

## FLOWERS AND FRUITS IN FLACOURTIACEAE

### I. SCAPHOCALYX SPATHACEA RIDL.

W. A. VAN HEEL

Rijksherbarium, Leiden, Netherlands

#### SUMMARY

Descriptions are given of the flowers, fruits, and seeds. The petals have basal scales. The pistil is an urceolate structure issuing in 5—7 stigmas. In it are two whorls of ovules along the wall, the lower whorl in the same radial planes as are the stigmas, the upper whorl in alternate radii. The pistil wall is entirely covered by nectariferous hairs. There is a peculiar vascular bundle pattern. The ovule is sessile and atropous, the nucellus is beaked, the inner integument terminates into 2—4 projections, the outer integument into 2—4 lobes. The ovules develop into inferior seeds mainly by proximal growth. Lobes of the endocarp grow around the ectostome. The testa has its hard layer in the middle. The seeds consist of two parts, a hard container containing a free kernel, an air mantle being enclosed. This is probably a swimming device. As, moreover, the fruit is pulpous, the species probably is diplochorous. The results are put against the theory of metamorphosis and the carpel theory. It is thought that this Malaysian plant is a very unusual, possibly ancient, monotype.

#### THE PLANT AND ITS FLOWERS

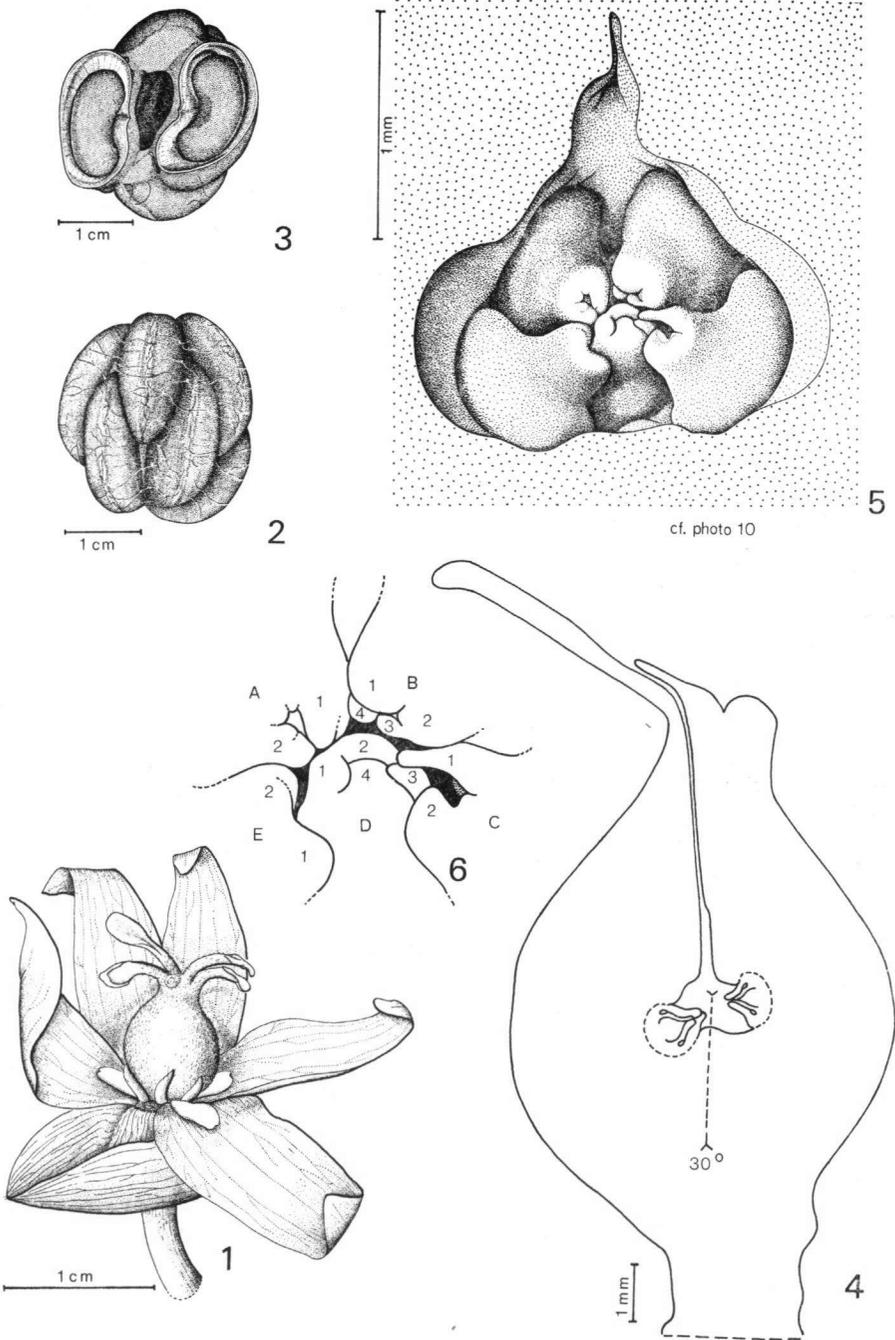
*Scaphocalyx spathacea* is a small Malaysian tree. It is a member of the *Flacourtiaceae*, a tropical plant family of which the reproductive morphology is very insufficiently known. For a taxonomic description the reader is referred to Sleumer (1954). When he revised *Scaphocalyx* the female flowers were unknown.

Both male and female flowers are on the same tree, the males flowering in advance of the females. The calyx and the petals are similar in the male and female flowers. The calyx is a spatha, tearing down on one side. There are 5—7 petals, which are oblong and up to 2.5 cm long.

In the male flowers there are as many stamens as petals, and their whorls alternate. The petals bear small nectariferous stubs at their inside base, but in one flower were found to have basal bilobed scales. Sleumer pictured a double bladed petal. The stamens have stiff, persistent filaments, which bear versatile introrse anthers on top. In the male flowers there is no sign of pistil formation.

In the female flowers (fig. 1) a whorl of 5—7 short subulate sterile structures is present between the petals and the pistil. Because of their position they could be called staminodes. However, they do not have reduced anthers on top, and there may be more or fewer than there are petals. In fact, they are always in the same number as, and alternate to the styles.

The solitary and terminal, one-celled pistil is an urceolate structure issuing around the top in 5—7 tube-shaped styles, which flare into spoon-shaped stigmas. Frequently the number of styles is unequal to that of the petals. The wall of the pistil is clad with nectariferous hairs. The ovules are placed on the wall in two alternating whorls and are atropous (fig. 4).



*Saphocalyx spathacea*. — Fig. 1. Female flower, one petal and one stigma omitted. — Fig. 2. Bunch of seeds from dried fruit. — Fig. 3. Ibid., halved. — Fig. 4. Hexamerous pistil, halved, schematic. — Fig. 5. Halved ovary with five ovules. — Fig. 6. Ibid., scheme of lobes of outer integuments.

