

## ON THE ARILLOIDS OF NEPHELIUM, EUPHORIA, LITCHI AND AESCULUS, AND THE SEEDS OF SAPINDACEAE IN GENERAL

L. VAN DER PIJL  
(*Rijksherbarium, Leyden*)

(received July 16th, 1957)

### A. INTRODUCTION

The seeds of the *Sapindaceae* show some remarkable features. One of them is the “*Wurzeltasche*” or radicular pocket, separated from the main part of the seed by a “deep fold of the testa”.

Another noteworthy feature is the pluriformity of the fleshy parts round or near the seed. The fleshy part may belong either to the seed itself or to the pericarp. RADLKOFER, the well-known specialist on the *Sapindaceae*, originally used the term aril for all these fleshy parts, which means that he used it in an ecological sense. In his study on the “aril” of *Sapindaceae* (1878) he proposed to use the terms: *a*) arillo epispermatico, *b*) a. esostomatico, *c*) a. ombelicale-esostomatico, *d*) a. ombelicalo and *e*) a. endocarpico, for those, morphologically heterogeneous, structures. In this paper these structures will be designated as follows, *a*) sarcotesta (fleshy testa), *b*) micropylar arillode, *c*) micropylar-chalazal arillode (*b* and *c* are fleshy parts of the testa restricted to a definite area), *d*) true aril, and *e*) endocarp pulpa.

In later years RADLKOFER (1895) gave a short review of the fruit forms occurring in this family, in which he designated the fleshy layers with the conventional names. He seemed to think that the phylogenetic sequence of the structures *a*, *b*, *c*, *d* was *d-c-b-a*, which means that he regarded the sarcotesta, of e.g. *Talisia*, as the final stage. On the seeds of *Xerospermum*, which apparently are provided with a sarcotesta, he said that they possessed a fleshy aril that was completely fused with the seedcoat. The sarcotesta of the genera *Synima* and *Lychnodiscus* was presumably interpreted by him in the same way.

In his large monograph of 1933/1934 he gave no general review, but inserted many remarks on the arilloid structures found in individual species. In this work he criticized at several points the current fashion to describe every fleshy part that does not belong to the outer pericarp as an aril.

In later years the morphological investigation of the various kinds of testa found in the *Sapindaceae* has made but little progress.

MAURITZON (1936a) figured the ovules of some species of *Sapindus*, *Xanthoceras*, *Nephelium*, *Koelreuteria*, *Dodonaea*, *Diplopeltis* and *Cardio-*

*spermum*. He described cases in which the thick nucellus was, during anthesis, gradually resorbed, of an unusually broad insertion of the ovule, of the campylotropous incurvation of the ovule during its later development, and of the outer integument's tendency to swell in the micropylar region. He paid, however, little attention to the vascular supply of the ovule and to the development of the testa.

CORNER (1953) paid some attention to the family when he was in search for support for his "Durian Theory", which regards the arillate seed as primitive.

The sarcotesta of the *Melicocceae* was by him too considered as "a modification of the aril: in some obscure manner the aril becomes adnate to the testa in many allied *Nephelieae*". In some of them (*Nephelium*, *Cubilia*, *Pometia*) and also in *Blighia*, *Paullinia* and *Schleichera* he considered the fleshy part on the outside of the seed as an aril.

In 1955 I published a study on the typological derivation, or, possibly, the evolution, of fleshy parts in the fruits of the *Angiosperms*. I tried to prove the primitiveness of the fleshy seedcoat, or sarcotesta (phase *a*), and adduced arguments in support of Corner's idea that the current notion of the primitive seed as a small, hard, dry and dormant organ is to be abandoned. I criticized, however, his indiscriminate use of the term aril, and I demonstrated that in contrast to Corner's opinion, most so-called arils are arillodes and that even parts that are usually designated as a "true funicular aril" are in many instances derivative products, viz. specialized and individualized outgrowths of the integument. I already found support for this view in some *Sapindaceae*, where many "arils" are in reality arillodes, arising from the integument.<sup>1)</sup>

I have already elaborated my view on the primitive character of the sarcotesta for the *Leguminosae* (1956), and wish to do now the same for the *Sapindaceae*, in order to show that, here too, the same above already mentioned developmental range *a-e* is present.

First of all, however, I wish to make some general remarks.

The discussion on the nature of the aril is, as I perceived a short time ago, the revival of a controversy which arose a century earlier (cf. the review given by PFEIFFER (1891)). BAILLON (1875) took, in a study not reviewed by PFEIFFER, the same stand as I do now. He regarded an "*arille généralisée*" (our sarcotesta) as the starting point from which various arilloid structures arose by reduction; the latter were his "*arilles localisées*". He demonstrated this in *Myristica*, some *Zingiberaceae*, *Euphorbiaceae* and *Rhizophoraceae*. MAURITZON (1936*b*) studied "arils" from some of the families which according to Corner are provided with arillate seeds. In *Careya arborea* (*Lecythidaceae*), *Strelitzia*, *Costus*, *Globba* and *Alpinia* (*Scitamineae*) these "arils" proved

<sup>1)</sup> I wish to make here a correction in the table given in my study of 1955. Among the *Palmae* the *Lepidocaryae* (*Zalacca*, *Metroxylon*, *Daemonorops*, *Plectocomiopsis*, *Calamus*, etc) are not provided with a pulpy endocarp, as stated there with a question mark. According to BECCARI (1918) the fleshy mass around the seed is part of the latter.

to be arillodes developed from the integument parts indicated in Fig. 1 by *a* and *c*.

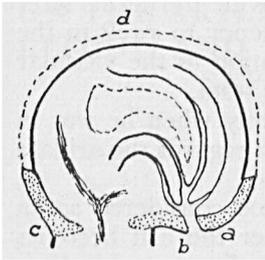


Fig. 1. Schematic median section of a sapindaceous ovule with the regions of the outer integument which may contribute to the development of arillodes dotted. In a complete sarcotesta *d* too is fleshy.

Finally I have to discuss some definitions of terms used in this paper.

PFEIFFER (1891) defined the aril as an outgrowth of a part near the seed and attached only at its place of origin. Although this definition agrees in the main with my own conception, does not prevent us from regarding the aril as a secondary structure, and excludes the sarcotesta, it seems to me too wide, as it would include also Radlkofers "arillo endocarpico", the endocarp pulpa (found in some *Guioa* and *Pseudima* species).

Though MAURITZON (1936*b*, 1939) showed that arilloid structures may sometimes be developed before fertilization has taken place, I propose to define the aril more or less in the same way as Gaertner did of old, viz. as a secondary, usually postfloral outgrowth of the funicle and therefore entirely free from the seed. This definition is independant of whatever view we may hold with regard to the phygenetical origin of the aril.

While maintaining the old term "arillode" for an outgrowth of the integument in the vicinity of the micropyle, I shall use the term "arilloid" for every kind of outgrowth on and near the seed that resembles the apparently entirely independent aril.

## B. OBSERVATIONS

### *Cupania hirsuta* Radlkofer (*Cupanieae*)

I could study the ovules of flowers in anthesis. They show a slightly curved nucellus, which in this species persists up to this period, but might nevertheless be described as anatropous.

There is no distinct funicle, and the ovule is inserted directly on a horizontal outgrowth, apparently of the central "axis". The outgrowth is widened transversely, and acts as a kind of secondary placenta. It projects past the place of insertion of the ovule, and forms underneath the micropyle a kind of obturator (Fig. 2).

The outgrowth of the placenta possesses a vascular supply consisting of several bundles. A large bundle enters the ovule; this is the raphal bundle. It does not branch into separate integumental bundles as is frequently seen in the family. The raphal region is more or less swollen.

