

## ON THE FLORAL STRUCTURE OF *SCYPHOSTEGIA*

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The genus *Scyphostegia* was founded upon the basis of a single collection of female plants from Mount Kinabalu, Borneo (Stapf, 1894). The genus, represented by the single species *S. borneensis*, was referred to the family Monimiaceae on account of a few superficial resemblances presented by the plant with the members of the family. For example, the foliage of *Scyphostegia* was compared with that of *Daphnandra repandula* F. v. M.; the so-called disc was interpreted to be homologous with the receptacle of the monimiaceous genera.

Engler (1897), in his supplement to the monimiaceae, considered *Scyphostegia* as a genus of dubious affinities. In a more detailed monograph of the family Perkins and Gilg (1901) excluded the genus from the Monimiaceae on account of the following reasons: (i) Absence of ethereal oil cells (a feature also recorded by Stapf), (ii) Tepals being inserted at the base of the receptacle, (iii) Carpel having scaly outgrowths at its base, and (iv) the inflorescence belonging to a basically different structural type from those met with in the Monimiaceae.

In 1926, Hutchinson created a new family, the Scyphostegiaceae, to accommodate the genus and tentatively placed the family in the Urticales. He further surmised that 'when male flowers are known this genus may be found to belong to Moraceae'.

The male plants of *Scyphostegia* were collected by J. Clemens and M. S. Clemens (field No. 26361) in the type locality of the female plant (Mount Kinabalu) nearly 40 years after Stapf's establishment of the genus, and was described in 1937 (Baehni). In the succeeding year appeared a contribution dealing with a more detailed study of the structure of the inflorescence and flowers in the male as well as in the female plants (Baehni, 1938). In this paper, the author disagreed for placing the family Scyphostegiaceae in the Urticales as was done by Hutchinson, and strongly felt that the genus 'ne peuvent pas être placés dans une position très éloignée des Monimiacées'.

In the latest study dealing with the comparative morphology and relationships of the Monimiaceae (Money, Bailey and Swamy, 1950) *Scyphostegia* was found to possess a trilacunar nodal structure and a tricolpate type of pollen in contrast to the typically unilacunar nodal types and monocolpate, dicolpate or acolpate types of pollen characterising the Monimiaceae. On the basis of these features presented by *Scyphostegia*, as well as on the grounds that the genus furthermore differed from the other members of the family in the absence of ethereal oil cells and in the possession of a unique type of floral structure, the genus was excluded from the Monimiaceae. It was also suggested that a summation of the known anatomical and morphological characters of *Scyphostegia* do not indicate any relationship with the allied families of the Monimiaceae either.

In view of the fact that Baehni (1938), on the basis of floral structure, visualised a close relationship of the Scyphostegiaceae not only with the Monimiaceae but also with certain other putative ranalian families, an extended study of the reproductive structures—as limited by herbarium specimens—was undertaken in order to verify his contention. The results are incorporated in the present contribution.

Herbarium specimens bearing the following collector's name and number were available for study:

<i>Haviland 1377</i>	..	female (TYPE).
<i>Orolfo 3079</i>	..	female.
<i>Clemens 26062</i>	..	female.
<i>Clemens 26361</i>	..	male (TYPE).
<i>Burot Ho 1758</i>	..	male.
<i>Puasa 3171</i>	..	male.

#### INFLORESCENCE.

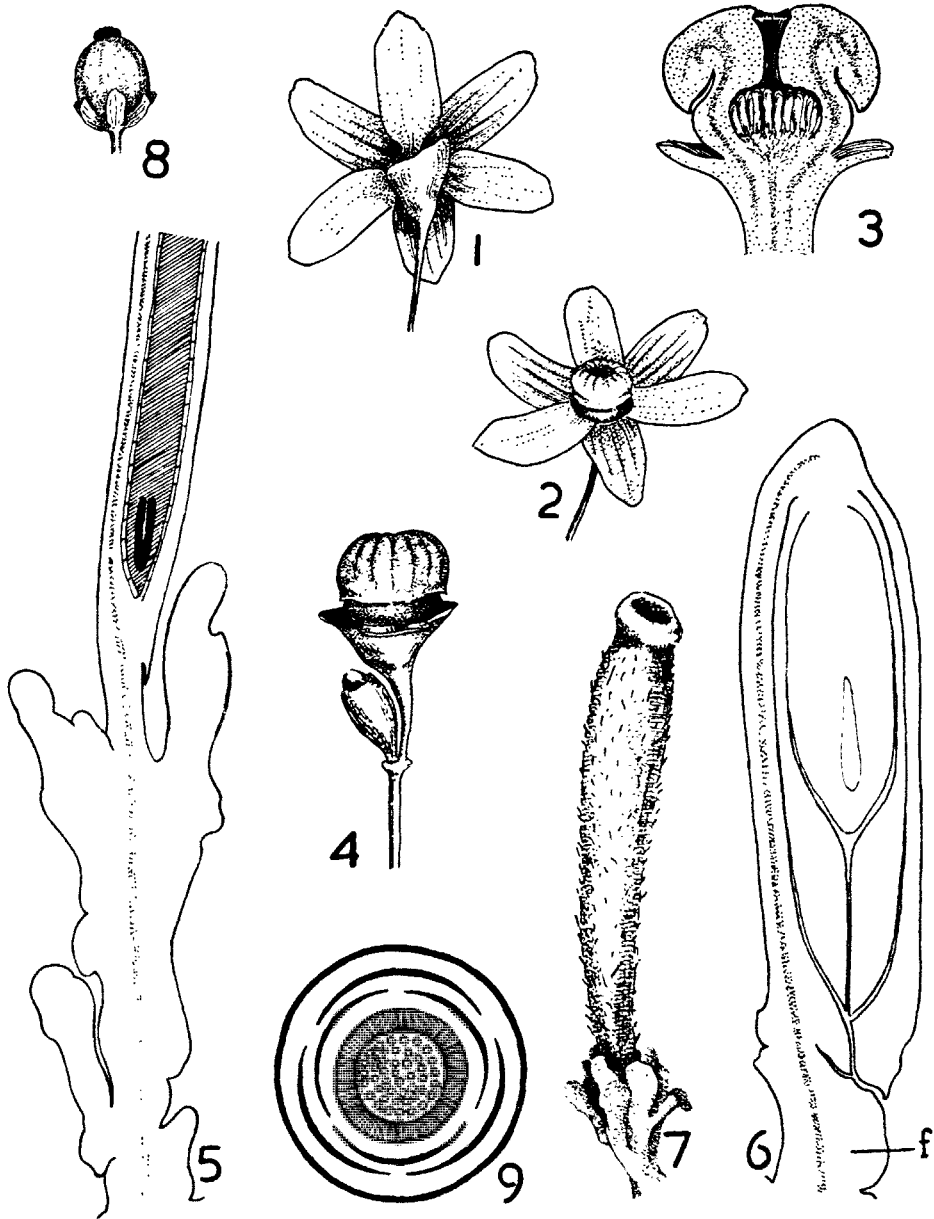
The male as well as the female inflorescences of *Scyphostegia* conform to one and the same structural plan. The lax raceme takes its origin from the leaf axil and gives out shorter lateral branches in a more or less alternating fashion throughout its length, the branch situated nearest to the leaf axil being the first to develop ontogenetically. Each branch at its apex bears a cluster of 5–10 flowers in the male and 5–8 in the female. A diagram of such a cluster as seen in serial transverse sections is reconstructed in Fig. 17. The central double cross-hatched circle represents the axis of a lateral branch of the inflorescence, the stippled circles the individual flowers, and the heavy circles the infundibulous bracts subtending the respective flowers. As may be appreciated from the relative sizes of the stippled circles, the outermost bract encloses the oldest flower, the one placed in its immediate interior the next younger flower, and so on (compare Figs. 18–20 for male, and Figs. 1 and 4 for female). In Fig. 18, a cluster of male flowers is shown as occurring *in situ* at the tip of a lateral branch of the inflorescence. When the outermost infundibulous bract is dissected out, the long slender pedicel of the oldest flower and the next younger flower in the axil of the first are exposed to view (Fig. 19); the removal of the bract of the second flower would in turn show the presence of the third flower bud (Fig. 20). That exactly a similar relationship holds for the female flowers may be seen in Fig. 1, which depicts an entire flower cluster and in Fig. 4, showing the next younger flower bud in the axil of the first. Thus each lateral branch of the inflorescence—whether in the male or in the female—has the construction of a raceme, although the flower-bearing part of the branch axis is greatly condensed. The inflorescence *as a whole* may rightly be interpreted as a compound raceme.