The large, round, leathery walled fruits contain 10—14 large reniform seeds, which are radially placed and are embedded in soft tissue (figs. 2 and 3).

It is the purpose of this paper to present a detailed account of the structure of the pistil and its ovules as well as of the fruit and its seeds. It is my intention to publish some more contributions on different plants of the same family in the future.

The material of *Scaphocalyx* came from trees in the Arboretum of the Forest Research Institute (Pusat Penyelidikan Hutan) at Kepong, Malaysia. I acknowledge the valuable cooperation of the staff of this institute, especially of Dr. C. T. Whitmore\*.

#### ANATOMY OF THE PISTIL

The material consisted of flowers at anthesis, or just before or after that.

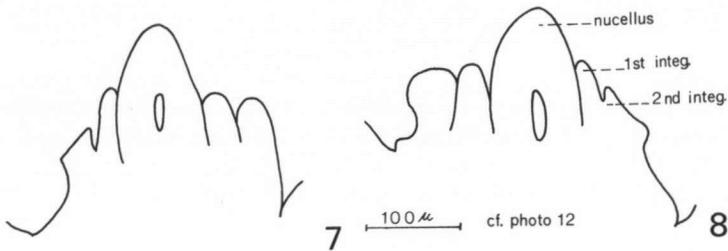
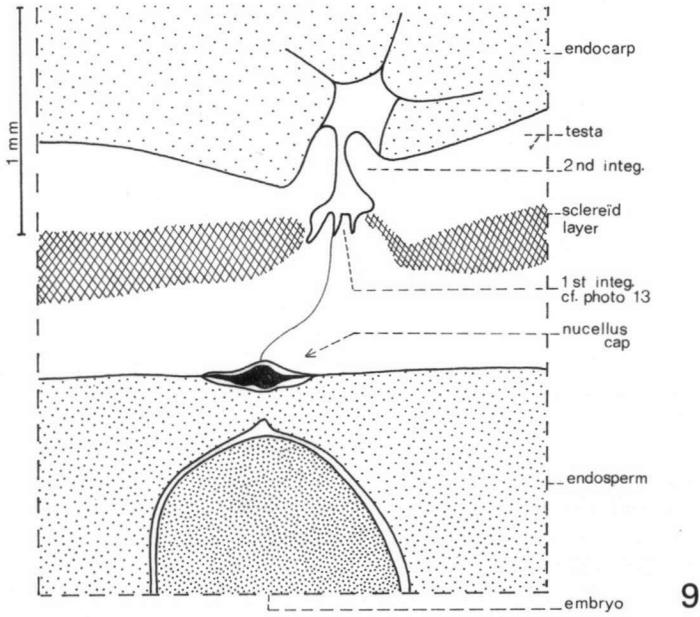
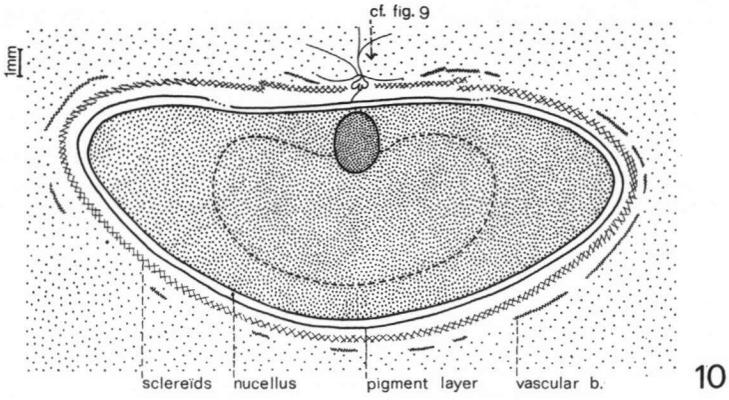
The wall of the pistil is traversed by a whorl of equidistant parallel main vascular bundles, numbering twice as many as the stylar tubes (photos 1, 2, and 3). These bundles are located in the stylar and in the alternistylar radii. When studying the cross-sections of the pistil in upward sequence, we notice the progressive projection into the upper part of the lumen of the pistil of alternistylar ridges, which eventually meet in the centre and fuse, sparing the stylar tubes. The main bundles in the stylar radii moderately fan out in small bundles into the dorsal regions of style and stigma. Those in alternistylar radii — if followed in upward direction — first divide into two equal collateral branches; these branches fan out in the lateral walls of two adjoining stylar tubes and stigmas (fig. 20). In the centre of the pistil the stylar ridges are extended slightly downwards; these parts receive a basipetal anastomosing vascular supply from the lateral stylar bundles. At their basal ends these ridges can show a slight subdivision into two collateral parts.

There is another set of parallel, smaller, bundles running in the wall of the pistil. They are as many as the main vascular bundles and alternate with these (photo 2). I call these bundles the anatropous bundles, because they run downwards, after a double origin from two neighbouring main bundles at about three quarters of the height of the pistil. At the same time they branch into ovular bundles inwards and into cortical bundles outwards (fig. 18, 20). By branching profusely, the cortical bundles form the minute subsurface vascularization for the nectariferous tissue and hairs of the pistil wall. In the stylar region the cortical bundles take their origin directly from the main vascular bundles. From each anatropous bundle one to five ovular traces are derived in a row. They move downwards first, into the direction of the centre, then turn again (fig. 20). At the turning point the lowermost ovular bundles together form a kind of stele with several small anastomoses. Presumably these traces represent the vascular bundle supply towards the ovules; the stages were not old enough to show the lignified connections with the vascular bundle traces which are already present in the bases of the ovules.

#### THE STRUCTURE OF THE OVULES

As mentioned above, the ovules are placed on the wall half-way up the pistil in two alternating whorls, one whorl above the other, but at the same time slightly interlocking. Whereas the lower whorl of ovules is situated in the radii of the styles, the upper whorl occupies the alternate radii. There are no placental ridges on which the ovules are inserted (photos 1, 2, and fig. 4). The ovules have no contact with the alternistylar ridges mentioned above.

\* Now at Saffron Waldon, Essex.



Figs. 7, 8. Young ovules, median l.s. — Fig. 9. Seed, micropylar region l.s. — Fig. 10. Seed in median l.s.