As I did not have older stadia, I could not make out from what part the cupuliform aril, whose presence has been reported for the genus, arises.

I started with the description of the situation found in this species, as it seems to be a rather simple one, from which that which we will meet in other genera may be derived.

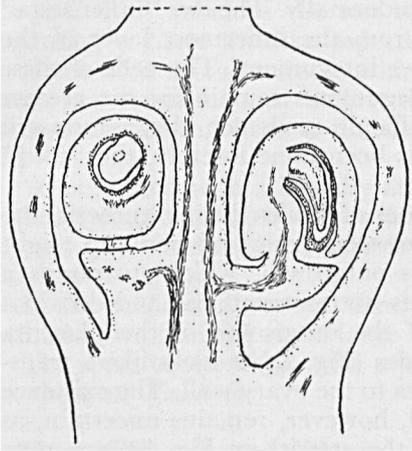


Fig. 2. *Cupania hirsuta*. Longitudinal section of ovary during anthesis. Left ovule cut obliquely, right one according to the plane of symmetry.

### ***Nephelium lappaceum* L. (Nephelieae)**

RADLKOFEK (1933) says that the edible part of the fruit is an aril, adnate to the thin testa, and only free from the latter around the micropyle. He considers it as a far advanced stage in the developmental range mentioned in the introduction.

However, a study of the ontogeny of the seed shows that the fleshy layer is in reality the swollen outer integument (Fig. 3). The broadly

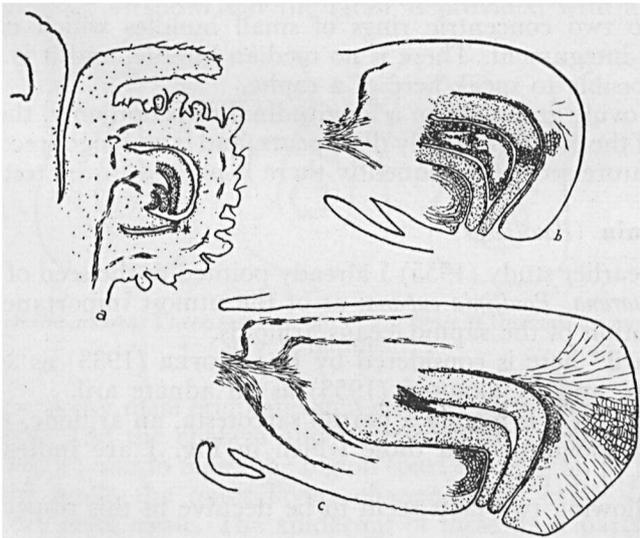


Fig. 3. *Nephelium lappaceum*. Longitudinal sections of ovarium and ovules, *a*, very young ovary, *b*, ovule at the time of fertilization, *c*, a long time after fertilization.

attached ovule grows out in a longitudinal direction, and the cells of the outer integument become very large. Near the tip they are arranged in rows that radiate fanwise. Sometimes these rows of cells end in the epidermis, which suggests an epidermal origin, but sometimes they end (or better start) subepidermally. The dry "inner testa" underneath it probably originates from the innermost layer of the outer integument and from the inner integument. The cells of these layers remain small. As the two integuments remain for the greater part firmly connected, it proves difficult to detach the pseudo-aril from the inner layers. When this has been done forcibly, the "seed" shows, of course, no true hilum.

When we study longitudinal sections of ovules during anthesis, the triangular outgrowth in the angle between ovule and pericarp might suggest a future aril. However, this outgrowth, which surrounds a large part of the base of the ovule, is not meristematic and does not develop further. It reminds one of the outgrowth of the placenta found in *Cupania*. In very young ovules (Fig. 3a) it looks like a transverse sept extending from the placenta to the ovary wall. The existence of a connection with the ovary wall, however, remains uncertain, as the supposed connecting cells near the asterisk in Fig. 3a are more or less free from each other and desintegrate entirely in a subsequent stage. This situation elucidates to some extent the one found in *Cupania*. There, however, the ovule proper still shows something like a real raphal bundle. It looks as if in *Nephelium* the basal part of the ovule is not just an unusually broad funicle, but that it includes placental tissue.

In transverse sections of fertilized ovules we have studied the vascularization. A very thick vascular column composed of radially arranged bundles, runs through the basal part. At a higher level it splits into two concentric rings of small bundles which enter into the outer integument. There is no median bundle, and it is therefore hardly possible to speak here of a raphe.

As the ovule grows out in a longitudinal direction only, the campylotropy of the ovule gradually disappears, and is no longer recognizable in the mature seed. Consequently there is no fold in the testa.

### **Paullinia** (*Paullineae*)

In my earlier study (1955) I already pointed to the seed of the well-known *guarana*, *Paullinia cupana*, as of the utmost importance for the interpretation of the sapindaceus arilloids.

The "aril" here is considered by RADLKOEFER (1933) as an adnate arillodium, and by CORNER (1953) as an adnate aril.

I found that it is merely a partial sarcotesta, an arillode, the fleshy parts corresponding with those which in Fig. 1 are indicated with the letters *a*, *b* and *c*.

The following two facts seem to be decisive in this respect:

- a) the micropyle is visible in the middle of the arillode, which would be impossible if an aril had grown over it,

b) the so-called "aril" does not consist of a distinct tissue fused with that of the testa, but is to be regarded as a mere change in the texture of the testa itself (cf. *Cardiospermum*).

In *Paullinia boliviana* Radlk. the arillode shows an outgrowth at its rim. This envelops the rest of the seed for some distance, thus assuming a more aril-like aspect.

If the zone of the testa to which the arillode is attached becomes narrower the latter may at first sight be hardly distinguishable from a true aril arising from a funicle and remaining entirely free from the testa.

When a seed with a broadly attached arillode like that of *Paullinia* is detached, the hilum becomes visible. When subsequently the arillode is torn off, a much larger scar is left. We shall call this second scar the pseudo-hilum.

In the seeds of *Durio* and *Euonymus*, which also are provided with arillodes, we find the same large scar on the seed.

The seeds of *Aporrhiza*, with a half dry, half fleshy testa are similar to those of *Paullinia*.

### **Harpullia arborea** (Blanco) Merr. (*Harpullieae*)

The almost mature seeds I could investigate, were dark brownish-green and bore the fleshy, orange outgrowth that is characteristic for the genus, and which generally has been described as an aril. RADLKOFER (1933) calls this species exarillate, but in all the herbarium specimens seen by me the arillode was well recognizable, though strongly shrivelled.

It is easy to prove that it is an arillode of the *Paullinia*-type, not adnate to the testa, but part of it. Sections of an ovule shortly after fertilization (Fig. 4) show that the latter is provided with a funicle,

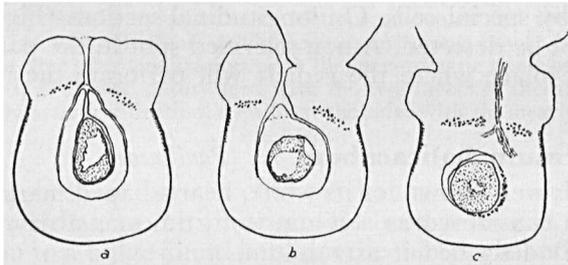


Fig. 4. *Harpullia arborea*. Three sections out of a series cut through an ovule shortly after fertilization.

and that the fleshy mass originates in a circular zone which surrounds the micropyle and the chalaza and belongs to the outer integument (part *a* in Fig. 1) and to the raphe region (part *c* in Fig. 1). In the other parts of the ovule the outer layers change at an early stage into ordinary, dry testa tissue. The epidermis of these dark parts extends for some distance over the arillode, and this too seems to prove that the arillode can not be regarded as an originally distinct part.

