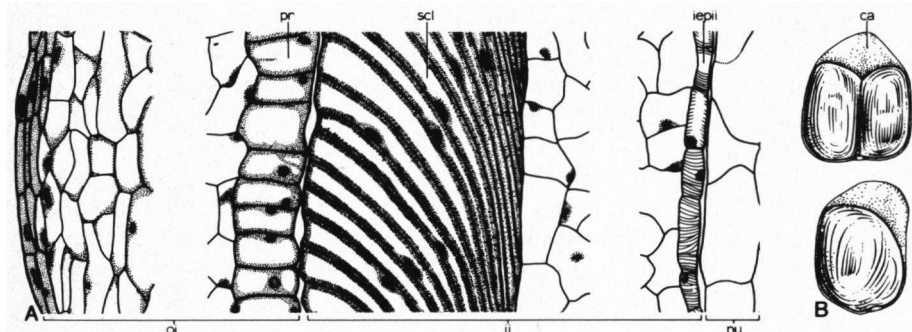


Fig. 5 A-B – *C. obliqua*, seed and seed coat (*ca*, caruncle; *iepii*, inner epidermis of inner integument; *ii*, inner integument; *nu*, nucellus; *oi*, outer integument; *pr*, prismatic layer; *scl*, sclerotic layer).

A: Part of seed coat of young seed; intervening tissue of outer and inner integuments has not been shown, l.s. $\times 260$.

B: Mature seeds, front and side views. $\times 3$.

teristics and result in the multi-layered structure of the integument. During gametogenesis peripheral provascular elements differentiate in the outer envelope. This strand extends further into the integument after fertilization to reach almost as far as the apex, and during seed development tracheary elements are discernible (fig. 4A, F, G). The inner epidermis differentiates into a prismatic layer, whose cells enlarge, particularly in the micropylar region (fig. 5).

Seed and Seed Coat – The remaining layers of the outer integument become flattened during seed maturation and form, together with the prismatic layer, the soft, whitish, membranous covering of the seed coat. The tissues of obturator, nucellar beak and central nucellus, and the inner layers of the inner integument are crushed or resorbed, the latter persisting as a thin membrane in the seed. The outer epidermis of the inner integument forms the sclerotic palisade layer whose macrosclereids taper on the inner side, and are not uniformly elongated (as is also the case with the prismatic cells of the outer integument), to form the ridges on the surface of the seed, especially in the micropylar and chalazal regions.

A caruncle develops around the straight micropyle, primarily as a result of the proliferation of both dermal and subdermal apical cells of the outer integument (fig. 4G). The caruncle is more conspicuous on the ventral side of the seed due to a noteworthy swelling of the funicular integumentary “bulge”. Later its central cells enlarge appreciably and become aerenchymatous. Contrary to the condition in *Micranthemum* (BERG 1975), the basal peripheral cells of the caruncle do not develop into stone cells.

5. DISCUSSION

Taxonomic Significance – Although during the last decades pollenmorpho-

logical, and chemo- and cytotaxonomic researches, for example, have progressed significantly in unravelling the complicated relationship between various taxa, only a few authors have emphasized the importance of ovule and seed characters in taxonomic and evolutionary inquiries. Most of these studies are based on distinctive features derived from fertilized ovules and seeds (NETOLITZKY 1926; B. SINGH 1964; WUNDERLICH 1967; MOHANA RAO 1974; PHILIPSON 1974; R. DAHLGREN 1975; CORNER 1976), or the differentiation of sarcotesta and arils in connection with seed dispersal (CORNER 1949, 1964; TAKHTAJAN 1959, 1969; VAN DER PIJL 1972; BERG 1975), and "... represent adaptations for increasing the efficiency with which angiosperms exploit their environment." (STEBBINS 1976). Since the ovule is considered to be one of the most protected and conservative plant organs (see, e.g., MEEUSE 1975, p. 98), it can be expected that detailed ontogenetic studies would also furnish important data for taxonomic expositions at various levels of affinity. In Euphorbiaceae, especially, ovule and seed characters may be conclusive as: "*Die einzigen durchgreifenden Merkmale, die allen Gliedern der Familie zukommen, sind die Anheftung, Form und Zahl der Samenanlagen...*" (PAX & HOFFMANN 1931, pp. 13–14).

