

ANATOMICAL AND ONTOGENETIC INVESTIGATIONS ON THE MORPHOLOGY OF THE FLOWERS AND THE FRUIT OF *SCYPHOSTEGIA BORNEENSIS* STAPF (SCYPHOSTEGIACEAE)

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ABSTRACT

New details could be derived from the study of fixed male and female flowers of *Scyphostegia borneensis* Stapf. Of prime importance among these is the exact structure of the female reproductive units. They correspond to what are generally recognized as ovules. These anatropous ovules have a constriction separating funicle and raphe, an aril (loid) of mixed character, a distal integumental extension, and a five-lobed exostome. Their placentation is basal. Together, they are enclosed by an urceolate wall consisting of three-trace units which are apically stigmatic. These sterile units form septa growing downwards between the tips of the ovules, giving rise to locules which are open below. The morphological interest of some of these details was discussed. The embryosack development could be followed. The fruit appeared to be a fleshy capsule.

The striking similarity with certain formations in the *Monimiaceae* is not based on affinity. As to the above characters the alleged affinity with the *Flacourtiaceae* could not be checked because comparable characters in that family have never been studied. However, there is a correspondence with such details known in the *Tamaricaceae*. Moreover, in the *Tamaricaceae* the placentation is intermediate between basal and parietal. This was considered to favour the inclusion of the *Scyphostegiaceae* in the *Parietales*. Of all the *Parietales* families they must be nearest to the *Flacourtiaceae*, as judged from external characters.

INTRODUCTION

Scyphostegia is a curious, endemic, monotypic genus from Borneo. Its affinity is an intriguing problem in plant taxonomy. In this paper it is tried to get nearer to a decision. The investigation was carried out on the instigation of Prof. Dr. C. G. G. J. van Steenis. For a full description the reader is referred to the original publication by Stapf (1894) and to Van Steenis (1957).

It is a small dioecious tree with alternate, simple, penninerved, dentate leaves with inconspicuous stipules. The inflorescences are racemi of spikes. The spikes are most remarkable because the axis bears a number of telescoped infundibuliform bracts. Each bract bears one flower in its axil. Only one flower at a time is expanded (fig. 2a). Both male and female flowers have six perianth segments. In addition the male flowers have three stubs — looking like glands — in front of the three inner perianth segments, and furthermore, in front of the three stubs, three stamens with bithecous, four-loculed, extrorse anthers with protruded connectives. The stamens are fused forming a column in the centre of the flower. The female flowers have the vexed urceolate structure, consisting of a wall crowned with a large recurved collar like a sessile stigma that leaves a minute opening in the centre. This structure encloses a single cell filled with many upright reproductive units, scaly at the base, that are inserted on a slightly raised bottom.

HISTORY OF CLASSIFICATION

Stapf (1894) placed *Scyphostegia* in the *Monimiaceae*. He derived the urceolate female structure from the 'torus more or less crowned with perianth parts' in certain *Monimiaceae*.

According to him the reproductive units are stalked carpels with an involucre of emergences at the base. This involucre is not a perianth like in the *Moraceae*, but is rather comparable with protrusions of the torus between the carpels in the *Monimiaceae*.

Perkins and Gilg (1901) and Perkins (1925), monographing the *Monimiaceae*, excluded *Scyphostegia* from this family because of 1) the spikes with telescoping bracts, 2) the tepals down on the receptacle, 3) the absence of etherial oil cells in the leaves, 4) the scales at the base of the carpels.

Hutchinson (1926) established the family *Scyphostegiaceae*, which he included in the *Urticales* near to the *Moraceae*, accepting the female flower to be fig-like. However, in 1959, basing himself on essentially the same description, he placed the family in the *Celastrales*. In his opinion the reproductive units are stipitate mono-ovulate carpels with three hyaline receptacular lobules at the base and with a terminal stigma. Numerous free carpels are enclosed by a fleshy disk. Also in the *Capusiaceae* (*Celastrales*) the fruit is enclosed by an enlarged disk. Thus Hutchinson changed his mind from inflorescence to flower.

Baehni (1937, 1938) thought that female flowers, not inflorescences, must correspond with male flowers. Therefore — and for some other reasons — he rejected the inclusion of *Scyphostegia* in the *Urticales* by Hutchinson. The stubs in the male flowers represent petals, the female urceolate structure a corolla. Stipitate carpels are surrounded at the base by a whorl of non-vascularised trichomes of epidermal origin. The genus should not be included in the *Monimiaceae* because of 1) the small number of stamens, and 2) the dehiscence of the thecae being neither transversal nor valvate. Yet it cannot be very far from the *Monimiaceae*.

Money, Bailey, and Swamy (1950) added some arguments to those of Perkins and Gilg in order to remove *Scyphostegia* from the *Monimiaceae*. *Scyphostegia* has 1) trilacunar nodes, 2) large druses and crystal cells in the leaves, 3) tricolpate pollen, 4) stipules. *Monimiaceae* have unilacunar nodes, no large druses and crystal cells, 2(—3) sulcate pollen, and no stipules.

Swamy (1953) published a valuable anatomical study on *Scyphostegia*, using herbarium-material. As to the male flower Swamy remarked that the stub-like structures must be related not to the perianth parts, but rather to the stamens, because stubs and stamens are supplied by common vascular cords. The stubs cannot be remnant stamens, however, because they are situated in the radii of the extant stamens. As a hypothesis it was stated that the stubs could represent the two marginal parts of extrorse foliar microsporophylls that separated, bent outwards, and fused together.

For the female flower Swamy presented new details together with a corresponding dissimilar interpretation. From prefertilization stages it became clear that the reproductive units are unmistakably bitegmic ovules. Both integuments form the micropyle; they are unvascularised. The funiculus forms a kind of pedestal. Later, this part sends out a whorl of spongy parenchymatous lobes towards the chalazal end. This outgrowth is carried with by the seed. There is a chalazal protuberance, not a style. Swamy gave a convincing figure of a by all means quite normal anatropous ovule with a raphe bundle. The endosperm is cellular. He furthermore gave a description of the gynoecium wall, which forms a berry later on. Its mouth is lined with stigmatic tissue. The urceolate structure was thought to consist of 8—12 carpels, judged from the number of ridges on the deflexed stigma and the number of main vascular bundles. Of course in this interpretation the basal placentation is aberrant. Therefore it was assumed that an originally parietal placentation receded centripetally, retaining the centrifugal development of the ovules, and that the marginal carpellary bundles receded in conformity. The *Scypho-*

stegiaceae are a monotypic family neither related with the *Urticales*, nor with the *Monimiaceae*. They do not even stand in the *Ranales*.

Metcalf (1956), who on request of Van Steenis examined the anatomy, found two more characters on the ground of which *Scyphostegia* could be excluded from the *Monimiaceae*, namely the paracytic stomata and uniseriate rays. He listed eight vegetative anatomical characters, the combination of which is common to *Scyphostegia* and certain *Flacourtiaceae*. From this he concluded to a possible, though not close, relationship with the *Flacourtiaceae*. With this Metcalfe offered a quite new outlook on the affinity of the genus.