#### MALE FLOWER.

*External morphology:* The short pedicel of the young male flower (Fig. 20) becomes elongated into a slender structure nearly half as long as the perianth towards maturity (Figs. 19, 22). The perianth is united into a tube, the individual lobes becoming free about the mid-height of the flower (Figs. 19, 21). The lobes of the outer whorl are somewhat fleshy, three in number, and pronouncedly concave. The lobes of the inner set are again three, in alternating disposition in relation to the outer, thinner, and significantly smaller both in longitudinal and latitudinal dimensions (Fig. 21). The third inner whorl consists of three fleshy knob-like 'glands' taking their position opposite to the lobes of the second whorl (Figs. 22, 23). The innermost whorl is represented by three stamens that are confluent by their adaxial surfaces (Fig. 23). The dehiscence of the anthers is extrorse. The pollen grains are typically tricolpate (Fig. 24).

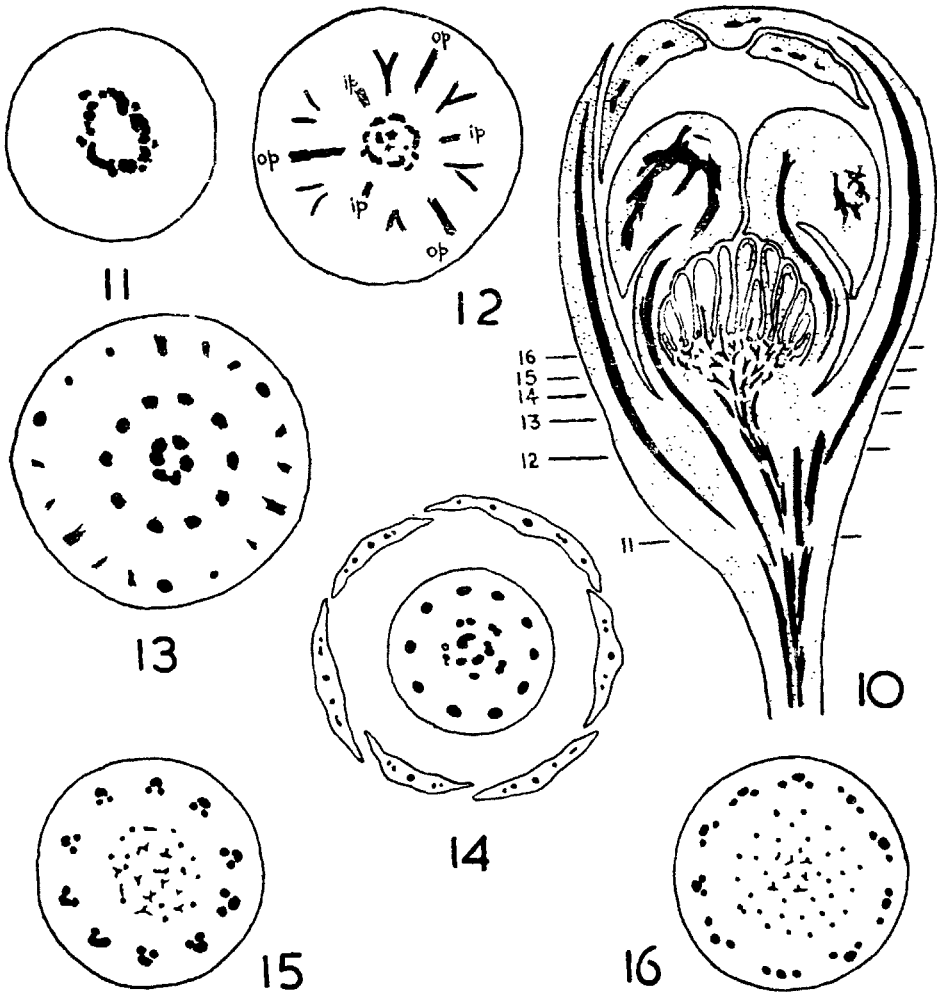
*Anatomical structure:* The pedicel contains two strands of vascular tissue (Fig. 26) each of which trifurcates below the insertion level of the perianth to give rise to six bundles<sup>1</sup> (Fig. 27). They soon arrange themselves in two whorls of

<sup>1</sup> The phraseologies employed here are purely descriptive of phenomena seen in successive serial sections and do not involve developmental implications of vascular tissues.



FIGS. 1-9: Fig. 1. Female flower as seen from the stalk end. Fig. 2. Same, as seen from above. Fig. 3. Median longitudinal section of female flower; perianth removed. Fig. 4. Female flower (perianth trimmed off) after removal of the subtending infundibulous bract; note the flower bud in the axil of the flower. Fig. 5. Longisection (micropylar part) of an immature seed with its funicular outgrowths. Fig. 6. Longisection of an ovule at anthesis showing the pedestal-like funicle (*f*), two integuments, and crassinucellus with an outline of the female gametophyte. Fig. 7. A seed at the stage shown in Fig. 5, showing funicular outgrowths. Fig. 8. Mature fruit. Fig. 9. Floral diagram of the female flower.

three each (Fig. 28), the peripheral set of bundles later contributing to the vascular system of the outer whorl perianth lobes (Figs. 29-35). The three bundles of the inner set undergo trifurcation (Fig. 28) and one strand from each group moves out (Fig. 29) and occupies an alternating position with and in the same circumference of the bundles supplying the outer perianth whorl (Fig. 30). These strands vascularise the lobes of the inner perianth whorl (Figs. 33-35). The main bundle of the sepals and petals remains unbranched throughout the tubular part of the



Figs. 10-16: Fig. 10. Longisection of a female flower slightly before anthesis. Figs. 11-16. Transections of female flower at levels as indicated by corresponding numbers in Fig. 10.

perianth (Figs. 31-33) and splits up into the median and lateral veins only as the individual perianth lobes become separated (Figs. 34, 35). Vascularisation of the two outer whorls of the flower thus being completed, there remain in the centre of the floral axis three strands (Fig. 29). At a slightly higher level (Fig. 30) each of these divides by a tangential split. The outer three branches supply the corresponding 'glands' constituting the third whorl (Figs. 31, 32) and undergo some degree of proliferation into short branches (Fig. 25). The remaining three branches

constitute vasculature of the stamens (Figs. 25, 31-35). These bundles at the point of their origin are endarch as is the situation in other floral appendages, but after entering the anther assume exarch disposition.