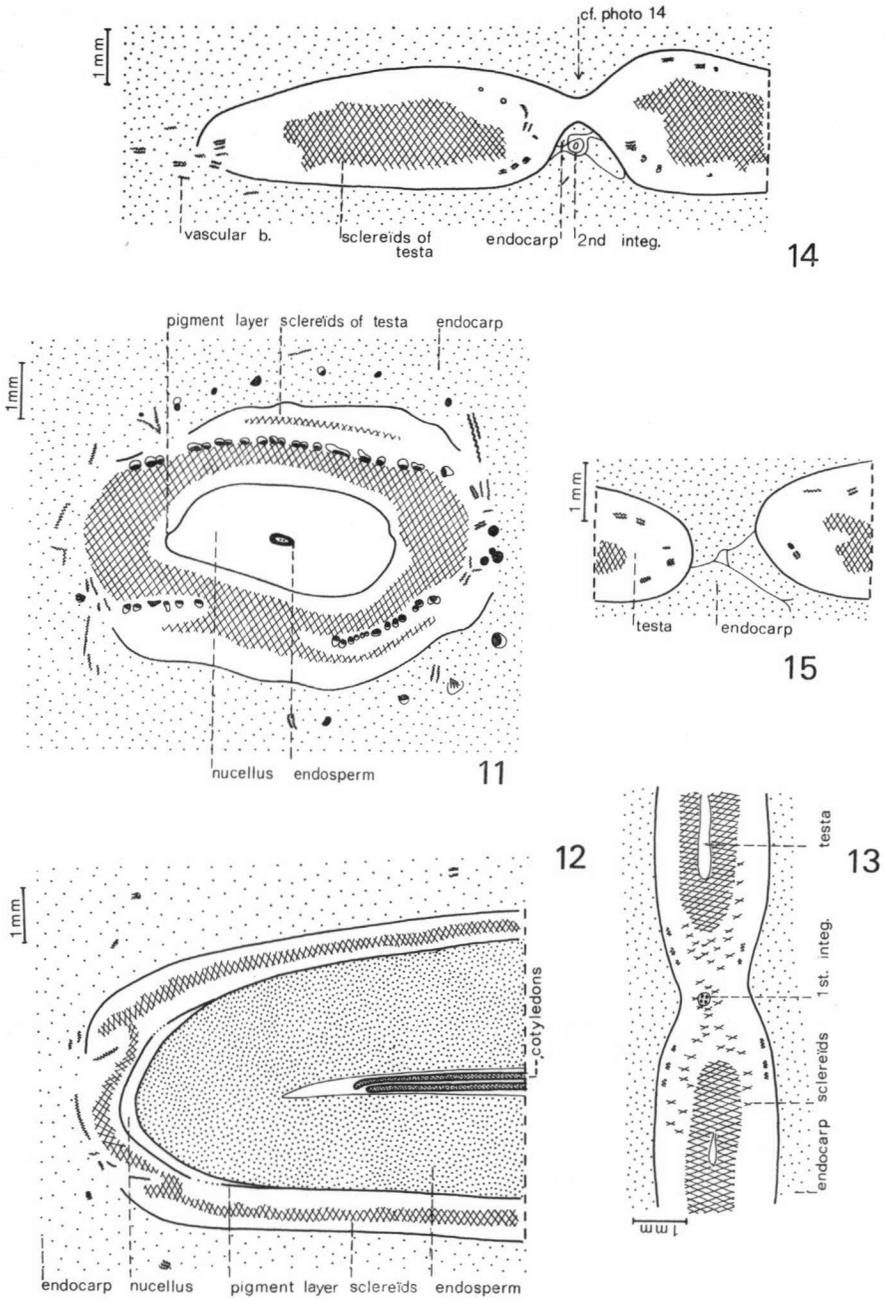
The ovule is a sessile transverse-ellipsoid body which, however, tapers into the integuments towards the pistil centre (fig. 5). Its median longitudinal plane lies in a radial plane of the pistil. In median longitudinal section the insertion line of the ovule shows as a semi-elliptic curve (photo 4). In transverse longitudinal section the ovules appear narrow at the base, broadening up to half-way and then tapering into the tip (photo 5). In cross-section the ovule is elliptic below and round to polygonal above. The peculiar shape of the ovule is mainly caused by extreme division of cells in its proximal part. This division occurs in a radial direction, both upwards and downwards; the tissue of that region can be observed to consist of extensive cell-families.

The nucellus forms a conspicuous beak which, however, does not protrude from the micropyle in the stages that could be studied. It is formed by rows of cells fanning upwards, as can be seen well in transverse longitudinal section. Its cells stain densely. The beak does not take part in the extreme radial division of cells of the base of the ovule, so that, later on, it stands out on top of an expanded nucellus. The proximal radial growth of the ovule is carried through to such an extent that ultimately the seeds become reniform, as we shall see below. The ovule becomes buried in the endocarp tissue, not only by its own proximal expansion, but also by the growth of the endocarp tissue around its proximal part by means of dermal and subdermal divisions.

The integuments are inserted on the broadest part of the ovule along an elliptic line which, to be precise, is higher in the median plane than in the transverse plane. This insertion is parallel to the base line of the whole ovule. The integuments are either appressed to the nucellus, or largely free from the nucellus and from one another. About anthesis both integuments are five or more cell layers thick, showing active dermal cell-divisions on the inside, especially in their distal regions. Each terminates into four discrete parts. Whereas the tips of the inner integument are rather cylindrical in shape, the free parts of the outer integument are triangular lobes (fig. 5, photo 10). However, frequently separation or form are unequal. Often the outer integument terminates in two median lobes double the size of the lobes in case there are four. In that case the upper median lobe is frequently longer than the lower. In a few cases these median lobes seemed slightly bilobed. The inner integument can show the same features. When studying upward cross-sections of the distal integument regions, we notice that the separation into four terminal free parts is announced by the appearance of four inward-projecting ridges which enclose a four-starred micropyle (photos 6—9). On the level of the tips of the inner integument, the outer integument still is cylindrical, the latter separating into four lobes higher up. The relative position of the free parts of the outer and inner integuments is variable. If the integuments are two-lipped all parts are median. Four lobes in the outer integument are practically always placed median and transversally. If both integuments have four distal free parts, the parts alternate.

At this stage the vascular bundle supply of the ovule consists of a comb of small traces median in the very base of the ovule. These traces did not yet show lignified outward connections, as stated above.

Unfortunately, only one young pistil was present in my material. It contained ovules at the megaspore stage. These ovules show the early stages of the two integuments, boat-shaped around the base of the nucellus and on a platform (photos 11, 12 and figs. 7 and 8). The platform is formed by the early cell divisions, mentioned above, which produce the peculiar proximal radial growth of the ovule, that in the end leads to reniform seeds. The proximal growth has not yet spread to the nucellus at this stage. The inner integument is three cell layers thick now, but the outer integument has more layers. It is furthermore evident that the outer integument grows fastest in its median plane, giving rise to a



Figs. 11—15. In upward sequence: C.s. of seed.

bilobed appearance, which probably marks the beginning of the two median lips that frequently can be observed terminating this integument in later stages.

#### THE STRUCTURE OF THE SEEDS

The development of the ovule into a seed can be analysed into a number of processes as follows.

The gameto- and embryogenesis, which the material did not permit to study, result in a young embryo with two reniform foliaceous cotyledons lying face to face in the median longitudinal plane of the seed (cf. Sleumer 1954, fig. 11j). The embryo is surrounded by a copious rather hard endosperm. Around the endosperm lies a dark brown layer. This layer is formed by the inner cell layers of the testa, including the pigmented inner epidermis, which have separated from the rest of the testa (photo 15). The embryo, the endosperm, and the pigment layer together form a solid kidney-shaped body, which is lying loose within the outer, remaining, hard part of the testa (fig. 13). The seeds lie buried in the pulposus endocarp, together forming a bunch, firmly held together by the leathery ectocarp. Evidently the endosperm functions mainly at germination.