Dark-coloured, sclerified or cutinized cells are seen at an early stage in the deeper layers of the arillode where they form the continuation of the dry parts of the testa, and serve as a protective shield underneath the arillode. When the arillode is removed, a pseudohilum is left.

A view of the mature arillode from above (Fig. 5*b*) and a section of it perpendicular to the micropylar canal (Fig. 5*c*) show that the region indicated in Fig. 1 by *b*, does not develop into arillode tissue. This part is covered by extensions of the tissue formed in the parts

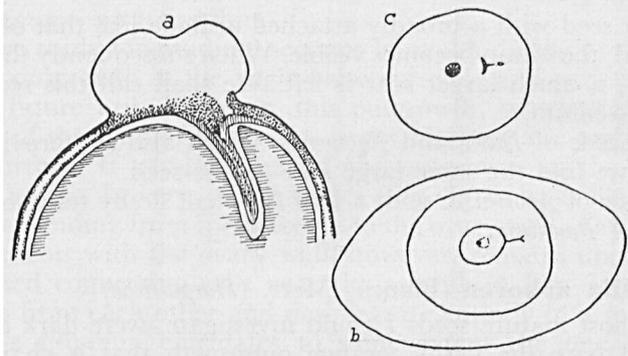


Fig. 5. *Harpullia arborea*. Arillode of mature seed. *a*. longitudinal section, almost median, with intrusion and embryo, *b*. surface view from above with arillode, hilum, suture and micropyle, *c*. cross section of upper part of arillode with bundle, suture and canal.

*a* and *c*. The groove between these two parts of the arillode persists even in the ripe seed. The micropylar canal in the upper part of the arillode is extremely narrow, and disappears in its lower part; it is not lined by special cells. On longitudinal sections (Fig. 5*a*) it can, therefore, not be detected. A non-sclerified spot in the partition layer indicates the place where the radicle will perforate the testa at germination.

### **Cardiospermum halicacabum** L. (*Paullineae*)

The seed is well-known for its white, heart-shaped mark. The latter is sometimes considered as a hilum, sometimes as a dry aril. RADL-KOFER (1933) described it as a hilum.

In the heart-shaped mark we find the micropyle near the notch and the scar of the vascular bundle near the point.

We possess three studies dealing with the ontogeny of the seeds, viz. by GUÉRIN (1901), MAURITZON (1936*a*) and KADRY (1946). (The more general study on the sapindaceous testa promised by Guérin, has never appeared, as far as I know). The study by Mauritzon gives no details that might interest us here. The other two studies contradict each other in some respects. Guérin gave drawings which leave us in some doubt with regard to the exact origin of the arillode. He regarded it as an extra-layer over the testa.

Kadry interpreted his Fig. 15a as showing a micropylar beak, a massive mucilaginous tissue originating from the tip of the nucellus and from part of the inner integument. He contested the correctness of Guérin's opinion that this beak surrounds a micropylar canal.

Guérin's Fig. 1, the structure generally found in the ovules of the family and my own sections through these ovules make it clear that this beak is nothing but the tip of the solid looking inner integument, and that the nucellus has been resorbed by this time (Fig. 6b), as was stated expressly by Guérin.

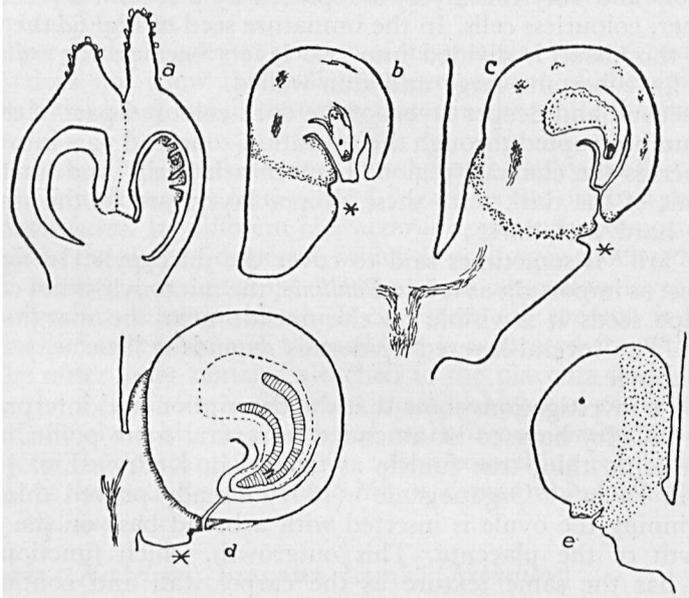


Fig. 6. *Cardiopermum halicacabum*. a-d. Sections of ovules and seeds of successive age, at different magnification. a. Gynoecium in young flower bud, b. in open flower, c. some time after fertilization, with the meristematic tissue of the developing arillode dotted, d. almost mature seed with the two layers of the arillode hatched, e. ovule shortly after fertilization, seen from the side, with the nearly white arillode dotted.

Obviously because he was convinced that every ovule must have a funicle and that an "aril" originates from a funicle, Kadry drew the attention to a bulge found between the micropyle and the placenta (which bulge is in fact the outgrowth of the placenta which acts as a funicle) which is present before fertilization and would according to him develop into an aril. According to him this bulge (indicated by an asterisk in my figures) is an outgrowth of the funicle, which later on surrounds the micropyle as well. At this place inside the curvature the outer integument, though recognizable in young ovules, is said to become undistinguishable in older ovules. We can, however, discern it in his drawing, and it is clearly recognizable in Guérin's drawings as well as in my own sections (Fig. 6). The part of the outer integument situated inside the fold shows in a section through the

plane of symmetry the semi-circular shape that is so characteristic for the *Sapindaceae*.

The "aril" is certainly not, as said by Kadry, an extra-layer fused with the testa (outer integument). Apart from direct observations to be described further on, the arguments against this view are the same as those given in our discussion of the corresponding part in the seed of *Paullinia*. In mature seeds we see in the transition zone between the white "aril" and the dark "testa" that the latter has a typical dark pallissade epidermis with thick outer walls, and that in the "aril" this layer (and only this layer) is replaced by a several-layered tissue of thinner, colourless cells. In the immature seed of Fig. 6*d* the central part of this tissue is divided into two layers because the cells in its middle have become large and thin-walled.

The second and deeper layers of the dark-coloured part of the testa extend uninterrupted through the transition-zone and pass into similar layers across the chalazal region. Underneath "aril" and unchanged epidermis of the dark testa these deeper layers are in the ripe seed equally hard and dark.

The "aril" is sometimes said to cover the micropyle. In fact, and this is just as important as it is in *Paullinia*, the micropyle is not covered. In unripe seeds it is visible on the outside near the margin of the arillode. The several-layered epidermis extends a little way beyond the micropyle.

My own investigations show that the description and interpretation given by Kadry have to be amended in several more points.

There is no thin, true funicle as figured in Kadry's Fig. 14. The figures in Payer's "Organogénie" (1857) already proved this. From the beginning the ovule is inserted with a broad base on the typical outgrowth of the placenta. This outgrowth, which functions as a funicle, has the same texture as the carpel wall and contains the same, heavily colouring idioblasts.

The outgrowth forms a brownish bulge below the ovule. That it looks as if this bulge grows out over the ripening seed, is due to the fact that internal changes in the arillodal part of the testa (splitting of its layers) proceed upwards, so that it looks as if the brownish colour of the bulge on the outgrowth of the placenta spreads upwards. The outgrowth of the placenta itself does not develop any further.

My sections (Fig. 6) show that the fertilized ovule develops an arillode from the usual regions near the micropyle indicated in Fig. 1.