Van Steenis (1957), in his description of *Scyphostegia* in the Flora Malesiana, accepted an urceolate ovary containing ovules. The seeds are surrounded at their base by lamellae of placental origin. He was convinced by the results of both Swamy and Metcalfe. Moreover, in his opinion a combination of 'distichous crenate leaves with stipules, dioecious, trimerous flowers with a deepened receptacle, a unilocular ovary with parietal ovules and a sessile stigma, connate stamens and extrastaminal disk glands fits excellently with *Flacourtiaceae*.'

Melchior (1964) also put his faith in Metcalfe and placed the *Scyphostegiaceae* near the *Flacourtiaceae*. Incorrectly he cited Van Steenis as well as Swamy for holding an affinity with the *Monimiaceae* and the *Moraceae* respectively.

In three subsequent papers Croizat (1960, 1964 ed., 1962) widely discussed *Scyphostegia borneensis*, which he called one of the world's most striking and significant monotypes. It is a limit-case, a nascent structure developing in between two conventionally definable extremes, viz. ovule and ovary. One morphogeny underlies many morphologies: the building of a system of scales or enations around a nucellus, the ovule becoming an ovary. This is accompanied by a transference of the pollen bearing function to the outer envelopes. As a consequence Croizat thought that the systematic position of *Scyphostegia* is intermediate between the *Berberidaceae/Flacourtiaceae* on one hand, the *Moraceae/Monimiaceae* on the other.

NEW MORPHOLOGICAL INVESTIGATIONS

THE FEMALE FLOWER

The reproductive unit.

This unit most approximates what every botanist would describe as an anatropous, crassinucellate, bitegmatic ovule (fig. 5). It has a raphe vascular bundle which, when at the chalaza turning towards the nucellus, spreads into a small stele with patches of inverted medullary vascular tissue (figs. 1b and 8). Vascular bundles are absent in the integuments and in the nucellus. Both integuments are inserted below the nucellar base; they are appressed. Both take part in the micropyle formation, endo- and exostome being often not in line. The endostome is slightly prolonged on its adaxial side. Towards the seed-stage additional growth makes endo- and exostome no longer easily recognizable. The ovules cover the bottom of the pistil without any pattern (fig. 1a). However, it is noteworthy that all ovules are directed towards the centre with their raphe-sides (fig. 7m). The xylem of all collateral raphe bundles is directed away from the centre. The appearance of the ovule primordia on the floral apex takes place in a strictly centrifugal sequence.

Most probably a single archesporic cell is formed in each nucellus. In several preparations this cell was seen to give rise to a linear tetrad of spores, the chalazal one of which functions as the embryosack mothercell. Other preparations were more suggestive

of a tetra- or bisporic development. The sac when completed is eight-nucleate with an egg-apparatus, two polar and three antipodal cells (fig. 5c). Thus, according to the scheme, *Scyphostegia* follows the Polygonum-type of embryosack formation, save for some variation. During development a conspicuous nucellar cap (fig. 10) is formed by periclinal divisions in the epiderm of the upper half of the nucellus. Radiating alignments

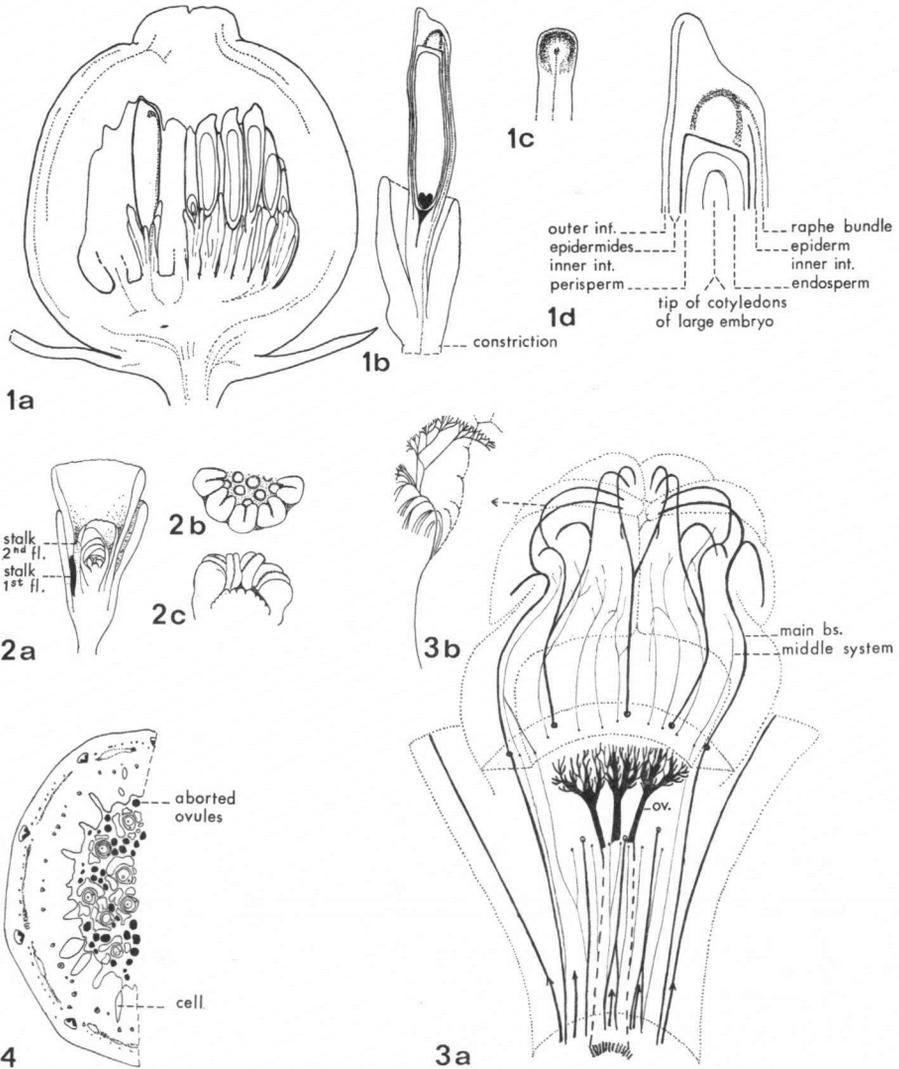


Fig. 1a. Fruit before opening, l.s. (2.5 ×), b. one of the young seeds with small embryo, l.s. (5 ×), c. raphe side tip of seed, s.v., d. details. — Fig. 2a. Female inflorescence with third flower, fourth floral primordium behind the third, l.s. (2.5 ×), b. primordial female flower, s.v. (17 ×), c. half of another primordial female flower (17 ×). — Fig. 3a. Cleaned half of young female flower showing vascular bundles, schematically, b. detail. — Fig. 4. Wall of female flower showing irregular inward protrusions.

of cells are the result. From below this cap is continuously being 'absorbed' by the growing embryosack. However, it keeps on restoring itself by the periclinal divisions. At about the four-nucleate stage the embryosack starts 'absorbing' the cap. Before that stage it 'absorbs' hypodermic cell-layers which also originated by additional divisions. At mature embryosack stage the cap counts mostly four layers of cells. Finally, in the ripe seed, the nucellar cap still persists.

Since in different fruits ovules with mature embryosacks can be found of very different size, it is suggested that the embryosack can prolong its mature state during a certain time. Nevertheless many ovules are not fertilized (fig. 4). Usually the peripheral ones wither. Those which do become fertilized form a free nuclear endosperm and a somewhat delayed zygote (fig. 5d). In vigorous young fruits the funicles, the distal region of the inner integument, and the endosperm may be light green, the outer integument light brownish.

