

FLOWERS AND FRUITS IN FLACOURTIACEAE III. SOME ONCOBEAE

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SUMMARY

Data are presented on *Oncoba*, *Caloncoba*, *Camptostylus*, *Dasylepsis*, *Scottellia*, *Berberidopsis*, *Lindackeria*, and *Peterodendron*, with special emphasis on development and anatomy of the gynoeceum. A neutral view is preferred to the carpel theory. There appears to be a link between parietal and basal placentation. It is proposed to refer to this placentation as cupular. Several peculiarities are found, such as 'ramification' of the stigmatic canals, penetration of the embryosac into the chalaza, distal lobes on integuments, separate vascular traces to the lowermost ovules, etc.

MATERIALS

Oncoba spinosa Forsk.: *Botanic Garden Pretoria s.n.*; *Story* 4748; *Leeuwenberg* 9552; *Seegeler s.n.* — *Caloncoba welwitschii* (Oliv.) Gilg.: *J. J. F. E. de Wilde* 2007; *Bos* 6453, 6681. — *C. glauca* (P. Beauv.) Gilg: *Bos* 5821. — *C. echinata* (Oliv) Gilg: *Botanic Garden Wageningen s.n.* — *Camptostylus mannii* (Oliv.) Gilg: *Bos* 3845, 4877, 6714. — *Dasylepsis brevipedicellata* Chipp.: *Oldeman* 958. — *Scottellia mimifensis* Gilg: *Meikle* 526. — *Berberidopsis corallina* Hook. f.: *Sleumer s.n.*, culta, England. — *Lindackeria dentata* (Oliv.) Gilg: *Breteler* 1664, 2759; *Bos* 3707, 6254. — *Peterodendron ovatum* (Sleumer) Sleumer: *Leeuwenberg* 10843.

I extend my sincere thanks to my colleagues of the Laboratory for Plant Systematics at Wageningen, and to the Chief of the Botanical Research Institute at Pretoria for collecting most of the material. Voucher specimens in alcohol or F.A.A. are in L, PRE, or in WAG.

ONCOBA SPINOSA FORSK.

GENERAL

Oncoba spinosa is a well known spiny shrub or small tree of Africa. Its flowers are rather large and showy, with about ten long white petals and numerous slender stamens. Four broad sepals are well demarcated from the petals. The pistil in the centre carries a long style which flares into a crater-shaped stigma with a knotted rim. Often, functionally male flowers have less well developed pistils. Many longitudinal septa reach inwards from the wall into the ovary, carrying many ovules along their flanks and rims (photo 3). The ovules are atropous and radially symmetrical in cross-section. However, frequently the stalk is at an angle with the body of the ovule, in which case the ovules may be slightly bilateral. A thick nucellus is surrounded by two integuments; at the top the outer integument does not extend beyond the inner one. The fruits are woody balls, filled with pulp when ripe, in which many hard seeds are immersed. Each hard seed is covered by a thin soft layer. The fruits do not dehisce. Everard & Morley (1970) present a fine illustration of the plant. I may add here that the staminal primordia can be seen to arise on the floral

apex in centrifugal sequence. For a taxonomic description the reader is referred to Sleumer (1975).

ONTOGENY OF THE PISTIL

Around the floral apex a sinuate girdling meristematic wall arises which develops immediately into a distally lobed and radially septate cupule. Cells are produced downwards, and at the same time, but increasingly so later on, cells are produced outwards in the radii of the inward curves of the sinuate wall. As a result the wall grows upwards and inwards leaving deep clefts in the radii of the outer curves of the sinuate wall. Moreover, as the floral apex itself continues growing as well for some time, the clefts are extended downwards. In this way the septs and locules are shaped simultaneously by differential meristematic growth (photo 1, fig. 1).

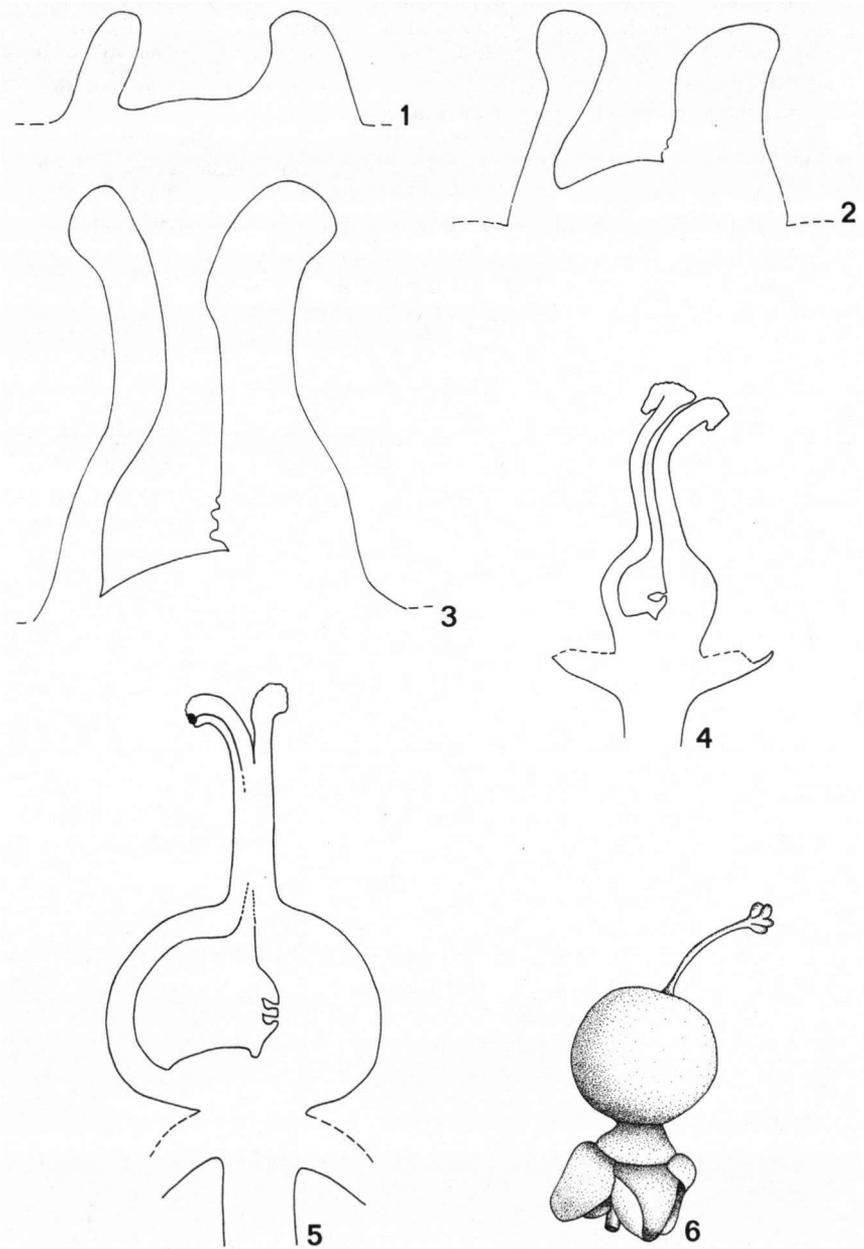
After the initiation of the ovules, the septs touch one another in the subdistal part of the pistil, and a style is completed there by intercalary growth. It is only after anthesis that the septs start fusing with one another in the centre of the style. As they do so a whorl of separate styler canals is formed around a solid central column (fig. 5).

The sinuate apex of the meristematic wall develops directly into the young stigma as a lobed rim of a cupule. Subsequently the stigma attains a crater-like form and becomes plugged in its centre because the septs touch and fuse. Later on lobulation of the stigma occurs, resulting in the peculiar ramification of each styler canal firstly into two collateral ones and then into two to five serial or fan-shaped smaller ones, all subsidiaries ultimately leading to the stigmatic surface (fig. 11). The growth of the style and stigma is continued (up to a stage shown in fig. 6) together with the later growth of the ovary into a fruit. On the surface of such a 'supermature' stigma the openings of the subsidiaries of the styler canals can be observed quite clearly (photo 4).

THE OVULES AND SEEDS

The ovular primordia appear in accordance with the primary modelling of the pistil, that is chiefly in acropetal succession (photo 2, figs. 2 and 3). The ovules originate on the lateral sides of the septs as well as on their rims. Slightly later on the ovules located on the rims develop more quickly than those located on the sides.