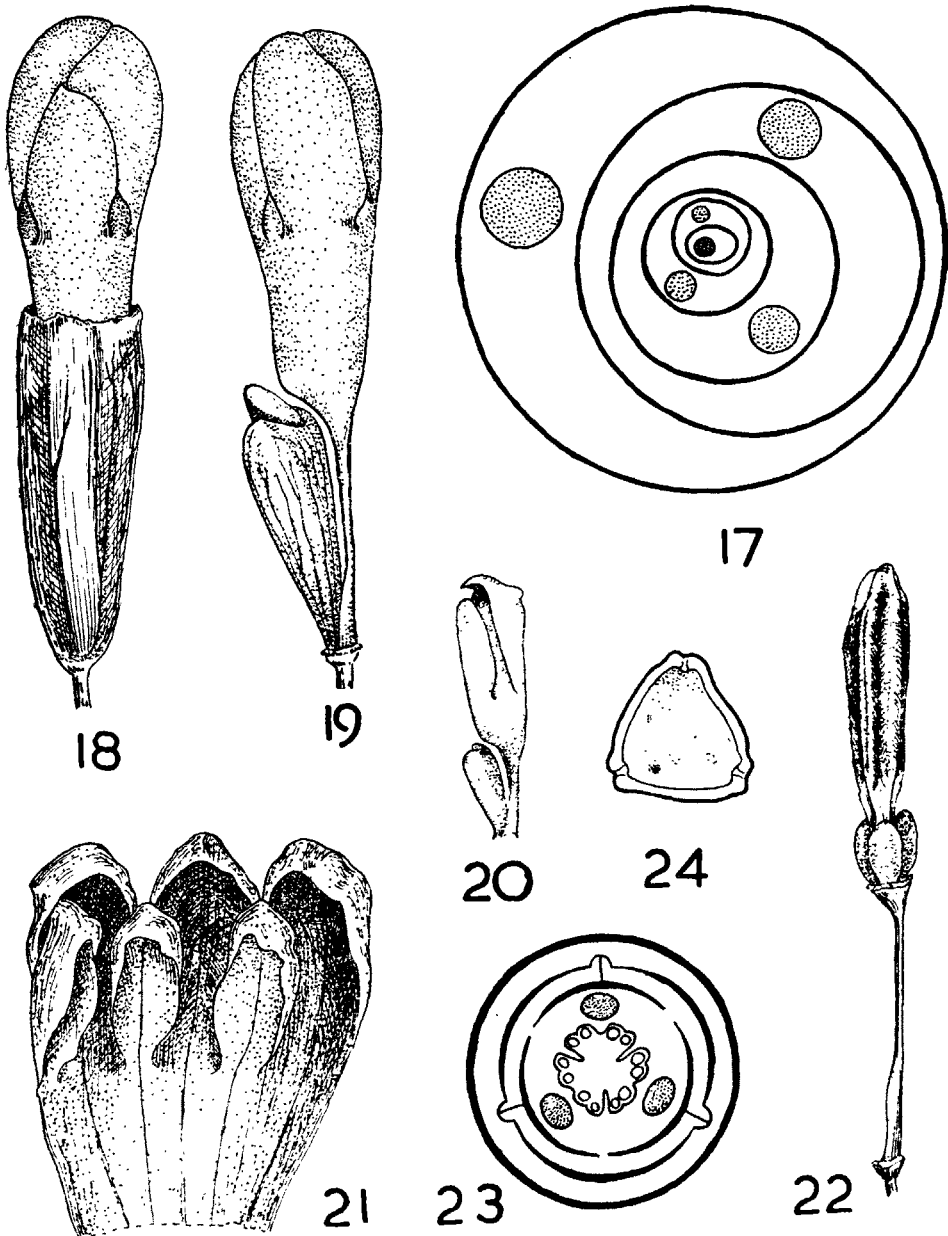
#### FEMALE FLOWER.

*External morphology:* Just like in the male flower, six perianth lobes in two alternating sets constitute the first and second whorls. In contrast, however, the lobes of both the whorls are not only free from the base, but also morphologically similar to each other (Figs. 1, 2). Furthermore, the resemblance is reflected in their histological structure as well. The lobes are somewhat fleshy with a toughened exterior and persist in the mature fruit (Fig. 8).

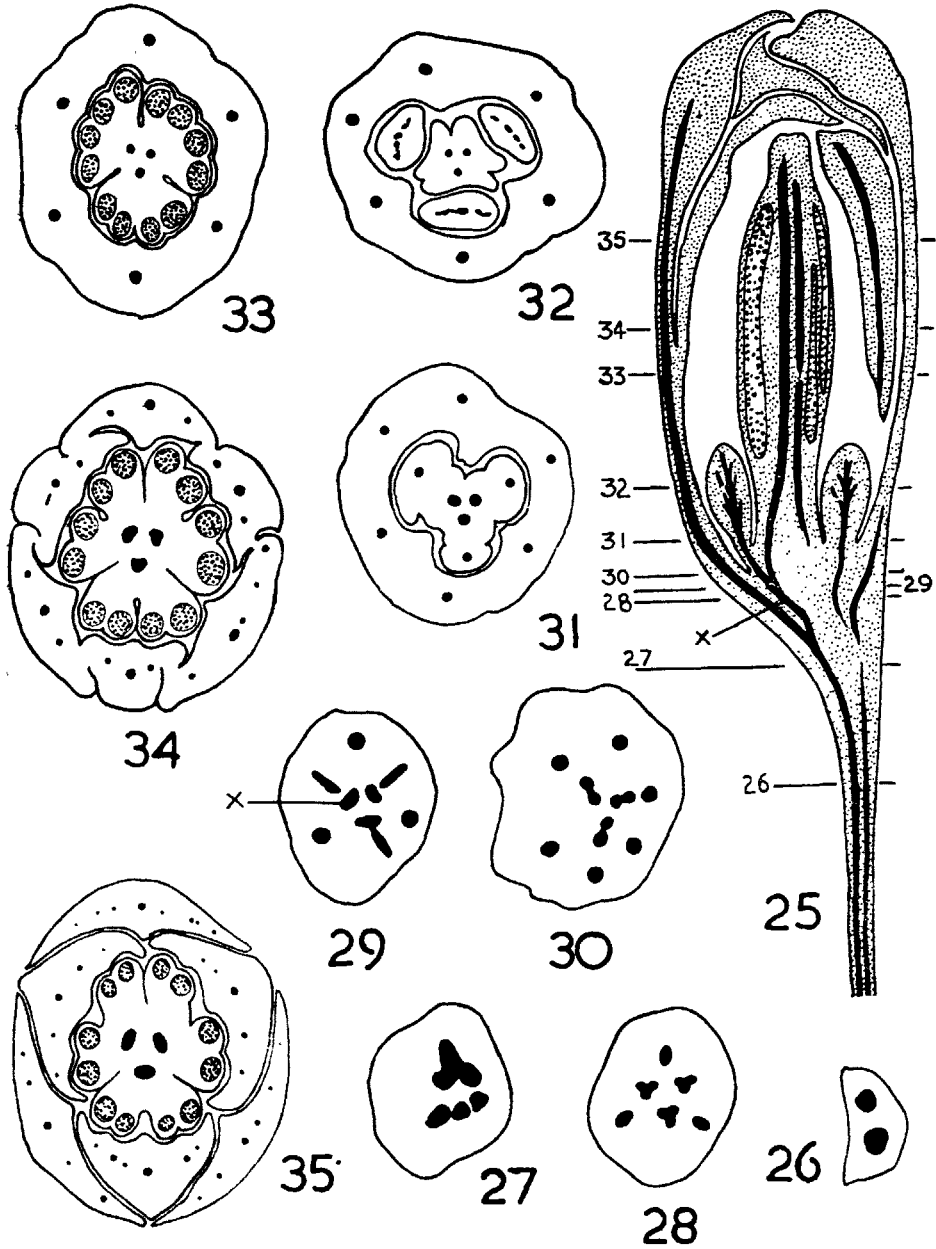
Structures corresponding to the third whorl of the male flower (the 'glands') are absent here. Instead, an urceolate structure occupies the position of this whorl (Figs. 2, 9) which at the same time is also the innermost. The free margin of this structure is pronouncedly deflexed so as to cover nearly the upper half (Figs. 4, 3). The exterior of the deflexed surface presents 8-12 longitudinally running ribs. The wall of the urceole is rather fleshy and encloses a single cavity that communicates with the outside through a narrow passage at the apex (Fig. 3). Two to four cell layers surrounding the passage show a conspicuously glandular texture, presumably a feature connected with the growth and passage of the pollen tube. Although the superficial cell layers of the extensive deflexed surface also present a more or less similar histological character, an examination of adequately preserved material of relevant developmental stages is necessary to confirm its stigmatic function or otherwise. The neck of the urceole is greatly compressed vertically and as such the gynoecium is devoid of a style. The floor of the urceolar cavity is slightly raised and functions as the placenta on which numerous anatropous ovules arise (Figs. 3, 10). In the prefertilisation stage the funiculus part of the ovule presents the appearance of a stub-like pedestal (Fig. 6, *f*), which later undergoes significant modifications as will be explained on a subsequent page. The ovule has two closely adpressed integuments, both of which take part in the organisation of the micropyle, and a fairly massive nucellus whose vertical dimension is nearly twice its width (Fig. 6).