During the growth of the embryosack, chiefly after fertilization, the nucellar tissue is constantly being absorbed by the sac (fig. 10). However, since divisions take place in every direction, it is replaced by new tissue. Yet the nucellus loses ground, and in mature seeds there is left only a thin irregular sheath of one or two cell-layers lining the testa (figs. 1b, d and 9). As said above the cap persists too. The conclusion is that the nucellus forms a definite nutritive tissue as a whole and particularly by its cap. It is a transient perisperm. Sooner or later, probably depending on the time of fertilization, the endosperm changes from free-nuclear to cellular (fig. 9), tending to form radial rows of cells. It surrounds a dicotyledonous, white, rectilinear embryo that may be large or small, presumably also depending on the time of fertilization.

Developmental series show that the outer integument is not specially adapted for its function as a layer of the testa. The cells of the outer epiderm may appear somewhat inflated. On the other hand the inner integument shows two important changes (figs. 1d and 9). First the walls of the cells of its outer epiderm are heavily lignified and the cells become tubiform, probably by the breakdown of transverse walls. Second the cells of the inner epiderm develop a special contents, staining deeply red with saffranin, without nuclei. This adaptation also runs over the nucellar base (fig. 1d), connecting the inner epiderm by a transverse plate. By this layer the whole nucellus with its embryosack is encased. Except distally both integuments have only 3—4 cell layers. Distally both integuments increase in thickness surrounding the micropyle. The so-called stipe of the ripe seed is formed by secondary extension and growth of the ovule itself, namely of its basal raphe-side region, and of the distal parts of the integuments. The mesophyll of the inner integument may become strongly lignified.

So far features are not uncommon. However, the ovules do show some remarkable characters, namely a pedestal funicle, an aril(loid), a protuberance on the chalazal side, and a five-lobed exostome.

During development (fig. 5b) the funicle forms a kind of pedestal on which the ovule is placed. This is caused by a circular transverse constriction developing just below the level of the knob of the outer integument (figs. 5c, d). There are no special cellular details marking this constriction level. It is assumed that at this constriction the seed will be abscised (fig. 1a, b). However, stages showing this were lacking in my material.

Right above this constriction there is a circular obliquely transverse region of the ovule which forms an aril(loid). This structure surrounds the basal half of the ovule like a fringed collar (fig. 1b). Studying its development we see that the first divisions occur on the adaxial raphe side only (figs. 5d, 6), and that afterwards they spread towards

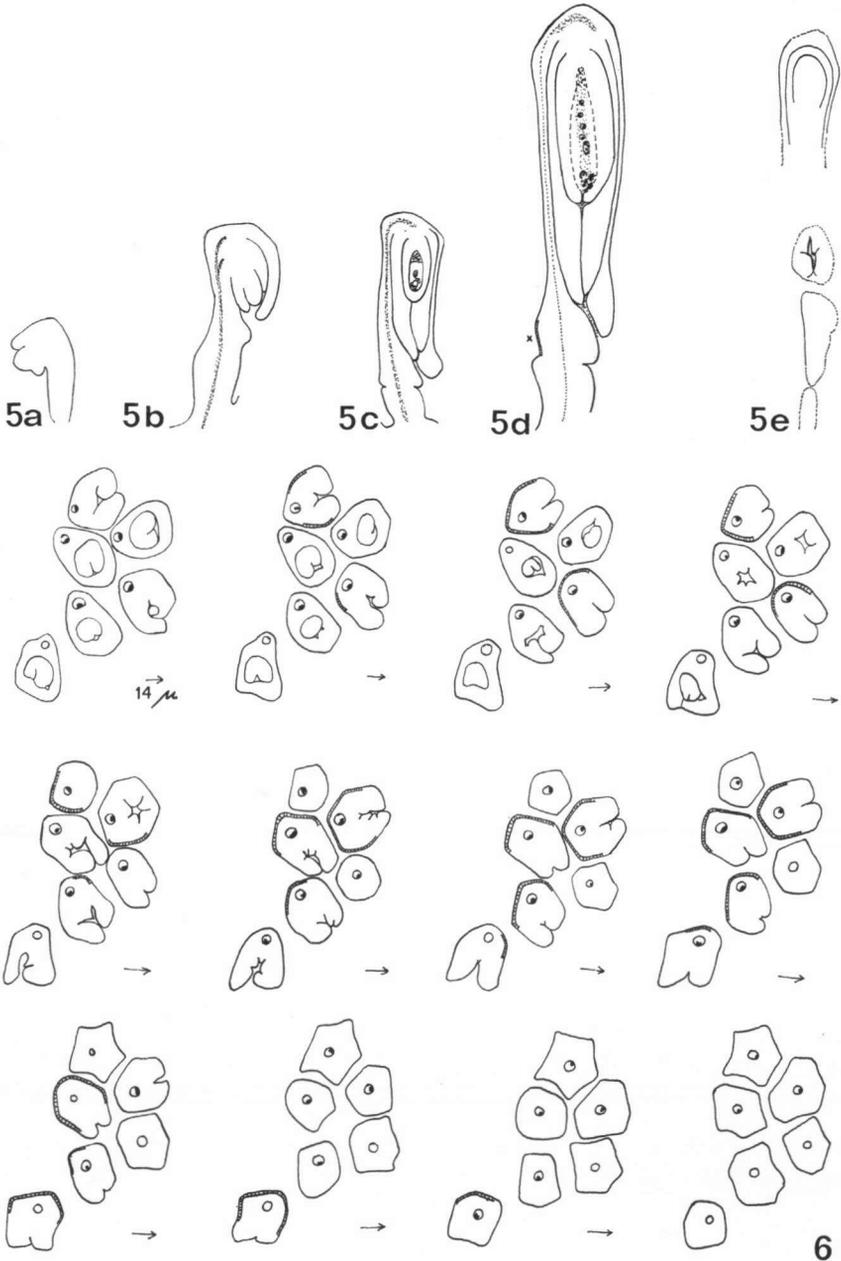


Fig. 5a—d. Ovules, l.s.; meristem of arilloid at ×; a. initial development of integuments (70 ×), b. archesporic cell stage (70 ×), c. embryo sac completed (70 ×), d. first formation of nuclear endosperm (the nuclei are given as if in one plane, in reality they are distributed over $5 \times 7 \mu$; 35 ×), e. same stage as d; tangential section showing lobed exostome. — Fig. 6. Series of c.s. through 6 ovules at micropyle level (17 ×). Developmental stage same as in fig. 5d. Note lobed exostomes.

the sides of the exostome (fig. 11) and above it. A ring of tissue is formed that in some places becomes thicker than in others. This is caused by periclinal epidermal divisions in the first place, accompanied by subdermal ones. Somewhat later the thicker regions grow upwards as lobes, this time chiefly by hypodermal periclinal divisions. First there are three lobes, a smaller median adaxial one and two larger lateral-adaxial or lateral ones. Next two further lobes are formed at the sides of the exostome, not as an apical prolongation of the outer integument but like an accessory lateral formation of its distal region. This pattern of lobing can only be observed in definite early stages of aril(loid) formation. Immediately afterwards, lobing becomes irregular, especially so above the exostome. The minute region below the exostome takes hardly any part in the thickening. Below the constriction the funicle has no share at all in the aril(loid) formation; it grows slowly in thickness, chiefly by hypodermal periclinal divisions, and becomes polygonal in cross-section. Its epidermal cells may inflate, burst, and free their contents into the crevices separating the ovules. The aril(loid) has a densely homogeneous parenchymatic tissue, strongly cutinized. However, in mature but still unopened fruits in herbarium material (*J. & M. S. Clemens 26062; Nieuwenhuis 1306*) the needle-like bases of the seeds are surrounded by membranaceous lamellae, irregularly longitudinally fused. Evidently this membranaceous character is an effect of drying, whereas soaking does not recover the original condition. In material preserved in liquid the aril(loid) remains fleshy even in the opened fruit. It appears that the growth of the aril(loid) is released to a good extent only after fertilization (fig. 5d).