The first cell divisions leading to both integuments are observed in the dermal cell layer of the ovular primordium. However, in a later stage middle cell layers may become included in the proximal part of the outer integument, which are of subdermal origin (*cf.* Hakki, 1974). For the greater part the outer integument consists of two cell layers, but there is a secondary multiplication of the cells of the inner epidermis, resulting in a thin sarcotesta. The inner integument has four cell layers, but around the micropyle it becomes thicker by the development of more cell layers. The inner epidermis differentiates into the 'pigment layer', but around the micropyle more cell layers can contribute to a 'pigment plug' occluding the developing seed. Moreover, this occlusion is achieved by the lignification of the middle cell layers of the inner integument. The cells of the outer epidermis of the inner integument differentiate into palisade sclereids. The 'pigment layer' fences off the seed towards its base, the sclereids do not develop there. The nucellus possesses a distinct epidermis of cylindrical cells. The nucellus is resorbed entirely by the developing embryosac, except for a thin layer of empty cells distally. Apically the nucellus is penetrated by the growing embryosac. However, the embryosac does not protrude out



Oncoba spinosa—Figs. 1—5. Developmental series of the pistil, longitudinal sections. On the left: sectioned through the ovules, on the right: sectioned through the septa. — Fig. 1. $60\times$. — Fig. 2. Ovule initiation. $30\times$. — Fig. 3. Style formation. $30\times$. — Fig. 4. At stage prior to anthesis. $3.5\times$. — Fig. 5. At stage after anthesis. $3.5\times$. — Fig. 6. Fruit just before style and stigma will fall off. $1\times$.

of the micropyle. The endosperm becomes cellular. Distally in the seed a thick cuticle is situated between the integument and the residual nucellar tissue. The embryo has two large appressed foliar cotyledons, which are located in the median plane of the seed in case it is bilateral. Towards the maturation of the ovule a slight extra growth occurs in the region below the insertion of the inner integument.

On entering the ovule the vascular bundle divides into a peripheral whorl of short vascular bundles and into some diffuse vascular tissue in the middle reaching the base of the nucellus. In the mature seed the peripheral vascular bundles run higher up into the sarcotesta, in the median plane of a bilateral seed even up to micropylar level.

After completing my manuscript Corner's book on seeds (1976) appeared. The description of the seed of *Oncoba spinosa* given therein is in agreement with mine. The remarks of Vaughan (1970) on *Oncoba echinata* disagree with my findings.

THE FRUITS

The pulp in the fruit is formed by the placental septa. Immediately after the appearance of the ovule primordia strong periclinal division takes place in the peripheral cell layers of the septa. Finally the seeds become surrounded by irregular lobes of the placental tissue (cf. *Scaphocalyx*, Van Heel, 1973). At first the enlarged placentas, although contiguous, remain separate, but in the end a mass of globular cells results, which contain starch and pyrenoids.

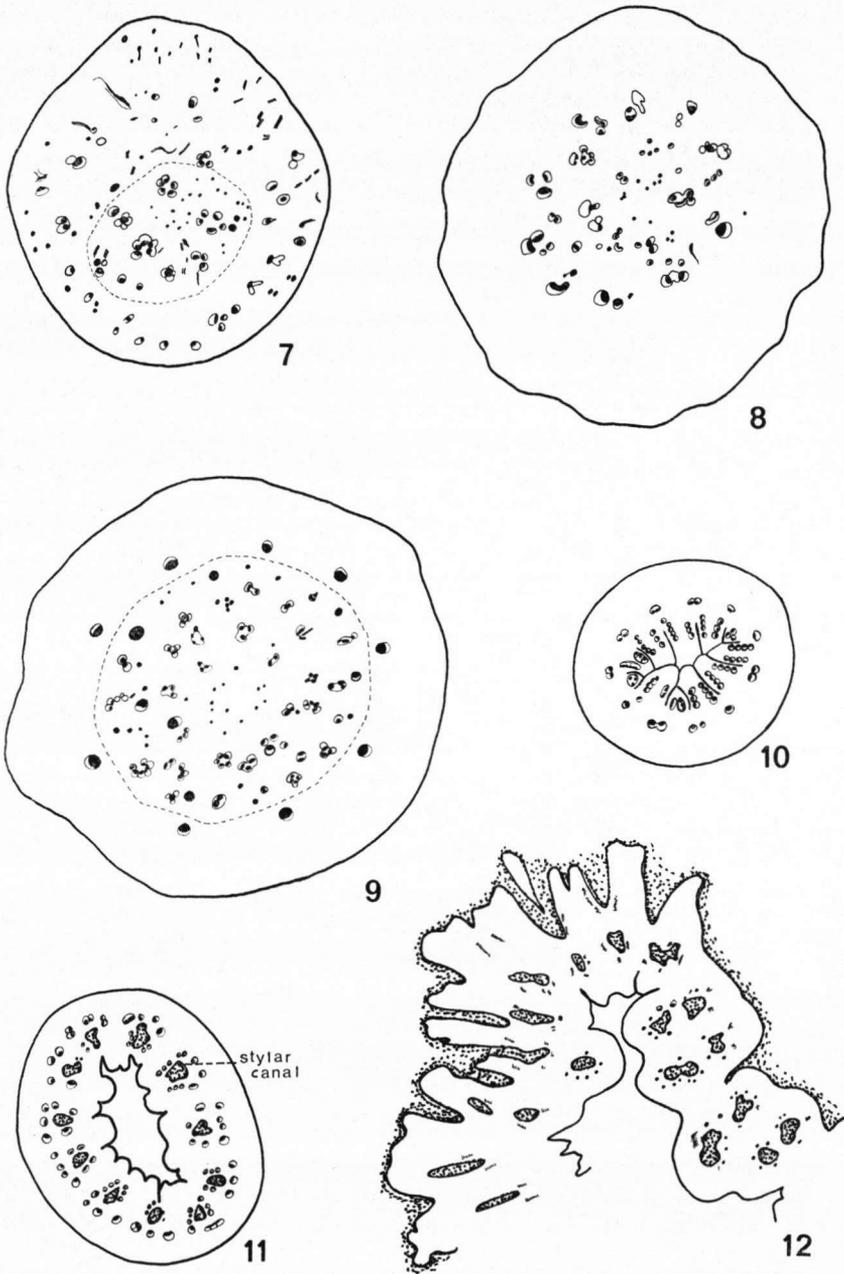
The fruit wall consists of a leathery layer of small parenchyma cells which surrounds a very hard matted layer of long sclereids. This mantle of sclereids projects into the base of the placental septa with lengthwise ribs.

PATTERN OF VASCULAR BUNDLES

In cross-section, the pedicel of old flowers or of young fruits shows circular groups of vascular bundles, which together are again arranged in a circle. In each group the xylem of all constituting bundles faces the centre. If the pedicels are small the circular groups are condensed into large concentric vascular bundles. In large pedicels there may occur many small 'medullary' and also 'cortical' bundles.

Outer and lateral portions of the groups of vascular bundles turn and bend outwards, and ramify into the vascular supply of the perianth and the androecium. The supply toward the calyx is clearly separate. Many traces enter the calyx, dividing collaterally, and forming girdling anastomoses just below its base. The supply towards the androecium and the corolla is combined, quite in conformity with the close association in the flower of small upper petals and stamens. Many traces branch repeatedly, giving off corolla bundles downwards and stamen bundles upwards, the uppermost traces branching into stamen bundles only.