The reniform shape of the seed is brought about by the extreme proximal growth of the ovule, described above. This growth is first mainly lateral (that is in a radial plane of the fruit upwards and downwards), but later on also turns upwards (that is towards the centre of the fruit). The insertion line of the seed on the pistil wall, and that of the endospermic body on the testa, by this reniform growth, is expanded into a narrow basal zone of more than half-elliptic shape (figs. 2 and 10). The terminal part of the seed is to be found in the sinus of the kidney-shaped whole. It is evident that the reniform growth is copied by both the endosperm and the cotyledons in later stages of development of the seed. It is by the interplay of the reniform growth of the seed and the inward growth of the endocarp that the seeds become located in a parenchymatous, finally pulposus, endocarp tissue.

Young fruit stages would have permitted the study of the development of the seed. Unfortunately, they were lacking in my material. As a consequence, it was only by careful study of the very limited terminal area of the seed that its structure could be understood, and something on its development deduced. Lengthwise sections show that the testa carries both the original free integuments on top, separated by a small micropylar chamber (fig. 9). This chamber is roofed over by the distal lobes of the outer integument, forming an ectostome. Into the chamber the four tips of the inner integument project, heavily lignified or suberized, forming the distal part of an endostome (fig. 13). Thus it appeared that the testa proper, except for its apical part, must be formed by a basal growth common to both integuments, resembling an intercalary growth (figs. 10 and 17). A possible fusion between the two integuments, with loss of cuticles, was not observed. The growth of the testa should be checked as soon as young fruit stages are available for study.

Furthermore, the endocarp growing around the seeds divides into a number of lobes (3) that, on attenuating, bend over the ectostome, forming as it were an extra ectostome (figs. 9, 14—16).

The tissue of the testa is stratified, it is composed of three about equally thick layers, the endo-, the ecto-, and the mesotesta. The endo- and the ectotesta consist of parenchymatous cells. Both epidermides become pigmented (figs. 10 and 17). The mesotesta consists of elongate, lignified, pitted cells, which are arranged in two crossing sublayers (cf. Sleumer 1938 for *Hydnocarpus*).

In the seeds nothing is left of the nucellus, except for its densely staining nucellar cap.

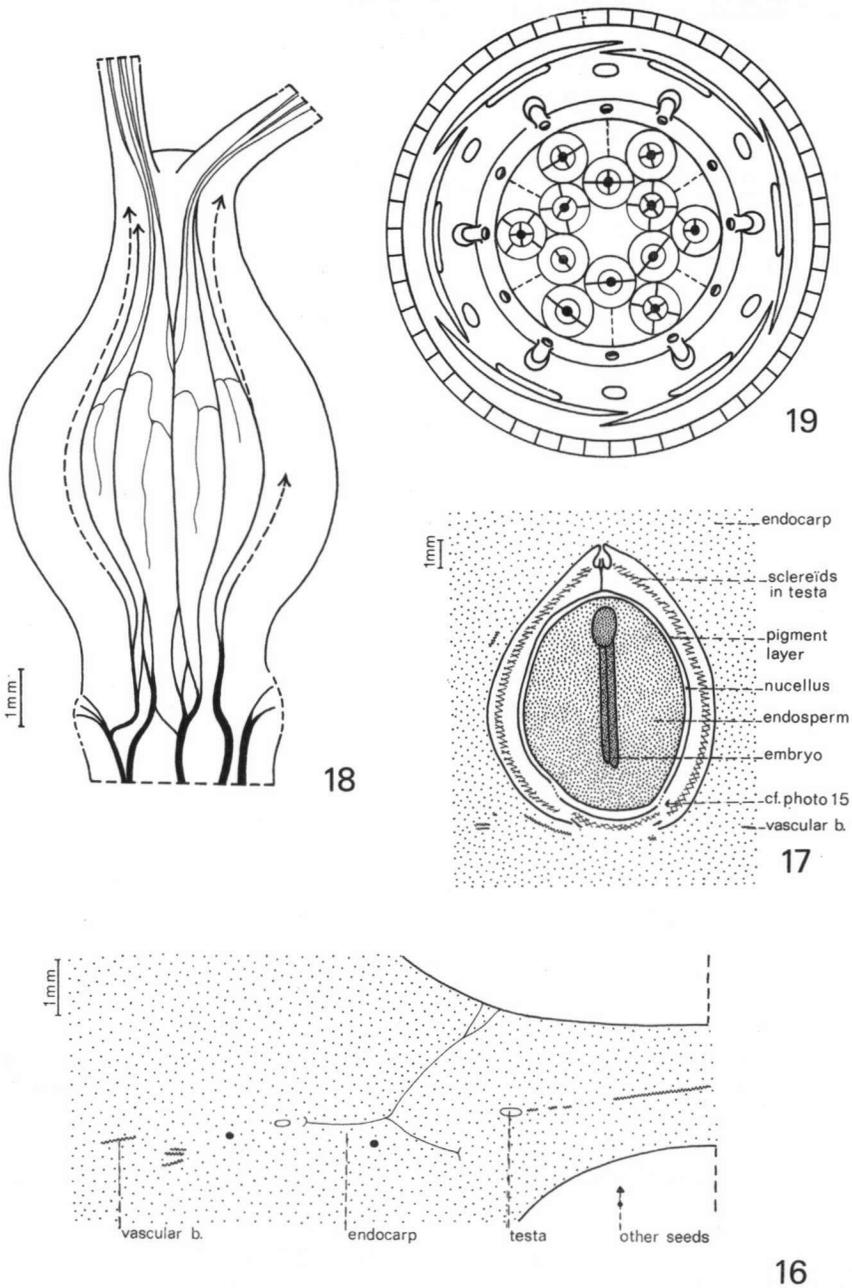


Fig. 16. Most distal c.s. of seed. — Fig. 17. Seed, transverse l.s. — Fig. 18. Main vascular bundles in pistil wall seen from the outside, in halved and cleared pistil. — Fig. 19. Diagram of female flower including the ovules and lobes of the integuments, and main vascular bundles.

At the ovule base the distinction into what possibly is remaining nucellar tissue and what not, seems arbitrary.

The final fencing of the seed at its insertion and micropylar region is effectuated by secondary sclerification or pigmentation of cells in those regions. In the insertion region a sclerified layer of cells differentiates connecting the base of the corresponding layer in the testa (figs. 10, 12—17). Besides, a pigmented cell layer differentiates here, forming a continuation of the pigmented inner epidermis of the testa. In this way the testa is as it were protracted over the seed base. Quite similarly, in the micropylar region between the endo- and ectostome level, radiating strands of sclereids are formed in the testa, which connect the sclerified layers of cells of the testa over the micropyle (photo 13, fig. 13). The sclereids are also formed projecting into the micropylar chamber.