A comparative study of the existing reports on euphorbiaceous ovules (for general references, consult NETOLITZKY 1926, pp. 184–189; B. SINGH 1964, pp. 43–46; DAVIS 1966, pp. 117–120; and furthermore, BERG 1975; BOR & BOUMAN 1974; BOR & KAPIL 1975; CHOPRA & SINGH 1969; JOHRI & KAPIL 1953; LANDES 1946; RAO 1970; R. P. SINGH 1962, 1965, 1969, 1970a, b, 1972, SINGH & CHOPRA 1970; SINGH & PAL 1968; WARMING 1872; WUNDERLICH 1967; for a detailed account of the seeds and seed coats the reader is referred to the recent and magnificent contribution by CORNER 1976, pp. 129–142), supported by our own ontogenetic research in a number of taxa, provides the following systematical characters for the subfamilies Acalyphoideae, Crotonoideae and Euphorbioideae (cf. WEBSTER 1975; BAILLON 1858; PAX & HOFFMANN 1931):

(1) Ovules anatropous (with a tendency to hemitropy), suspended, solitary and bitegmic.

(2) Ovules crassinucellar; nucellar apex showing a heterogeneous size and organization: in *Acalypha*, *Micrococca*, *Ricinus*, and *Excoecaria*, a nucellar "cap" is formed by a limited mitotic activity in the apical dermal region; in *Chrozophora*, *Codiaeum*, *Croton*, *Jatropha*, *Hevea* this activity is extended and a long nucellar "beak" is organized; *Euphorbia* still shows another unique development of the apical nucellar region (BOR & KAPIL 1975), whereas in *Dalechampia* the nucellar dermatogen does not divide at all.

(3) Pre-fertilization differentiation of a group of thick-walled nucellar cells at the antipodal end of the embryo sac: "hypostase"⁴; and post-fertilization development of a saucer-like structure ("podium") in the nucellar base below

* Although we omitted to report it earlier, this type of hypostase is also present, but in a very reduced form, in species of *Euphorbia* (BOR & KAPIL 1975). In *Codiaeum* both the hypostase and podium are absent.

the hypostase, which structure persists in the mature seed.

(4) Inner integument initiated by a subdermal initial (or a group of initials); its apical rim consists of dermal rows of cells originated by periclinal divisions in the inner epidermis; outer epidermis forming a stony layer (i.e., radially elongated macro-sclereids) of the seed coat. The inner integument develops into a massive sheath, especially in those taxa where the integument is vascularised as well (e.g., *Aleurites*, *Baliospermum*, *Codiaeum*, *Croton*, *Givotia*, *Hevea*, *Jatropha*, *Manihot*, *Pimelioidendron*). In *Ricinus* and several other genera the nucellar base proliferates excessively during the pre- and post-fertilization stages and the inner integument is broadly inserted on this vascularised region. CORNER (1976) applies the term 'tegmic pachychalaza' and suggests a relation between these two types of ovular vascularisation.

(5) Outer integument also initiated by a subdermal initial; sometimes thin: 3-layered in *Acalypha*, *Micrococca*, *Croton*, *Euphorbia helioscopia*, but one or several periclinal⁵ divisions in the subdermal layer give rise to 4-layered (e.g. *Codiaeum* and many species of *Euphorbia*) or multi-layered integuments (*Jatropha*, *Ricinus*, *Excoecaria*), which may be vascularised as well (*Chrozophora*, *Dalechampia*, *Macaranga*, *Trewia*). Inner epidermis usually forming the prismatic layer of the seed coat.