Slightly above the perianth insertion, at the very base of the pistil, the residual vascular bundles recombine into a circle of five or more circular groups of small vascular bundles with opposing xylem (fig. 7). Consequently the position of the vascular bundles on this level is similar to that in the pedicel below the perianth insertion. However, immediately upwards the groups spread into numerous bundles, single or in small mutually opposed groups, which are distributed evenly in the tissue. Slightly upwards again out of this mass of bundles about ten bundles proceed outwards and are separated from the main mass of bundles by the mantle of young sclereids that is developing in the fruit wall, as



Oncoba spinosa — Figs. 7—11. Transverse sections of pistil at anthesis. 15 \times . — Fig. 7. Traces towards the pistil amidst the androecium supply. — Fig. 8. At base of pistil. — Fig. 9. At base of 'carpel dorsal' bundles. — Fig. 10. At the level of the style. — Fig. 11. At base of stigma. — Fig. 12. Ramification of stigmatic canals.

mentioned above (fig. 9). By classical terminology they are the 'carpel dorsal bundles'. Slightly upwards the mass of vascular bundles withdraws from the central part, although leaving there tiny bundles. A broad ring of (groups of) vascular bundles is formed, as seen in cross-section, which become organized into sets of the different placental septs. The sets consist of bundles which are distributed evenly in the base of the placental septs. They divide into upward ramifications which may divide again and turn towards the periphery of the placentas in order to supply the ovules (photo 3). In the upper part of the ovary the septal vascular bundles turn inwards and proceed towards the base of the style. However, the central bundles end up in ovule traces only. Also, the most peripheral ramifications end blindly. In general the course of the vascular bundles in the placental septs is in conformity with the overarching growth of the pistil wall and the ribs of sclereids. The 'dorsal' bundles outside the sclereid mantle bend inwards also and enter the base of the style; upwards they divide collaterally into two large and some minor bundles. Together, the bundles in the style, as seen in cross-section, form a sinuate circular pattern with the inner bends weakly developed or missing in the lower parts. The xylem of all bundles faces the stylar clefts (fig. 10). Distally in the style, where the septs fuse laterally leaving stylar canals as described above, the dorsal bundles continue to divide collaterally. Together with the septal bundles they form a sheath of bundles around the canals, except centrally (fig. 11). Together with the upward division of the stylar canals in the stigma the vascular bundles divide also and continue to enclose the canals (fig. 12).

CALONCOBA AND CAMPTOSTYLUS

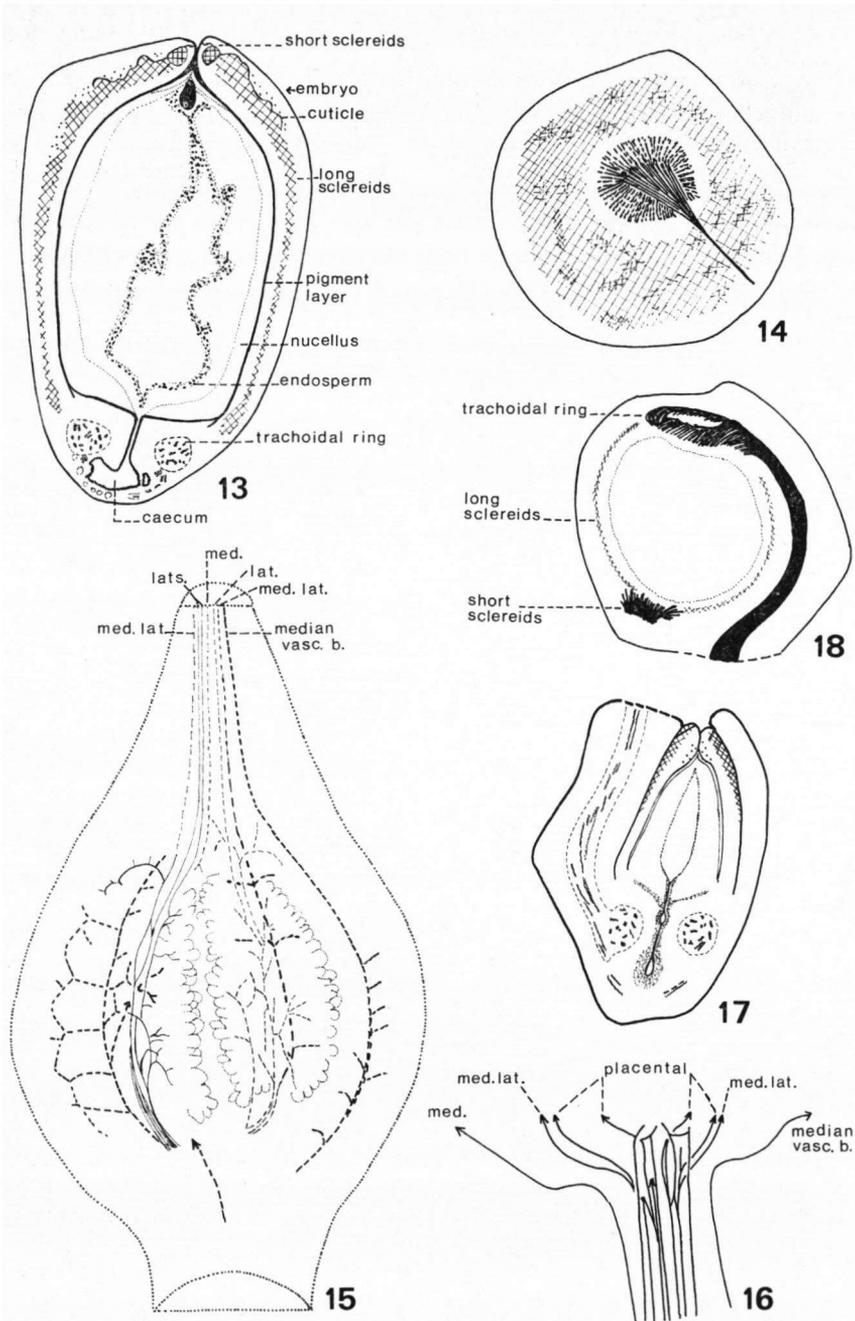
COMPARISON WITH ONCOBA

I can confirm the report for *Caloncoba echinata* given by Endress & Voser (1975) stating that the first visible development of the stamens takes place irregularly on a flat apex. However, as mentioned above, the development is centrifugal in *Oncoba*.

Whereas the pistil in *Oncoba* is polymerous and shows 'ramification' of the stylar canal into the stigma, in *Caloncoba* and *Camptostylus* the pistil is pentamerous or hexamerous and does not show the ramification of the stylar canal. The anatomy of the pistils is not similar in every respect (see below).

Like in *Oncoba* the ovules cover the whole surface of the septs, that is also the rims. However, upwards where the septs approach in the centre of the pistil, and still higher up where they touch, there is no ovule formation (fig. 23). Because the ovule formation is continued along the sides of the placentas for a short distance, on this level one gets the impression of a sub-marginal placentation in transverse sections. Evidently, when the septal margins approach and touch, the placental function gets lost.

Like in *Oncoba* the ovules have two integuments, and the micropyle is formed by the inner integument only. Also, the outer integument matures into a sarcotesta, and the epidermides of the inner integument develop into a layer of elongated sclereids and a pigment layer. However, in *Caloncoba* and *Camptostylus* the sarcotesta becomes much thicker than in *Oncoba*, and the sclereid layer consists of more than one cell layer. In *Caloncoba* and *Camptostylus* the ovules are anatropous, not atropous as in *Oncoba*. Whereas the embryosac penetrates the apical part of the nucellus in *Oncoba*, in *Caloncoba* and *Camptostylus* it penetrates the basal part of the nucellus and grows into the chalazal region (see below) (figs. 13, 17). Toward seed maturation the inner integument in all species studied becomes slightly thicker apically, and isodiametric sclereids are differentiated from mesophyll cells in that place (photo 5, fig. 18). The isodiametric sclereids mature earlier



Caloncoba glauca — Fig. 13. Young seed, transverse longitudinal section. 15 ×. — Fig. 14. Seed at chalaza, cleared. 7 ×. — Fig. 15. Portion of young pistil, cut lengthwise and cleared. — Fig. 16. Receptacle of young flower, cut lengthwise in halves, and cleared.

Campostylus mannii — Fig. 17. Post-fertilisation ovule, longitudinal section. 15 ×. — Fig. 18. Young seed, cleared. 4 ×.

than the elongated sclereids of epidermal derivation, so that the top of the seed is fenced off rather early, while the development of the seed as a whole proceeds (fig. 18).

The pigment layer that differentiates from parenchyma cells at the base of the seed between nucellus and chalaza appears to be discontinuous at its borders with the integumental pigment layer (fig. 13). It fences off the seed below.

