FLOWERS AND FRUITS IN FLACOURTIACEAE. IV. HYDNOCARPUS SPP., KIGGELARIA AFRICANA L., CASEARIA SPP., BERBERIDOPSIS CORALLINA HOOK. F.

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SUMMARY

In Hydnocarpus the hard layers of the seed coat develop from the epidermides of both integuments where they are contiguous. This does not conform with the division of the Angiosperm seeds into testal or tegmic. Corner's suggestion of two unallied groups in the Flacourtiaceae, namely an integumental and a pachychalazal one, cannot be corroborated. The seeds of Kiggelaria closely resemble those of Hydnocarpus.

In Casearia the development of the fruit wall and its vascular bundles is different for the Asian and the American species studied. The three parietal placentae are confluent over the base of the ovary. The seeds are exotegmic, as described by Corner; the ovules are atropous. The berries and seeds of Berberidopsis are described for the first time. The seeds have a softly parenchymatic raphe. The embryo is small. The inner integument is absorbed during development. The inner epidermis of the outer integument forms a lignified crystalliferous layer. The affinity of Berberidopsis is discussed.

Hydnocarpus spp.

The flowers of Hydnocarpus are unisexual. Mostly they have 4 or 5 sepals, an equal number of petals, and many stamens or staminodes. The petals have a basal ventral scale. The pistil has mostly 4 or 5 parietal placentae covered with anatropous ovules. The sessile stigma is composed of as many reflexed, widening, bifid lobes as there are placentae, and alternating with these. The fruits are indehiscent, large and hard, and contain hard seeds. The reader may find detailed descriptions in Sleumer (1954). The anatomical structure of the seed was described by Sleumer (1938) and recently by Vaughan (1970) and Corner (1976). In the following some more anatomical data, especially as to the relation of the pistil, ovule, and seeds, are presented.

As regards the pistil it is notable that the style is very short. At the stylar level the septa at most just touch in the centre, but they do not fuse secondarily there, and do not form stylar canals corresponding with the carpels which constitute the pistil. As a result the cavity of the pistil continues upwards into a five-fluted, or irregular, central split, which issues on the surface of the stigma above. This is illustrated by a series of cleared thick slices of a pistil in figs. 5—8.

The locules are small as compared with the massive wall of the pistil. As the pistil matures, the endocarp forms a soft mass of tissue, especially in the regions of the placentae, even small lobes can be formed here. However, the pulposus tissue in the mature fruit is not formed by the endocarp but is entirely due to the confluent sarcotestae of the seeds. At the very bottom of the pistil there is either no placental...
Hydnocarpus polypetala. Fig. 1. Ovule l.s., 60 x. Figs. 3—8. Vascular bundle pattern of pistil, cleared t.s., 7 x. — Hydnocarpus kurzii. Fig. 2. Vascular bundles in half of young seed, cleared, 7 x.
tissue, or the placentae may be sterile at their base and they may touch each other in the centre of the pistil, forming sterile locules in that region.

As regards the vascular supply of the pistil (figs. 3—8), it is notable that the massive wall is supplied by a 'cortical' system of anastomosing bundles which is largely separate from the main vascular bundle system, but has some connections with the latter at the base and in the upward tapering region of the pistil. The placentae are provided with their own vascular bundle strands which run from the base upwards. They have their xylem on the outside (fig. 6), and many inward traces to the ovules split off from them. Above, they have ramifications which end blindly in the sterile regions of the placentae. Below, they originate from the vascular bundles in the base of the pistil, on a level above the origin of the basal lateral carpellary vascular bundles. Upwards, the median and lateral carpellary bundles divide into a number of smaller bundles toward the stigma. In the stigmatic lobes they ramify profusely and fan-like.

The ovules are anatropous, bitegmic, and have large nucelli (fig. 1). The vascular bundle of the ovule branches fan-like in the distal part of the raphe, and the branches curve and spread into the outer integument. Short anastomoses move into the direction of the nucellar base, coming from the base of the recurved branches (fig. 2). In the ovules the outer integument does not reach beyond the inner one. In less well developing or small seeds this is unchanged, so that there is no ectopyle. However, in well developing ovules and seeds an ectopyle is formed as a short slit by the prolonged distal parts of the outer integument. The inner integument always forms a definite endopyle. In H. polypetala the inner integument has two terminal and lateral lobes.