Still later in appearance is a purely parenchymatic protuberance at the chalazal end (fig. 1b, c, d). This structure is somewhat depressed in the median line on the raphe side. It is really a boat-shaped or obliquely cylindrical protuberance, longest in the median abaxial line, gradually becoming shorter towards the adaxial side or even not reaching there. If the protuberance does not reach the adaxial region, the raphe may appear like a small knob or ridge on the inside of the protuberance. The protuberance is parenchymatic, it is sometimes green in its subperipheral tissue. The cell-layers of the outer integument and the outer lignified cell-layer of the inner integument can be seen to extend directly into it. Part of the ovular tissue between the ascending and descending vascular bundle is also extending and it shows a prolongation of the lignified layer of the inner integument on the adaxial side. Judged by the affiliation of cells the protuberance is a late abaxial extension of the two integuments, which grows sideways and sometimes even overgrows the raphe side, causing there a small pit. The lignified layer makes the protuberance hard on the abaxial surface. I also found seeds with still more lignified cells joining the lignified layer on the inside. However, the adaxial inner surface remains soft even in ripe seeds, so that the tissue could be eaten there by animals. Of course also the fleshy aril(loid) is edible. The protuberance bears a number of soft unicellular hairs like the whole testa. It has no stigmatic surface. In its curve towards the nucellus the raphe bundle may show some irregular tiny spears into the direction of the chalazal protuberance.

In a series of cross-sections the inside of the exostome proves to be clearly five-lobed (fig. 6 and 11), to wit by one lobe at the raphe side and two pairs of lateral lobes. The lateral lobes on the raphe side are often not well developed, they may be shorter. In a later stage the lobing is no longer evident.

The urceolate organ enveloping the ovules.

Very young stages, less than 1 mm across, present a not unusual picture. About ten horseshoe-shaped primordia are raised on a low circular wall (figs. 2b, c). They surround

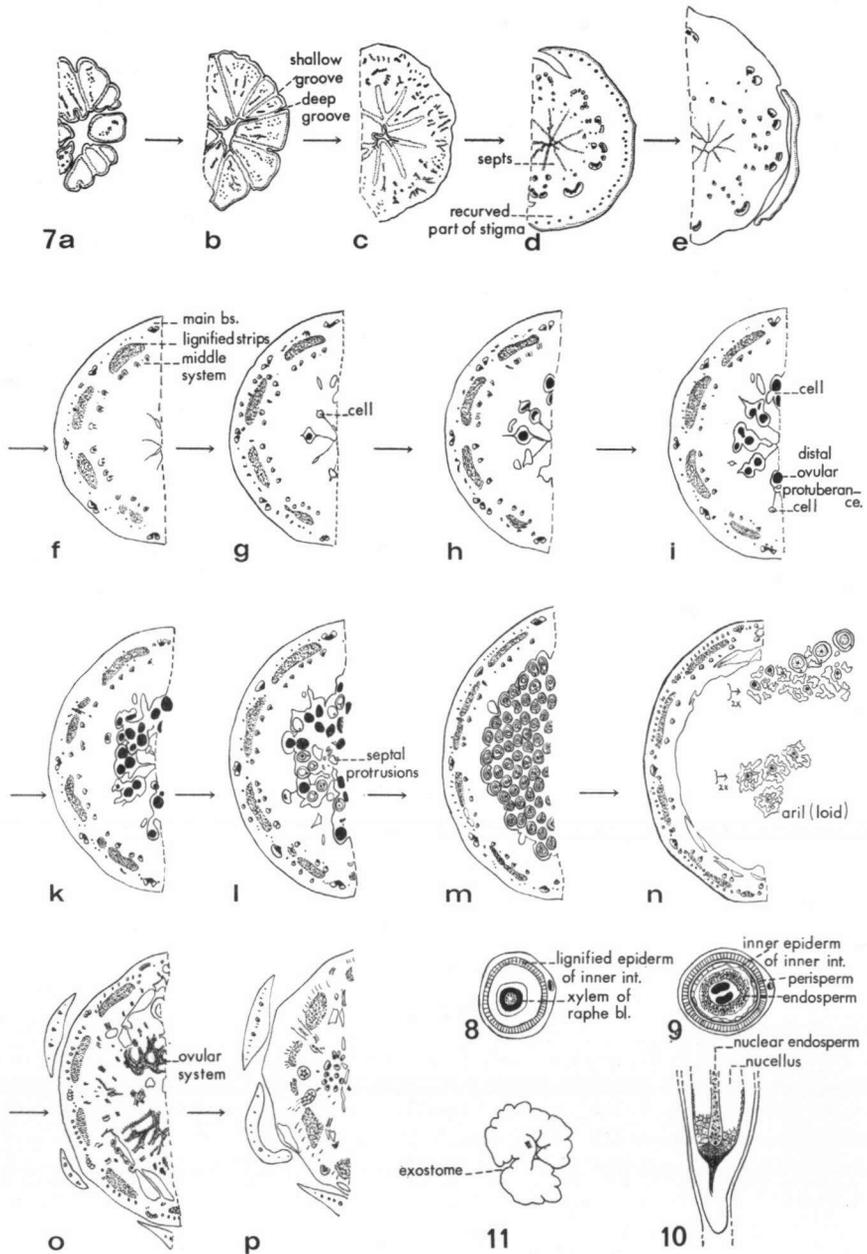


Fig. 7a—p. Cross-sections of young fruit of the stage of fig. 1 from the stigma downwards (a—e $\times 5$; f—p $2\frac{1}{2} \times$). — Fig. 8. Young seed of the stage of fig. 1b, l.s. at chalaza ($17 \times$). — Fig. 9. Ibidem, near micropyle, c.s. ($17 \times$). — Fig. 10. Ibidem, with very small embryo, l.s. ($17 \times$). — Fig. 11. Exostome with aril(loid) formation, t.s. ($17 \times$).

a relatively early and large convex floral apex along its periphery. The apex is covered with centrifugally arising ovular initials. The primordia, growing over the floral apex, develop into a stigmatic part which is relatively large, at fertilization stage about half the size of the whole urceole. At this stage the whole structure is not more than $\frac{1}{2}$ cm across. It is only afterwards that an enormous growth seizes the underlying wall part, so that in the end the formerly stigmatic cap is placed like a small plug on top of the fruit (fig. 1a).

