

Flowers and Inflorescences in the Genus *Balanophora*.

By FOLKE FAGERLIND.

The construction of the flowers and inflorescences of the genus *Balanophora* have been represented by a large number of researchers (e.g. HOFMEISTERS 1858, VAN TIEGHEM 1896, 1907, EICHLER 1868, TREUB 1898, LOTSY 1899, ZWEIFEL 1939, EKAMBARAM and PANJE 1935). But these works differ much from each other. Neither the descriptions of the male nor those of the female flowers agree. Also they could not agree on whether the female inflorescences are simple or branched. In order to extend where possible our knowledge in these areas, I have collected plentiful material of *Balanophora elongata* and a smaller quantity of *B. globosa* in Tjibodas, the branch of the Botani garden of Buitenzorg, Java, on the slope of the Pangerango Gedeh. The part of my studies, which concerns the formation and development of the embryo sac, was already represented (FAGERLIND 1945). The result of my studies on the morphology and development of the flowers and inflorescences and the conclusions from it are described in the following.

**1. Construction of the male inflorescences and the male flower.** *Balanophora elongata* is dioecious. The male and female inflorescences are, as with the remaining genera, endogenous and spadiceous (see e.g. HARMS 1935). On the first sits a relatively small number of male flowers, which are arranged in the form of a flat spiral. The arrangement of the male *Balanophora* flowers is described by HARMS in summary with the following words: "male flowers ... in the axil of a very broad half-moon-shaped scale-like supporting leaf or surrounded at the base of usually short bracts often united with one another into a kind honeycomb."

Each *B. elongata* flower sits in the center of a flat pit in the axil of the inflorescences (Fig. 1 c). Obviously these pits are due to the "honeycomb" formation. If one examines tangential profiles that are lain far at the periphery, those which do not meet the "honeycomb" system, then it is shown that the system dissolves here into "scale" structures X-shaped in cross section (Fig. 1 b). The two upper sides of this structure are importantly longer than the others. The first form together a furrow, which encloses a male flower. The points of these sides show a claviform hump in cross section. One of the lower sides on the right and the other one almost affects the left side of two X-structures sitting under it. In still far portions which were because of the periphery the two lower sides are united to a median rib (Fig. 1 C). Each segment, which clearly develops out from the lower surface of each cell of the "honeycomb" system, thus changes its appearance depending upon the situation between base and the point. The scales are somewhat bent and completely swollen above into shieldlike structures, which cover the male flowers that are for a while interconnected. The flowers become visible by the fact that this connection is later broken by a strong aspect ratio of the basal parts of the male flowers. The "honeycomb" formation obviously came about in *B. elongata* by the fusion of the basal portions of the bordering scales. My material was not sufficient to be able to decide surely whether this process acts during development or whether the connection is already present in the young plant (congenitally fused). It looks in such a way, however, as if the latter would be the case.

*Balanophora elongata* thus has "honeycomb" formation, although one can observe broad, "half moon-shaped", free "subtending bracts" between the flowers. This genus might be located thus in its construction between the two types mentioned by HARMS. The descriptions of the "subtending bract" condition of the male flowers in the different *Balanophora* species are,

however, so superficial that one cannot decide from them whether the presence always excludes the large “subtending bracts” from the “honeycombs” in a more or less pronounced form. I do not consider it improbable that the “honeycomb” formation is usual with the genus *Balanophora*.

As is the case for other species of *Balanophora*, subgenus *Balaniella* (see e.g. HARMS 1935 and ZWEIFEL 1939), with *B. elongata* the male flower consists of a stalk of 4, or more rarely 3, 5 or 6 tepals as well as of a central short-stalked, capitate structure with a rather large number of anther lobes (Fig. 1 d). The flower is, as usual with this subgenus, somewhat elongated in a transverse direction. The perianth is valvate. The two lateral tepals are importantly smaller than the others. The small spheridium shows a number of costae, which are separated from each other by deep furrows. Each costa proceeds from the base of the small spheridium, runs then parallel to the floral axis up along the sides of the small spheridium and then runs out above or unites with one or rarely with several neighboring costae which come from the opposite side. On the inside of the costae are the anther lobes, which are thus tube-shaped and mostly show the same fusion tendencies as the costae themselves. Therefore one gets the impression (Fig. 7 d-e) that in cross sections of the median and basal parts of the spheridia a larger number of pollen sacs (20-30) is present than in the cross section of the apical parts (8-16). If one projects the anther lobe system of *B. elongata* on one level, then one gets different pictures (Fig. 1 f-g). Likewise apparently *B. indica* complies, which after ZWEIFEL has 20 to 30 anther lobes, and probably with all *Balaniella* species with 8-20 or more anther lobes (see composition by HARMS).