The vascular supply of the seeds is a basal stele which, by the extreme proximal reniform growth of the ovule, has been expanded into a reniform loop. Of course this form corresponds with the insertion zone of the seed. The stele divides into a ring of bundles into the very base of the testa and the region below (fig. 11). The stele takes its multiple origin from the ovular traces which, moving downwards and then upwards again in the pistil wall, are derived from the anatropous bundles described above.

## SUMMARY OF THE RESULTS

### General flower structure

The calyx is spathaceous, the petals are provided with a scale. There is no trace of a pistil in the male flowers, but there are staminodes in the female flowers. The pistil is one-celled and has parietal ovules. Large pulposus fruits contain seeds with abundant endosperm and an embryo with foliaceous cotyledons.

### The pistil

The pistil wall is traversed by main vascular bundles in the styler and in alternate radii. They supply the styles and stigmas. Between them double-based bundles move downwards, ramifying into a peripheral system which supplies the nectariferous surface of the pistil, and into a central system which supplies the ovules.

### The ovules

The ovules are sessile and atropous. There is a lower whorl in the styler radii and an upper whorl in alternate radii. The nucellus is beaked. The integuments terminate into two to four projections or lobes. The main growth of the ovule takes place in its proximal region. The testa is formed at the base of both integuments; it has a thick layer of lignified cells in the middle.

### The seeds

The seeds attain a reniform shape and are buried in the endocarp tissue, the latter forming small lobes over the ectostome. They are supplied with a basal stele that does not penetrate the testa. They are fenced off basally and apically by layers of cells imitating the testa. There is a lignified mesotesta. Later the testa splits into an outer hard case and an inner dark sheath, that eventually firmly encloses the body of the endosperm and embryo. Between these two parts a free space is left.

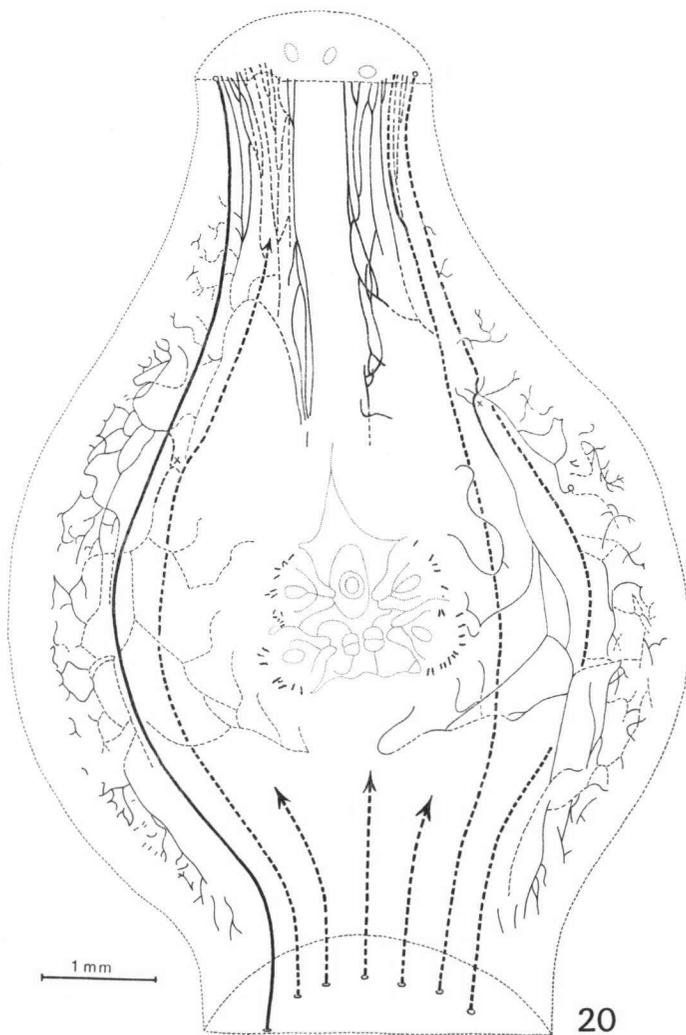


Fig. 20. Vascular bundles in halved and cleared pistil, seen from the inside. Arrows indicate that the further course of the bundles is not given in the figure. Interrupted lines indicate bundles in the background. Dotted lines indicate the outlines of pistil and ovules. The attachment of the 'anatropous' bundles is marked by crosses.

Many of the above characters are uncommon and need some comment. They should be compared with the results in other groups of plants and confronted with general theories. It is an intriguing question how the results could match to the carpel theory. Of course it is unfortunate that no other Flacourtiaceous flowers were studied thus far.

## DISCUSSION

### The unisexual flowers

In taxonomic literature *Scaphocalyx* is reported to be dioecious. Yet, from informations collectors gave me, I conclude that the same trees give staminate flowers first, and then pistillate flowers. Of course there is no way of establishing whether the immediate fore-runners of this species had unisexual or bisexual flowers. The male flowers show no traces of pistils. Pistillate flowers have sterile appendages which from their location and subulate form could be called staminodes. In that case the typological inference is that the stamens are reduced in the pistillate flowers. In this reasoning the full bisexual stage is taken as the normal primary condition, and the unisexual as secondarily derived. However, this reasoning is no more than a convenient way of understanding, and should not be translated in the phylogenetic way, meaning that the bisexual condition antedated the unisexual. In fact, since it is reasonable to assume that Angiosperms arose from early Gymnosperms, which had staminate and ovulate organs separately, it is also logical to assume that Angiosperm lineages may persist that are still unisexual (*cf.* Heslop Harrison, 1958). Other lineages may have combined staminate and ovulate organs into one blossom, still others could be on the verge of making that combination in the present time. Why could not the staminodes be proof of that — as yet unbalanced — union of sexes into one blossom? The ovuliferous parts have to develop as a proliferation of the staminate structures when flowering periods of the two come to overlap on the same tree. Species showing this kind of overlapping would offer opportunity to study these phenomena. However, as stated above, there is no way of rejecting or confirming the one or the other possibility. Not even by a correlation with other characters, the semophylesis of which is equally uncertain.

### The petals and metamorphosis

At their base the petals have structures ranging in form between nectariferous stubs and bilobed scales. I consider this feature to be the product of the mixing of bract and stamen characters. From the stamens comes the four-sidedness, from the bracts the foliarity. The result is a more or less double bladed (diplofoliar) structure, the blades of which adhere in the median plane. They possibly became fixed as an entomophilous device. This view asks for some comment on the concept of metamorphosis.

In flower morphology, discussions continue on whether the petals of different species should be derived from the sepals or rather from the stamens. At the background stands the conviction that all floral and vegetative appendages are homologous. Mostly in these discussions typological thinking refers floral organs to foliage leaves, and this in turn is quite wrongly given a phylogenetic meaning.