At anthesis the stigma looks chiefly like a collar curved outwards (figs. 3a, 7d), consisting of 9–13 radiating ridges (figs. 7b, 12b). However, it may be noted that, starting from the peripheral horseshoe-shaped primordia there is an important inward growth leading to the ultimate roofing of the whole floral apex, save for a small entrance. Moreover, there is a downward growth into the cavity with the young ovules (fig. 3a). Through this inward and downward growth septa are formed which can be located below the radiating ridges on the surface of the stigma. These septa are formed by the fused lateral parts of two originally free but adjoining horseshoe-shaped primordia. These parts come together near the centre and are appressed (fig. 7c, 12d). A faint shallow groove runs radially over each radiating stigmatic ridge (figs. 7a, b, 12b). They represent the outcome of the grooves separating the sides of the originally distinct primordia (fig. 2b). The radiating ridges on the surface and their underlying septa are separated by deep radial grooves which become narrower as the stigma grows older. The deep grooves represent the inside grooves originally enclosed by each horseshoe-shaped primordium (fig. 2b); they are absent in the most distal recurved region of the stigma. As a consequence, in transverse sections, the uppermost level of the stigma appears as 9–13 separate portions, each in two halves. Thus, if the terminology of carpels be accepted for the horseshoe-shaped primordia, the radiating ridges on the stigmatic surface may be called commissural (fig. 7d, e, 12e).

Though the septa of the stigmatic part are appressed, they may on a low level delimit cavities which, in cross-section, look like carpellary cells (figs. 7f–k, 12d–g), sometimes even with 'false' septa (fig. 7h). These cells are the result of the inward and downward growth of the septa between the distal tips of one or a few ovules. Lower down the septa recede, forming irregular protrusions (figs. 7i, 12h). The inside surface of the wall part of the urceole is lined with irregular ridges between the outer ovules (fig. 7m), sometimes its tissue may delimit cavities without enclosing ovules and without relation to any structure (fig. 4). In its lower part the wall is smoother. There are nowhere protrusions suggesting abortive ovules. The surface of the stigmatic part and the appressed surfaces of the septa are formed by 1–6 layers of small cells, the epidermal cells of which have a dense cytoplasm. This surface is assumed to be stigmatic.

As the fruit develops, the walls of parenchyma cells in definite regions are lignified (fig. 7l, 12g). These regions are 9–13 longitudinal subsurface strips, in line with the stigmatic ridges and between the main vascular bundles. From epibasal levels these strips reach to just below the stigmatic part. No doubt they have something to do with the opening of the capsule (fig. 13). The opening occurs by valves which recurve entirely, separating the halves of the double main vascular bundles. Each valve contains one of the lignified strips. The tips of the valves show some of the irregular septal outgrowths on the inside. The stigma is torn loose and adheres to one of the valve tips. In this way the seeds, inserted with their needle-like bases, provided with fleshy aril(loid)s and partly soft distal protuberances, are fully exposed.

In essentials the vascular bundle supply of the urceolate wall was described by Swamy. My observations agree with his. Since I can add some important details it seems the obvious way to present a full picture here.

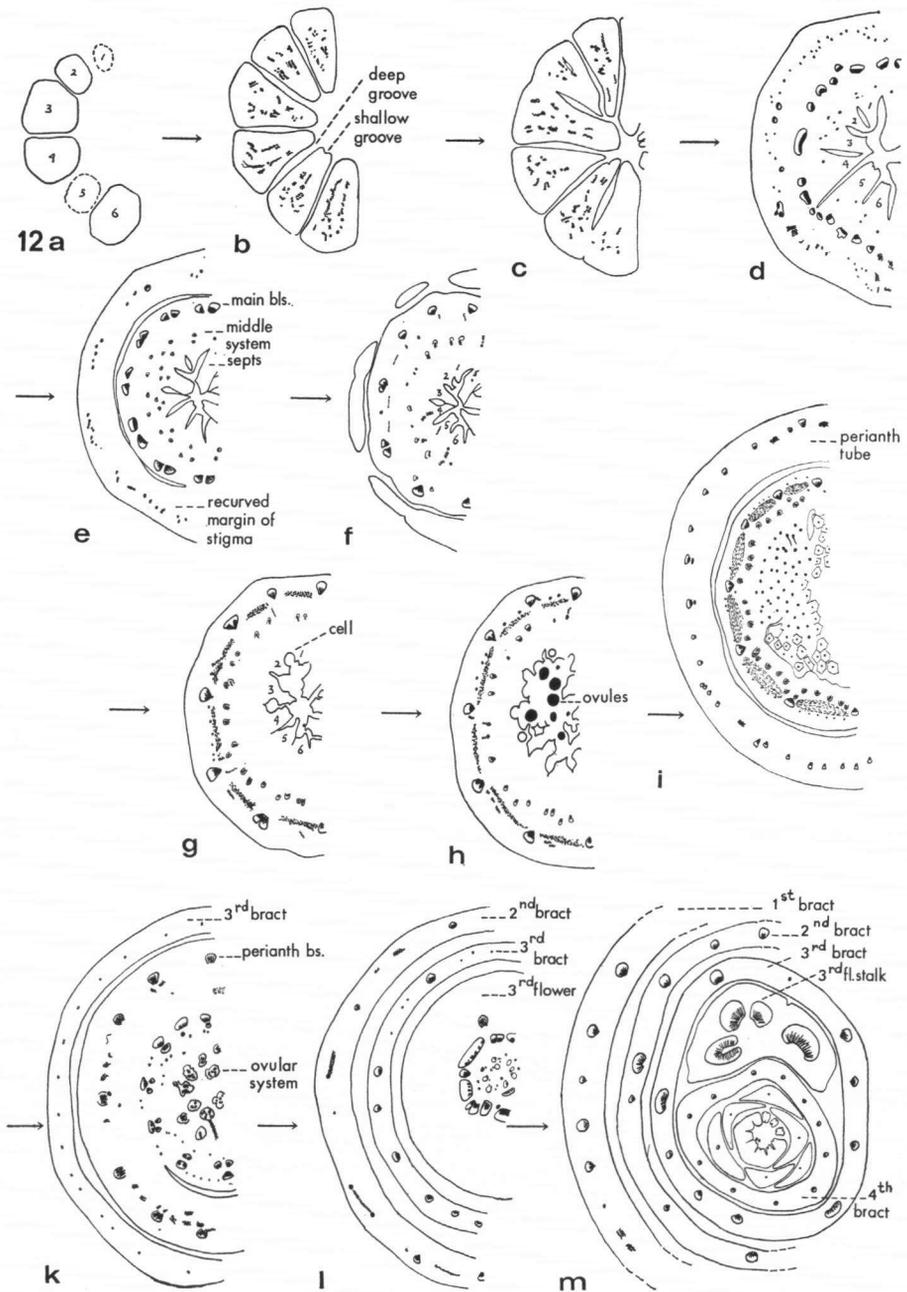


Fig. 12a—m. Downward cross-sections of the third female flower in an inflorescence at about the time of fertilization (a—i 9 ×; m 18 ×).

Three systems can be distinguished in the vascular bundle supply to the urceolate structure (fig. 3a). First is an independent system to the ovules, rooting at the common stele deep in the flower base. This system falls apart into five or fewer trunks of a histologically irregular structure. The trunks, during their upward course, ramify into ever smaller branches until ovule traces result. Anastomoses are frequent, also between branches deriving from adjacent trunks.