(6) Caruncle, i.e., proliferation of the outer integumentary rim around the exostome, commonly present in mature seeds⁵.

(7) Placental obturator always present, but variable in size and structure.

On the basis of these ovular characters it should be noted that WEBSTER's (1975) subfamily Crotonoideae forms a homogeneous group, since all the investigated taxa have a massive nucellus with protruding nucellar beak, and either a thick, subdermally derived and vascularised inner integument or a vascularised tegmic pachychalaza. Especially the latter features, have a conclusive diagnostic value because the occurrence of vascular bundles (together forming a vascular sheath) in subdermally initiated inner integuments is a rather unique phenomenon among angiospermous ovules (cf. KÜHN 1928; LANDES 1946; CORNER 1976). A number of taxa grouped in the subfamily Acalyphoideae have thick, vascularised outer integuments, but other taxa of the same subfamily have thin, 3-layered outer integuments. Whether the above-mentioned ovular features reveal definite phylogenetic trends within this complex family can only be determined after the ontogeny of more taxa is investigated.

Ovular Morphology – That ontogenetic studies can throw more light on the morphological interpretation of the ovule and its accessory appendages is evident from the following discussion. The ovular primordium (WARMING 1878: "mamelon ovulaire") is the protuberance that differentiates into nucel-

⁵ Although its development may be very reduced in many species of *Euphorbia*, morphologically speaking there is a slight proliferation and consequently a tendency toward caruncle formation.

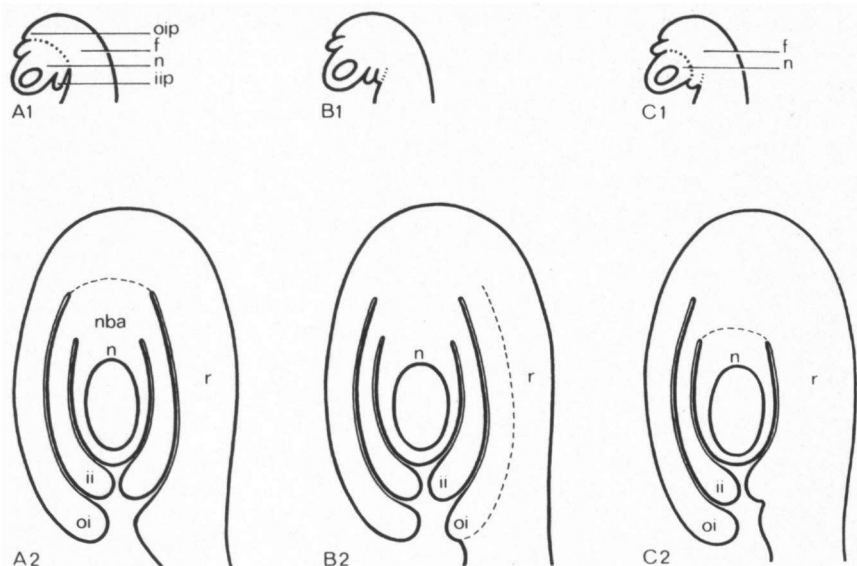


Fig. 6 A-C – Diagrams of longitudinal sections of three bitegmic anatropous ovules, showing two developmental stages for each of them (*f*, funicle; *ii*, inner integument; *n*, nucellus; *nba*, nucellar base; *oi*, outer integument; *r*, raphe).

A1, 2: Outer integument is a unilateral outgrowth of the distal funicular region, and inner integument an additional ring-shaped appendage of the nucellar base.

B1, 2: Outer integument is a ring-shaped outgrowth of the distal funicular region, and "fusion" of this integument and funicle is "congenital".

C1, 2: Both inner and outer integuments are unilateral outgrowths of the terminal funicular region.