Metamorphosis has had various shades of meaning (Baron 1931, Guédès 1969, 1972). In its pure form it says that there is one general plan, realized into various appendages on one shoot, which therefore are homologous. Proof is thought to lie in the continuous phyllotaxis and the intermediate forms. However, the phyllotaxis can only be considered

as continuous by adducing numerous subsidiary hypothesis (Plantefol 1949). Thus the series of intermediate forms, occurring naturally and teratologically, or as a result of experiments, remain the most important evidence (the homonomy or serial homology).

By several authors the general principle was thought to be present in the fact that the appendicular primordia are undetermined during the first phases of their development. After that phase, the ontogeny could take the one or the other direction, depending on metabolic conditions. However, recent experimentally produced form-transitions (Bos 1957, Astié 1962, Dupuy 1963) have shown that the primordial meristems, after having started their development in a certain direction, can switch over to another. In that way elegant series of intermediate forms can be produced on a series of developing primordia, on the condition that the primordia are in successive phases of development at the time of the intervention which causes the switching (viruses, varying conditions of floral induction, spray of growth substances, etc.). This means that meristems can change in another — not entirely arbitrary — direction any time, the more profoundly so as they are younger at the time of intervention (*cf.* Maresquelle, 1973). The mechanism underlying this capacity is unknown, but should be revealed by future morphogenetic investigations, guided by morphological knowledge.

By detailed study of the teratological or experimentally produced intermediate forms, one can '*faire de la morphologie idéaliste*' (Guédès, 1972) and try to grasp ('*saisir*') refined homologies. From the latter one can construct a vague '*Urpflanze*', not as a phylogenetic model, but as a simple structure from which one can mentally deduce ('*dériver par la pensée*') the various actual forms. This could be called a '*harmless pastime*' (as phylogeny was called by Guédès 1966, citing Davis and Heywood). It is for instance interesting to note that Guédès (1965) thought that the ovules were integral parts of the carpel wall, not meaning by this homology any possible phylogenetic relation, except perhaps that the ovules as well as the carpel walls might both originate from syntelomes. However, this would seem to be a homology based on events so far away in the distant past, that it does not lead to understanding of the history of the Angiosperm flower. Evidently, Guédès tries to think of the syntelomes as the basic principle underlying the metamorphosis.

The term 'transformation' has muddled thinking to a great extent. It means that the metamorphosis of the phyllome on one shoot is equivalent to the conversion of bracts to carpels during the ontogeny of one shoot. This opinion has led to all the 'derivations' between bracts, petals, and stamens in one or the other direction, and to its misapplied phylogenetic interpretation.

Hiepko (1965) put it as follows: '*Mit der Frage der Herkunft ist nur gemeint: stehen die Petala morphologisch näher den Staubblättern oder den Hochblättern (Kelch)?*' He answered the question for many *Magnoliales* and *Ranales*. He thought that the oldest members possibly have '*allmählich fortschreitende Differenzierungsgefälle*', and that in the youngest members several different levels in this scale have been advanced in different lines. Thus the gradual homonomy in one plant can give indications toward the interpretation of special, suddenly fixed, intermediate forms between floral appendages in related plants (Remane 1956). For me this means that the 'mixing' of characters — Zimmermann (1965) wrote on the determining processes shifting their levels along the shoot — may be an important evolutionary mechanism.

I assume that the mixing of characters led to the formation of semophylls and nectaries, on the event of entomophily, in a hologenetic process. The basic, at the time genetically different, organs were bracts and stamens. They could have been assembled in stamiferous cupules, as these are known in fossil Gymnosperms. Strasburger (1879) admitted a certain antagonism between vegetative and floral sphere (so did Heslop Harrison, 1952).

He thought that the intermediate forms were mixed forms. Mixing may also take place between 'inflorescences' and 'flowers'. Nozeran (1955) and Emberger have shown the evolutionary significance of it. Rohweder and Treu-Koene in *Houttuynia* (1971), and Van Heel in *Hyacinthus terata* (1962) spoke of the fertilization of bracts; this theoretically may also lead to intermediate forms by mixing. In *Nymphaeaceae*, also, I consider the intermediate series between calyx and stamens as a gradual mixture of characters which gave rise to a cantharophilous flower (cf. Heinsbroek and Van Heel, 1969, and Carlquist, 1969). These appendages are not primitive because of their being flat and foliar, but because they were formed early in flower history by foliarity of the originally slender microsporangiophores, through the influence of intermixing bract characters. In many other plants the stamens became only slightly foliarized outwards. According to Hiepko among Dicots the staminal petals are predominant. In others plants a single definite intermediate stage was effectuated, or became fixed. So, for instance, the nectaries of *Eranthis*. Such a case is also the basally scaled petal of *Scaphocalyx*.

### The pistil and the carpel theory

The pistil in this species is strikingly simple and symmetrical: an urceolate structure issuing in a number of tubes, supplied with twice that number of vascular bundles — in line with and between the tubes —, bearing as many ovules along its wall — also in line with and between the tubes. In addition supplied with a cortical and an ovular vascular system which together are based on twice the number of anatropous bundles alternating with the main bundles. Although this pistil in its regularity would seem a most rational system, it cannot be understood under the classical carpel theory. According to that theory the pistil would be composed of a number of carpels coinciding with the styles and stigmas, and the portions of the pistil wall below them. Correspondingly, the main vascular bundles would represent the median and the commissural marginal carpel bundles. From the present structure no objections can be raised against this part of the explanation. However, also according to the classical carpel theory, the ovules are located at or near the margin of the carpels. Now if the above analysis is correct, the ovules are in reality located in the median carpellary regions — namely the lower whorl — as well as in the commissural planes — namely the upper whorl, which is not permissible under the theory. Therefore the theory does not apply to the *Scaphocalyx* pistil.

In some cases the ovules are located 'on the blade' of the carpel. *Nymphaea*, *Viola*, *Butomus*, *Lardizabala*, and other plants, have 'laminal' placentation. However, in these cases the ovules happen to be absent in the median regions of the carpels. There are authors who think of processes of shifting to bring these laminal cases back to the type, others think that the ovule-bearing surfaces represent the thickness of the edges of the carpels. No doubt, the placentation of *Scaphocalyx* could be harboured safely into the type by imaginative auxiliary hypotheses concerning 'shifting'. However, 'shifting' should be made feasible anatomically, and should, if possible, be corroborated by intermediate stages. This I am unable to do.

On the other hand, other authors considered the laminal placentation basic, and the marginal derived. Eames (1961) advanced this idea, coupled with the supposed 'emergence' nature of Angiosperm ovules. He wrote: 'the position of the ovules on the lamina, primitively scattered, and the relation of the ovule traces to the vascular system — largely or wholly derived, primitively, from the minor veins of the vascular network (derivation from strong, lateral veins is secondary) — support the emergence interpretation'.

Here Eames accepted the three idealistic categories stem, leaf, and root, and added the

ovules as emergences on the leaf. However, I do not accept the idealistic viewpoints. Moreover, the results of paleobotany do not support the emergence origin of the ovules. Therefore, in my opinion, an explanation of 'laminal' placentation was brought not closer that way. In the *Scaphocalyx* pistils too, the traces toward the ovules come from the minor vascular bundles.