*Anatomical structure:* In the basal part of the pedicel the vascular strands are arranged in the form of a somewhat irregular ring as seen in transverse sections (Fig. 11). As the two perianth whorls arise in close succession, the vascular strands supplying them also differentiate almost simultaneously at the same level (Fig. 12. *op*—outer perianth: *ip*—inner perianth). The main strand of each perianth lobe soon breaks up into the median and marginal bundles, the latter again branching into two whereby a transection at the base of a perianth lobe shows the presence of five bundles (Fig. 14). Higher up in the lobe the bundles undergo further ramification and webbing.

After the differentiation of strands for the perianth, the remaining vasculature soon resolves into two concentric systems of strands (Fig. 13). The outer ring consists of 8-12 strands (corresponding to the number of ribs present on the deflexed part of the gynoecium) and supply the wall of the gynoecium. During their course, each strand trifurcates into a central larger and two smaller bundles one on its either lateral side. This 'triplet' condition remains distinct even at higher levels of the gynoecium (Figs. 15, 16). At the region of the deflexed part, the bundles become rather massive, undergo considerable ramification and anastomoses, and form sprays in conformity with the deflexion (Fig. 10). The inner ring of strands (Fig. 13) consisting generally about half the number as that of the outer, almost immediately begin to undergo an extensive system of branching, the branches spreading rather uniformly in the floor of the gynoecium (Figs. 10, 14-16). Each ultimate branchlet of this system forms the vascular strand of an ovule (Figs. 10, 6).



Figs. 17-24: Fig. 17. Diagram showing the plan of construction of inflorescence; double cross-hatched area—inflorescence axis; stippled areas—individual flower; heavy circles—infundibulous bracts subtending a corresponding flower. Fig. 18. A branch of male inflorescence, the basal region being enveloped by the infundibulous bract. Fig. 19. Same, bract removed; axillary bud is exposed. Fig. 20. Continuation of the inflorescence after the removal of involucre of the axillary bud in Fig. 19. Fig. 21. Perianth of male flower longitudinally split and spread in one plane, as seen from the abaxial side of the perianth. Fig. 22. Male flower after removal of perianth, showing three 'glands' and stamens. Fig. 23. Floral diagram of male flower. Fig. 24. Section of pollen grain at the equatorial region showing three germ pores.



Figs. 25-35: Fig. 25. Longisection of a male flower just before anthesis. Figs. 26-35. Transsections of male flower at levels as indicated by corresponding numbers in Fig. 25.

FRUIT AND SEED.

During post-fertilization development, the ovules and ovary undergo considerable morphological modifications. The ovary develops into a fleshy pericarp, lodging within its cavity a large number of seeds, and thus the fruit of *Scyphostegia* may aptly be classified as a berry. The most significant modification appears to

be the change undergone by the funiculus. Keeping pace with the development of the fruit, the stub-like funiculus (Fig. 6) sends out spongy parenchymatous lobes towards the chalazal end of the seed. The lobes, often exhibiting a considerable degree of irregular branching, grow rapidly in the disposition of a whorl and envelope the micropylar region of the seed (Figs. 7, 5). It may be mentioned in passing that it is the inaccurate interpretation of these structures in the past that has been responsible not only for the misconception of the floral structure of *Scyphostegia* as a whole, but also for the diverse opinions expressed with regard to the systematic relationships of the family based on such misconceived premise.

The seed is vertically elongate, slender, and somewhat cylindrical. When detached from the placenta (from herbarium specimens) it carries with it the whorl of funicular outgrowth (Fig. 7). The chalazal end shows a slight constriction, the apex being depressed; the histological features of this part of the seed could not be studied for want of suitably killed material. As far as could be ascertained from herbarium specimens after re-expansion, the seed coat appears to be formed essentially by the outer integument, the cells of its innermost layer having undergone vertical elongation and hardening. The outer surface of the seed becomes uniformly but sparsely distributed with unicellular trichomes (Fig. 7). No traces of the inner integument could be made out. The vascular strand of the ovule remains unbranched in the funicular region as well as in the tissues of the seed coat (Fig. 5). In the oldest stage available for examination, the seed cavity is filled with cellular endosperm and the young embryo lies near the micropyle (Fig. 5).

#### DISCUSSION.

*Perianth of the male and female flowers*: In both sexes the perianth consists of two whorls, the individual members of one whorl alternating with those of the second. In the male, the basal half of the perianth lobes is fused to form a single tube whereas in the female, the individual lobes are completely free; furthermore, in the male, the outer perianth members are unlike those of the inner in regard to size, shape and degree of succulence, but in the female all perianth appendages are exactly alike. In view of the distinctive characters exhibited in the two perianth whorls of the male flower, the outer whorl may presumably be regarded as sepaline and the inner, petaline. Stapf (1894) considered the outermost two whorls of the female flower as perianth, Hutchinson (1926) as 'bracts' or 'involucre', and Baeni (1938) as 'calyx'. Although there are no morphologically distinctive characters in the two outer whorls of the female flower, an interpretation of these structures on a homologous rank with those of the male flower fits harmoniously with the relation the perianth bears to its succeeding whorl. Whether the outer and inner whorls of the female flower should then be designated literally as sepals and petals in descriptive phraseology is a matter of personal opinion and is not of any direct consequence for an understanding of the true, fundamental nature and relation of other floral appendages. On the other hand, the term tepal could as well be employed if one prefers to do so, provided he appreciates the homology of the concerned structures in the flowers of the two sexes.