B and C hypothetical cases.

lus and funicle; although the nucellar and funicular tissues are indistinguishable as distinct regions before the appearance of integuments, the sharply curved region may be designated as the funicle and the distal region as the nucellus (megasporangium; *fig. 6A*). As soon as the latter gives rise to the primordium of the inner integument (just above the bent funicle), the nucellus is more clearly delimited at its base.

The primordium of the outer integument arises on the ovular region below the ring-shaped protrusion of the inner integument. Its initial mitotic activity is much more pronounced on the outer, convex side of the young curved ovule, but periclinal divisions occur also in the dermatogen at the inner side of the funicle. However, the advanced growth and curvature of the funicle affect the unilateral ontogeny of the outer integument, thus obscuring its further development on the funicular side. Consequently, many eminent morphologists were led to believe that in anatropous ovules the outer integument and funicle are fused "congenitally", or that the development of the outer integument is completely suppressed on the side next to the funicle. These workers seem to assume

that the outer integument is an outgrowth of the nucellar base, and wrongly derive the anatropous condition from atropy by simply inverting mature erect ovules (*fig. 6B*).

Another group of theorists who consider both integuments as (foliar) extensions of the distal funicular (axial) region have never explained, however, why in anatropous ovules only the development of the outer, and not that of the inner integument is suppressed on the funicular side (*fig. 6C*). The only plausible explanation of this phenomenon, supported by ontogenetic studies, is that the inner integument originates independently as an additional outgrowth of the nucellus, whereas the outer integument and raphe are considered to be derivatives of the funicle. Consequently, the concept of "congenital fusion" lacks an empirical basis and must be rejected (*cf. SATTLER 1974*).

In this way the bitegmic ovule is interpretable as consisting of two structural units: the funicle (*viz.*, raphe) plus outer integument, and the nucellus plus inner integument. Such an interpretation leads to the following propositions and definitions:

(1) The nucellus is that part of the ovule which is completely surrounded by inner integument (see also K.V.O. DAHLGREN 1927). Contrary to this definition the term "nucellus" has generally been applied to the ovular region which is situated above the integuments (SCHLEIDEN 1837; VAN WISSELINGH 1919; NETOLITZKY 1926, p. 31; CORNER 1976). As early as 1878 WARMING objected to this narrow view, stating that: "... *la base du nucelle est située à peine plus bas que la ligne d'insertion supérieure du tégument interne... ou à la même hauteur*" (p. 203).

In many plants the nucellar tissue at the base of the embryo sac differentiates into a hypostase. In addition, there is often a characteristic proliferation of the basal nucellar tissue, *i.e.*, the podium (K.V.O. DAHLGREN 1940). Such nucellar structures are frequently referred to as "chalazal" cork tissue, a denomination which is topographical rather than indicative of the histogenetic nature of this tissue. When such a secondary tissue formation does not take place there is usually no histological differentiation in the tissues of the (free) distal nucellar region, and the portion situated between the attachment zone of the inner integument and the terminal ramifications of the raphe bundle. Therefore it is proposed to designate the latter zone as the "nucellar base".

(2) The inner and outer integuments are not homologous from an ontogenetic and histological point of view. Although in the investigated euphorbiaceous ovules both integuments have a subdermal origin, the inner integument of the large majority of angiospermous taxa develops as an exclusively dermal outgrowth from the nucellar base.

Teratological phenomena also point in the direction of a different origin of the two integuments. STRASBURGER (1879, p. 42) observed, for instance, that in oolyses of *Rumex scutata*: "*Oberhalb der Insertionsebene des äusseren Integuments stirbt der Funiculus entweder sofort... ab, oder er streckt sich noch zu einer oft bedeutenden Länge, um an seiner Spitze schliesslich abzusterben. Hier*

lässt sich dann oft noch eine mehr oder weniger vorgerückte Anlage eines inneren Integuments erkennen, während die Funicularspitze selbst in einer verschrumpften Nucellaranlage endet". In other words, the development (or degeneration in oolysis) of both the nucellus and the inner integument are strongly correlated with one another (see also STRASBURGER 1872, p. 425). Our observation that in *Euphorbia geniculata* the basal cells of the inner integument contribute to the formation of the podium also supports the idea that this integument is an extension of the megasporangium (BOR & KAPIL 1975; for other arguments, see MEEUSE & BOUMAN 1974; STEBBINS 1976).