The development of the ovule is marked by enlargement of the cells of the outer integment and by profuse division of small cells of the inner integment especially in its proximal half. Thus the outer and the inner integment are both multiplicative, sensu Corner, and may be distinguished by the dimensions of their cells. The cuticle between the adjacent outer and inner integument vanishes gradually, at first persisting in places. On the endopyle level either the cuticles persist, so that the outer and inner integument composing the young testa can be distinguished, or the outer and inner integument remain partly free from each other on that level. According to Corner the seeds of Hydnocarpus are pachychalazal, because of cell divisions occurring below the insertion of the integuments. However, in my opinion the testa is entirely integumental by the loss of the cuticle between the integuments, and no such pachychalazal growth of tissue occurs.

Towards seed formation, the inner integument differentiates into a tegmen consisting of three different thick layers of cells, namely an outer layer of periclinous sclereids which are elongate in the direction of the longitudinal axis of the seed, an inner pigmented layer, and a middle layer of undifferentiated parenchymatic cells. The middle layer desinigrates later on, so that the pigment layer is separated as a dark sheath around the endosperm-embryo body (‘Kernhaut’). The outer integument differentiates into two layers, namely an outer parenchymatic one giving rise to the soft layer (sarcotesta sensu Van der Pijl, aril acc. to Sleumer) which forms the pulpous mass in the fruits, and an inner layer of anticlinous elongate sclereids. The inner layer originates by the formation of radial cell rows on the inside of the outer integument, starting from the distal regions of the young seed. Later the innermost cells of these radial rows elongate as radial cells which are sclerified. The outermost cells of these radial rows are also sclerified, but do not first elongate radially, and in
Hydnocarpus glaucescens. 1. Differentiation of the integuments into seed coat, l.s. (see text); 2. Ibidem, t.s., slightly younger.
this way they differentiate into small isodiametric sclereids. Consequently, the three sclerified layers of the seed coat, as they have been described by Sleumer (1938), are derived from both integuments. The hardness of the seed is mainly caused by the dominant layer of antinclinous sclereids, the middle layer of Sleumer, which is formed by the outer integument. The outer layer sensu Sleumer is formed by the rest of the radial cell rows formed by the outer integument which sclerify without prior radial elongation. The inner layer sensu Sleumer is formed by the periclinous longitudinal sclereids, which are less heavily lignified and are derived from the outer dermal layer of the inner integument. Around the endopyle this layer is absent, the pigment layer dominant. In the subdistal part of the seed the sclereid layer of the inner integument forms many outgrowths protruding peak-like into the outer integument.

It should be stressed that the differentiation of the testa, as described above, frequently starts after the multiplication of the cells of the integuments, and only after the cuticles between the integuments have vanished. In those cases it is difficult to ascertain which share each integument has in the differentiation. However, in H. glaucescens young seed stages (photos 1–3) were found in which the differentiations start before the entire loss of the cuticles, so that the share of each integument could be ascertained. Moreover, the integuments are less multiplicative in this species, which has comparatively small fruits and seeds. Anyway, the share of each integument into the testa differentiation can be ascertained by comparison at the distal parts of the seed if the integuments remain free in that region.

The conclusion is that the hard part of the seed coat originates from both integuments, with loss of the cuticular boundary. Corner also recognizes the composition of the seed as described above (cf. his fig. 279) but according to him the observed differentiation of the testa and the tegmen has diversified in a similar way into the new growth of the pachychalaza. As a consequence, Corner thinks the Flacouriaceae are an unnatural assemblage in so far as there is a Hydnocarpus group with pachychalazal seeds and a Flacouritia group with exotegmic integumental seeds. In my opinion, however, the seeds of the Hydnocarpus group are integumental as well, which pleads for a natural unity of the Flacouriaceae as regards this character. The fact that in Hydnocarpus the seed coat is endotestal as well as exotegmic, may indicate a relation of the Flacouriaceae with Dilleniidae. The important difference between testal and tegmic seeds, which plays a role at family and even ordinal level, possibly has its border cases.