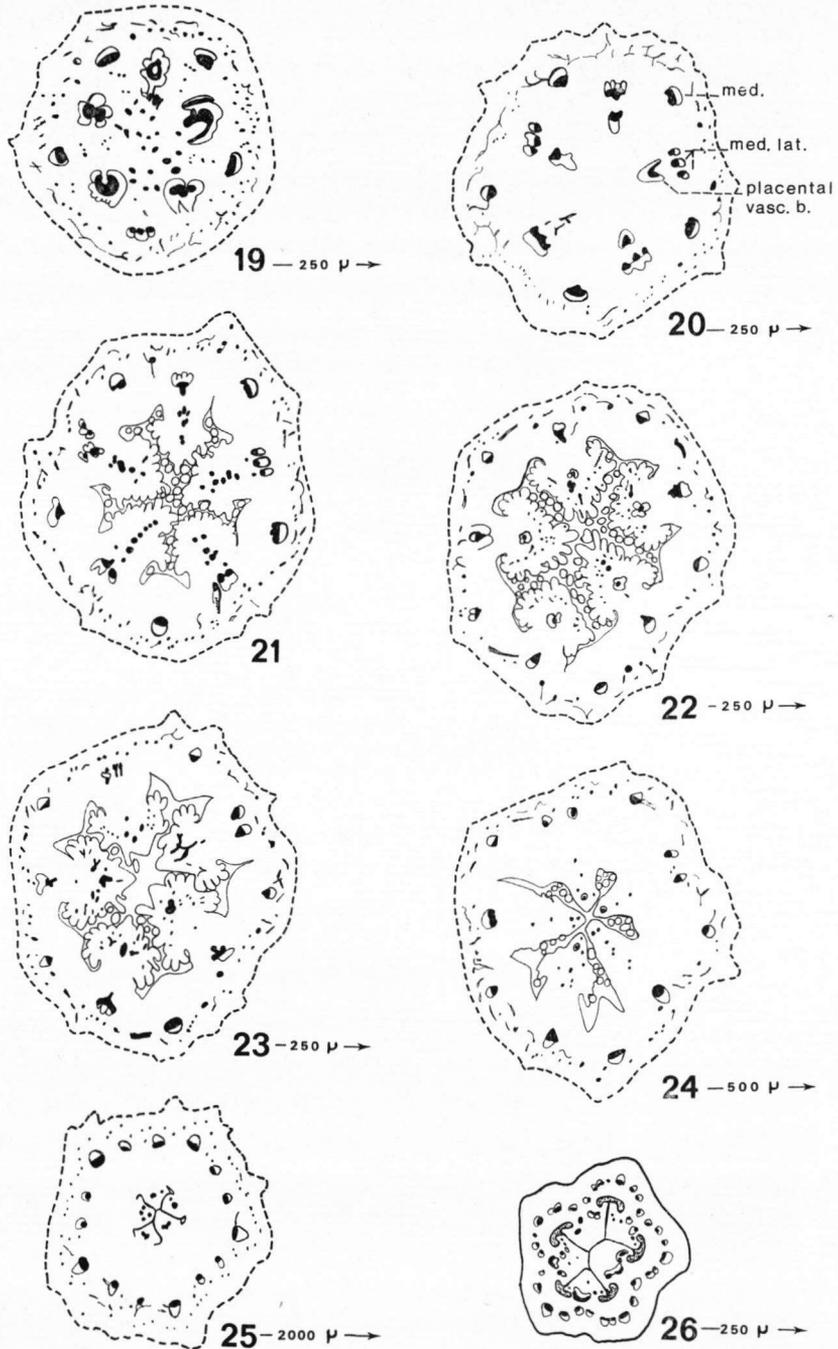
Both *Caloncoba* and *Camplostylus* have been revised taxonomically by Sleumer (1974). The separate status of *Oncoba* is fully endorsed by flower anatomical characters. However, the similarity of these characters in *Caloncoba* spp. and *Camplostylus mannii*, and the occurrence in both of an odd feature as the embryosac penetrating downwards and forming a caecum in the chalazal region (photo 6), certainly pleads for considering *Caloncoba* and *Camplostylus* closely allied. The chief difference, as advanced by Sleumer, is to be found in the form of the inflorescences, the flower characters seem to overlap. The species are distinct, however.

SPECIAL FEATURES

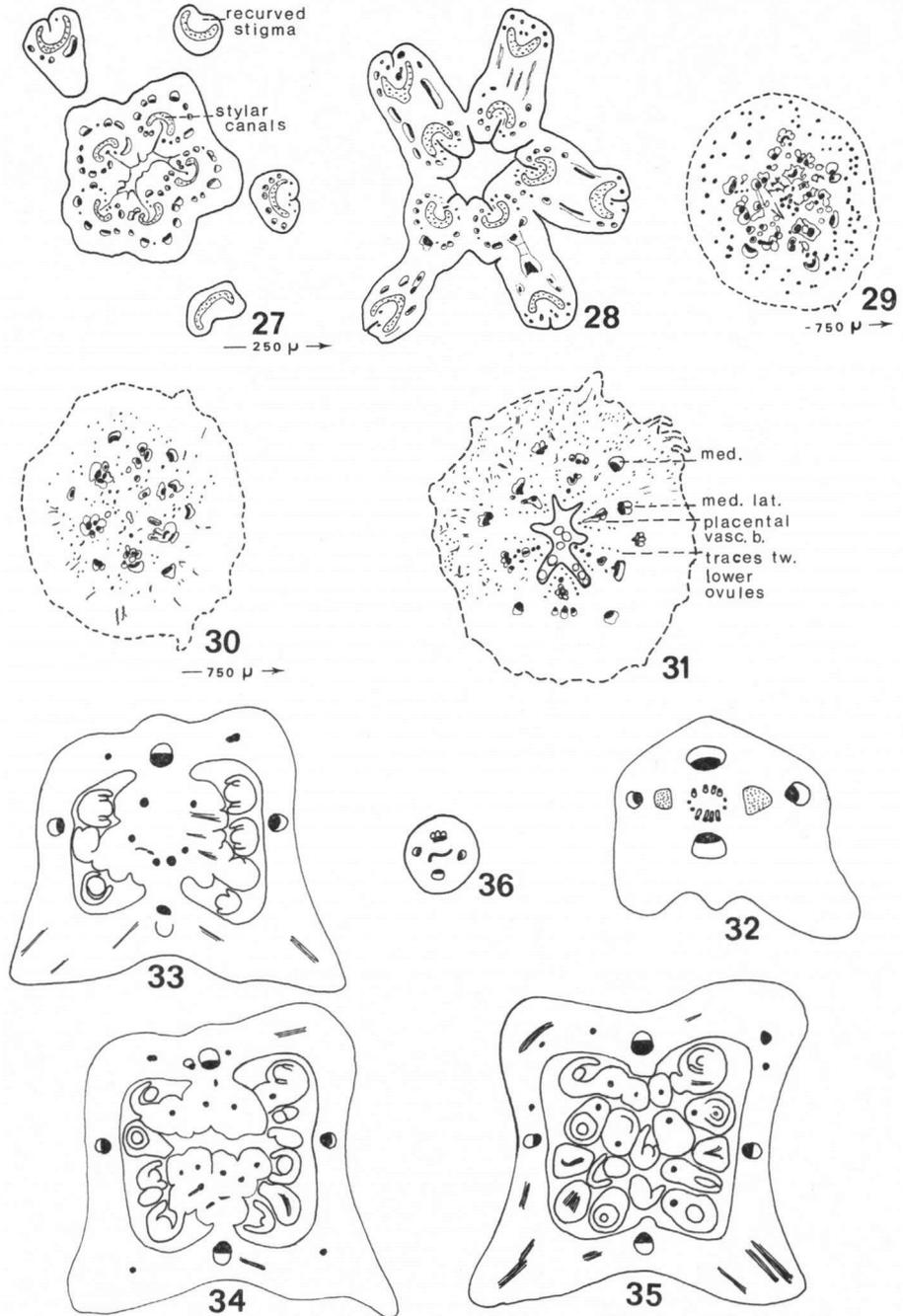
In 1970 I described the presence of distal lobes on the outer integument of *Caloncoba welwitschii*. During the present study I noticed the occurrence of four-tipped inner integuments in ovules of *Camplostylus mannii* (like in *Scaphocalyx*, Van Heel, 1973). Moreover, in young seeds of the same species I discovered inner integuments which terminated into two lateral lobes which themselves are slightly lobulated. The exostomes had the form of short slits.