With *B. elongata* the stalk contains two vascular strands occupying the midpoint at the transverse level of the flower. These contain tracheids and parenchyma. At the base of the small spheridium the strands divide into two each, which still are at the mentioned level. The tracheids disappear gradually. The two outside strands in the middle part of the small spheridia then exhibit the tendency to split again (Fig. 1 d). The two daughter strands, which also continue to be on one level with the mother strands, are themselves, however, hardly stretched at all.

The data concerning the construction the pollen sac walls in the genus *Balanophora* are extremely poor. ZWEIFEL indicates that the outermost walls of the epidermis consist of a tapetum and a subepidermal layer which are soon absorbed. No “fibrose layer” forms. Just like ZWEIFEL, I had the opportunity to pursue all phases in the formation and development of the archesporium. It is, however, unmistakable that at the least *B. elongata* occasionally has a specialized external wall of the anther lobe which is developed for the most part from a four cell layered epidermis, tapetum and two layers lying between them (Fig. 1 h-j). The fact is unmistakable that for the latter, and/or the intermediate layer, it results from tangential division of common mother cells. Secondly then at least anticlinal divisions (Fig. 1 h) take place in the central and intermediate layer. Locally the external wall can even be only two- or three-layered (Fig. 1 h-i). Since the cells in the different layers lie opposite to each other, the formation of the archesporium and the cell walls in the same way have to be carried out as with most (all? see FAGERLIND 1937) angiosperms. A fibrous layer is not formed however. ZWEIFEL indicates that the central layer is absorbed briefly before degeneration of the tapetal cells soon occurs. My material shows that the intermediate layer dissolves before the central layer and that degeneration precedes later than that of the tapetal cells. Nevertheless remainders of the three layers are retained for a long time (Fig. 1 j). The anther lobes open as shown in previous studies by longitudinal fissures. The pollen formation could not be observed.

**2. Construction of the female flower and the female inflorescences.** Apart from certain details, the descriptions of the female flower by TREUB 1898 agrees with LOTSY 1899, EKAMBARAM and PANJE 1935 and ZWEIFEL 1939. They stand, however, in sharp contrast to the earlier descriptions by HOFMEISTER 1858 and EICHLER 1868 (see also HARMS 1935),

which were certainly incorrect (see and S. 000). Due to the above-mentioned agreement I can briefly condense my description of *B. elongata* from my own observations.

On the young axis, which comes out later than primary axis, the female inflorescence promptly forms a large number of whorls in decussate rings or more probably arranged in flat spirals (Fig. 2 a). These soon grow, much reminiscent of leaf primordia, and lay themselves on top of each other in a tiled roof arrangement. In agreement with TREUB, LOTSY, UMIKER and ZWEIFEL they are called “scales” below. The scales are first arranged diagonally upward and then for a shorter time diagonally downward (Fig. 2 b). Finally they stand, however, nearly perpendicular to the inflorescence axis. Gradually they are converted into stalked claviform formations. The apical parts of these form “clubs” in such a way that they occasionally touch each other and then cover the female flowers.

During the time, in which the scales change their direction, one observes a change of the epidermis and the hypodermal layer which are under them at the base of the furrow system, which lies between them. The cells of these layers become larger (Fig. 2 a-b), and their protoplasm consolidates. The hypodermal cells stretch in a radial direction. From repeated division of the epidermis cells and further linear stretching of the hypodermal cells, which are under it and which soon divide, gradually a papilliform structure results (Fig. 2 b-c) whose epidermal coat in the cross section shows usually four cell rows (Fig. 2 i). The papillae mentioned above develop later into what is generally called the *Balanophora* female flowers.