Second are 9—13 main vascular bundles (figs. 7f, 12e) passing from below upwards through the wall of the urceole just under its outer surface. They are either a direct continuation of stelar parts, quite independent of the ovular supply, or they are attached in a double or multiple way to the very base of perianth traces. Their location is important. They are situated in the same radii as are the deep grooves separating the radiating ridges or septa of the stigma (figs. 7e—k, 12e—h). As a consequence, they appear as 'dorsals' to the horseshoe-shaped primordia mentioned above. Their xylem portion is collaterally double. In the base of the stigma they are separated into two bundles side by side. These branches curve upwards and inwards towards the upper central parts of the stigma, to be precise: also slightly sideways, namely to the tips of two adjacent radial ridges of the stigma (fig. 3a). During this whole curving course each of the branches falls apart into smaller branches which recurve outwards (fig. 3b, 7d, 12d). The smallest branches become brush-shaped and anastomose beneath the stigmatic surface.

Third is a middle system which supplies the inside part of both wall and stigma (fig. 3a). In cross-section it is represented by tangential series of 3—6 normally oriented bundles separated by the radii of the main bundles in which they are absent (figs. 7f, 12g). The bundles of each set result from the ramification of 2—4 traces which are mainly attached to both basal flanks, with opposed xylem, of the main bundles, (figs. 3a, 12k). In later stages concentric bundles may be formed there (fig. 7p). Some others that happen to lie closer to the inner surface of the wall, are attached to the trunks belonging to the ovular system (fig. 3a).

On the level of the constricted part of the urceole anastomoses occur between the main bundles and the middle system bundles. In each series of middle system bundles the bundles may converge or come to an anastomosing end before they move into the stigma. Finally 1—3, frequently 2, bundles per series move into the stigma (figs. 3a, 12f), supplying there the innermost regions of the stigma which grew inwards and downwards over the ovule tips. Moving upwards into the stigma these bundles ramify into some short branchlets inwards and downwards (fig. 3a). In that way each series forms mostly two more or less reniform minor formations of tiny branchlets chiefly inwards, which can be compared with those formed chiefly outwards by the main bundles. In cross section, these branchlets come to lie in two more or less radial half-series on both sides of a groove separating two septa. They have opposed xylem parts. A well-known image is thus produced, be it with double 'dorsal' main bundles (figs. 7e, 12e).

Apart from these three systems, in later phases quite a number of more or less parallel small bundles occur just beneath the periphery of the wall between the main bundles (figs. 7f—o, 12h, i). Their xylem parts are directed towards the centre. They end blindly both upwards and downwards. Anastomoses occur among them, especially higher up. Sometimes they are connected with the main bundles. It is between these bundles 'looking like cortical bundles' and those of the middle system that the strips of lignified cells are situated.

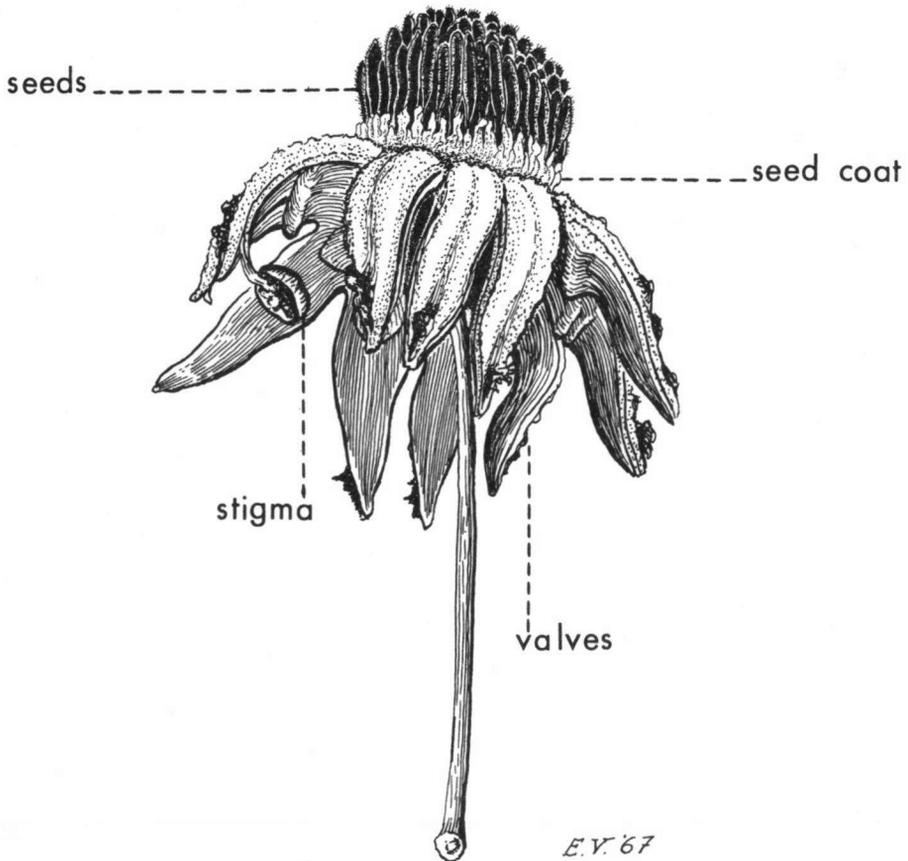


Fig. 13. Open fruit (2 ×). For this drawing I am indebted to our artist Mr. Ed Vijsma.

THE MALE FLOWERS

The central column consists of three extrorse, bithecous, four-loculed anthers and their filaments, adnate back to back. That this is so is corroborated by 1) the three sterile prolongations of the connectives which are distally free later on, 2) the three parts that can be distinguished in the column in a very young stage, 3) the three vascular bundles. The three stamens are situated in the same radii as the inner perigone-segments. The vascular bundle is exarch directly above the level of attachment, not endarch below and exarch above as Swamy mentioned. Half way the anther the bundle splits into two collateral halves, leaving some fading vascular tissue in the middle and sometimes slightly outwards. In the upper half of the anther the bundles are not exactly exarch. Their xylem shows an intermediate orientation, half way between a direction toward the periphery and towards the median plane of the anther.

Swamy reported a clear distinction between two circles of vascular bundles in the flower base, an outer for the perigone, an inner common supply for the stub-like 'glands' and the stamens. I am unable to corroborate this. I found the pattern to be rather variable.

The clearing by means of chloral-lactophenol, revealing the slightest lignification, showed the bases of the stamen traces, and still more so those of the stub-like structures, to be multiple or to be even attached in a diffuse way to the perigone traces. All bundles arise from the two traces in the ribbon-like pedicel. These flat pedicels are appressed between the next younger flowers and the tubular bracts (for the female counterparts see figs. 2a, 12m).

The stubs are variable in size and form. They are stained intensely. Their upper regions are covered with many anomocytic stomata, according to the descriptive terminology of Metcalfe. Therefore the histological features indicate a glandular function. In a well developed gland at the base the single vascular bundle is irregularly concentric. On moving upwards this bundle splits into a dense tangentially elongated system of minor bundles. Adaxial minor bundles tend to fade.

The pollen are about spherical, about 15μ , and tricolpate.

DISCUSSION

MORPHOLOGY

A summary together with a discussion of what is new in the above descriptions may follow here.

1) Both ontogeny and anatomy support the common opinion on the composition of the staminal column. A more precise account was presented on the exarch vascular bundles in the stamens. The extrorse and exarch characters find their counterparts in the ovular system (see 9).