During ovule development a rather ample growth of the chalazal region sets in, which is followed by a penetration into that region by the embryosac through a very narrow canal. The canal widens into an irregular cavity in which the chalazal tissue becomes resorbed gradually. The differentiation of the basal pigment layer extends downwards along the canal, and in *Camplostylus mannii* also forms a 'postament' upwards into the base of the nucellus (fig. 17). In literature (Maheshwari, 1950; Johri, 1963) this structure is called an embryosac haustorium or caecum. Although reported for most cases, in this case I could not detect endosperm formation in the caecum. The formation of the absorbing cavity is accompanied by a special vascularization. The complex raphe bundle of the anatropous ovule spreads into a ring of tracheids in the chalaza around the resorbing cavity (figs. 13, 14, 17, 18, photo 6). In a later stage tracheids can be formed also beneath the cavity, so that a cup of tracheids results, which extends around and below the cavity. Martens (1974) described a cup of tracheids in the ovules of *Welwitschia*, but without resorbing cavity.

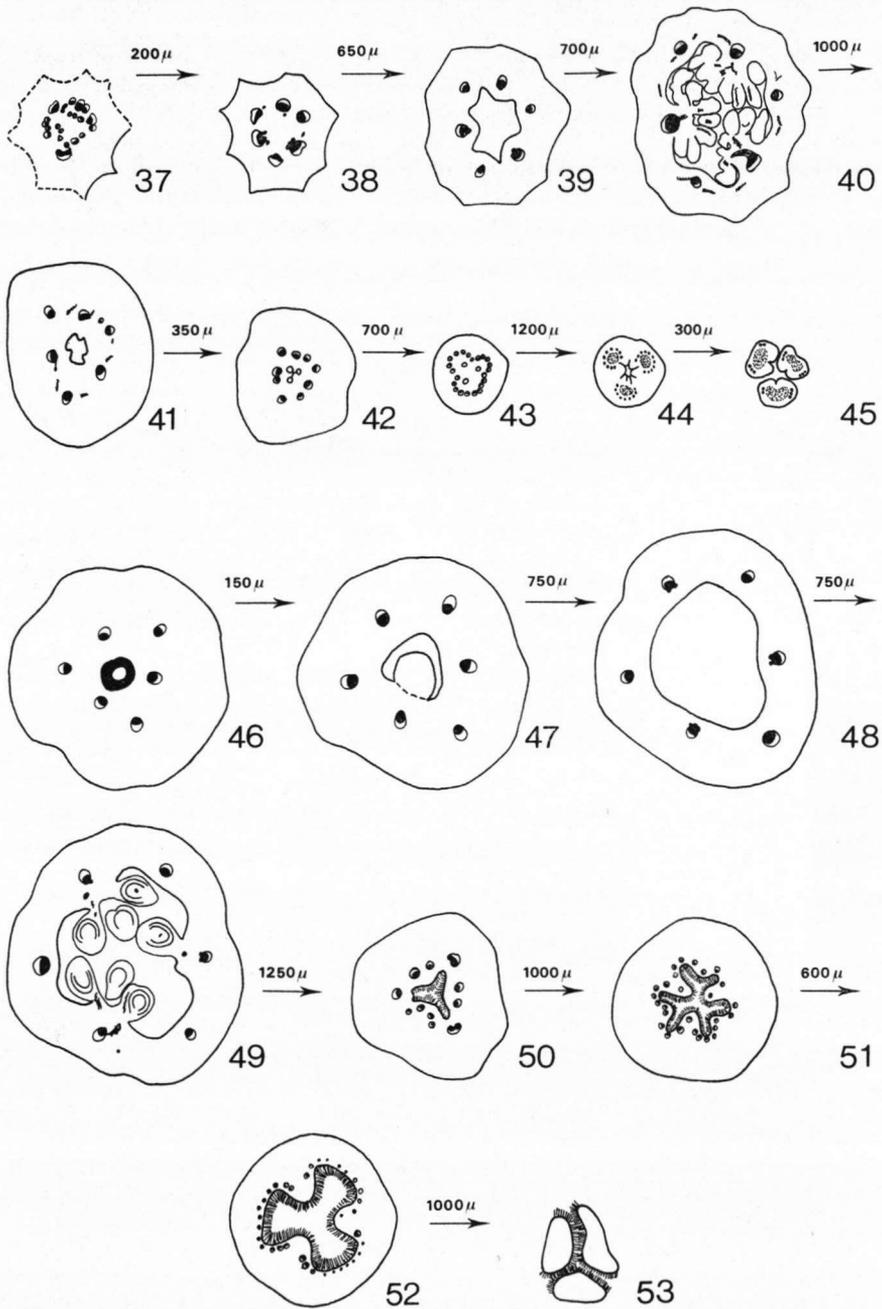
When the seeds develop, the cuticle separating the outer and the inner integument vanishes entirely, after that it at first persisted in some places (fig. 13). The interplay between strong periclinal divisions in the inner cell layer of the outer integument and the folding of the layer of elongated sclereids of the inner integument leads to many sclereid projections into the sarcotesta of the mature seed (photo 5). Finally the fusion of the integuments is complete. The sarcotesta is filled with starch and its inner cell layers become pigmented. Also the pigment layer of the inner integument finally comprises several cell layers next to the inner epidermis. In the seed the epidermis of the nucellus persists in places. The nuclear endosperm becomes cellular and oily. The embryo also contains oil. The first embryo development would present a case of 'delayed' histogen differentiation in the sense of Haccius & Bhandari (1975).



Caloncoba welwitschii — Figs. 19—26. Cross sections of a young pistil, from base to stigma. 15 \times .



Caloncoba welwitschii — Figs. 27—28. Cross sections of a young pistil, from base to stigma. 15×. Continuation. — Figs. 29—31. Cross sections of base of older pistil. 7×.
Peterodendron ovatum — Figs. 32—36. Pistil at anthesis. Cross sections from base to style. 30×.



Dasylepsis brevipedicellata — Figs. 37—45. Pistil at anthesis. Cross sections from base to stigma. 15 ×.
Berberidopsis corallina — Figs. 46—53. Pistil at anthesis. Cross sections from base to stigma. 30 ×.

ANATOMY OF THE PISTIL

Below the very base of the pistil the traces toward the pistil reconstitute a stele, which in the base of the pistil changes into an outer whorl of five 'carpel dorsal' bundles alternating with an inner whorl of more or less concentric complexes of bundles (figs. 19, 30). In addition there are 'cortical' bundles and bundles in the centre that could be residual stelar bundles. The concentric complexes divide into outer portions which form the 'median — or commissural — lateral carpel' bundles, and inner portions which run upwards as placental bundles (figs. 20, 31). The latter have inverted xylem and phloem basally. They separate each into a radial series of smaller complex bundles, of which the inner ones ramify into lower ovules, and the outer ones into the progressively higher placed ovules (figs. 15, 21). It is curious that there are no cross connections between the placental bundles and the main pistil wall bundles during their upward course. Now and then irregularities occur, such as ovule traces connected with the minor pistil wall vascular bundles (fig. 15, at left).

Moreover, from the residual stele small bundles arise which branch towards the lowermost ovules, and which in transverse section appear as lateral radial rows in the placentas, reminiscent of the curious supply towards the ovules in *Scaphocalyx* (Van Heel 1973) (figs. 16, 31).

The basal connection of the placental bundles with the 'median lateral carpel' bundles in *Caloncoba* contrasts with the more diffuse location of the placental bundles and the absence of 'median laterals' in *Oncoba*. Possibly the difference is related with the fact that the transgression between septa and floral apex at the time of ovule origin in *Oncoba spinosa* is more gradual than in *Caloncoba echinata*, in which species I could observe a more distinct demarcation. In other words: in *Oncoba* the placentation would be more basal, in *Caloncoba* more parietal.

More upwards, in the sterile septal parts, some bundles of the placental complex end blindly, other bundles constitute inverted bundles facing the bundles of the pistil wall. Farther upwards all bundles fall apart into the lateral and marginal bundles of two adjoining stylar lobes (figs. 24—28). On this level transverse sections of the stylar lobes enclosing the stylar canals show the normal picture of five or six laterally connate carpels with submarginal placentas (here sterile) into which small vascular ramifications are given off.

DASYLEPIS BREVIPEDICELLATA CHIPP.