Because the floral primordia develop in the “furrows”, one gets the impression that they are arranged in circles around the base of the scales. Whether they belong to these, or whether they develop directly in the axil, is not possible to decide since the scales stand so closely that actually no “internode” is present. In each furrow first a simple set or several simple series of flowers forms, and gradually new rows develop closely on the first. If the scales grow, the flower rows at the base of the furrows shift to the stalk-shaped basal part of the scale. This shift is still more obvious with *B. globosa*, with which most female flowers move up on the scale stalk (see TREUB 1898). With several other genera the female flowers, at least at a late stage, sit clearly on the scales. Judging from the pictorial material of HARMS the scales of *B. pedicellaris* and *papuana* are obviously developed on the secondary axis, which carry the flowers in an annular [Kranz] or spiral form, while on the primary axis no flowers are present. Also EICHLER assigned this view.

Two different statements are present in the literature over the further fate of the central cell of the floral primordium:

1. EKAMBARAM and PANJE maintain that the central cell goes through a row of transverse pitches, whereby a simple cell row develops. In the basal part of this cell row divisions in different directions then take place, so that the row is converted into a three-dimensional cell tissue. A cell lying in the center of this tissue becomes the egg mother cell.

2. The remaining *Balanophora* researchers, who essentially correctly understood the flower formation, regard the original central cell, or a cell derived from that simple cell row, as the egg mother cell. The cells which are next to the epidermis could also be regarded as derivatives of the epidermis.

The second view is certainly the correct one. With *B. elongata* a short, usually simple cell row develops from the central position through transverse divisions, with *B. globosa* this cell row is still shorter. The apical cell of the row proves to be the archesporial cell. Sometimes a longitudinal or slanted division occurs. The cell row can therefore be “doubled” in an particular place. Every now and then two archesporial cells form, which was also observed in former times. They lie then closely over or next to each other (see FAGERLIND 1945). That the tissue, which surrounds the central row and the archesporial cell on the sides, is altogether a product of the

epidermis resulting from periclinal divisions of the epidermal cells, derives clearly from my pictorial material (Fig. 2 c-k). I recently described (FAGERLIND 1945) the development of the archesporial cell to the egg mother cell and to the embryo sac.

Owing to the divisions of the epidermis and the enlargement of the archesporial cell, the floral primordium strongly swells at the center. Meanwhile, above the swelling, a thin, style-like structure develops. About the nature of the development of this “style” the opinions diverge. Two different views are present.

1. TREUB states that the apical epidermal cell transforms from the recent papilliform floral primordium into an apical cell, which then provides for the later formation of the style. After his view a similar process obviously takes place with the liverworts in which the apical cell takes over the formation of the stems.

2. VAN TIEGHEM as well as EKAMBARAM and PANJE maintain that the epidermal cells, which surround the apical point of the central row divide in one level nearly perpendicular to the longitudinal axis of the papillae. The daughter cells likewise divide later, and in this way gradually the style develops. The reason for the formation of the apparent apical cell is that one of the apical cells grows faster and is thereby bent over the others.

Certainly the latter opinion is correct, which comes out from my pictorial material (Fig. 2 c-h). The formation of an apparent apical cell, as with EKAMBARAM and PANJE who found it with *Balanophora dioica*, I have found sporadically in *B. elongata* and *globosa*. With these species the apex of the primary central cell is surrounded by a coat, which consists of four epidermal cells lying closely together (Fig. 2 i). These later divide straightforwardly, as is described by EKAMBARAM and PANJE (Fig.). Sometimes one of the cell rows formed in such a regressive way does not continue with development, their cells no longer divide. In this way the apical part of the style, at least temporarily, becomes three-ranked. By a repetition of this procedure in a further row more apical parts of the style become double-storied or even single-storied. The single-storied is, however, limited to only one cells “story [layer]”. Each time, if a new cell row remains, it shifts the part of the style, which consists of the still active rows, so that gradually it lies symmetrically towards its foundation. The emergence of the apparent apical cell is nothing other than this straightforward process. Tangential divisions at the periphery of the spadix show the indicated variations (Fig. 21 - m). With both TREUB and EKAMBARAM and PANJE as well as with ZWEIFEL cells in the “style” are described or shown, which are not exposed. Such cells really occur, as shown by cross sections of *Balanophora* flowers (Fig. 21-m). They result from the fact that individual epidermal cells of the style divide periclinally, after they developed, how in the cross section is evident, dominating size and position. Such divisions take place in the middle and basal parts of the style. However, they hardly develop - at least not with the species studied by me - a long central cell row, which could be regarded as a continuation of the original central row. Such a case would occur, however, with *B. dioica*, if one corrects the EKAMBARAM and PANJES data concerning the formation of the “ovarian portion” of the female flower. I believe that the alleged central cell row is nothing different here than exposed epidermal cells, which were met by the section, because no pure profiles were taken.