(3) Anatropy in bitegmic ovules is caused by the early bending of the primordial funicular region, and affects primarily the unilateral development of the outer integument. As the meristematic zone, which induces the inception of the outer integument, originates always from the terminal funicular region, this zone is more or less ring-shaped, which is particularly obvious in those plants where the ovules have a tendency to curve to a lesser degree (hemitropy). As a consequence of the subsequent elongation and curvature of the funicle, however, the development of the outer integument is unilateral, but a dermal integumentary outgrowth can be discerned on the proximal inner side of the funicle as well. Sometimes the meristematic zone is crescent-shaped, and the development of the outer integument is completely obscured on the inner side of the funicle. In all these cases, apparently, the primary enveloping function of the integument has been transferred to the funicle (viz., to the raphe).

As indicated above, very few morphologists have explained this phenomenon correctly. VAN WISSELINGH (1919) and NETOLITZKY (1926, p. 25) pointed to the fact that the peripheral layers of raphe, chalaza, and outer integument exhibit a similar configuration, and together form the outer portion of the seed coat. Frequently applied statements such as: "*Both integuments as well as lower part of chalaza are mainly concerned with formation of seed coat*" (B. SINGH 1964) should rather be avoided as, in this general context, the "chalaza" is merely a topographical denomination of the basal ovular region, which together with the raphe and outer integument is a derivative of the funicle.

Note added in proof:

In a recent paper STEBBINS (1976) relates the anatropous position and double integuments of the ovule to the origin of angiosperms.

ACKNOWLEDGEMENTS

The first author wishes to acknowledge the kind invitation of Professors B. M. Johri and H. Y. Mohan Ram to undertake research in the Department of Botany, University of Delhi. His stay in Delhi was made possible by a grant of the Ministerie van Onderwijs en Wetenschappen (Dutch Ministry of Education and Sciences). Thanks are expressed to Prof. A. D. J. Meeuse for his support in securing the scholarship, and to Dr. F. Bouman for discussions and suggestions.