2) That the stub-like structures in the male flowers are glandular can be confirmed from their anatomy. Neither anatomy nor ontogeny permits considering the stamens as prophylls to the radially constructed glands.

3) The so-called stalks, or stipitate bases of the carpels of some authors, or the needle-like bases of seeds of others, are formed by extreme post-fertilization extension of the basal raphe-side and the adjacent distal parts of the integuments of strongly anatropous ovules.

4) The 'emergences' at the base of the seed-stalks are not really inserted on the receptacle. They are separated from the receptacle by the pedestal-funicles. However, towards fruit maturation, the funicles become of small size as compared with the extended basal ovule parts. That is the reason why they were overlooked by Hutchinson and Van Steenis who both studied dried material. These authors considered the 'emergences' as hyaline receptacular lobes or scarious lamellae of placental origin.

5) During early ovule development a constriction is formed immediately below exostome level, leading to the pedalled appearance of the funicle. This level is assumed to function as an abscission level. It makes one think of similar structures in the pedicels of many flowers and in the stamens of *Euphorbia*.

6) The 'emergences', making a collar of homogeneously parenchymatic lobes, are not formed by the funicle, as Swamy reported. They are accessory post-fertilization formations of the basal raphe-side and the distal sides of the outer integument of the ovule. The collar must be understood as an aril(loid).

According to Pfeiffer (1891) Gaertner and Planchon have called arilli what is formed near the hilum and by the funicle, arilloid what is formed by the exostome. With respect to this hypothetical distinction there has been a discussion on the mace of *Myristica*. If the distinction is valid the mace would be a mixed structure. In my opinion the best study on the mace subject dates back to Voigt (1885). He found that the development

of the mace starts at the raphe side and from there spreads to the exostome side. First a superficial thickening is formed that later develops into a collar. Yet Voigt seems not certain whether in still younger stages than those studied by him a clear separation between aril and arilloid could not be demonstrated. Pfeiffer did not believe in this separation. On this issue a recent paper of Swamy (1964) is noteworthy. He stated for the aril(loid) of *Stemona* that, although initiated towards the free face of the funicle, the division activity gradually spreads in the antiraphe direction along the rim of the outer integument, finally affecting the extreme antiraphe point of the latter. Here also there is first a thickening, the edges of which are thrown into lobes. So there is a curious feature common to *Myristica*, *Stemona*, and *Scyphostegia*, namely a certain period of time during which the primary aril(loid) development spreads from the raphe towards the exostome side. However, a discontinuity in the course of this development has never been proven. In *Scyphostegia* too, I could not observe a separation at any time between an aril and an arilloid. Van der Pijl (1955) mentioned the same coincidence of the two categories for the *Bombacaceae*. Maybe that, on closer study, the 'mixed' aril could prove to be of more frequent occurrence. Evidently here lies a field for detailed ontogenetic research. For the present problem the investigation of some *Flacourtiaceae* with aril(loid)s could be elucidating. This will form part of my future study.

Of course the rating of the reproductive units as ovules — as structures like these are commonly called — provided with arilloids, arils, or both — as these are taken descriptively — does not mean that we are closer to an understanding of their nature. The regularity in the developmental course, mentioned above, and the pattern in the initial lobing in *Scyphostegia* are indicative of a not purely accessory nature. For these reasons the aril(loid) may be thought to represent — in these cases and probably in part only — a reduced structure in connection with the basal raphe region of the ovule. However, this does not affect taxonomy immediately.

7) The chalazal protuberance is not stigmatic, as was supposed by Hutchinson and others. Histologically this extension was shown to be a prolongation of the abaxial side of the integuments on the chalazal level. Since it arises a long time after fertilization, it simply cannot function in the capture of pollen. Nor does it show a stigmatic structure of cells. Chalazal or subchalazal extensions on seeds are not rare. It is my guess that they are not necessarily all of the same nature (see for instance Nast & Bailey, 1945). The exact histology of practically all of them needs further study.

8) The development of the convex floral apex takes place very early as compared with that of the enveloping pistillary parts. The ovules arise centrifugally, covering the apex without pattern. However they are all directed away from the centre of the apex, also with their xylem.

9) The embryosack development varies according to the Polygonum type. The endosperm is nuclear at first, but later changes into cellular. There remains a thin layer of nucellar perisperm lining the testa. Nucellar perisperm is of rare occurrence according to Maheshwari's text-book. A conspicuous nutritive function is exerted by an epidermal nucellar cap. This cap compensates its disorganisation below by continued periclinal division of its cells. The partaking of the integuments in the testa was followed in detail.

10) In young stages the exostome can be observed to be five-lobed.

De Haan (1920) reached the conclusion that in Pteridosperms and Gymnosperms the integuments are originally composed of units, the nature of which is still uncertain. This is corroborated by the distal lobing and the presence of separate vascular bundles corresponding with the lobe parts. That today this is generally recognized appears from a paper by Smith (1964). Smith demonstrated upward series of fossils in which the

original composition of units became increasingly obscure. In Angiosperms the evidence seems to be meagre. Nevertheless Warming (1878) cited a few examples in endo- as well as exostome, among them *Juglans*. Leroy (1955) described bilobed integuments in *Platycarya* (*Juglandaceae*); the integument would be composed of two units. Boesewinkel and Bouman (in press) demonstrated histogenetically that these two units arise as two separate primordia in *Juglans* and *Pterocarya* (notably also in flowers with a basal placentation). The lobing in the distal parts of the outer integument of *Scyphostegia* may mean another trace in Angiosperms of the originally multiple nature of the integuments. In *Scyphostegia* the lobing develops late, in contradistinction to the early development in *Juglans*.

11) The fruit is a fleshy capsule, not a berry. It has lignified (commissural) valves. In dehiscing the valves split the double main vascular bundles of the pistil wall into two halves.

12) Initial stages of the pistil wall show about ten horseshoe-shaped primordia which will develop into the sessile stigma. Basally the primordia are fused, developing into the pistil wall. The stigma has a surface of commissural radial ridges. Faint radial grooves over these ridges demarcate the original primordia. The adjacent halves of two neighbouring radial ridges are formed by the sides of the original primordia. The outcome of each primordium is considered as a unit of the pistil, with the restriction that these units do not bear ovules. Apically the units grow down between the tips of the ovules by means of septa, forming cells that are open basally. The units are supplied by the branching of a triple vascular trace. A full picture of this branching was presented. Their middle vascular bundles — the main vascular bundles of the pistil wall — are double. The lateral traces form two sets of bundles with opposing xylem in the sides of the units.

Though in itself the term carpel could serve as a convenient tool for description, I will refrain from calling the wall units carpels, in order not to imply that they could be freely compared with the carpels in the *Ranales*, or that they, although foliar, could be compared with foliage leaves. It is obvious that *Scyphostegia* has no affinity with the *Ranales*. Comparisons should be made only within well-established groups. As long as we are still in the dark on almost every morphological detail of important groups, as there are the *Monimiaceae* or the *Flacourtiaceae*, it is preferable to wait until the morphology of these and of many more diverse groups — each on a broad comparative basis — has been attacked by sound standard methods, involving the combined approach of external morphology, ontogeny, histogenesis, and vascular anatomy, reconciling their results.