Whereas the main part of the ovule is covered by a typical epidermis with smooth cuticle, and underneath the epidermis with parenchymatous tissue, the parts of the integument which are dotted in Fig. 6 remain for a longer time meristematic; they are rich in protoplasm, consist of very small, thin-walled cells, and show an uneven surface. The meristematic region between ovule and pseudo-funicle, clearly belongs to the integument, even in the raphal region.

The outer integument also produces a meristematic bulge situated between micropyle and pseudo-funicle. During anthesis (Fig. 6*b*) this

bulge is still united with the part inside the fold of the inner integument which later on is separated.

Seen from the outside this arillode is clearly distinguishable in young seeds, as shown in Fig. 6*e*, which represents a slightly older stage than Fig. 6*b*. The colour of the arillode is nearly white and dull, whereas the rest of the testa is brown and glistening.

The arillodal region is traversed by a single vascular bundle, which might be regarded as a raphal bundle. However, shortly after entering the outer integument above the arillodal layer, it divides into two branches, one on each side of the median plane, and the latter split into several bundles.

In larger seeds the greater portion of the nucellar part (the radicular pocket) does not show the arillodal development of the epidermis, and forms the black notch that penetrates in the white, heart-shaped arillode.

The tissue of the arillode does not become fleshy, and it differs, therefore, in this respect from what I regard as the original condition in the *Sapindaceae*. Its different character is apparently connected with a change in the way of dispersal, which is no longer zoöchorous. The arillode persists, but functions merely as an abscission layer.

In herbarium material in which ripe seeds are present, it is easily seen that the outer layer of the arillode is separated from the inner one. The outer layer remains attached to the placenta and the inner layer to the seed. It forms the white mark, which can easily be scratched off. So the white heart-shaped mark is not something sticking to the testa, but a scar, i.e. a place where something is missing. This remnant of the arillode is a pseudo-hilum, comparable to that described for *Paullinia*, etc.

### **Euphoria** (*Nephelium*) **longana** Lamk. (*Nephelieae*)

RADLKOFE (1895) considered the fleshy, edible layer round the seed as a free aril. This interpretation looks plausible as the "aril" arises at the base of the seed from a narrow ring which contrasts by its white colour with the brown testa.

The ring remains dormant for a long time after fertilization. In fruits of 2.5 cm length i.e. in a fairly advanced stage of development (seed 1.6 cm) the ring is 2.5 mm high, in another fruit of 2.9 cm length the "aril" has grown out to  $\frac{1}{3}$  the length of the seed, in an almost ripe fruit of 3.5 cm length the "aril" entirely surrounds the seed and overlaps the top with its lobes.

I could study the nature of the ring in sections.

In young ovules (Fig. 7*a*) a situation is found resembling that in *Cupania*. The horizontal body below the ovule is easily recognizable as a fold of the carpel. Its epidermis is continuous with the internal lining of the latter, and its subepidermal layer contains the same kind of idioblasts as the corresponding layer on the inside of the pericarp. It has a double layer of vascular bundles, the upper one connected with the bundles of the central axis, which below the plane of section pass into the style, the lower one connected with more peri-

pheral bundles in the torus. There are, however, anastomoses between the two.

The ovule proper is here too inserted with a broad base, and consists of a different kind of cells.

The situation is schematically represented in Fig. 7*b*, where the pseudo-funicle is interpreted as an outgrowth of the "Querzone", the rim of the lower, peltate part of the carpel, which is horizontally

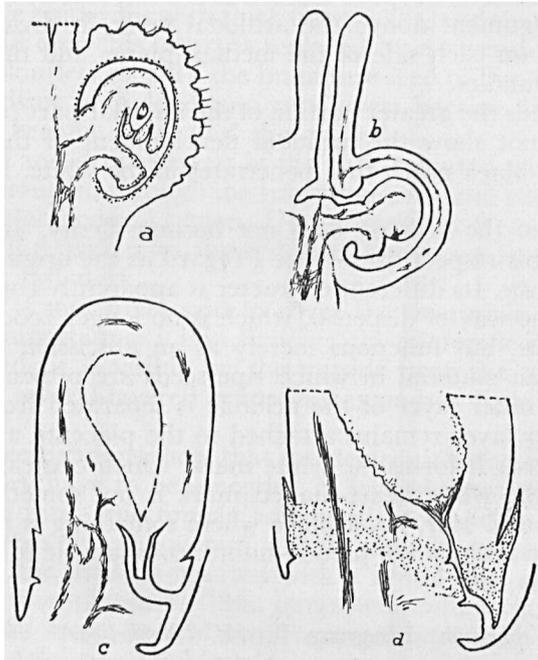


Fig. 7. *Euphoria longana*. *a*. One cell of the ovary of an open flower, *b*. Schema of the structure of an ovary cell, *c*. young seed of 3½ mm length, *d*. basal region of young seed of 5 mm length; arillodal region dotted.

incurved. This ovary would differ therefore from those found in many other families, where the ovules are borne in vertical rows on or near the margin of the upper carpel parts.

Fig. 7*c* represents a longitudinal section of a young seed of 3.5 cm length. Above the groove between seed and pseudo-funicle the white ring which is to grow out into the arillode, is visible; it is separated from the rest of the seed by a second groove. The ring is a differentiation of the outer integument and runs internally from its tip across the seed to the chalazal region; therefore a typical arillode. The upper part of the seed has a one cell thick, smooth epidermis, whereas in the arillode the epidermis, just as in *Cardiospermum*, is not sharply delimited.

In older seeds, like that of Fig. 7*d*, the ring grows out in an upward direction. The tissue remains white and soft (dotted in Fig. 7*d*). At the micropylar side of the seed the ring extends beyond the micropyle, which is so well hidden by it that it is difficult to find, except in

microtome sections. When the seed is detached from the basal part of the arillode, it exhibits a pseudo-hilum.

The campylotropy of the ovule is but weakly expressed, and in the seed it is no more recognizable, as the endosperm in the embryonic sack develops, just as in *Nephelium*, in a longitudinal direction only.

### **Litchi chinensis** Sonn. (*Nephelieae*)

The genus *Litchi* has according to RADLKOFER (1933) a free aril. In the drawing given by RADLKOFER in 1898 (Fig. 167B) the "aril" is wrongly represented as fully closed around the seed, while in fact it is open at the top between the overlapping folds.

The "aril" develops just as in *Euphoria* from a white ring round the base of the seed. It takes here even longer before it grows out than it does in *Euphoria*. In fruits of 2.5 cm with seeds of 1.6 cm length the ring was 2.5 mm high, whereas in fruits of 2.9 cm with seeds of 1.9 cm it covered one third of the seed. Only in almost mature fruits of 3.5 cm (seeds 2.3 cm) the "aril" had reached its ultimate size.

The question now arises again, of what nature the ring is.

BANERJEE (1944) gave a figure (his Fig. 13) with an "obturator" over the micropyle, and thought that from this organ and the likewise papillated tissue at the raphal side the aril might develop. I could confirm the presence of these tissues, but am certain that the "obturator" is the usual outgrowth of the carpel, here covered with papillae. It does not develop any further (Figs. 8a and 8d), and is still recognizable in rather large seeds as a white parenchymatous tissue situated under the meristematic ring.