**Kiggelaria africana**

The flowers and fruits differ from those of Hydnocarpus in some minor aspects, such as the anthers opening by pores and the dehiscent fruits. The dehiscence of the fruits could not be studied from my material. In contrast to the genus Hydnocarpus, which is Asian, Kiggelaria is African. Young pistils are not very different from those of Hydnocarpus (figs. 9–18), except in that the placentae bear only two rows of ovules. Correspondingly, the placentae do not have their own strong placental strands. Inverting ovule traces are given off directly by the commissural lateral carpel bundles.

The ovules are anatropous, bitemgic, and have large nucelli. The endopyle is a porus, the ectopyle a median slit. Mauritzon (1936) reports that, when the en-
Hydnocarpus glaucescens. 3. Differentiation of the integuments into seed coat, l.s. at micropyle (see text). — Casearia tuberculata. 4. Differentiation of sclereid mantle on inside of pistil wall, t.s.
dosperm is formed, the outer integument is seven cell layers thick, the inner integument four cell layers. The integuments are multiplicative (sensu Corner). Young fruits, with a diameter of 6–7 mm, show the disappearance of the cuticle between the outer and inner integument at places; in this stage the inside surface cells of the outer integument start to divide into radial cell rows (which are also reported by Mauritzon), and on the outside of the inner integument an acropetal differentiation into longitudinal cells begins. There is no difference here with Hydnocarpus glaucescens. In fruits with a diameter of 17 mm, which contained seeds with complete embryos and endosperm, the stony layer of the seed coat was found to consist of two equally thick sublayers, an outer one of isodiametric cells, and an inner one of cells stretched longitudinally according to the axis of the seed. It is logical to presume that these two sublayers are the result of the differentiation of the outer and the inner integument respectively, as described above. Therefore the pattern is similar to Hydnocarpus, except that the radial elongation of the inside part of the radial cell rows, prior to their lignification, does not take place. A pigment layer is present as in Hydnocarpus, but here this layer also stretches over the basal boundary of nucellus and chalaza. Also in the chalazal region a short prolongation of the differentiation of sclereids is present, in line with the outer integument. These results corroborate my opinion that the seed coat of the Hydnocarpus group is integumental with loss of the cuticle, and testal as well as tegmic.

The vascular bundle of the raphe curves and divides irregularly into the chalaza, forming a tracheidal cup. There is no prolongation into the outer part of the outer integument, as there is in Hydnocarpus. However, in later stages (fruits 6–7 mm in diameter) two lateral bundles have developed from the base of the raphe bundle which ramify mainly into the antiraphe side of the outer integument and grow into the direction of the chalaza, that is opposite to usual (figs. 19–23).

**Casearia spp.**

The flowers of Casearia have a five-lobed calyx, no petals, about ten stamens, a number of staminodes, and a trimerous pistil. The pistil has three parietal placentae with atropous ovules, a short style, and three short stigmatic parts in line with the placentae. The fruit is a three-valved capsule, exposing arillate seeds medianly on the valves. The reader may find detailed descriptions in taxonomic contributions, for instance by Sleumer (1954). The anatomy of the seed is described by Corner (1976). In the following some more data on pistil, ovule, and seed are given.

In the American spp. *C. arborea* and *C. sylvestris* the adaxial tissue of the wall of the pistil remains meristematic for some time and is responsible for the growth in thickness. It forms to the outside the mesophyll with many secretory spaces lined with a distinct epithelium. Finally, its meristematic activity is confined to the adaxial subepidermal cell layers, where radial cell families are formed. In the Asian spp. studied such a specialised growth in thickness is absent. In all species subepidermal layers give rise to a mantle of initial sclereids. This meristematic mantle differentiates centripetally into tangentially stretched cells which later become sclerified (fig. 30, photo 4). Presumably, this sclereid layer gives toughness to the wall of the young fruit and plays a role in the opening mechanism of the commissural valves. The dehiscence will be facilitated by the fact that in the radii of the main vascular bundles, where the valves separate, the meristematic mantle does not become sclerified, but remains composed of small parenchymatic cells. The bulk of
*Kiggelaria africana.* Figs. 9—18. Young pistil, series of t.s., 15 x. Figs. 19—26. Young seed, series of t.s., 7.5 x (fig. 24: 15 x). Distance between sections indicated in µm. — *Casearia flavovirens.* Fig. 27. Vascular bundle pattern of pistil. Base, cleared t.s., 15 x. Fig. 28. Ibidem. Half, cleared., 15 x.
the fruit wall is formed by a marked radial expansion of the cells of the mesophyll tissue outside the sclerifying mantle. As a result of this expansion the secretory spaces are extended as radial slits. In relation to the whole fruit the differentiation described above starts at the top and pursues downwards. It is remarkable that the development of the meristematic mantle and its differentiation is not continuous over the surface of the placenta where the ovules are inserted: Instead, this layer forms a boundary running between the pericarp and the placenta (a 'short-cut'), creating a separate position of the placenta with their independent vascular bundle strands. In *C. arborea* and *C. sylvestris* this boundary becomes much thicker, because cells on the side of the placenta become stretched radially or irregularly prior to the lignification of their walls. Moreover, in these species a radial expansion of the mesophyll cells of the pericarp is less evident, the mesophyll growing by multiplication of cells mainly.