See figs. 37—45. Three placentas are situated along the sides of the ovary, which bear the ovules along their whole surface. However, in their distal parts they are sterile; here, in the centre of the attenuating ovary, they touch and fuse into the style giving rise to three narrow stylar canals. Where the style grades into the stigma three carpellary components appear, each with a ventral split. Proximally the pistils are also sterile.

Above the level of the separation of the calyx system and the petal-stamen vascular bundle system, a pistillary stele is sharply demarcated. The stele consists of an outer and an inner irregular ring of vascular bundles. The position of the xylem of the bundles in the inner ring is either irregular or tends to face that of the outer ring. Upwards the pistillary stele condenses into three (carpellary dorsal) bundles and three alternating complex bundles. To be precise, the inner ring of bundles condenses into the inner parts of the complex bundles which higher up turn inwards as many ovular traces. Towards the stigma each carpellary component has its own semi-circle of vascular bundles, derived

from the lateral branching of the six main pistillary bundles, among them the outer parts of the complex bundles.

The ovules are anatropous and have two integuments. In the pre-anthesis stages studied, the inner integument is not longer than the nucellus, and consists of two cell layers. As a contrast, the outer integument is very much longer than the nucellus, and consists of a few cell layers.

SCOTTELLIA MIMFIENSIS GILG

The ovules are anatropous and possess a large nucellus which, at the time of anthesis, is not surrounded by the inner integument in its distal parts. At that time both integuments have few cell layers. The outer integument forms a lateral micropyle facing the raphe, which is caused by the fact that its rim overarches the nucellus on one side.

Sections of young seeds show that both integuments have increased in thickness. Whereas the inner epidermis of the inner integument forms a pigment layer, which continues over the base of the seed, the outer epidermis differentiates into a number of elongate sclereid cell layers, except around the micropyle where the young sclereids are isodiametric. The inner cell layers of the outer integument divide anticlinally inwards in conformity with outward extrusions of the young sclereids of the inner integument. The outer cell layers of the outer integument form a pigmented outer layer of the seed.

BERBERIDOPSIS CORALLINA HOOK.F.

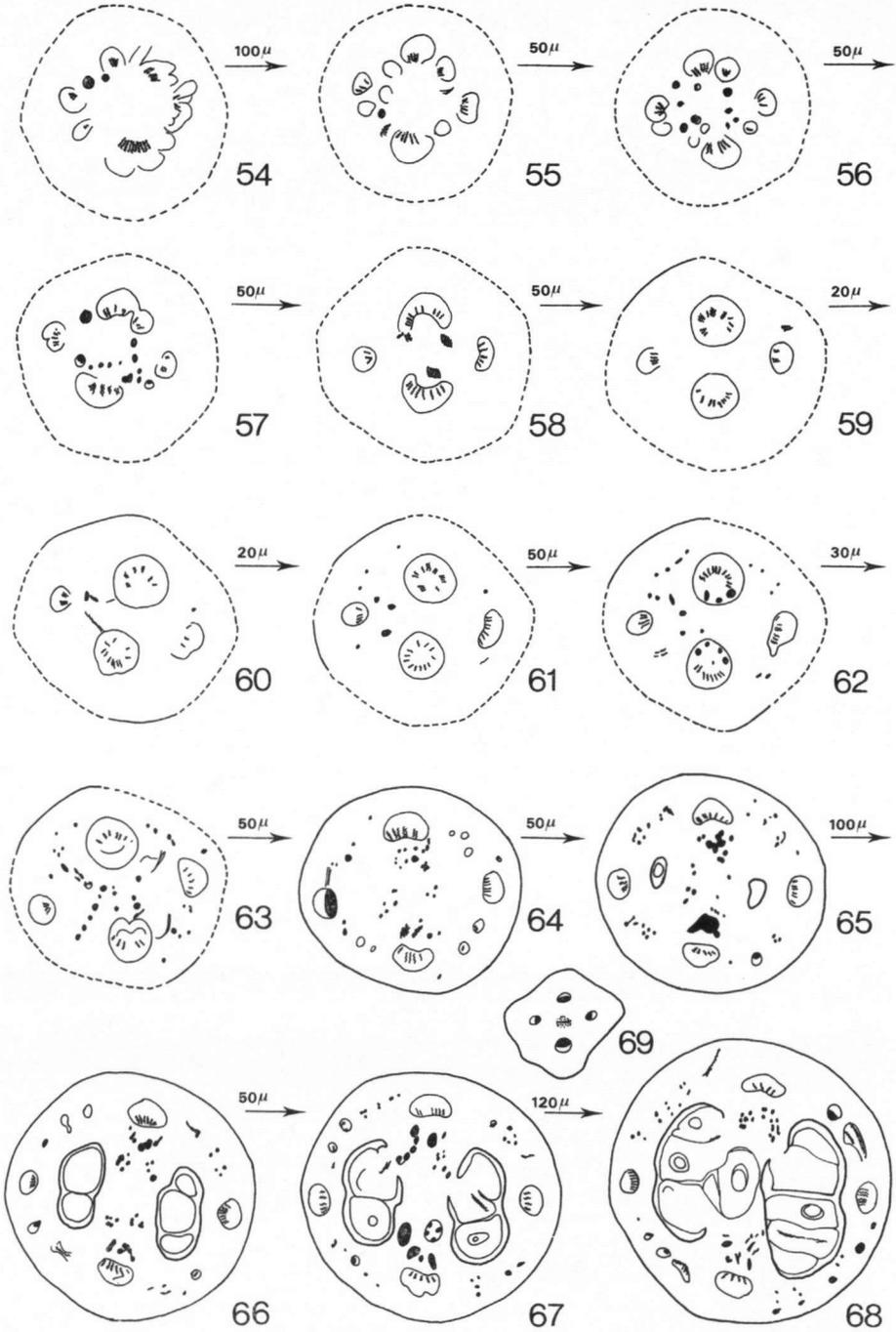
See figs. 46—53. The pistils differ from those of the preceding species, in that the ovules are inserted directly on the pistil wall. The pistils are sterile over a large proximal part. There are six vascular bundles in the pistil wall, three carpel dorsal bundles in the corners and three alternating bundles in the middle of the pistil sides. From the flanks of the alternating bundles portions become separated, invert, and abruptly turn inward as the supply of the ovules. The ovules are located on both sides of the radial planes of the alternating bundles, but some lower ones can be placed exactly in those radial planes. At levels above the tepals and the stamens, a floral stele is completely reconstituted. Also above the level of departure of the six pistil traces, the stele is reconstituted, tapers upwards, and ends. Correspondingly, the axis protrudes very shortly into the base of the locule. This pattern is unlike that reported hitherto in this study for other members of *Flacourtiaceae*. The locule narrows upwards into a central three-fluted styler canal filled with stigmatoid papillae; in the stigma it may become six-fluted. Along the styler canal the alternating bundles first divide collaterally, subsequently the division products divide frequently. Because also the dorsal bundles divide, a sheath of small bundles is formed which surrounds the styler cavity.

The ovules are anatropous and have two integuments; the micropyle is formed by the inner one. Both epidermides of both integuments are in a stage of special differentiation, those of the inner integument probably forming a pigment and sclereid layer. The large isodiametric cells of the outer epidermis of the outer integument form a pigmented layer, like in *Scottellia*.

The fruits and seeds are unknown.

LINDACKERIA DENTATA (OLIV.) GILG

See figs. 54—69. For a description of the species the reader is referred to Sleumer, 1974. The gynoecea have one locule with two parietal placentas which carry the ovules over



Lindackeria dentata — Figs. 54—69. Pistil at anthesis. Cross sections from base to style. 30 ×.

their whole surface. Downwards the pistil may have a two- or four loculed sterile base, upwards it has a central style canal.

The vascular stele toward the pistil gives off two carpel dorsal bundles (three-traced). In alternating radii two large parts of the stele are demarcated. The four diagonal parts in between proceed inwards and upwards, divide, form commissurals, and partly twist to form inverted parts of the two large stelar parts demarcated. In this way characteristically four major bundles can be distinguished, two carpel-dorsals and two alternating 'median lateral' (placental) concentric complexes. Slightly higher up the inverted parts of the concentric complexes give off small bundles which proceed inwards and form a complex pattern of small bundles in the centre which has connections with the numerous lateral carpel bundles leading to the spines on the wall. Also two small placental bundle complexes result in this way, from which the lowermost ovules are supplied. The remaining inverted part of the two concentric basal pistil bundles becomes separated from the outer part, and divides into the placental bundles leading upwards and which supply the higher placed ovules. Lower placed ovules may have also a double-based vascular supply.