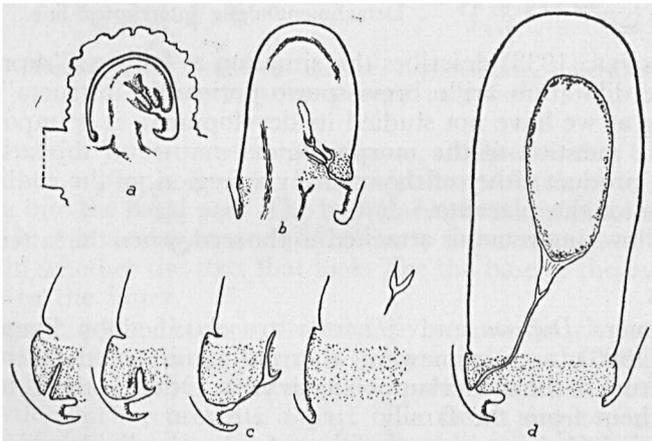


Fig. 8. *Litchi chinensis*. a. one ovary cell of open flower, b. ovule considerably swollen, c. subsequent sections through the micropylar region of a young seed forming part of a series, d. seed of  $\pm 1$  cm length; endosperm freenucleate.

Some time after fertilization (Fig. 8b) the outer integument appears to be distinctly swollen at the places a, b and c of Fig. 1. At the place b the thickening is still diffuse. In older seeds the zones a and c have differentiated outwardly into the protruding ring of meristematic

tissue that we found also in *Euphoria*, whereas the rest of the seed is covered by a smooth epidermis. The ring is separated from the main part of the integument by a groove. The micropyle lies below the ring. If the latter were an aril, the micropyle should lie above it. The ring is clearly the narrowed partial sarcotesta predicted in the description of *Paullinia*.

In the vicinity of the micropyle part *b* of the outer integument also grows out, so that in this region the ring consists of a double layer (Fig. 8*c*). The inner integument remains as a cap much higher in the seed, as shown in the schematic drawing given in Fig. 8*d*.

The cup which develops out of the ring is, just as in *Euphoria*, an arillode. From the rim of the outer integument it extends to the raphal side. The ripe seed shows (in contrast to what we find in an arillate seed) the micropyle inside the pseudo-hilum (cf. Fig. 12).

### **Toechima plurinerve** Radlk. (*Cupanieae*)

A figure of a longitudinal section through an almost mature fruit is given in Fig. 9.

The seed seems to be attached with a wide base to the placenta, i.e. without the intermediary of a funicle. At its base it is enveloped by a yellow, fleshy ring (dotted in the drawing).

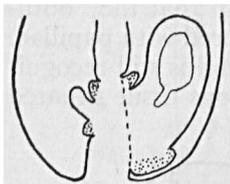


Fig. 9. *Toechima plurinerve*. Longitudinal section of almost ripe fruit with one ovule aborted. Arilloid dotted. Detachment along interrupted line.

RADLKOFER (1933) describes this situation as follows: "supra hilum transverse dilatatum arillo brevi spurio pericarpio instructa".

As long as we have not studied its development, it is impossible to decide the question of the morphological nature of this arilloid; it may be a product either of the micropylar region, of the rudimentary funicle, or of the placenta.

The yellow ring remains attached to the seed, when the latter is shed.

### **Didierea**

The genera *Didierea* and *Alluandia* are classified by PERROT and GUÉRIN (1903), as a, somewhat aberrant, group of the *Sapindaceae*. The structure of the ovules supports this view. Other authors, however, exclude them from the family.

Perrot and Guérin give a drawing of a longitudinal section (their Fig. 7) through a seed, and mention a small aril arising from the funicle, near the micropyle. As it is attached in the notch of the seed at the side of the radicle (and micropyle), it seems more probable that this "aril" originates from the integument. A comparison with their Fig. 3, which represents a mature ovule, confirms this view. We find here at the corresponding place, which corresponds also with area *b* of our Fig. 1, an outgrowth of the outer integument.

***Pometia pinnata* Forst. (*Nephelieae*)**

The ripe seeds are surrounded by a fleshy layer. RADLKOFER (1933) regarded the latter as an adnate aril. Corner followed him.

My material contained young fruits and unswollen ovaries. The latter were obviously derived from unfertilized flowers, as sections (Fig. 10a) show that their ovules are already degenerating. These ovules, however, give a good idea of the various layers in the mature stage, and show that the campylotropous curvature has at this stage not progressed very far. The nucellus has been resorbed by the embryosac, by now also obliterated, though in the remaining, basal part of the nucellus the cavity in which it was originally enclosed, is still recognizable. In the shrivelled apical part of the embryosac the egg apparatus may still be visible. Cross sections through the micropylar region show the presence of a micropylar canal.

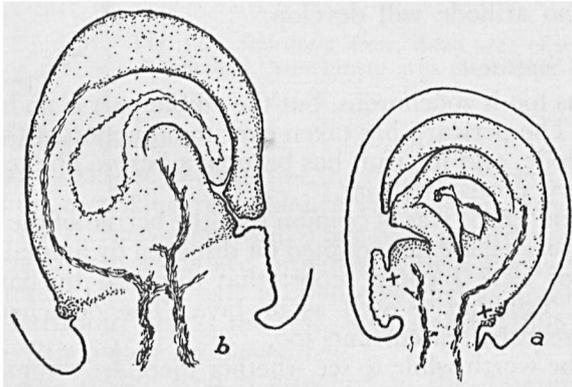


Fig. 10. *Pometia pinnata* ovules, a. mature, degenerating, unfertilized, b. from young fruit, less strongly magnified.

The ovule is, just as in other *Sapindaceae*, attached with a broad base, i.e. without a proper funicle. Some separate strands enter from the placenta into the basal part. The boundaries between placenta, funicle and ovule are as vague as in *Nephelium*, *Cupania*, etc., so that it is uncertain whether the part that looks like the base of the ovule really belongs to the latter.

Inside the notch between the micropylar and the chalazal part of the ovule the outer integument is represented by the typical, semi-circular, bulge. Further we recognize in the section on both sides an outgrowth which represents a part of a tissue ring separated from the rest of the ovule by grooves. The basal groove runs in Fig. 10a between the two crosses. The region below it may represent the outgrowth of the placenta (obturator), with which we have become familiar in the seeds of other genera.

In transverse sections of the fertilized ovules two parallel rows of strands, perpendicular to the median plane of the ovule, are seen to enter the ovule. The row at the right in Fig. 10a enters the outer integument splitting into many bundles. The bundles of the row at

the left show some anastomoses with those of the row on the right, but remain mainly inside the enclosed part of the integument.

Fig. 10*b* represents a median section through an ovule a long time after fertilization. It had already increased to twice its original size. The basal part is especially rich in protoplasm, and reminds one of the arillodal ring found in other genera. This zone forms a disk which separates the seed from the placenta (dotted in Fig. 10*b*).

It seems plausible to assume that the mature seed will possess a fleshy "aril" developed from this meristematic tissue, and that it will later on be detached at this place from the placenta.

The outgrowth below this part (the obturator) shows no meristematic character. Its cells are large and uncoloured.

In herbarium material we found fruits up to 17 mm in length, with seeds up to 7 mm long. The latter showed as yet no distinct arillode. In the light of our observations on similar fruits of *Litchi* this does not mean that no arillode will develop.

### **Sapindus** (*Sapindeae*)

This genus too is zoöchorous, but the edible part is no longer found in the seed. The pericarp has taken over the function of the sarcotesta and the arillode, and the fruit has become a berry. The testa is a very hard and dry protective coat.

RADLKOFER (1895) was of opinion that the berries of the best-known species, *S. saponaria*, are not adapted for dispersal by animals. However, in a study of 1957 I could report that dispersal by bats has been observed in Trinidad as well as in Java. The detached seeds are probably spread by sea-currents too.