In my paper on *Scyphostegia* (1967), another endemic plant with some affinity with the *Flacourtiaceae*, I refrained from calling the units composing the pistil wall — enclosing numerous basal ovules — carpellary. I called them just pistillary units. This I did, because if I had called the units carpels, I would have declared for the carpellary (classic or ranalian) theory of the Angiosperm gynoecia, a theory which is supposed to cover all Angiosperm gynoecia on account of the unity of plan — or monophyly — of the Angiosperms. Rudolf Schmid (1972) purposely avoided designating bundles related to the ovular supply as 'ventral carpellary' bundles: 'since I am uncertain of the homology of ventral bundles in other families and those bundles of *Eugenia s.l.*'.

Maybe there are two characters common to all Angiosperms. Firstly the double fertilization and the secondary endosperm, secondly the enclosure of ovules (angiovuly, Van der Pijl, 1966). This implies that the means of enclosing the ovules might have been different in different lineages — for example *Ranales* and others (cf. Kalkman, 1972). Kubitzki (1972) thinks the *Ranales* are a rather isolated group. Croizat (1973) states that the *Euphorbiaceae* and related families were separate from the *Magnoliales* on the level of pre-angiospermy. Moreover, I am not certain whether all ovules are perfectly homologous, as the research on them has been very insufficient (Van Heel & Bouman, 1972).

Freed from the idea of only one possible way for the enclosure of the ovules, I can look again on the *Scaphocalyx* pistil as a unity, a terminal utricular structure, a cupule crowned with stigmatic lobes, bearing the ovules on its inside wall in a symmetrical pattern.

Rohweder (1967) suggested that the carpel of the *Ranales* may be interpreted as a principally ascidiate structure. And of course the, consistently typological, work of Leinfellner points in that direction. Moseley (1972), on *Nuphar*, suggested that the basic shape is probably utricular. Likewise Uhl, on the gynoecium of *Nypa* palm (1972). The utricular, ascidiate, cupular view is in disaccord with the views from the school of Bailey and Eames. They spoke of phylogenetic closure of conduplicate carpels (Eames 1961: 228—229), treating the idealistic reference model phylogenetically. It also directed their interpretation of the pistils in *Winteraceae*. In my opinion, this was a mistake.

In 1937 Arber wrote very clearly and plainly: '... the nature of the carpel can be understood by comparing it to an infolded foliage leaf bearing ovules on its marginal regions. This is a very different thing from saying, in a literal sense, that the carpel is an infolded foliage leaf'. And Puri (1963) wrote: 'the classical concept is essentially a morphological concept (as against phylogenetic) which attempts to explain Angiosperm stamens and carpels as we see them here and now, in terms of vegetative leaves. It is just a means of understanding flower by comparing it with vegetative bud without implying anything as to its past history or evolution in time. It aims at achieving uniformity, avoiding phylogenetic speculation'. In my opinion 'pure' morphology is a reference system, through careful observations reflecting relations in plant structure by means of a consistent set of terms. However, these terms may be valueless from the historical point of view. As a contrast phylogenetic morphology, if it is not entirely deductive, can be guided by its retrospection into the fossil world and it can be comparative-morphogenetic (or holo-genetic) in its method. It probably will be more rewarding in the end, because it can make contact with — genetical, biochemical, and physiological — morphogenesis in the future.

The covering with nectariferous hairs of the entire wall of the pistil is a rare feature in

Angiosperms. It is not mentioned by Bonnier (1878), nor by Faegri & Van der Pijl (1971). The nectariferous surface is supplied by a rich cortical vascular system. This system, together with the ovular bundles, has its origin in the 'anatropous' bundles running downwards. The pattern could be understood under the assumption that the hairy cover and the ovules originate rather late during the ontogeny of the pistil, namely during a period of predominate basipetal growth of the proximal region. However, my material did not permit to study this phase of development. In general I think that the time of ovule initiation, related to the degree of maturation of the pistil, could be an interesting character, which hitherto escaped attention. I noticed that in some *Winteraceae* the ovules originate surprisingly late. The same was noticed in *Cananga* by Periasamy & Swamy (1961). The early origin of ovules — as well as of stigmatic pistil parts — could have a function in the early pollination. All the other developmental processes, including the lodging of the fertilized ovules in the proximal utricular pistil parts, can be postponed until pollination has been secured.

Corner (1958, 1963) expressed ideas with which the structure of the *Scaphocalyx* pistil would seem to fit well. According to Corner the syncarpous ovary is a new intercalated unit proximal to the vestigial carpel-primordia. Free carpels are exchanged for a carpellary tube, like free petals for a petal tube. The property of ovule and fruit development is transferred to the new structure. The whole structure appears only as if consisting of congenitally fused carpels. I think this idea in the first place points to the sad lack of our knowledge on the meristematic processes taking place after the horseshoe-shaped ridges announcing the pistil have appeared. These processes should be studied in a comparative way (Van Heel, 1969) and should replace, and at the same time materialize the concept of 'congenital fusion', which was a panacea for all that could not be explained by the comparison of mature stages only (as frequently, but not exclusively, applied in idealistic morphology). The disadvantage of the idea is that every property of the carpels — placenta with ovules, the vascular supply, the post-fertilization development, and the method of dehiscence — has to be transferred to the new intercalation (as Corner wrote). The problem is that this happens in a way reflecting the former positions. Evidently the receptacular processes, on which we are so badly informed, do not entirely disturb the original positional interrelationships (thus, on comparison, creating the effect of fusion and conservatism of the vascular bundle pattern). Furthermore, the objection could be raised that the idea implies the acceptance of the carpel theory.

One could theorize that in some lineages the phylogenetical processes would happen just the reverse, the ovules becoming transferred from a symmetrical position within cupules to the margins of the cupular lobes, through accelerated development.

Sattler (1973) also thinks there are gynoecea to which the carpel concept cannot be applied. He offers a number of tools (gynoeccial appendage, placenta and ovules) and a number of processes (zonal growth, transference of function, etc.) with which to start a renewed empirical validation. He too rejects the notion of 'congenital fusion' as a mental construction to explain syncarpy, the inferior ovary, and other phenomena. It should be replaced by the study of meristematic activity. He offers several instances of arcipellate taxa. *Scaphocalyx* would certainly offer a perfect example. The scheme presented by Sattler would — if worked out — seem to be a more neutral scheme, of service in trying to reach more precise comparative morphogenetic knowledge leading to better theories.

### The ovules

A critical paper on the present knowledge of the ovules was published by Van Heel & Bouman (1972). Except for the location in the pistil, the ovules of *Scaphocalyx* show some

more unusual characters, such as the sessile atropous condition, the predominate basal 'intercalary' growth, and also the tips, lobes, and beaks terminating the integuments and nucelli.