The triple structure as present in the wall units appears of frequent occurrence in diverse organs. It is well-known in many foliage leaves and perianth parts, also in stamens (see e.g. Wilson 1942) and in stamen groups (Van Heel, 1966). It should be recognized as a main building scheme. The innervation of the units resembles that described for similar units in *Drosera*, *Carica*, and *Clethra* by Hunt (1937). For *Drosera* Hunt noted a close correspondence with the innervation of the foliage leaves. However, in general foliage leaves with these details of innervation would seem to be rare. The double main bundle surpasses the lateral systems and separates into two collateral halves. Double bundles in carpels can be anticipated in all groups with loculicid capsules.

As said above, the pistil wall units do not bear the ovules. It is useless to search for a syncarp part in the base of the pistil. Proleptic independent cross-zones, if at all conceivable, simply cannot be demonstrated. Moreover, I would not like to infer their 'typical' presence from a possibly unwarranted comparison with different groups. The convex

floral apex homogeneously gives rise to centrifugally developing ovules, and that at a very early stage in floral development. The apex is advanced over the surrounding peripheral wall units. Swamy, clinging to the Ranalian carpel theory, forwarded the hypothesis that in *Scyphostegia* the lateral parts of macrosporophylls, originally parietal, receded towards the base of the locule. In this respect it is important to note that indeed in the *Tamaricaceae* we meet with placentae in between parietal and basal. Likewise Swamy supposed that the lateral parts of microsporophylls separated and formed the glandular stub-like structures which stand in line with the stamens. This makes one think of similar possibilities in the *Lauraceae* and *Hernandiaceae*. However that may be, the point is that with the introduction of receding or separating lateral parts of carpels Swamy attached to these parts individuality to such an extent as to undermine efficiently the classical carpel concept. That is in favour of those authors (e.g. Lam, 1948 etc.) who suppose that placentae could be or could have been organs distinct from sterile parts.

Moeliono (1966; a more detailed and fully illustrated English version will shortly appear) histogenetically demonstrated that the placentae arise directly from the floral axis in the *Caryophyllaceae* and other *Centrospermae*. Only secondarily they fuse with the units of the pistil wall. The septa grow inwards, meeting the placentae, and form locules. This secondary fusion takes place by a special course of events, called postgenital fusion, that can be followed histogenetically step by step. Later the septa are dissolved along other lines than those of the secondary fusion, causing the free central placentation. Thus in these cases the placentae, whatever their nature, are individual structures.

This discovery may bear a direct relation with the basal placentation of *Scyphostegia*. The septa, being the outcome of the combined halves of the horseshoe-shaped primordia of the wall units, grow inwards and downwards over the tips of the ovules, forming cells which partly enclose the latter. Hereby the formation of extra cells is possible. Moreover, in view of a relationship of *Scyphostegia* with *Tamaricaceae-Flacourtiaceae* which will be dealt with in the following, it is significant that Murty (1954) reported a trilocular condition not only in the lower, but also in the upper part of the attenuate pistil cell of *Tamarix*. He considered this as evidence against the explanation given for the parietal placentation by Troll.

TAXONOMY

My observations lead to the conclusion that the reproductive units are clear-cut ovules. In this I fully agree with Swamy. It is only incomplete investigation that could mislead workers before Swamy. Quoting Swamy (1953): 'With due regard to these botanists, it must be said that it is most unfortunate that the female flower of *Scyphostegia* has not received as critical an examination as it should have deserved in their hands.' The present paper, made possible by well-fixed developmental series, is an extension of that by Swamy who had access to herbarium specimens only. Therefore certain details escaped his attention and he did not recognize the aril(loid).

I also fully agree with Swamy that the affinity of *Scyphostegia* is not with the *Ranales*. The genus cannot be related with the *Monimiaceae*. For the same reasons it cannot be referred to the *Celastrales* as was the second opinion of Hutchinson. Earlier authors listed in all twelve important characters to exclude *Scyphostegia* from the *Monimiaceae*. To these must be added that in the *Monimiaceae* the ovules contained by the receptacle are always each enclosed by a third covering, the carpel of the *Ranales*. The figures of Money, Bailey, and Swamy (1950) show that, even in reduced Monimiaceous flowers in which the ventral carpel bundle may extend directly as the ovule trace, there is a definite dorsal carpel bundle.

The Monimiaceous genus *Hennecartia* was stated by Poisson (1885) and by Perkins and Gilg (1901) to be provided with a stigmatiform mouth of the urceolate receptacle. According to the latter this mouth would actually capture the pollen. However, until this is proven by a thorough anatomical study, I will not take it for granted. In this respect it needs to be stated that we know deplorably little on such an important group as the *Monimiaceae*. Let us assume that in the *Monimiaceae* flowering structures can be discovered consisting of an apically stigmatiform, urceolate envelope containing some ovules which are each coated with reduced carpels. In that case a state would be reached which in superficial structure (*Gestalt*) would be completely similar to that in *Scyphostegia*. This analogy would have been reached in completely different lines, the one listed in the *Ranales*, the other in the *Parietales*.

In general I can follow Croizat in that there is a tendency for reproductive units to be sheathed by ever more telescoping coverings, leading from 'ovule to ovary' and from 'flower to inflorescence' or vice versa. Both of the lines disclosed above could show this tendency, as such they could be compared as to their structural themes. However, this does not necessarily imply any close affinity. I cannot follow Croizat in every detail he presented on the female flowers of *Scyphostegia*.

The *Ranales* being excluded, the only possibility left lies in the *Parietales*. Metcalfe advanced a remote relationship with the *Flacourtiaceae* on the ground of anatomical characters. Van Steenis was of the same opinion basing himself moreover on a number of external characters, as mentioned above. To these may be added that in the *Flacourtiaceae* stamens with prolonged connectives, extrorse stamens, and stamens in a column sometimes occur. A capsule instead of a berry is also frequently reported in that family. The question in how far there are precise structural similarities with gynoeceum forms in *Flacourtiaceae* — e. g. in *Hydnocarpus* pistils or in *Casearia* aril(loid)s — awaits further study, as most unfortunately important detailed morphological knowledge on the *Flacourtiaceae* is lacking.

As it is, the difference between the *basal* placentation in *Scyphostegia* and the *lateral-parietal* placentation in the *Flacourtiaceae* remains the only discrepancy. Evidently Van Steenis found no difficulty here, as he included 'parietal ovules' in the combination of characters corroborating the supposed affinity with certain *Flacourtiaceae*. May this be not a serious abstacle in taxonomy, to morphology it is a major challenge. Luckily the placentation in the *Tamaricaceae*, also listed in the *Parietales*, seems intermediate. It is recorded as '*basal-parietal*' by Niedenzu. This will form a subject of my investigation in the immediate future.

I could not compare some of my specialized results with similar characters in *Flacourtiaceae*, because in that family these have never been studied. However, it is noteworthy that some characters, namely a chalazal protuberance bearing unicellular hairs, the endosperm changing from nuclear to cellular, the outer layer of the nucellus forming a scanty perisperm lining the testa, and the presence of tricolpate pollen, being all special characters of *Scyphostegia*, were also reported by Johri and Kak (1954) for *Tamaricaceae*.

From this correspondence an affinity to the *Tamaricaceae* with their special habit and habitat and their pentamerous flower structure cannot be claimed. However, it does once more indicate that the *Scyphostegiaceae* must be placed in the *Parietales*. Of all the families in that order they must be nearest to the *Flacourtiaceae*, as judged from external characters.

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