It would be worth while to see whether there are remnants of older conditions in the form of vestigial arilloids. This seems the more desirable as MAURITZON (1936*a*) gave in his Fig. 3*D* a section of an ovule of *S. mukorossi*, which shows the presence of an outgrowth below the ovule. The drawing is reproduced here as Fig. 11. Mauritzon



Fig. 11. *Sapindus mukorossi*, after Mauritzon.

obviously thinks that the outer integument is absent at the side of the "funicle", and that at this spot there is an outgrowth from the carpel which covers the micropyle, a kind of "obturator" therefore. There is no proper funicle, and the base of the ovule is in the well-known way broadly attached to the placenta. In several species the ripe seeds remain over some distance attached to the placenta, and when detached they show a linear scar. There is no aril, but sometimes a hair felt is found on seed and placenta.

**Schleichera oleosa** Merr. (*Schleichereae*)

There is a fleshy "aril" round the ripe seed. I could obtain no material for a study of its development. The way of attachment of the "aril", however, shows (Fig. 12) that the latter is an arillode, developed from the regions *a* and *c* in Fig. 1. It surrounds the micro-pyle,—just as in *Litchi*.

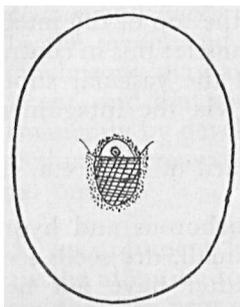


Fig. 12. *Schleichera oleosa*. Basal area of seed. Hilum hatched. Attachment area of arillode dotted.

**Paranephelium** (*Cupanieae*)

RADLKOFEK (1933) remarked that the fruits and seeds of this tropical genus show a striking resemblance to those of *Aesculus*.

I saw fruits of *P.costophyllum* Miq. They have a hard, spiny pericarp, and the large brown seeds are provided with a partly smooth and partly dull testa. The dull part is often regarded as an aril, although it is just as hard and dry as the rest. RADLKOFEK (1895) considered it as "eine arillöse Schicht der Samenschale".

The dull part of the seed is attached to the dissepiment. When the seeds are detached, the centre of the dull part shows as a remnant of the vascular strands a large, sunken scar, and herein the seed differs from that of *Aesculus*. Obviously the ovule had in its youth a very broad base with many bundles entering.

The place where the smooth surface penetrates for some distance into the dull surface, is the pocket in which the short radicle is hidden. The testa is here very thin, whereas the adjoining dull part is extremely thick.

**C. CONCLUSIONS**

Our observations on the seeds of the *Sapindaceae*, though limited to a few genera, have given us an insight into the nature of the arilloid structures occurring in the family. The majority of the tribes recognized by Radlkofer were represented in our material and the genera discussed here belong to the most divergent among them.

Our impression that the fruits in this family originally contained large seeds provided with a fleshy testa originating from the outer integument, was strengthened.

That such a sarcotesta may be present, had, as I remarked in the introduction, already been recognized by RADLKOFEK (1895) in some of the genera. We found it now also in a *Nepheleum* species, and we

also discovered instances of incomplete sarcotestas (arillodes) in several other genera. In *Cardiospermum*, *Harpullia*, *Litchi*, *Euphoria* and *Paullinia* they had been described so far as arils arising from a funicle. However, no true funicle, and therefore no aril, is present in any of the plants investigated.

In some species of *Litchi* and *Euphoria* the meristematic part of the integument forms a ring, which grows out a long time after fertilization. The meristematic arillode extends from the top of the integument across the base of the ovule to the pseudo-funicle; this in contrast to a real aril arising from a true funicle. That the vascular supply makes a detour, entering into the fleshy part via the integument, also distinguishes the latter from an aril.

The connection with the so-called endocarp-aril of *Guioa* e.a. has not been investigated.

The non-dehiscent bladder-fruits with anemochorous and hydrochorous dispersal and the dehiscent fruits with small, dry seeds seem to represent side-lines of development. The latter have not been investigated here. The drupaceous fruits seem to be a later zoöchorous development.

It may seem strange that the morphological nature of so many sapindaceous table-fruits had so far not been properly investigated. As items on the list for future research parade other important table-fruits like *Blighia sapida*, *Diploglottis australis* and *Alectryon excelsus*. That their study has so long been neglected may be due to the false conviction that the fleshy parts are everywhere of the same kind and that they are adequately described by the term "aril".

It does not seem plausible to assume that the funicular, true aril is the arche-type out of which the fleshy structures found on the surface of the seed itself, arose by "adnation". An exostome-arillode seems to be morphologically different from a true aril. Returning to the question of the sequence in the series of structures mentioned in the introduction, I have to admit that a typological range of structures can be interpreted historically (if deemed necessary) in different ways; we can start at any point. This does not mean, however, that we should refrain from every historical interpretation; this seems the less desirable as others have already proceeded in this direction.

Of course, transfer of functions between various layers may have taken place. A transfer of function from endocarp or aril to testa is here, however, morphologically improbable. It seems plausible to regard the undifferentiated, complete sarcotesta as the starting point for the development of more localized and specialized structures, which seem ecologically better adapted for dispersal by birds, as they are more easily detached.

Notwithstanding this differentiation in structure, we recognize in all of them (aril, endocarp-pulpa, arillode, sarcotesta) the original sarcotesta-function, viz. that of presenting an edible layer inside the purely protective pericarp.

At an earlier occasion (1955) I tried to find a historical background for the presence of this condition in various group of *Angiosperms* by

regarding it as the persistence of a condition that occurred already in the seed of *Gymnosperms*.

Possible implications of our finds for the subdivision of the family may be left to taxonomists. The pluriformity in fruits and seeds seems to some extent to be independent of the accepted taxonomical delimitations, as it may vary even within genera. The gap between *Nephelium* and *Euphoria* nevertheless seems to be widened by our finds.

In the ovules and seeds themselves we found once more that the campylotropy may appear at a comparatively late stage in the development, and that some of them retain the campylotropous structure permanently by developing in a transverse as well as in a longitudinal direction, whereas others lose it by developing mainly in a longitudinal one.

As an argument for the primitiveness of the sarcotesta I wish to draw the attention to its presence in groups in which other characters occur that are primitive. In my general study (1955) I reported the presence of such a correlation in various families belonging to the *Monocotyledones*, viz. in many *Liliaceae*, *Amaryllidaceae* and *Iridaceae* as well as to the *Dicotyledones*, viz. in *Degeneriaceae*, *Magnoliaceae*, *Ranunculaceae*, *Winteraceae*, *Annonaceae*, *Berberidaceae*, *Connaraceae* and in some primitive *Leguminosae*.

On the other hand I have to admit that in the *Sapindaceae* this character may have arisen anew, and that it may be here merely a parallel to the *Gymnosperm* condition, one note in the extensive gamma of means the family uses to attract dispersers. That it is no primitive character in the *Sapindaceae* may seem indicated by the wide range of fruits found in this family and the rather advanced position of this family in the natural system, where the families in the various taxonomical groups are often arranged in a rectilinear sequence. When we accept the position of the family at the end of the series *Ranales-Rosales-Malvales-Tricoccae-Geraniales-Rutales*, we should, however, not overlook that a sarcotesta and structures derived of the latter occur also in some of the "intermediate" families, viz. the *Sterculiaceae*, *Bombacaceae*, *Euphorbiaceae* (very pronounced here), *Oxalidaceae*, *Polygalaceae*, *Tremandraceae* and *Meliaceae*, as well as in the "succeeding" member of the series, the *Celastraceae*. This does not plead for a development *de novo*.

SPORNE (1945) gave a new, revolutionary arrangement of the families of the *Angiosperms*, based on the statistical frequency of "primitive" characters as expressed in his "advancement index". The *Sapindaceae* are there placed very low, as the eighth from below of the dicotyledonous families.