One may speculate on the functional significance of sessile versus stiped ovules, but nothing really is known of it. The atropous, *versus* the anatropous, condition has no doubt consequences for the path the pollen tubes have to take to reach the micropyle. How do the tubes reach the nucellar beaks in case the atropous ovules — as in *Scaphocalyx* — point freely toward the centre of the ovarian space? In my material I did not find an extension of beaks or integuments up to the stigmatic surfaces, nor did I find a kind of obturation.

A functional explanation of the nucellar beak and of the distal tips of the inner integument may be sought in the conduction of the pollen tube. Whereas the beaks and the tips consist of metabolically active cells (i.e. they become deeply stained), the lobes of the outer integuments are normally parenchymatic and their function could be thought of as being limited to the angiovuly. However, nothing could be made sure on the histogeny of these peculiar structural details.

In literature, reference to nucellar beaks is frequent. They occur in Pteridosperms, Cycads, *Euphorbiaceae* (Davis, 1966), and in *Polygonum* (Souèges, 1919). The initiation of the single integument in the form of two lobes is common in Gymnosperms. Schnarf (1937) mentioned it for *Taxus*, *Austrotaxus*, *Torreya*, *Pinus*, *Abies*, *Larix*, *Thuja*, *Cupressus*, *Cryptomeria*, and several *Cycadaceae*. For *Cryptomeria* it was mentioned by Strasburger (1879), and photographed by Bierhorst (1971). For the integuments in Angiosperms a distal separation of parts was recorded in *Scyphostegia*, *Caloncoba*, *Juglans*, and *Sterculia* (Van Heel, 1970), and now in *Scaphocalyx*. Furthermore, I noticed two-lobed inner integuments in *Exochorda*. In Pteridosperms integuments as well as cupules separate into parts distally. However, it should be remembered that the homology of cupules and integuments in the groups mentioned is uncertain. As stated by us (Van Heel & Bouman, 1972), there is some anatomical indication to regard the outer integument as a bipartite structure in some Angiosperms. Also in *Scaphocalyx* it can have two lobes. Sterling (1972) noticed that in *Dipidax* — a Liliaceous plant with only one integument instead of the usual two in that family — there are two lateral protuberances at the ovule base. Could they represent the outer, missing, integument?

Van Wisselingh (1920) described the structure of the integuments in *Eranthis* and in *Tropaeolum*. In their seeds the original integuments form a minor part of the seed coat and can be detected near the micropyle. The main portion of the testa is produced by extreme growth in the chalazal region. Both cases were recorded by Netolitsky (1926). Voigt (1885) wrote for *Myristica* (transl.): 'the growth of the ovule is produced mainly beneath the insertion of the inner integument. Consequently, on the mature seed the latter is limited to a very small region of the tip. The embryosac penetrates into the enlarging base of the nucellus'. In *Myristica* the proximal growth elevates the inner integument only. For some *Euphorbiaceae* something similar was described (Singh, 1954, for *Ricinus*). Corner (1949) gave a precise description of the ovule development in some *Annonaceae*, which shows the same features. The ovules remain bilateral (as in *Scaphocalyx*), and the integuments remain free along the flanks of the ovules and seeds. However, here *Scaphocalyx* differs in that the testa along the flanks of the older ovules and seeds is an 'intercalated' structure and develops as a single sheath beneath the two original integuments. The latter, in the end, show only at the topmost part of the seed. How the intercalated testa is effectuated histogenetically I could not study. Periasamy (1964) described similar proximal growth in *Coccoloba*. I described a similar case in *Hernandia* (Van Heel, 1971). It is striking that a number of cases on record also have labyrinth seeds. All the cases are due to growth

intercalated between the micropylar part and the base of the ovule, at or below the level of insertion of the integuments. This growth is followed by that of the nucellus, the endosperm, and the embryo, they become sunken in the proximal ovular tissue. In Gymnosperms the proximal growth — with variations — is recorded for *Pinus*, *Torreya*, *Gnetum*, and *Cycadaceae*. Generally, we could name seeds and ovules, as they are described above, inferior (*cf.* Schnarf). In how far this inferiority plays a role in mesozoic and paleozoic seeds, is often not easy to make out from the descriptions.

The ovule as a whole, on developing into a seed, becomes buried deeply into the endocarp tissue, which adds to the process by some inward growth, finally enclosing the micropylar part of the seed with a small number of lobes. In this case the endocarp growth can possibly be compared with the aril formation on stiped ovules in *Flacourtiaceae*, namely in the equally atropous *Caseariaceae*.

### The seeds

Finally a pulpos fruit results, in which hard reniform seeds are embedded. It is a peculiar fact that the testa has a compound hard layer of cells in the middle — a mesotesta — because this is not reported elsewhere in Angiosperms, but is frequent in the single integument of Gymnosperms. All inferior seeds have in common that the layers present in the testa are copied in the outer part of the chalazal extension, so that there too the seeds are provided with sclerified cell layers — and in *Scaphocalyx* also by a chemically resistant layer — and thus are fenced from their milieu. Netolitzky called these layers the *Hartschicht* and the *Pigmentschicht* respectively. Bierhorst (1971) described them in *Zamia*.

As described in the first part of this paper, a free space develops between the hard part of the testa and the kernel of the seed which consists of the endosperm and the embryo. This is brought about by disruption of the cells within the inner soft layer of cells of the testa. Its inside parts, including the inner pigmented epidermis, become separated and finally firmly enclose the kernel. Schnarf called this layer the 'Innenhäutchen', which according to him is present in *Ginkgo*, *Cycadaceae*, *Cephalotaxus*, and *Pinaceae*, originating in much the same way. It had already been mentioned by Strasburger (1872). Its presence in fossil Gymnospermous seed is not recorded. In Angiosperms it is probably present in some *Cucurbitaceae* (Singh 1953, cited by Esau 1965). Netolitzky mentioned it in *Cistaceae*. Possibly it is present in *Scyphostegia* (Ding Hou, 1972). Interesting remarks on this feature were made by Guttenberg (1971). This author stated that generally air spaces can be formed in fruits and seeds between an outer envelope and a kernel. In small seeds they may be a means for flying, but in large seeds they may serve as a swimming device.

The air content of the inner part of the testa of *Cycas* makes its seed capable of swimming. In *Nymphoides peltata* the testa surrounds the body of the seed only loosely. Correspondingly, I consider these features in the *Scaphocalyx* seeds as a means towards dispersal by water. Therefore — as judged from structure — *Scaphocalyx* should be diplochorous (*cf.* Van der Pijl, 1972), firstly its pulpos fruits being conveyed by animals, and secondly its seeds by water.

### Conclusion

Some arguments may be summed up in favour of the view that this Malaysian monotype possibly is a very ancient one. Main properties are frequent in Gymnosperms, rare in Angiosperms. Firstly the projections or lobes terminating the nucellus and both integuments, secondly the inferior seeds and the three layered testa. Furthermore, but in

minor degree, the atrophy of the ovules, the unisexuality, and the pulpous fruits. The placentation of the ovules cannot be assessed at present. The covering of the pistil with nectariferous hairs is also a special feature.

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