The anthers have four irregularly but distinctly septate pollen sacs, like in *Caloncoba echinata* (Endress & Voser 1975). There is no horizontal correlation in the position of the compartments of the sporangia within one anther. Each theca opens by a single continuous slit.

The anatropous ovules have two integuments. At anthesis the micropyle is formed by both integuments, but prior to anthesis the inner integument does not reach over the top of the nucellus. The outer integument forms a moderately thick parenchymatous outer part of the testa, which does not become juicy, in contrast to the sarcotestae in *Oncoba*, *Caloncoba* and *Camptostylus*. The inner epidermis of the inner integument develops into a pigment layer, the outer epidermis forms a multi-layered smooth sclereid layer. The seed is completed with a large arilloid (*sensu* Van der Pijl 1972) developing from the raphe. Like in *Caloncoba* and *Camptostylus* an absorbing cavity is formed in the chalaza, surrounded by a whorl of chalazal vascular bundles. Likewise there is no endosperm formation in this cavity.

PETERODENDRON OVATUM (SLEUMER) SLEUMER

The structure of the pistil is in some respects unlike that in the *Oncobeeae* as described above. Transverse sections from below upwards (figs. 32—36) reveal that the ovary is two-celled below and one-celled above. At the very base and in the top region the ovary is sterile. At mid-level the central column bears ovules, a situation approached in *Lindackeria*. Upwards it splits into two parietal placentas which terminate into ovules. Distally the sterile carpel margins approach centrally to form a stylar canal. The 'median lateral' vascular bundles are not accompanied by inverted placental strands.

The ovules are anatropous. At anthesis both integuments do not reach over the top of the large nucellus.

CONCLUSION

Summarising my findings may be described as follows. The pistil grows as a lobed — stigmatic — and a septated — placental — cupule (in *Oncoba*). The placentas bear the ovules on their surface everywhere. There is a transition between parietal and basal placentation, reflected in anatomy. Often basal concentric complexes of alternating vascular bundles in the pistil base give rise to inverted placental traces. Lowermost ovules may receive

vascular traces separately in several ways, either as sets from the residual stele, or as traces from the minor pistil wall bundles, or as parts from low down the normal placental traces.

The ovules are anatropous, in *Oncoba* atropous. The embryosac may form extensions upwards into the nucellar cap (*Oncoba*), or downwards into the chalaza accompanied by a ring or cup of tracheids (*Caloncoba*, *Camptostylus*, *Lindackeria*). The seeds are tegmic (Corner, 1976) by differentiation of the outer epidermis and the inner epidermis of the inner integument into a sclereid and a pigment layer respectively. The sclereid layer may comprise one (*Oncoba*) or more cell layers. The sarcotesta, formed by the outer integument, may be thin or thick, or partially thick in the case of the raphal ariloid in *Lindackeria*. Brachysclereids are around the ectostome, and a pigment layer fences off the seed on the chalazal side. There are distal lobes on the integuments in *Caloncoba* and *Camptostylus*. A 'ramification' of the styler canals and a late extra growth marks the stigma in *Oncoba*.

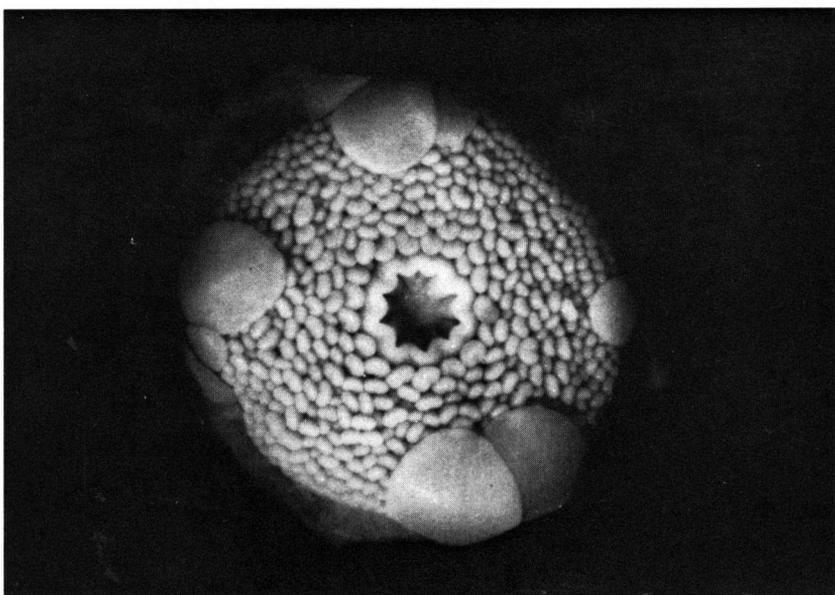
In the descriptions above I have tried to take an unbiased view by using 'neutral' developmental terms, so as to leave out theoretical implications, especially those of the carpel theory. A similar view was recently advocated by Sattler (1973, 1974). The placental regions neither by their ontogeny nor by their anatomy betray their 'typical nature' of fused carpellary margins. Nevertheless, they are continuous with the margins of the stigmatic lobes above. In the initial stages of development of *Oncoba* (fig. 1, photo 1) it is impossible to draw a sharp line between the growing apex of the pistil itself and those regions of the sinuate girdling meristematic wall that are to give rise to the ovules. This fact is reflected in the diffuse position of the placental vascular traces. We are dealing with a basal-parietal placentation. In general one may ask whether it is useful to attempt to draw a clear demarcation between axis and leaf (appendage, meristematic wall) on a growing apex. From the morphogenetic point of view the sharp distinction, derived from the field of the morphology of mature stages only, seems less sharp and less meaningful.

It is possible to regard the sinuate girdling meristem as the result of a fusion (cf. Corner, 1958; Stebbins, 1974). Horseshoe-shaped primordia — whether bract or carpel is at present immaterial — touch laterally and fuse gradually, but the process has never been actually demonstrated!. The growth that follows is possibly at first apical, but later mainly intercalary. The intercalary growth does not take place by a definitely localized meristem, but by the overall formation of recognisable cell families in such a way that an ovarian cup results. The main vascular bundle pattern, derived from the traces towards the initial primordia, is not disturbed by the fusion and the subsequent growth of the cup. However, a secondary pattern or mass of vascular bundles may be consequent upon the growth of the cup in width and thickness. The — idealistic — distinction of marginal bract regions in the cup is not possible. The transition of the ovary cup and the growing pistil apex may become gradual. Placental fields develop on those parts of the sinuate cup which are closest to the apex. This may be called 'cupular placentation'. A possible extension of the placentation to free (carpel) margins is not present in this group of plants.

In conclusion a 'neutral' descriptive terminology, devoid of theoretical implications or bias is preferred. The pistil of the *Flacourtiaceae* studied may then be described as a lobed stigmatic ovarian cupule with basal-parietal placental fields on the inside ridges alternating with the lobes. This leaves room for a 'heterotopy', or rather plasticity, of the origin of the placentas and ovules. This approach makes it also possible to relate *Scyphostegia* with its many strictly basal ovules with the *Flacourtiaceae* (Van Heel, 1967).