As this arrangement rests *inter alia* on the seed-characters (seeds arillate, seeds few, integument bundles present) its reliability depends partly on the acceptability of the opinion that the arilloid testa of the *Sapindaceae* should be considered as a primitive character and not as an incidental, i.e. secondary, adaptation, viz. to zoöchorous dispersal.

Sporne himself remarked that two of his other criteria, viz. "apetaly" and "small number of seeds" are in themselves not reliable indicators of advancement, because they may occur *a*) as ancestral characters in very primitive groups, and *b*) as the result of a process of retrogression in some very advanced families. The combination of the two characters forms, as already indicated by Stebbins, an "adaptive peak", indicating anemophily. It is clear therefore that *a*) and *b*) refer to resp. primary and secondary anemophily.

Considering all this, and recognizing that ariloid structures are often parts of the integument, it seems necessary to point out that the correlation found by Sporne between the characters "seeds arillate" and "integument bundles present", does not necessarily prove them to be both primitive ones. As I tried to show for the seeds of the *Sapindaceae* the correlation may be due to ecological factors (see below). Whether they may at the same time be regarded as primitive characters, is an independent problem.

Another point of general interest is that the pseudo-funicle, as MAURITZON (1936a) already indicated for *Dodonaea*, is, as a rule, wholly or partly an outgrowth of the carpel wall. A true funicle is usually absent. The ovule is attached with a broad base, it is without a raphe and provided already at the very base with several vascular bundles.

Vascularization of the ovule by several bundles is exceptional in the *Angiosperms*. As far as I know the phenomenon is limited to some ovules of sea-shore plants as *Hymenocallis occidentalis* and *Typhonium lindleyanum*, where it may be correlated with definite ecological needs, viz. resp. water-storage in the testa and germination of viviparous seeds. In the plants investigated here there is also a special need in the strongly developing integument. It is noteworthy that especially in *Litchi* and *Euphoria* the water supply to the succulent arillode has to make a detour via the integument up to its micropylar region.

The boundary between ovular and placental tissue is rather vague, and it is therefore no wonder that the place of attachment of the seed sometimes grows out with the placenta, a phenomenon usually called adnation, but which may perhaps better be indicated as nondisjunction of placenta, pseudo-funicle and seed.

The situation in the *Sapotaceae* shows some resemblance to that in the *Sapindaceae*, and its development deserves a special study. There too the micropyle is often situated inside a large "scar", the "Ansatzfläche" or "area umbilicalis".

#### D. AESCULUS

We will discuss the seeds of the genus *Aesculus* in connection with those of the narrowly related *Sapindaceae*. The structure of the latter may shed light on the rather unusual aspect of the first. The genus may be regarded as a northern outpost of the tropical *Sapindaceae*. It has a near relative in the tropical genus *Billia*.

The seeds of *Aesculus* are large, but the outer integument, although

at first strongly developed, changes later on as a whole into a hard, dry testa. They may remain for a long time dormant, but possess no special dispersal mechanisms, a situation also met with in *Paranephelium*.

The European species, *A. hippocastanum*, was driven southwards by the last glaciation, and did since then not recover its former area, although the climate in N.W.-Europe is not unfit for it. This may be due to the absence of special means of dispersal. The seeds of the related tropical-American genus *Billia* are said to be provided with an aril (cf. CORNER (1953)). Alas these seeds were not obtainable.

The first feature that strikes us in the seed of *Aesculus*, is the very large "hilum". Though some textbooks call it a "macula hilaris", most of them simply refer to it as a hilum. The micropyle is situated just outside the hilum, so that the radicular pocket also ends outside it, a situation often misrepresented in the literature.

The outer surface of the radicular pocket lies as a whole outside the "hilum"; it often forms a triangular notch in the latter's dull surface, just as in some *Sapindaceae* with a bilobate pseudo-hilum. This fact, together with the large size of the hilum, suggests that the "hilum" may in reality be the scar of a detached arillode, a pseudo-hilum.

On the other hand the dull spot also is the place where the seed originally was attached to the dissepiment.

It is, therefore, noteworthy that shortly after fertilization a funicle seems to be present (Fig. 13). This "funicle" is separated from the

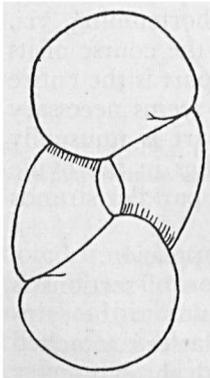


Fig. 13. *Aesculus hippocastanum*, two ovules from opened ovary cell attached to underlying placenta, shortly after fertilization.

ovule proper by a deep transverse groove. The funicular part is often greenish, whereas the ovular part proper is white.

These seemingly contradictory facts require a closer inspection. The situation in the ovary then appears to be complicated by fusions and bends. In the study of KAYSER (1893) this has been well analysed. We derive from it the following details:

The ovules are inserted on the dissepiment and not in the axil of the ovary cell (Fig. 14). Popularly said the basal part of the funicle seems to be fused with or incorporated into the dissepiment. This situation is already anticipated in many *Sapindaceae*, where the so-called funicle seems to belong at least partly to the wall of the carpel. On

transverse sections of the ovary which I made myself, the vascular bundle of the ovule appears to arise from the axillary strands of the placenta. It runs more or less horizontal through the dissepiment and leaves the latter halfway.

In Kayser's Fig. 1, a transverse section of the ovary, the basal part of the obliquely cut ovule, the pseudo-funcle, appears to be broadened laterally, and to form a distinct part.

My own transverse sections (Fig. 14) show that this part, which contains an undivided vascular bundle, consists, before fertilization, for the greater part of a large-celled, rather loose parenchyma of a

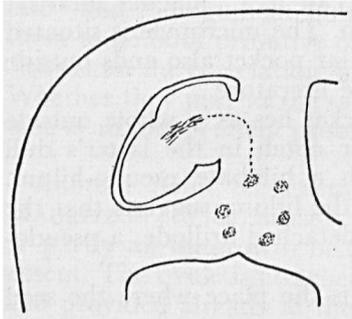


Fig. 14. *Aesculus octandra*. Cross section of ovary in anthesis. Course of strand outside plane of section indicated by dotted line.

similar kind as that in the pericarp, whereas the apical, nucellar part consists of a denser tissue.

Kayser's drawing of longitudinal sections of the ovule (cf. her Fig. 3), which fully agree with my own ones, have one shortcoming, viz. that they do not represent the entire basal part and the course of its bundle, which gives the impression that the nucellar part is the entire ovule and that the funicular part is the placenta. It seems necessary to add that the vascular bundle in the funicular part is unusually stout and seems compound. It forks into two branches in the ovule proper. These two branches split into a number of parallel strands which pass into the outer integument.

Fig. 96 of KÜHN (1927) gives the same wrong impression.

The neglect of the funicular part in the description of sections is caused by the circumstance that it stands perpendicular to the symmetry plane of the ovule proper, which means that the latter is attached more or less laterally. In a longitudinal section through the symmetry plane of the ovule the funicular part, therefore, is missing.

In Fig. 15 I reconstructed by the aid of a number of longitudinal and transverse sections a scheme of the structure peculiar to the ovule of *A. octandra* and *A. hippocastanum*.

It is clear that the green, basal part is not an ordinary funicle, but that it is homologous to the "obturator", the outgrowth of the carpel found in the *Sapindaceae*. In its central zone it is not delimited from and may contain tissue of the outer integument by a kind of fusion and contraction. Internally it may thus have become more or less arilloid, but at the periphery it is morphologically not comparable to the arillode of *Litchi* and its allies. This complex mass is separated

from the nucellar part, the ovule proper, by the groove mentioned above and indicated in Fig. 15 by a dotted line. This groove is in my opinion comparable to the first, basal groove in *Pometia*, *Litchi*, etc.