It is a special feature of the *Casearia* spp. studied that, in the base of the pistil, the three placental ridges are confluent and give rise to a three-rayed ridge separating three small locules (figs. 30 – 32, photos 5 and 6). As this structure is not developed by a secondary approximation of the placental ridges, the pistillary apex possibly may develop into this three-rayed configuration at once, after the initiation of the pistillary wall. However, my material did not permit to study this development. In *C. arborea* this phenomenon is prominent. Epibasally, the three placenta can be recognized as ridges along the pistil wall. Upwards, the ridges fall apart into many ovular stalks over their whole surface. Distally the ridges are sterile, and, on the narrowing of the pistil, fuse secondarily in the middle, leaving a three-fluted styal space (with small locules in *C. tuberculata*, see fig. 35). Apically, this space opens again on the level of the stigma. Unfortunately, ripe open fruits could not be studied.

The pattern of vascular bundles in the pistil may be illustrated by the figs. 27 – 37. A stele of many small vascular bundles diverges into the flower base. Five main bundles of the perianth parts separate off, followed by five alternate commissural lateral traces of two adjoining perianth parts each. The remaining bundles converge upwards forming the stele toward the pistil. The traces of the stamens are connected with the above mentioned vascular bundles on a lower or higher level, according to whether the stamens are placed more outwards or inwards.

The pistil stele gives off three main bundles to the pistil wall first; then, higher up, three alternate sets of two collateral traces are given off (in the Asian spp. studied here), which ramify as the lateral bundles of the pistil wall. On cross-section, these lateral bundles appear as a continuous tangential series, no ‘median laterals’ can be distinguished. In *C. arborea* and *C. sylvestris* the lateral bundles originate much later in the ontogeny of the pistil wall as ‘cortical bundles‘. Above the level of departure of the bundles of the pistil wall, the remaining bundles converge into the stele which then falls apart into three portions, forming the complex strands of vascular bundles of the placental ridges. There are either cross-connections (*C. tuberculata* and *flavovirens*) or there is a mass of bundles (*C. arborea*) in the base of the three-rayed confluent placental ridges. Portions of the placental strands are split off toward the ovules. In the upper sterile parts of the placental ridges the vascular strands fade out. The complex strands consist of (cf. figs. 28, 33) either an irregular array of bundles (*C. arborea*), or a more or less concentric arrangement of collateral bundles (*C. arborea*), or a more or less concentric arrangement of collateral bundles (*C. calodendron*), especially below, or an inverted large bundle (*C. tuberculata*), or
*Casearia tuberculata.* Figs. 29—37. Pistil, series of t.s., 15× (fig. 29: 30×). Figs. 38—43. Young seed t.s., 15× (fig. 41: 30×).
again a tangential series of bundles (C. cf. flavovirens). In no case the placental vascular strands have a connection with the lateral bundles of the pistil wall, they come directly from the vascular bundles in the flower base. This construction makes clear that at fruit maturation the supply of the placentae can be secured, as well as their protection by the sclerified mantle described above.