REFERENCES

- BAILLON, H. (1858): *Étude générale du groupe des Euphorbiacées*. 684 pp. Paris.
- (1876): *Dictionnaire de Botanique*. Vol. 1, 788 pp. Paris.
- BERG, R. Y. (1975): Fruit, seed, and myrmecochorous dispersal in *Micranthemum* (Euphorbiaceae). *Norw. J. Bot.* **22**: 173–194.
- BERSIER, J. D. (1960): L'ovule anatrophe: Ranunculaceae. *Ber. Schweiz. bot. Ges.* **70**: 171–176.
- BOCQUET, G. (1959): The campylotropous ovule. *Phytomorphology* **9**: 222–227.
- & J. D. BERSIER (1960): La valeur systématique de l'ovule: Développements tératologiques. *Arch. Sci (Genève)* **13**: 475–496.
- BOR, J. & F. BOUMAN (1974): Development of ovule and integuments in *Euphorbia milii* and *Codiaeum variegatum*. *Phytomorphology* **24**: 280–296.
- & R. N. KAPIL (1975): *Euphorbia geniculata* – Ovule to seed. *Acta Bot. Neerl.* **24**: 257–268.
- CHOPRA, S. & R. P. SINGH (1969): Structure and development of seed in *Phyllanthus urinaria* L. *J. Indian bot. Soc.* **48**: 212–216.
- CORNER, E. J. H. (1949): The Durian Theory or the origin of the modern tree. *Ann. Bot. (New Ser.)* **13**: 367–414.
- (1964): *The Life of Plants*. 315 pp. London.
- (1976): *The Seeds of Dicotyledons*. Vol. I, 311 pp. Cambridge.
- DAHLGREN, K. V. O. (1927): Die Morphologie des Nuzellus mit besonderer Berücksichtigung der deckzellosen Typen. *Jahrb. Wiss. Bot.* **67**: 347–426.
- (1940): Postamentbildungen in den Embryosäcken der Angiospermen. *Bot. Notiser* **1940**: 347–369.
- DAHLGREN, R. (1975): A system of classification of the Angiosperms to be used to demonstrate the distribution of characters. *Bot. Notiser* **1975**: 119–147.
- DAVIS, G. L. (1966): *Systematic Embryology of the Angiosperms*. 528 pp. New York.
- EAMES, A. J. (1961): *Morphology of the Angiosperms*. 518 pp. New York.
- FAHN, A. (1974): *Plant Anatomy*. 611 pp. Oxford.
- GOEBEL, K. (1923): *Organographie der Pflanzen – Insbesondere der Archegoniaten und Samenpflanzen*, 2nd ed., Vol. III: *Spezielle Organographie der Samenpflanzen*. pp.1210–1789.
- JOHRI, B. M. & R. N. KAPIL (1953): Contribution to the morphology and life history of *Acalypha indica* L. *Phytomorphology* **3**: 137–151.
- KAPIL, R. N. (1956a): Development of embryo sac and endosperm in *Chrozophora rottleri* A. Juss.: A reinvestigation. *Bot. Gaz.* **117**: 242–247.
- (1956b): A further contribution to the morphology and life history of *Chrozophora* Neck. *Phytomorphology* **6**: 278–288.
- KÜHN, G. (1928): Beiträge zur Kenntnis der intraseminalen Leitbündel bei den Angiospermen. *Bot. Jahrb. Syst.* **61**: 325–385.
- LANDES, M. (1946): Seed development in *Acalypha rhomboidea* and some other Euphorbiaceae. *Am. J. Bot.* **33**: 562–568.
- MCLEAN, R. C. & W. R. IVIMEY-COOK (1956): *Textbook of Theoretical Botany* Vol. II. pp. 1071–2201. London.
- MEEUSE, A. D. J. (1975): *Floral Evolution and Emended Anthocorm Theory*. 188 pp. In VARGHESE, T. M. (ed.): *International Bio-science Monographs-I*. Hissar.
- & F. BOUMAN (1974): The inner integument – Its probable origin and homology. *Acta Bot. Neerl.* **23**: 237–249.
- MIRBEL, C. F. B. (1829): Nouvelles recherches sur la structure et les développements de l'ovule végétale. *Ann. Sc. nat.* **17**: 302–318.
- MOHANA RAO, P. R. (1974): Seed anatomy in some Hamamelidaceae and phylogeny. *Phytomorphology* **24**: 113–139.
- NETOLITZKY, F. (1926): *Anatomie der Angiospermen-Samen*. 364 pp. In LINSBAUER, K. (ed.): *Handbuch der Pflanzenanatomie*, II Abt., 2. Teil, Bd. X. Berlin.
- PAX, F. & K. HOFFMANN (1931): Euphorbiaceae. pp. 11–233 in ENGLER, A. & K. PRANTL (eds.): *Die Natürlichen Pflanzenfamilien*. 2nd ed., Vol. 19c. Leipzig.