My investigations confirm the opinions of VAN TIEGHEM, TREUB, LOTSY and others that the female flower of *Balanophora* is a compact structure. A style channel, whose presence is defended by HOFMEISTER (1858), ENGLER (1889) and HARMS (1935), is completely missing.

### **3. Construction of the male flower for the remaining *Balanophora* species.**

**Interpretation of the male flower.** The following data on the small spheridium of the male flower is, to a large extent, taken from HARMS from the compilation of the different

*Balanophora* species with very unequal constructions. This circumstance compelled VAN TIEGHEM, who split the genus into several, which are regarded by HARMS as subgenus *Balanophorotypus* (with VAN TIEGHEM the genus *Balanophora* strictly speaking) which has 4-6 tepals and a small spheridium, which in the center of each tepal have two interleaved horseshoe-shaped bent anther lobes (Fig. 1 k). The flower of *B. indica* was described recently by ZWEIFEL (1939). *Balania* usually has 3 tepals. The small spheridium is split into three epitepaler parts. Each part carries two transversely posed anther lobes, one above the other (Fig. 11). The conditions for *Balaniella* agree with what was said above for *B. elongata*. *B. morrisonicola*, which one tends to count as the same subgenus, contains 100 or more irregularly distributed pollen sacs in its small spheridium. *Polyplethia* has 4-7 tepals as well as a flattened small spheridium with 20-60 very small marginal pollen sacs.

Incidentally, with the Balanophoraceae the various stamens often grow together into a synandrium (Helosidoideae, *Langsdorffia*) as well as those which belong to different elementary anthers of the synandria “merged” into the different anther lobes (Helosidoideae see FAGERLIND 1938 a and b). Allocation of the locules into a larger number of smaller ones comes to the fore (*Ditepalanthus* FAGERLIND 1938 b, *Rhopalocnemis* - LOTSY 1901, *Exorhopala* - VAN STEENIS 1931). At least with *Helosis* and *Ditepalanthus*, no fusion of the anther lobes can be proven during ontogeny. Evidently the subepidermal cells, which in other plants remain here somatic and are indeed that, lie between the positions of the subepidermal layers which develop into the archesporium, are also converted to the archesporium. Division must for their part probably be based on the fact that a certain primary archesporial cell or its derivative became somatic or on the fact that it is placed within the subepidermal tissue, which normally develop archespores, the somatic nature is retained.

If one knows the aforementioned conditions for Balanophoraceae, it is not difficult to interpret the nature of the *Balanophora* male spheridium. We certainly are dealing with a synandrium, which is also generally accepted (see e.g. HARMS 1935). With the subgenus *Balania*, fusion is obviously not as complete as with the other subgenera. The elementary anthers and the tepals are unmistakably **superponiert**. Thus it is retained in *Balania* (Fig. 11) and with all Balanophoraceae that have tepals. UMIKERS (1920) indication that stamens and tepals are alternating was corrected (FAGERLIND 1938 a). The demarcation of the different anthers with *Balanophorotypus* thus results automatically. The same applies also to the locular system. Appropriate locules of the anther lobe halves of the same anther are obviously “fused” at the upper end. The arrangement the anther lobes with *Balania* hardly differs from *Balanophorotypus*. The insignificant difference is reliably connected with the strong shortening of the small spheridia. With *Balaniella*, which usually has four tepals, the synandrium might mostly consist of four stamens. Since the median tepal is importantly larger than the remaining, it is not impossible that the median anther is also larger than the transverse one. Possibly both the median anthers and tepals are a fusion product. The transverse corners of the small spheridia (Figs. 1 d, f-g) are reminiscent of the elementary anther of *Balanophorotypus*. It is possible that these corners are elementary anthers. Binding conclusions cannot be drawn however. None of the three possibilities: lengthening locules, locular folding (see Cucurbitaceae) or fusion of a large number of elementary anthers, is impossible. There is, however, obviously a stronger tendency here for fusion of the locules as with *Balanophorotypus*. Therefore, speaking on the subject of locular fusion, they run up on opposite sides of the spheridia. Here concerning the locule, they must belong to different anthers.