The ovules are atropous. However, the nucellus with two integuments may be attached at the end of the funicle at an angle of up to ninety degrees or sometimes even more. The micropyle is formed by the inner integument in its proximal part, by the outer integument in its distal part. The ovules have an aril which probably originates from the dermal layer on the distal part of the funicle, subdermal layers being incorporated later. The distal half of the aril is lobed to laciniate, and consists of two dermal cell layers only. The embryosac absorbs the central distal part of the nucellus and protrudes into the endo- and ectostome at an early stage, always remaining covered by the distal cells of the outer integument. The outer integument has fewer cell layers and fewer but larger cells than the inner integument. Both integuments have only two dermal cell layers distally. The outer integument remains entirely parenchymatic and forms the outer soft cell layers of the testa, consisting of large cells (figs. 38—44). As regards the inner integument, its outer epidermis develops into ribbon-like (Corner) longitudinal sclereids, its inner epidermis into a pigment layer (photo 7). The endo- and ectostome become lined with the suberized cells of small radial cell rows formed by both epidermides of the inner integument and by the inner epidermis of the outer integument. In its proximal region the seed is protected by a concave plate of sclerified tissue more or less in continuity with the sclerified integumental layer. On top of it, the nucellar basal remains form a suberized plate of tissue. Moreover a rim of brachysclereids forms a prolongation of the integumental sclerified sheath downward into the chalazal tissue, enclosing the distal part of the vascular bundle cup. A large complex vascular bundle enters the seed, spreading cup-like in its base, but not reaching into the integuments. Many small longitudinal vascular bundles of the aril are connected with this large bundle later on. At an early stage of seed development a transverse abscission layer of small, thin walled parenchymatic cells is formed. A copious endosperm surrounds a moderately sized planate embryo, as is common in Flacourtiaceae.

**Berberidopsis corallina**

Newly received fruiting material of this species, collected in its natural habitat in Chile, leads to an addition of the descriptions given in my paper on some Oncoboeae (1977). Hitherto, taxonomic works gave no descriptions of the fruits and seeds. Possibly, the fruits in the present material are almost mature. The fruits are roundish, the largest one present measured 14 mm in length and 9 mm in width. They have a brown-red colour (in alcohol). The style and stigma are persisting. The fruits are attached to the fruit-stalks, a lobed hard rim persisting between the stalk and the fruit, which represents the enlarged torus or disc between the perianth and the stamens. Also some minor lobes may be present between the scars of the stamens and the pistil. Considering that the wall of the fruit is entirely parenchymatic, and that there are no indications of lignification, nor of dehiscence lines, it seems that the fruits are berries, with a small-celled rind and a softly parenchymatic endocarp which protrudes between the outer seeds. There is no differentiation into radial cells of the mesocarp.
Twenty to thirty seeds are present in one berry, they are angularovoid, 3 mm long and 2 mm wide, reddish brown (in alcohol) by the contents of the large polygonal surface cells. The seeds are marked by a protuberant raphe consisting of pale, softly parenchymatic tissue.

The ovules, at anthesis, are anatropous; they have two integuments, a narrow endopyle bordered by the inner integment, and a wide ectopyle bordered by the outer integment. The raphe vascular bundle spreads little in the chalaza, no ramifications entering the integuments. A patch of tissue, staining red, forms a kind of hypostase. The nucellus is thick. The outer epidermis of the ovule consists of large cuboid cells which stain red with safranine; at the raphe, however, they remain unstained. The inner epidermis of the outer integment consists of many small isodiametric cells containing large nuclei. The mesophyll consists of 1 or 2 layers of larger parenchymatic cells. The inner integment has four cell layers, two mesophyll layers, and two epidermides which are regular by their cell pattern, but do not show any differentiation. In ovules at post-anthesis the outer epidermis of the inner integment soon becomes absorbed, except at the endopyle and near the chalaza; it is the first integument cell layer to disappear.