- PHILIPSON, W. R. (1974): Ovular morphology and the major classification of the dicotyledons. *Bot. J. Linn. Soc.* **68**: 89–108.
- PIJL, L. VAN DER (1972): *Principles of Dispersal in Higher Plants*. 2nd ed., 162 pp. Berlin.
- PURI, V. (1970): The angiosperm ovule. *Proc. 57th Session Indian Sci. Congr. (Kharagpur)*: 1–36.
- RAO, P. N. (1970): Euphorbiaceae. pp. 136–141 in Proceedings of the symposium on comparative embryology of Angiosperms. 385 pp. *Bull. Indian Nat. Sci. Acad.* **41**.
- SATTLER, R. (1974): A new approach to gynoecial morphology. *Phytomorphology* **24**: 22–24.
- SCHLEIDEN, M. J. (1837): Einige Blicke auf die Entwicklungsgeschichte des vegetabilischen Organismus bei den Phanerogamen. *Arch. Bwl. Naturg.* (3) **1**: 289–320.
- (1839): Über die Bildung des Eichens und Entstehung des Embryos bei den Phanerogamen. *Verh. Kais. Leop.-Carol. Ak. Naturf.* **11**: 29–58.
- SCHWEIGER, J. (1905): Beiträge zur Kenntnis der Samenentwicklung der Euphorbiaceen. *Flora (Jena)* **94**: 339–379.
- SINGH, B. (1964): Development and structure of angiosperm seed. 1. *Bull. Nat. bot. Gdn. Lucknow* **89**: 1–115.
- SINGH, R. P. (1962): Forms of ovules in Euphorbiaceae. pp. 124–128 in MAHESHWARI, P. (ed.): *Plant Embryology – A Symposium*, 273 pp., CSIR, New Delhi.
- (1965): Structure and development of seeds in *Codiaeum variegatum* Blume. *J. Indian bot. Soc.* **44**: 205–210.
- (1969): Structure and development of seeds in *Euphorbia helioscopia*. *Bot. Mag. Tokyo* **82**: 287–293.
- (1970a): Structure and development of seeds in Euphorbiaceae: *Jatropha* species. *Beitr. Biol. Pflanzen* **47**: 79–90.
- (1970b): Structure and development of seeds in *Putranjiva roxburghii* Wall. *J. Indian bot. Soc.* **49**: 99–105.
- (1972): Structure and development of seed in *Phyllanthus niruri* L. *J. Indian bot. Soc.* **51**: 73–77.
- & S. CHOPRA (1970): Structure and development of seeds in *Croton bonplandianum*. *Phytomorphology* **20**: 83–87.
- & A. PAL (1968): Structure and development of seeds in Euphorbiaceae: *Dalechampia roezeliana* Muell. -Arg. *Tech. Com. Nat. bot. Gdn. Lucknow*: 65–74.
- STEBBINS, G. L. (1976): Seeds, seedlings, and the origin of angiosperms. p.p. 300–311. In: C. B. BECK (ed.): *Origin and early evolution of angiosperms*. New York.
- STRASBURGER, E. (1872): *Die Coniferen und die Gnetaceen. Eine Morphologische Studie*. 442 pp. Jena.
- (1879): *Die Angiospermen und die Gymnospermen*. 193 pp. Jena.
- TAKTHAJAN, A. L. (1959): *Die Evolution der Angiospermen*. 344 pp. Jena.
- (1969): *Flowering Plants – Origin and Dispersal*. 310 pp. Edinburgh.
- WARMING, E. (1872): Recherches sur la ramification des Phanerogames. *Kong. Danske Vidensk. Seelsk. Skr. 5R. Naturv. Math. Afd. 10. Band 1*: 50 pp.
- (1878): De l'ovule. *Ann. Sci. nat. Bot.* **5**: 177–266.
- & M. C. POTTER (1932): *A Handbook of Systematic Botany*. 2nd ed. 620 pp. London.
- WEBSTER, G. L. (1975): Conspectus of a new classification of the Euphorbiaceae. *Taxon* **24**: 593–601.
- WISSELINGH, C. VAN (1919): Bijdragen tot de kennis van de zaadhuid. Vierde bijdrage: Over de zaadhuid der Cruciferen. *Pharm. Weekblad*: 1245–1271.
- WUNDERLICH, R. (1967): Some remarks on the taxonomic significance of the seed coat. *Phytomorphology* **17**: 301–311.