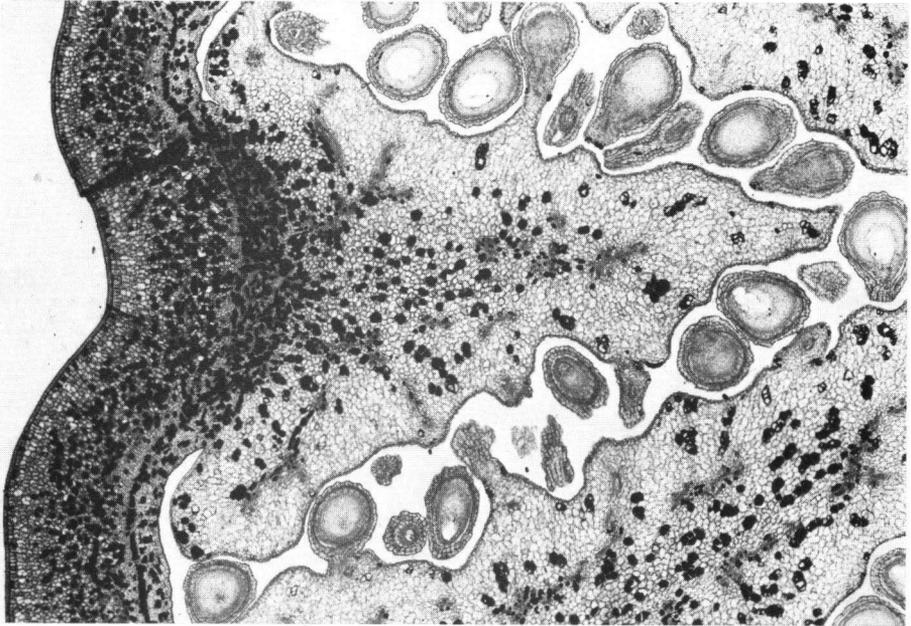


1

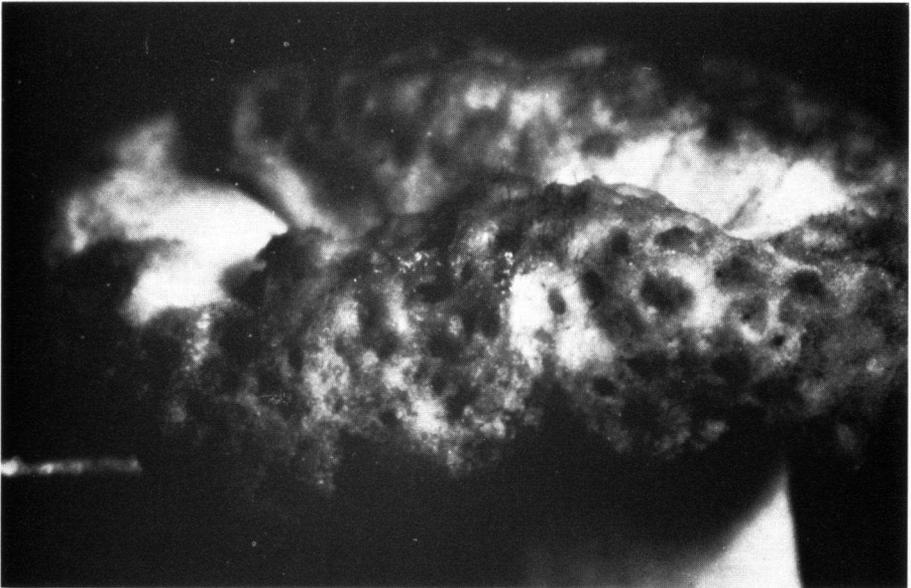


2

Oncoba spinosa — Photo 1. Early stage of development of the pistil, corresponding to fig. 1. — Photo 2. Appearance of ovule primordia, corresponding to fig. 2.



3

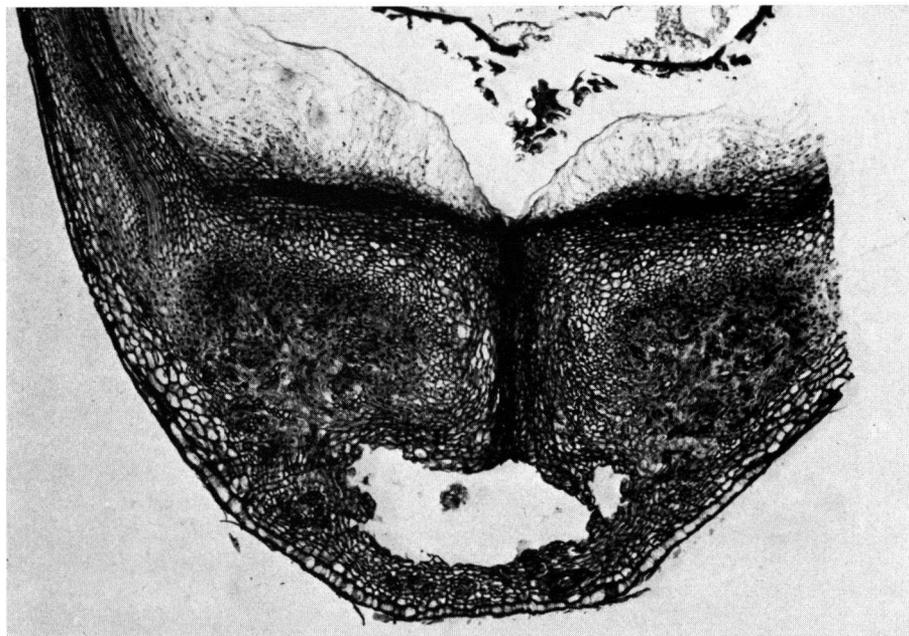


4

Oncoba spinosa — Photo 3. Placental septa, cross section. — Photo 4. Subsidiary styler canals issuing on stigma.



5



6

Caloncoba glauca — Photo 5. Top of young seed, longitudinal section. — Photo 6. Base of young seed, longitudinal section.

REFERENCES

- CORNER, E. J. H. 1958. Transference of function. *J. Linn. Soc. London, Zool.*, 44, 295 and *Bot.* 56, 365: 33—40.
- , 1976. *The seeds of Dicotyledons*. Vols. I, II. Cambridge Univ. Press.
- CUSICK, F. 1966. On phylogenetic and ontogenetic fusions. In: Cutter, E. ed. *Trends in Plant Morphogenesis*. Longmans, Green & Co.
- ENDRESS, P. & P. VOSER. 1975. Zur Androeciumanlage und Antherenentwicklung bei *Caloncoba echinata* (Flacourtiaceae). *Plant Syst. Evol.* 123: 241—253.
- EVERARD, B. & B. D. MORLEY. 1970. *Wild flowers of the world*.
- HACCIUS, B. & N. N. BHANDARI. 1975. Delayed histogen differentiation as a common primitive character in all types of non-zygotic embryos. *Phytomorphology* 25: 91—94.
- HAKKI, M. J. 1974. Embryologische und morphologische Beobachtungen an *Succowia balearica* (L.) Medik. (Brassicaceae). *Bot. Jahrb. Syst.* 94: 360—382.
- HEEL, W. A. VAN. 1967. Anatomical and ontogenetic investigations on the morphology of the flowers and the fruit of *Scyphostegia borneensis* Stapf (Scyphostegiaceae). *Blumea* 15: 107—125.
- , 1970. Distally lobed integuments in some Angiosperm ovules. *Blumea* 18: 67—70.
- , 1973. Flowers and fruits in Flacourtiaceae I. *Scaphocalyx spathacea* Ridl. *Blumea* 21: 259—279.
- JOHRI, B. M. 1963. Female gametophyte. In Maheshwari, P. ed., *Rec. Adv. Embryol. Angiosperms*. Delhi.
- MAHESHWARI, P. 1950. *Embryology of Angiosperms*.
- MARTENS, P. 1974. La cupule trachéidale. *Recherches sur Welwitschia mirabilis* VI. *La Cellule* 70: 261—292. (*Trav. biol. Inst. Carnoy* nr. 111).
- PIJL, L. VAN DER. 1972. *Principles of Dispersal in Higher Plants*. Springer.
- SATTLER, R. 1973. *Organogenesis of flowers*. A photographic text-atlas.
- , 1974. A new approach to gynoeical morphology. *Phytomorphology* 24: 22—34.
- SLEUMER, H. 1974. Revision der Gattung *Caloncoba* Gilg (Flacourtiaceae). *Bot. Jahrb. Syst.* 94: 120—138.
- , 1974. Revision der Gattung *Camptostylus* Gilg (Flacourtiaceae). *Bot. Jahrb. Syst.* 94: 283—288.
- , 1974. De Afrikanischen Arten der Gattung *Lindackeria* Presl (Flacourtiaceae). *Bot. Jahrb. Syst.* 94: 311—326.
- , 1975. Flacourtiaceae. In: *Flora of tropical East Africa*.
- STEBBINS, G. L. 1974. Building bridges between evolutionary disciplines. *Taxon* 23: 11—20.
- VAUGHAN, J. G. 1970. *The structure and utilization of oil seeds*. Chapman & Hall.