The fusion of obturator and integument into a single mass is perhaps less complete in the ovule of its tropical relative *Billia*, and in that case the integumental part may be developed into an arillode, which remains attached to the seed at maturity.

The vascular supply of placenta and ovules in *A. parviflora* has recently been described by BAEHNI and BONNER (1953). Their Fig. 1 shows the origin of the ovular bundle from an axillary strand, after which it runs through the dissepiment. They believe in a fusion between the funicle and the dissepiment. One difference with the situation I

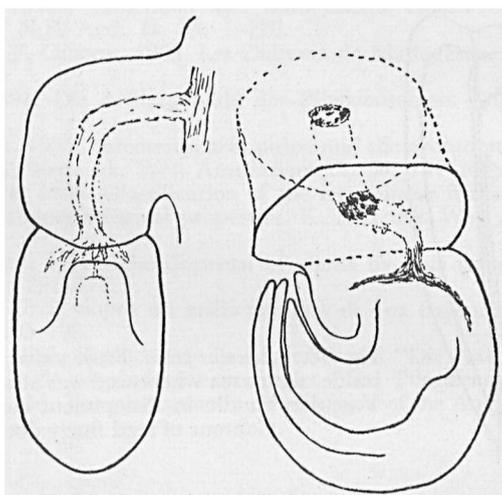


Fig. 15. *Aesculus*. Right: longitudinal median section of inferior ovule fully drawn. Vascular bundle and basal part of ovule outside plane of section in dotted lines. Left id. from the side.

noted in *A. hippocastanum*, is very interesting. The bundle in the "free part of the funicle" gives off a number of short branches. The authors say that this branching inside the "funicle" seems strange, but becomes comprehensible when we realize that part of the "funicle" may be regarded as arilloid.

When we compare this situation with that found in the *Sapindaceae*, and when we see that the ovule, attached by the broad, partly arilloid outgrowth to the dissepiment, develops in conjunction with the latter, we can understand the situation in the ripe fruit.

The parenchyma developing in the arilloid does at first not differ from the tissue of the dissepiment. In the ripe fruit, however, the arilloid is recognizable as a thin, but distinct part. When the seed is detached, the greater part of the arilloid remains behind as a distinct bulge on the surface of the dissepiment (Fig. 16)—just as part of the arillode remains behind on the placenta of *Cardiospermum*. It is cream-coloured in contrast to the rest of the surface and has a different

consistency, viz. soft and mealy. In its center we see the scar where the single vascular strand has been broken off. The course of the vascular strands passing into the seeds is then visible in the dissepiment to the naked eye.

At maturity the hardened layer of the testa which separates the seed from the obturator, is detached from the mealy layer, as described already by HINTZINGER (1927, p. 260). It has now become clear that by the absence of a raphe and a funicle and by the fusion of integumental and placental tissue into one layer, the scar may as well be described as a hilum as a pseudo-hilum and that the term "hilum" is here even no longer applicable.

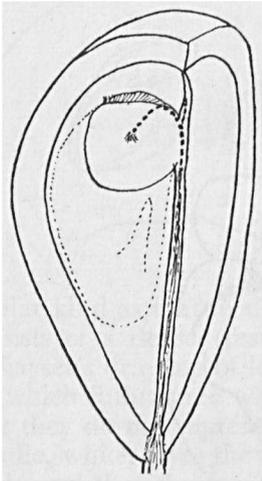


Fig. 16. *Aesculus pavia*. Fruit valve seen from the inside, with area where seed was attached in front. Vascular bundle in dissepiment coarsely dotted. Contour of seed finely dotted.

When we consider the structure of the testa from the ecological point of view, the completely sclerified testa may be seen as an adaptation to a life in extra-tropical regions. Still more clearly than the dry arillode of *Cardiospermum*, the contracted arilloid obturator has as the end of a line of development lost every zoöchoric importance, and has become an abscission layer.

I have to thank Dr. H. J. LAM, Director of the Rijks-herbarium, Leyden, for the liberally granted permission to work as a guest in his institute, and the Drs W. MEYER (Pajakumbuh), I. BANERJI (Calcutta), C. T. YUNG (Hongkong), J. A. FRAHM-LELIVELD (Wageningen) and S. NAKATA (Honolulu) for the sending of material.

#### REFERENCES

- BAEHNI, CH. and C. E. B. BONNER. 1953. Les faisceaux vasculaires dans l'ovaire de l'*Aesculus parviflora*. *Candollea* 14: 85-91.  
 BAILLON, H. 1875. Sur l'origine du macis de la muscade et des arilles en général. *Adansonia*, 11: 329-340.  
 BANERJI, I. and K. L. CHAUDHURI. 1944. A contribution to the life-history of *Litchi chinensis*. *Proc. Indian Ac. of Sci.*, 19: 19-27.

- BECCARI, O. 1918. Asiatic Palms. *Ann. R. Bot. G. Calcutta*, 12 (II): 67-98.
- CORNER, E. J. H. 1953. The Durian Theory extended - I. *Phytomorph.* 3: 465-476.
- GUÉRIN, P. 1901. Développement de la graine et en particulier du tegument seminal de quelques Sapindacées. *Journ. de Bot.* 15: 336-362.
- HINTZINGER, A. 1927. Über die Ablösung der Samen von der Placenta. *Sitz. ber. Ak. Wiss. Wien, M-N. Kl. Abt. I*, 136: 257-279.
- KADRY, A. E. R. 1946. Embryology of *Cardiospermum halicacabum*. *Svensk. Bot. Tidskr.* 40: 111-126.
- KAYSER, G. 1893. Beiträge zur Entwicklungsgeschichte der Samen mit besonderer Berücksichtigung des histogenetischen Aufbaues der Samenschale. *Jahrb. Wiss. Bot.* 25: 79-148.
- KUHN, G. 1927. Beiträge zur Kenntniss der intraseminalen Leitbündel bei den Angiospermen. *Bot. Jahrb.* 61: 325-379.
- MAURITZON, J. 1936a. Zur Embryologie und systematischen Abgrenzung der Reihen Terebinthales und Celastrales. *Bot. Notiser* 1936: 161-212.
- MAURITZON, J. 1936b. Samenbau und Embryologie einiger Scitamineen. *Lunds Univ. Årsskr. N.F. Avd. II*, 35: 1-120.
- PERROT, E. and P. GUÉRIN. 1903. Les *Didierea* de Madagascar. *Journ. de Bot.* 17: 233-251.
- PFEIFFER, A. 1891. Die Arillargebilde der Pflanzensamen. *Engl. Bot. Jahrb.* 13: 492-545.
- PIJL, L. VAN DER. 1955. Sarcotesta, aril, pulpa and the evolution of the Angiosperm fruit, I, II. *K. Ned. Ak. Wet. Amsterdam C.*, 58: 154-161, 307-312.
- PIJL, L. VAN DER. 1956. Classification of the leguminous fruits according to their ecological and morphological properties. *K. Ned. Ak. Wet. Amsterdam C.*, 59: 301-313.
- PIJL, L. VAN DER. 1957. The dispersal of plants by bats (chiropterochory). *Acta Bot. Neerl.* 6: 291-315.
- RADLKOFER, L. 1878. Sopra un arillo speciale di una Sapindacea. *Nuove Giorn. Bot. It.* 10: 105-109.
- RADLKOFER, L. 1895. Sapindaceae in Engler-Prantl "Die Nat. Pfl. Fam."
- RADLKOFER, L. 1934. Sapindaceae in Engler "Das Pflanzenreich", IV, 165.
- SPORNE, K. R. 1954. The phylogenetic classification of the Angiosperms. *Biol. Rev.* 31: 1-29.