Since the projection pictures of the arrangement the locules vary, they do not give reference points, to just as little as the course of the conducting tissue. The latter was, however, the case with *Helosis* (FAGERLIND 1938 A).

Conditions with *B. morrissonicola* and *Polyplethia* are too little known for them to be described and discussed.

**4. Interpretation of the female *Balanophora* flower.** The interpretations of the strongly degenerative female flowers of *Balanophora* differ to a large extent from each other. Some of the older attempts at explanation, which can only be partially understood with difficulty, rely on a wrong view of the construction of the flowers. After HOFMEISTER (1858), EICHLER (1868) and ENGLER (1889) the female flower consists of a very small, egg-shaped naked pistil with a hanging, laterally turned ovule without integuments that is fastened by means of a single-celled funiculus. This opinion divides HARMS still 1935 in the last edition of ENGLER PRANTL. After VAN TIEGHEM (1896, 1907) neither nucellus nor ovule can be distinguished (s. HARMS S. 329), but the egg mother cell forms directly in the cortex of the compact ovules. LOTSY maintained in 1899 that one cannot talk at all about flowers, carpels, placentae or gemmiform seeds: “a protuberance on the axis of the inflorescences forms, whose subepidermal cell forms the embryo sac, while from the covering epidermis a style-like organ grows. By comparing with other plants, in order to explain the morphology of this ‘flower’, construction of the term ‘carpel’ seems to me to be mistaken.” Later he obviously changed his opinion due to the degenerative ovules discovered in *Helosis* and *Rhopalocnemis*. “With Dr. TREUB I consider the flower of the *Balanophorae* to be reduced to a naked nucellus, the style being a mere prolongation of the nucellus; according to us there are no carpellae any more in the genus *Balanophore*.” One actually finds similar extensions of the nucellus within the Gentianaceae genus *Leiphaimos* (OEHLER 1927). GOEBEL (1929) did not view this structure as an actual flower. He assumes that their degenerative tepals have completely disappeared and that the strongly reduced ovule sits on a central placenta, which takes for its part the vegetative apex of the flower. The style should probably be more of a new formation or the last remainder of the lamina of the carpels. One gets the impression, as if GOEBEL would have thought also of the possibility, that the flower, through so-called congenital fusion of more or less degenerative ovules, central placenta and carpel, is developed from only one compact body. On the one hand it frequently appears that ovules and placentae are “fused”, on the other hand between placentae and inner wall of the ovary. In addition they can equally appear from the beginning (thus “congenital”), he wrote, without speaking directly of *Balanophora*. SVENSSON (1936) states that GOEBEL imagined the straightforward formation of the *Balanophora* flower in such a way, and in addition, adds that this opinion recognized by most modern researchers, however, I found was not confirmed.

Also for the remaining Balanophoraceae – of which the following information is, to a large extent, taken from the compilation by HARMS – the female flowers are reduced. Tepals appear only in the subfamily Mystropetaloidae, Dactylanthoideae and Helosidoideae (*Scybalium?*). The female flower here always consists of a more or less strongly reduced gynoecium. The perianth is epigynous. The tepals are strongly reduced. The latter cluster exists as a tiny, collar-shaped structure inserted around the apex of the ovary. With the remaining subfamilies these disappeared completely. All members of the family seem to have a central placenta (*Ombrophytum?*). With *Latrophytum* the central placenta carries two sessile ovules with broad bases, which are obviously not arranged into integument and nucellus (EICHLER 1868). With *Lophophytum* it probably behaves likewise (see EICHLER 1869). With the Helosidoideen the ovules are not an offshoot of the central placenta, and their situation corresponds to that of *Lathrophytum* (see FAGERLIND 1938 a and b).