Baehni (1937, 1938) looks upon the outer two whorls of appendages (at present interpreted as calyx and corolla) of the male flower as 'gamosepalous corolliform calyx' and designates the third whorl (at present regarded to be 'glands') as 'petals'. This view does not appear to be in harmony with known facts: the appendages of the outer two whorls alternate with one another; those of the third whorl is opposite to the second (as well as to the fourth) (Fig. 23). Thus, petal, gland and stamen, which belong to successive whorls lie, along one and the same radius. The vascular supply too of these structures likewise arise by the branching of the pedicellar strands along the same radius, and more or less in a periclinal plane (compare Figs. 30 and 31). This situation does not lend itself to the interpretation that the



first two whorls (whose members are in alternating position) as sepals made up of six lobes and those of the next inner whorl, as petals. On the other hand, it would be in conformity with morphological and anatomical structure to regard the outermost whorl as constituting the sepals and the immediately next whorl as constituting the petals (Fig. 35).

*The third whorl of the male flower:* The morphological nature of the third whorl of the male flower ('petals' of Baehni) is rather intriguing. This is largely because of its positional anomaly in being directly opposite to the appendages belonging to the immediately neighbouring whorls on either side. There are no significant features in the external form of the appendages to suggest their petaline nature. Histologically, the structure appears to be made up entirely of homogeneous parenchyma cells and is supplied with a well-developed vascular bundle. Neither 'vestigial structures' nor rudimentary vascular traces either between the second and third whorls or between the third and fourth whorls are present; thus the possibility of looking for any suppressed whorls is eliminated.

It is important to recall at this point that the vascular supply to the calyx and corolla are derived from one set of strands of the pedicel and that the supply to the structures of the third whorl as well as to the stamens are derived from a common cord (marked  $\times$  in Figs. 25, 29). This feature affords evidence to a considerable extent for the surmise that the first two whorls belong to one morphological category and that the third and fourth together belong to a second morphological entity. In other words, if the 'glands' of the third whorl are to be morphologically compared to any other appendage of the flower, it is most nearly related to the stamens than to the petals. Then how to account for the derivation of the third whorl?

The superposition of the 'gland' and stamen is a serious obstacle to admit the possibility of interpreting the 'glands' as remnants of an outer whorl of stamens. If a way can be found to explain this anomalous position of the glands, it would indeed be a contribution towards a clearer understanding of the floral structure. Data obtained through studies on ontogeny of a structure and information gathered through comparative morphology and anatomy of corresponding structures or of their modifications in closely related species often provide significant clues for the elucidation of the real nature and identity of intriguing floral appendages. Neither of these procedures is possible for *Scyphostegia* at present, because no suitable material is available to undertake developmental studies and the systematic position of the genus is so notoriously uncertain that any assumptions as to its presumed alliance would be unfounded.

Reserving a final conclusion as to the exact *modus operandi* in the derivation of the extant structures of the male flower of *Scyphostegia* for future, a speculation involving a series of hypothetical phylogenetic stages may be visualised, the purpose of which is only to serve as a working hypothesis for later investigations and discussion. The ancestral type of the male flower is conceived as consisting of just three whorls,—an outermost whorl of three sepals, a middle whorl of three petals, and an innermost whorl of three stamens (*s*, *p*, *st*, respectively in Fig. 36 A) having the shape of a microsporophyll, that is, a more or less dorsiventrally flattened structure with a median and two marginal veins; that the pairs of sporangia were situated between the median and marginal veins; that the sporangia dehiscence in an extrorse manner and that the vascular traces in the sporophyll had an exarch orientation, that is, the protoxylem points turned away from the floral axis (Fig. 36 A).<sup>1</sup> Microsporophylls of this kind are not wholly hypothetical; they are seen in a considerable number of the ranalian genera that exhibit in their tissues and organs a relatively low level of structural specialisation phylogenetically.

<sup>1</sup> In this series of figures only one sector of the flower is shown as seen in transections.

Whether the stamens in the ancestral type of *Scyphostegia* were syngenesious or free is a point which is immaterial for the present.

Subsequent phylogenetic modifications of the ancestral type of microsporophyll involve a pronounced activity of the marginal meristem of the sporophyll with simultaneous curvature of the margins so as to overlap the thecae. As a concomitance there is a shift in the disposition and orientation of the marginal bundles (Fig. 36, B, C). Finally the margins fuse (Fig. 36 D), so also the two vascular

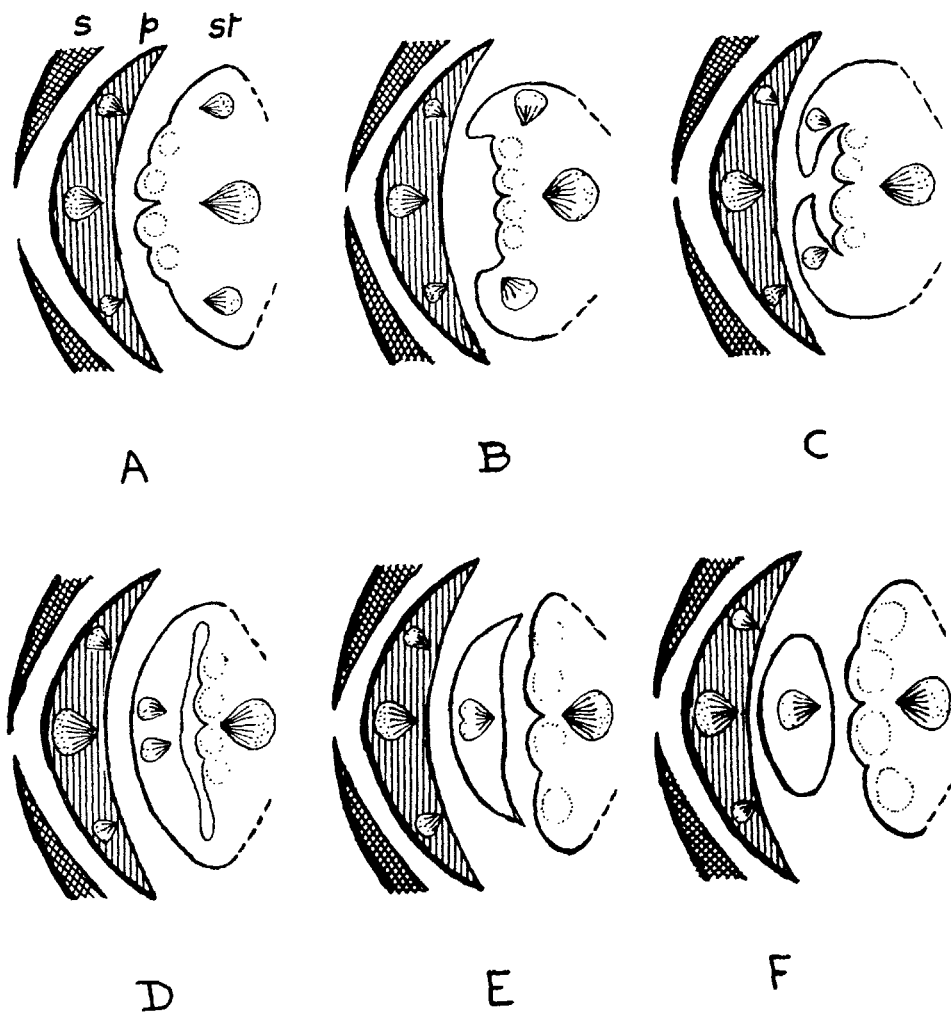


FIG. 36 A-F: Theoretical series of diagrams illustrating the derivation of the third whorl of the male flower. One sector of floral structures as seen in transection is shown. *s*—sepal, *p*—petal, *st*—stamen.