In the seed (figs. 47 and 48, photo 8) there is a conspicuous layer of palisade cells, the walls of which are undulatingly lignified and also pitted. Frequently, the lignification traverses the cell in the form of bars. Each cell contains a rhomboid crystal at one of its ends. As the distal parts of the integuments can be partly free from each other at the ectopyle, it could be verified by comparison with that region that the palisade layer represents the inner epidermis of the outer integment. This is in accordance with the observation of this layer as the only one that, in ovules at anthesis, shows signs of beginning differentiation in the form of cell activity. At the ectopyle also mesophyll cells show the undulating lignification of their walls. Except for the palisade layer, a conspicuous layer in the seed is formed by the thick cuticle which is present between the disrupted, but partly persisting, epidermis of the nucellus and the inner integment. All the cells of the inner integment become disrupted and partly absorbed. Only the inner epidermis persists in the form of its inside and radial walls, causing a polygonal pattern on the cuticle layer, or rather it
Casearia clutiaefolia. 7. Differentiation of the integuments into seed coat. — Berberidopsis corallina 8. 
Base of young seed, ± l.s.
may be the cuticle which penetrates between the inner epidermis cells. The seeds have a copious endosperm, consisting of cells, with a small embryo in it.

Four characters of the seed are very unusual for Flacourtiaceae, namely 1) the small embryo; 2) the endotestal development as a crystalliferous palissade layer; 3) the conspicuous notched cuticular layer; 4) the lack of differentiation of the inner integument. Presumably, the fleshy raphe is rare in Flacourtiaceae as well. For these reasons Berberidopsis must be considered as forming a separate tribe (cf. Berberidopsideae, Hutchinson, 1967), or must be given family rank. Warburg (1893), and Gilg (1925) placed the genus in the Flacourtiaceae. All prior authors considered Berberidopsis to be similar to Berberidaceae and Lardizabalaceae, judged from external appearance. However, Warburg placed the genus in the Flacourtiaceae on the strength of the longitudinally dehiscent anthers and the gynoecium with three parietal placenta. Another argument concerned the genus Erythrospermum, which has much similarity with Berberidopsis. However, I found that various specimens of Erythrospermum from New Guinea, present in our Herbarium, have a seed coat very much like that of Kigeliaaria. Furthermore, Erythrospermum has large embryos, as also Warburg reported. This means that Erythrospermum, although belonging to the Oncobeae, has a seed coat as in the Hydnocarpaceae group, viz. a mixed endotestal and exotegmic one. Evidently, Erythrospermum is Flacourtiaceous, more clearly than Berberidopsis. In Berberidopsis the indication of an affinity with Magnoliidae is of course much more evident by the purely endotestal seeds and the small embryos. Unfortunately, however, the rather diverse seed structure as far as known from such parietal Magnoliid families as Berberidaceae, Lardizabalaceae, and Papaveraceae does not present many points of contact. From a study of the pollen morphology (Keating, 1973), as well as from a study of the xylem anatomy (Miller, 1975) follows that Berberidopsis has a very primitive position within the Flacourtiaceae. Miller thinks many wood characters of Berberidopsis (and Strep- tothamus) occur especially in the Dilleniaceae, and also in the Theaceae. The seed coat anatomy of Berberidopsis, as described above, also occurs in Theaceae. Minute embryos are present in Dilleniaceae. Possibly, the structure of Berberidopsis, the partly endotestal seed in Hydnocarpus, and the perianth of Oncobeae, all indicate an ancient relation of the Flacourtiaceae with Dilleniidae.

ACKNOWLEDGEMENTS

My sincere thanks are due to the Directors of the Institutes mentioned, to Mr. P. Drijfhout (Stellenbosch), Dr. F. S. P. Ng (Kepong), Dr. C. G. G. J. van Steenis (Leiden), Dr. M. J. van Balgooy (Leiden), Dr. H. Sleumer (Leiden), all for collecting material in alcohol or in F. A. A. Part of the material, as indicated by *, was collected during my visit to the Kebun Raya at Bogor in 1969. This visit was subsidized by the Netherlands’ Foundation for the Advancement of Tropical Research (WOTRO), The Maatschappij voor Wetenschappelijk Onderzoek in de Tropen (Treub-Maatschappij), the Greshoff’s Rumphius Fonds, and the Van Leersumfonds. Another part of the material, as indicated by **, was collected during a short visit to the Botanic Garden of the University of Malaya at Kuala Lumpur. This visit was subsidized by the Netherlands’ Organization for the Advancement of Pure Research (ZWO).

MATERIALS

*Berberidopsis corallina.* Fig. 46. Ovule, l.s., 120 x. Fig. 47. Seed, transmedian s., 30 x. Fig. 48. Seed coat, t.s., 220 x.

For the meaning of* and** see under Acknowledgements.

REFERENCES