One finds the same design of the pistils as with *Lathrophytum* and Helosidoideae with the Loranthaceae, from which it appears that similar reduction features are present in this family as

with the Balanophoraceae. The [Kelle] of reduction phenomena is, however, here more gradual, which is possibly connected to the larger wealth of species. One also finds pistil types, which can be easily inserted into this chain, in the families Santalaceae and Myzodendraceae. For the above mentioned families cases are well-known, where the placenta has differentiated ovules with a clear funiculus and which show a tendency towards the demarcation of nucellus and integument (*Thesium* FAGERLIND 1939, see also SCHAEPPi and STEINDL 1937). Thus here the features deviate somewhat from the usual with the angiosperms. The reduction tendencies are only initially suggested. Furthermore, there are cases in which the ovules are developed, but exhibit a placenta with a broad, sessile base and extremely insignificant or no differentiation of the nucellus and integument (*Santalum*, *Osyris*, *Myzodendron* SCHAEPPi and STEINDL 1937, SKOTTSBERG 1913, FAGERLIND 1937). The next step is to describe cases of ovules present only as weak projections of the placenta (*Macrosolen*, *Dendrophthora* TREUB 1885, YORK 1913). Still further degeneration prospers in *Arceuthobium*, *Korthalsella*, *Ginalloa*, *Helosis*, *Rhopalocnemis* and *Ditepalanthus* (TREUB 1885, LOTSY 1901, RUTISHAUSER 1935, 1937, FAGERLIND 1938 a and b). Here the ovules are missing completely and their mother cells lie in the placenta. With *Korthalsella* the degeneration is particularly strong, which emanates from the insignificant size of the placenta. With *Viscum* (STEINDL 1935) and *Dendophthoë* (SMOKE 1936) the central placenta has disappeared completely. The basal egg mother cell here is subepidermal because of the rather clearly marked cavity of the ovary. This cavity is hardly extended with *Scurrula* (SMOKE 1936), but the egg mother cell is here subepidermal at the base of the style channel.

With the Rubiaceen (FAGERLIND 1937) I proved a reduction during the development of the nucellus and the ovule. Many species have integuments, which enclose a long micropylar canal, and projecting in these a strongly developed, typical tenuinucellus. With others the convexity of the nucellus became so small that it emerges only as an insignificant curvature at the base of the micropyle. The number of the cells in this curvature is very small with *Oldenlandia* and *Bolwardia*. With the first genus, in many cases only one epidermal cell is present, which forms the base of the micropyle. Finally with *Houstonia*, the micropyle has disappeared, because the completely apically situated cells of the ovule are involved in the formation of the “integumentary tissues”. Continued formation of integumentary tissues in connection with the complete disappearance of the nucellus leads here to the formation of an undifferentiated, compact ovule. Here we have thus striking proof of the fact that total reduction of the central part of a structure, which originally consisted of a central body and its surrounding mantel-shaped covering, can lead to the emergence of an undifferentiated, compact structure.

The reduction features of the Rubiaceae stand partly thereby in connection [with the fact] that the integuments are set ever more near to the point of the undifferentiated ovule, partly by the fact that the later volume increase of the young nucellus becomes ever smaller. The observation is very interesting that the differentiation of the common construction into central placenta and fruit wall with *Helosis* - probably the only case with the Loranthaceen and Balanophoraceen to which detailed studies were dedicated (UMIKER 1920, FAGERLIND 1938 a) – that such differentiation of the ovules proceeds in an analogous way in Rubiaceae. The fruit wall results from divisions of cells which lie below the apex of the plant. The apical part over the division zones becomes the central placenta. The divisions lead to the formation of the carpel. In the same way as the integument with Rubiaceae, the walls of the pistil with Loranthaceae, Balanophoraceae etc. form a coat; a coat forms around the nucellus around the central placenta. The reduction of the placenta to a bulge with a few cells forms a parallel to conditions with *Bouvardia*. Conditions with *Scurrula* can be composed in parallel to those of *Oldenlandia*. One thus sees clearly that a reinforcement of the reduction tendencies leads to the fact that the style

channel disappears in the same way as the micropylar canal with *Houstonia*. If such a process would take place in the pistil of *Viscum*, then easily the same conditions would also occur with *Balanophora*.

My judgements can therefore allow one to draw the conclusion that the female flower of *Balanophora* comes phylogenetically from a hypogynous flower with a central placenta and normal construction and that in the course of the phylogeny the following processes gradually took place: 1) reduction of the tepals up to completely disappearing, 2) reduction of the integuments up to complete disappearing, 3) reduction of the ovule up to disappearing, which leads to the egg mother cell and its derivatives being shifted into the central placenta, 4) reduction of the central placenta up to completely disappearing, which leads to the egg mother cell and its derivatives lying at the base of the fruit cavity, 5) reduction of the fruit cavity up to completely disappearing, which leads to the style channel disappearance and to the egg mother cell and its derivatives to be situated in a compact pistil. (the degenerations are illustrated in Fig. 3).