bundles therein (Fig. 36 E) and the newly formed adaxial part with its vasculature becomes detached from the sporangium-bearing part (Fig. 36 E). The final result of this series of changes is the interpolation of a new whorl consisting of three appendages that are placed on the same radius of the petal and stamen and between them (Fig. 36 F).

In the preceding hypothesis it will be seen that no attempt has been made to explain endarch orientation of the vascular bundle of the stamen. In fact such a situation has been assumed for the stamen of the ancestral hypothetical flower. Whether this situation preceded or followed the phylogenetic modifications surmised above, or was synchronous with them, does not interfere with the view suggested as to the anomalous position of the third whorl and as to how it might have been derived. That vascular bundles may often show various kinds and degrees of torsion or twisting not only in floral axes and their appendages but also in the vegetative axes and structures borne by them is a fairly common phenomenon although this fact seems to be not so well appreciated by anatomists who concentrate on the structures of only one part of the plant body, for example, on the flower. Furthermore, the behaviour of a vascular strand or bundle in regard to its orientation is quite often varied at different levels of one and the same structure. Thus at certain specific levels of a structure a bundle may be exarch and at certain other levels the same bundle may assume an endarch orientation. In the flower of *Scyphostegia* itself the staminal trace, soon after its formation, is endarch but assumes an exarch orientation only after entering the anther bearing part. Thus a certain mode of orientation of a bundle, in itself, may not be of much morphological significance.

With regard to the possible function of the structures belonging to the third whorl, no definite opinion can be expressed until suitably preserved material is examined. That the structures under consideration cannot be regarded as petals but that they are more nearly related to the stamens than to any other appendages of the flower makes one wonder if these modified parts of stamens could not have acquired some secondary function—as for example, a mechanism for the landing of the insect visitor, or as an organ for secretion of sugary solution, etc. Although in herbarium specimens the histological structure of these appendages fails to exhibit

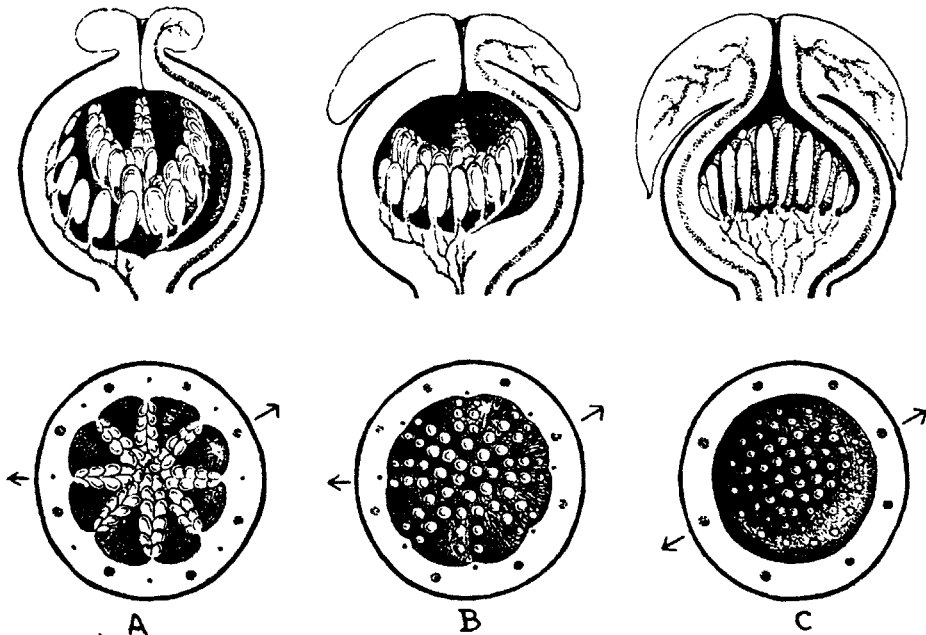


FIG. 37 A-C: Theoretical series of diagrams to illustrate the derivation of the extant gynoeceium. In the upper series, the gynoeceium is drawn as seen when cut longitudinally along the arrows in the lower series. In the lower series, transversely halved aspects of corresponding gynoeceia are shown.

the typical characteristics of secretory tissues, the probability of their playing this rôle is not altogether ruled out. Because, examples of stamens bearing accessory appendages in the form of lobes, glands, etc., that are known to take part in the secretion of sugary fluids are not wanting in the angiosperms. Future investigations and field observations alone should settle whether the corresponding structures in *Scyphostegia* are of the nature of nectaries or a device for ensuring efficient pollen dispersal through an insect visitor. Tentatively they may be referred to as 'glands' for purposes of description.

*The essential organ of the female flower*: Conflicting opinions have been expressed as to the nature of the centrally situated urceolate structure of the female flower. According to Stapf (1894) it is a 'disc' or 'receptacle' lodging a number of 'carpels'; to Hutchinson (1926) the wall of the urceole represents a 'receptacle resembling thick corolla' the cavity of which is occupied with 'female flowers'; and Baehni (1938) equates the wall of the urceole with 'corolla' and the structures within it to 'carpels' (Fig. 38). 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. Had they only dissected out the younger stages of the internally borne structures of an urceole and observed them under the microscope, it is certain that they would have reached altogether different conclusions. In fact, it is as a consequence of their interpretations of these structures that the authors were forced to misconstrue the entire structure of the flower.

That the structures within the urceole are nothing but ovules themselves has been demonstrated on a previous page. Then it is but logical to regard the urceole as no other structure than the gynoeceium. Furthermore, there is every reason to regard the tissue in the immediate neighbourhood of the opening of the urceole—though not all of the deflexed, morphologically inner surface of the urceole—as being stigmatic. The next two whorls of appendages outside the gynoeceium would naturally fall in the category of tepals (Fig. 38).