If one uses the expression “congenital” fusion for the degeneration phenomenon described above, then major agreement with certain trains of thought with GOEGEL show up (see above).

Except for the degeneration tendencies of the flower of Balanophoraceae and Loranthaceae represented above, the following also speak to the fact that my explanation is correct: the embryo sac of *Balanophora* is formed by the apical cell of the cellular tetrad. During growth it curves on its own, not in the previous announced way. The basal part of the embryo sac attains full growth after the sides bend upward and continue to grow so for a long time, until they reach a place directly over the original apical pole. In the original basal pole the egg apparatus later forms. The curvature movement is certainly reminiscence of the procedures of the ancestors. With *Korthalsella*, *Ginhalloa* and *Dendrophthora* RUTISHAUSER 1935, 1937, YORK 1913 obviously homologous curvature movements occur. Here we do not have to do it with one of the central placenta or to only an insignificantly defined ovule, in which a two-cellular tetrad develops, whose apical cell forms the embryo sac. The lowest part of the embryo sac grows down by the placental tissue, turns upward under the “seam” between the central placenta and fruit cavity wall, and grows into the tissue of the latter where it then forms the egg apparatus.

The existence of three or rarely as the case may be [and respectively] one standing phenomena as the strong degeneration of the pistil compartments, the formation of the embryo sac from the apical tetrad cell and the curved embryo sac with the Loranthaceae and *Balanophora*, can hardly be interpreted differently than the presence of a real relationship. Exceptions to these various agreeing features are available, e.g. the fusion tendencies of the androecium, disappearance of walls between bordering anther lobes, and the emergence of new walls in the anther lobes.

**5. Interpretation of the scale development of *Balanophora* inflorescences.** TREUB and LOTSY explained that there would be no sterile scales occurring on the female parts of the *Balanophora* spadix that are homologous to other plants. EICHLER had earlier regarded the scales as flower axes of the second order. Also he upheld subtending bracts (see UMIKER 1920). For the latter view he speaks of a temporary phylloid [Blattform]. The fact that the scales carry the female flowers with many *Balanophora* species in reality would have to be explained then with “displacement phenomena”. The impression that the female flowers are grouped in circles around the base of the scales or their starting points, however, is hardly compatible with this view.

Much speaks to the fact that EICHLERS view is correct. There are species of the Balanophoraceae in which the female inflorescences clearly stand out as secondary axes

(subfamily Sarcophytoideae see HARMS 1935). With *Lophophytum* (EICHLER 1869) and *Juelia* (ASPLUND 1928) both the male and female flowers sit in spirals on second order axes supported by bracts. In the first genus the apical portions of the bracts are converted to shieldlike structures, which temporarily form together a casing [armor, carapace] which covers the flowers. The subtending bracts soon drop. *Juelia* has in contrast to *Lophophytum* secondary axes whose apical parts are changed into shieldlike sterile disks. The remaining Lophophytoideae representatives do not have subtending bracts (or if they occur they nevertheless quickly fall off, see ASPLUND 1928 and HARMS 1935). The apex of the secondary axis is sterile and takes on the form of a stigma, a bowl or a disk. The Helosidoideae have between the flowers shieldlike scales which are provided with a stalk in their center (for *Scybalium* at the outer edge). At least with *Helosis* and *Ditepalanthus*, the flowers sit in concentric rings around the base of the scales (FAGERLIND 1938 a and b). EICHLER indicates that the flowers of *Scybalium* and *Helosis* sit slightly elevated over the principal axis of the small, flattened capitulae, which represent second order axes. With the *Helosis* material previously examined by me I could not notice such increases. They were more developed with *Ditepalanthus*, where the floral whorls sat symmetrically around the mantel of a broad cone, around its so called apex. Scales are attached. It appears to me completely unmistakably that the inflorescence and scale conditions differ from the Helosidoideae only a little and from those of most Lophophytoideae. The fertile part of the secondary axis of the inflorescence obviously expanded along the sides and at the same time became shorter, so that it increased only little over the surface of the primary axis. Without concern over such an “expansion processes”, the position of the flowers would be incomprehensible. The fact that *Ditepalanthus*, *Scybalium*, *Helosis* and the remaining Helosidoideae represent a series with constantly rising tendency towards flattening of the basal portion of the secondary axis thus clearly stands out. The stronger this tendency becomes, the more one gets the impression that the “scales”, thus the apical sterile portions of the secondary axes, sit directly upon the primary axis.