The structure of the gynoeceium of *Scyphostegia* is rather remarkable, particularly in regard to the nature of placentation. If the number of ridges on the deflexed (stigmatic?) part of the gynoeceium, the number of lobations protruding from these ridges into the 'stylar canal,' and the number of main vascular strands that run in the wall, may be taken as reasonably reliable indicators of the number of carpels that have entered into its construction, then it has to be surmised that the gynoeceium is made up of several carpels, their number being between 8 and 12. On this premise there is every reason to believe that the extant situation is an end product of a particular trend of phylogenetic modification. It is conceivable that the ancestral form of the gynoeceium of *Scyphostegia* was multicarpellary and unilocular; that the placentation was parietal; that the youngest ovules were borne towards the apical end of the placentae and the oldest towards the base; that the median vascular bundles of the individual carpels, after traversing the wall of the gynoeceium, entered the more or less small capitate stigma and proliferated into a few slender branchlets; and that the marginal bundles, situated beneath the placentae gave off vasculature to the ovules (Fig. 37 A). Such a gynoeceium could have undergone phylogenetic specialisation on the following lines: (i) the placentae receded centripetally, that is, towards the floor of the locule, at the same time retaining the centrifugal order of maturation of the ovules; (ii) the median vascular bundles of the individual carpels did not undergo any profound changes excepting that their distal region in the stigma acquired a greater degree of proliferation and spread, obviously with its pronounced abaxial deflexion and expansion; (iii) the marginal bundles receded in conformity with the placentae towards the base of the locule and began to proliferate into the vascular traces of the ovules at lower levels of the gynoeceium (Fig. 37 B). A culmination of these modifications would result in a gynoeceium as seen in *Scyphostegia* (Fig. 37 C).

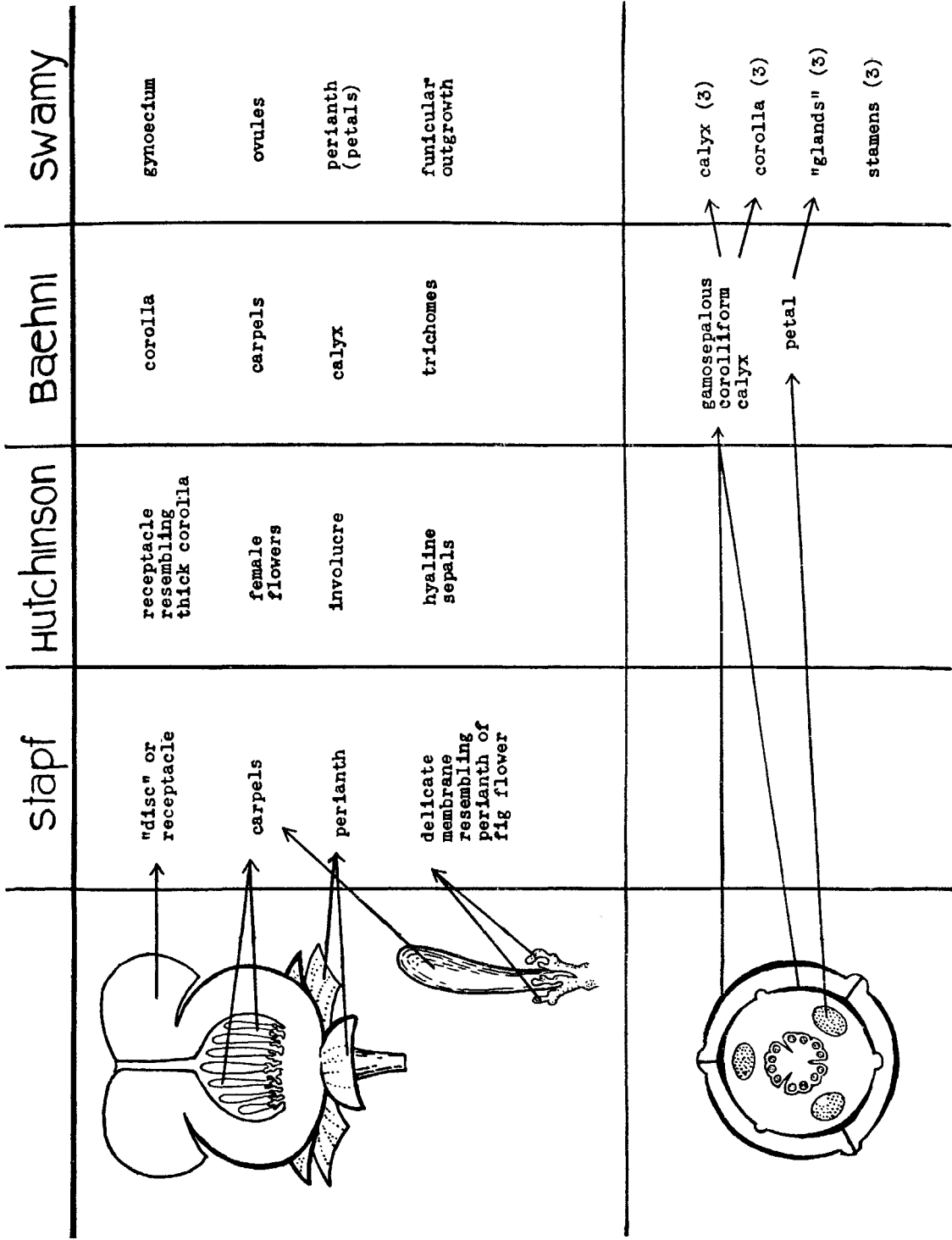


FIG. 38: Tabular diagram showing the interpretation of structure of the female and male flowers of *Scyphostegia* according to Stapf, Hutchinson, Baehni and the present author.

AFFINITIES OF *SCYPHOSTEGIA*.

Engler (1897) has treated the genus *Scyphostegia* as of 'unsicherer Stellung' under the Monimiaceae. Perkins and Gilg (1901) excluded the genus from the family (as also Money, *et al.*, 1950). After having accepted this procedure and after creating a new family, the Scyphostegiaceae, for the reception of the genus, two opinions have been expressed as to the relationships of the family—(i) that it could be related to the Moraceae (Hutchinson, 1926), and (ii) that it should be placed in a position not far removed from the Monimiaceae itself (Baehni, 1938).

In spite of viewing the male and female flowers of *Scyphostegia* in light of the new interpretations as given in the present contribution, the systematic position of the plant remains problematical. However, it has become increasingly clear that the combination of characters exhibited by this plant are so unique that there is ample justification to place the genus in a monotypic family of its own, the Scyphostegiaceae, as has already been done by Hutchinson (1926).

The monimiaceous affinity was contemplated essentially on the presumed homology between the urceolate structure of the female flower of *Scyphostegia* and the so-called receptacle of the monimiaceous flowers; and the urticaceous alliance on the interpretation of the internally borne structures of the urceole of *Scyphostegia* as true flowers. Now the genuine nature of the floral structure of *Scyphostegia* having been demonstrated, neither the suggested monimiaceous affinity nor the urticaceous relationship have any arguments in their favour.

A summation of anatomical, morphological and taxonomic characters of *Scyphostegia* affords strong supporting evidence to exclude the family from the above alliances, and also provides convincing arguments to negate a ranalian relationship. Speculations as to which other group of dicotyledons the plant is closely related should await the results of future investigations on the embryology, cytology, anatomy of the secondary xylem and phloem, and of other vegetative structures.

## TAXONOMIC RE-DESCRIPTION.

In view of the foregoing critical re-examination and the new interpretation derived therefrom of the reproductive structures of *Scyphostegia* (see Fig. 38 for an epitome) it becomes necessary to amend the original descriptions of the family (Hutchinson, 1926), of the epithets of the genus and of the female flower (Stapf, 1894), and of the male flower (Baehni, 1937).

*Scyphostegiaceae* Hutchinson, Fam. Flowering Plants, I. Dicotyledons  
(1927) 229. emend Swamy.

Arbores dioeciae; Folia alterna, simplicia, exstipulata. Flores in recemis; Perianthium 6-lobatum, lobis in duobus circulis, ad basim connatis in floribus masculinis, perfecte liberis in floribus femineis. *Flos masculinus*: circulis tertius tribus glandibus repraesentatus; stamina 3, syngenesica; gynoecium inchoatum nullum. *Flos femineus*: gynoecium superior, multicarpellatum, uniloculare; placentatio basalis; ovula multa, anatropa, bitegumentaria; semina multa, excrescentiis funicularibus stipetem circumdantibus; seminis operimentum ex modificato integumento exteriori constans; embryon amplum, cotyledones 2, ovati; hypocotyledon brevis et tenuis.

*Scyphostegia* Stapf in Trans Linn. Soc. Ser. II. 4 (1894) 217. emend Swamy.

Arbores dioeciae; Folia alterna, chartacea, crenulata. Inflorescentia racemus multiplex. Flores bracteati, bracteae infundibulares. *Flos masculinus*: Perianthium 6-lobatum, lobis forma tubuli in dividia parte inferiori unitis, in duobus circulis, tribus lobis exterioribus sepalinis, tribusque lobis interioribus petalinis;

circulus tertius ex tribus glandulibus lobis petalinis oppositis; stamina 3, longitudinaliter elongata, syngenesica secundum faciem adaxialem; filamentis brevissimis; antheris quadrilocularibus, extrorsis; gynoecium inchoatum nullum. *Flos femineus*: Perianthium 6, persistens; membris perfecte liberis, forma et mensuro similibus, in duobus circulis alternantibus dispositis; stamina inchoata nulla; gynoecium uniloculare, sine stylo, stigmatate prominenter deflexo; placentatione basali; ovulis multis, bitegumentariis, anatropis; funiculis stylobatae similibus. Fructus bacciformis, semina cylindrica, tenuia, excrescentia lobata ex funiculo oriente circumdata circa terminum micropylare; seminis operimentum exterior pilosum; endospermum minutum; embryon amplum.

*S. borneensis* Stapf in Trans. Linn. Soc. Ser. II. 4 (1894) 218. emend Swamy.

Arbor dioecia, glabra, 3-8 m. alta, trunco 30-60 cm. ambitu, ramis gracilibus, obscure angularibus. Folia oblonga 6×3, 10×4, 12×4.5 cm. longa et lata, apicibus abrupte acuminatis, basibus rotundatis-cuneatis, marginibus tenuiter crenulatis; nervis lateralibus 6-9-jugatis, angulo circa 60° a nervo principali orientibus; nervis inter nervos laterales notabiliter horizontali directione currentibus. Inflorescentia multiplex racemus, ramis lateralibus floriferis valde densis; ramis masculinis 5-10 flores ferentibus; ramis femineis 5-8 flores ferentibus; floribus novellis bracteis infundibularibus fere complete obductis; bracteis masculinis ad anthesim 8-12 mm. longis, 2.5-3.0 mm. diametro in parte latissima; bracteis femineis 5-8 mm. longis, 3.5 mm. latis in parte distante. *Flos masculinus*: 1.0-1.3 cm. longus, 2.5-3.5 mm. latus; perianthium tubiforme ad basim, liberum in parte superiori 6-lobatum, tribus lobis exterioribus amplioribus, sepalinis; tribus lobis interioribus parvioribus, tenuioribus petalinis; glandes 3, parenchymaticae, petalis oppositae; stamina 3, 8-9 mm. longa, syngenesica, glandibus opposita, apicibus sterilibus in stipitifimbriis et semicircularibus projectionibus terminantibus; sine filamentis definitis; anthera novella quadrilocularis tempore antheses bilocularis, verticaliter extensiva, extrorsa. *Flos femineus*: 1.0-1.5 cm. longus, 1.6-1.8 cm. latus tempore antheses; perianthii membra 6, 7-8×3.4 mm. longa et lata, in duobus circulis, forma et mensura perfecte similia, patentia, persistentia, tempore fructificationis in unicum circulum accommodata; gynoecium urceolatum, sessile, multicarpellatum, uniloculare cum 8-12 striis tenuibus et longitudinalibus, sine stylo, stigmatate extensive deflexo cum 8-12 striis tenuibus; placentatio basalis; ovula multa, subcylindrica, anatropa, bitegumentaria; funiculum parenchymaticum, stipitifforme. Fructus bacca 2.0-2.3×1.5-1.8 cm. longa et lata cum stigmatate persistente; paries carpellaris carnosus, 4-5 mm. densus; semina multa, stipitata, cylindrica, leviter curvata, 8-10 mm. longa, 1 mm. lata, cum depressione leviter obliqua termino chalazali; stipes et terminum papillatis eccrescentiis ex funiculo orientibus involuta; seminis operimentum unicellulo ribus trichomatibus sparse coopertum; endospermum nullum vel vix ullum; embryon dicotyledoneum, seminis cavum fere explens, cum brevi lenique hypocotyledone.

*British North Borneo*: Mount Kinabalu—*Clemens 26062* (female), August 11—September 31, 1931; near Koung, alt. 666.6 m. *Haviland 1377* (female TYPE); Beltolan, *Orolofo 3079* (female), April 10, 1933; Pony Trail-Mi Post, alt. 1,000-1,333.3 m., *Clemens 26361* (male TYPE), September-November, 1931; *Puasa 3171* (male), May 2, 1933; near Kinabatabgan, level land at Balu Puteh, *Burot Ho 1758* (male), May 27, 1932.

#### SUMMARY.

A critical re-examination of the male and female flowers of *Scyphostegia borneensis* Stapf reveals the following structural features:

- (i) The male flower has four whorls of appendages, the first two whorls from outside representing the perianth, the three outer lobes sepaline, the three inner petaline;

appendages of the third whorl constitute three 'glands' placed opposite to the petals; the innermost whorl is made up of three syngeneious stamens, lying again in a superposed seriation with the petals and glands.

- (ii) The female flower consists of three whorls of appendages, the outer two being homologous with the perianth of the male flower; the innermost whorl is the multicarpellary, unilocular gynoeceium itself, lodging many ovules.

There are objections to regard the appendages belonging to the third whorl of the male flower as petals. Arguments are provided to interpret these structures as 'glands' that have been derived from microsporophylls. Theoretical stages in their phylogenetic derivation are reconstructed.

Understanding of the structure and nature of the essential organ of the female flower by previous botanists is shown to be erroneous. What they interpreted as 'disc', or 'receptacle', or 'corolla' is demonstrated to be no other structure than the gynoeceium; what they thought to be 'carpels', or 'flowers' are shown to be the ovules. Hypothetical series of probable phylogenetic changes involved in the derivation of the extant situation in the gynoeceium of *Scyphostegia* is illustrated.

In view of these significant re-interpretations of structure and morphology, the taxonomic descriptions of the family, genus, and species are amended.

From a totality of evidence obtained from a study of morphological and anatomical characters, any relationship of the family *Scyphostegiaceae*, either with the *Monimiaceae*, or with the *Urticaceae*, or with any of the ranalian families is strongly negated.

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#### A CORRECTION.

In Fig. 38, last column, line 7 from bottom, read (tepals) instead of (petals).

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