From the basis of the above implementation one comes easily to the same conclusion about the scales of the female flowers of *Balanophora* as did EICHLER. He gives the impression of second order axes sterile in the apical part. In the case of e.g. *Balanophora elongata*, one rather gets the impression that the flowers sit between the basal parts of the scales, and that this is connected to the “expansion” of the basal parts of the secondary axis. The position of the flowers in relation to the scales is not incompatible with the mentioned view, even if their arrangement does not stand out as clearly in concentric circles or spirals as with the Helosidoideae and the Lophophytoideae. With the Helosidoideae and with *Balanophora*, obviously the sterile apical parts of the secondary axes in place of the subtending bracts, which have disappeared, the function of the subtending bracts of *Lophophytum* are to form a casing which protects the young flowers.

Concerning the male flowers, the evidence indicates for *Balanophora* the arrangement and the subtending bracts which are between the scales, later construct the subtending bracts of the flowers. This view is completely generally recognized (see HARMS 1935) and perhaps correct. ZWEIFEL, however, does not draw this conclusion. He calls the scales sterile spadices and obviously considers them homologous to those of the female inflorescence, which from the preceding are probably second order axes or apical portions of them. The debate over the scales of the female inflorescences shows that one must proceed very carefully with the evaluation. In my judgement of the scales of the male inflorescences, three different explanations are possible: They are 1. subtending bracts of the flowers, 2. inflorescence axes of second order, which are sterile at the apex and carry at the base only one flower, 3. subtending bracts of the strongly shortened single-flowered second order axes. Within the family, however, flower subtending

bracts are a rarity. Likewise a strong tendency stands out for the complete recovery of the subtending bracts of the secondary axes. Thus the nr. 2 explanation indicates that the scales of the male and female inflorescences are homologous, correct? With all Lophophytoideae except *Lathrophytum*, the male flowers sit in whorls or spirals on second order axes. With the latter genus each male flower sits “on a triangular, laterally squeezed together protrusion from whose apex is horizontally drawn downward in an inclined spiral.” This “protrusion” is regarded of EICHLER as male flower axis. Conditions with the subfamily in all other respects speak for the fact that ENGLER is right, if he explains his transformed single-flowered second order axes. One can possibly say the same of the scales of the male inflorescences with *Balanophora*. Since the subfamilies of the Balanophoraceae represents clearly different trends, which have, however, a whole number of common tendencies, one cannot conclude too much from the individual case of *Lathrophytum*. The question about the morphological nature of the scales of the male inflorescences with *Balanophora* must therefore remain provisionally unanswered. Possibly a study of those *Balanophora* species, with which the male and female flowers are evenly distributed over the same spadix, would bring a solution.

#### Summary.

1. The male and female flowering spadix of *Balanophora elongata* and the female of *B. globosa* were examined in the detail that the available material permitted.
2. With the male inflorescences scales between the flowers, whose basal portions grew together to a “honeycomb-like” pit system. In each “pit” sits a male flower.
3. With the female inflorescences one finds spadix-shaped [kolbenförmige] structures, “scales” between the flowers, around whose basal or originating portion the flowers are approximately concentrically arranged. The arrangement of the scales is described briefly. They give the impression of inflorescence axes of second order.
4. The male flower unmistakably contains a synandrium. The number the anther lobes is large. The different locules often gather in the top of the synandria. The large number is based on folding or splitting of the “original” or later locules, where more anthers are present than one expects from the number of the tepals.
5. The external walls the anther lobes consist of epidermis, central layer, intermediate layer and tapetum. One or two of the middle layers can be missing in parts. A fibrous layer is not formed. Everything speaks for the fact that the wall layers likewise form as with the remaining angiosperms.
6. The female flowers are strongly reduced. They consist only of an epidermal cell and their division derivative and a usually simple cell row, whose apical cell becomes the egg mother cell. The construction of the flower is explained as a result of complete reduction of all differentiation processes, which otherwise lead to the formation of ovarian pericarp, fruit area, placenta, ovule etc.
7. Homogeneous reduction processes during the flower formation of the Balanophoraceae and Loranthaceae, as well as different other features mentioned above, speak for the fact that the families themselves stand phylogenetically close.

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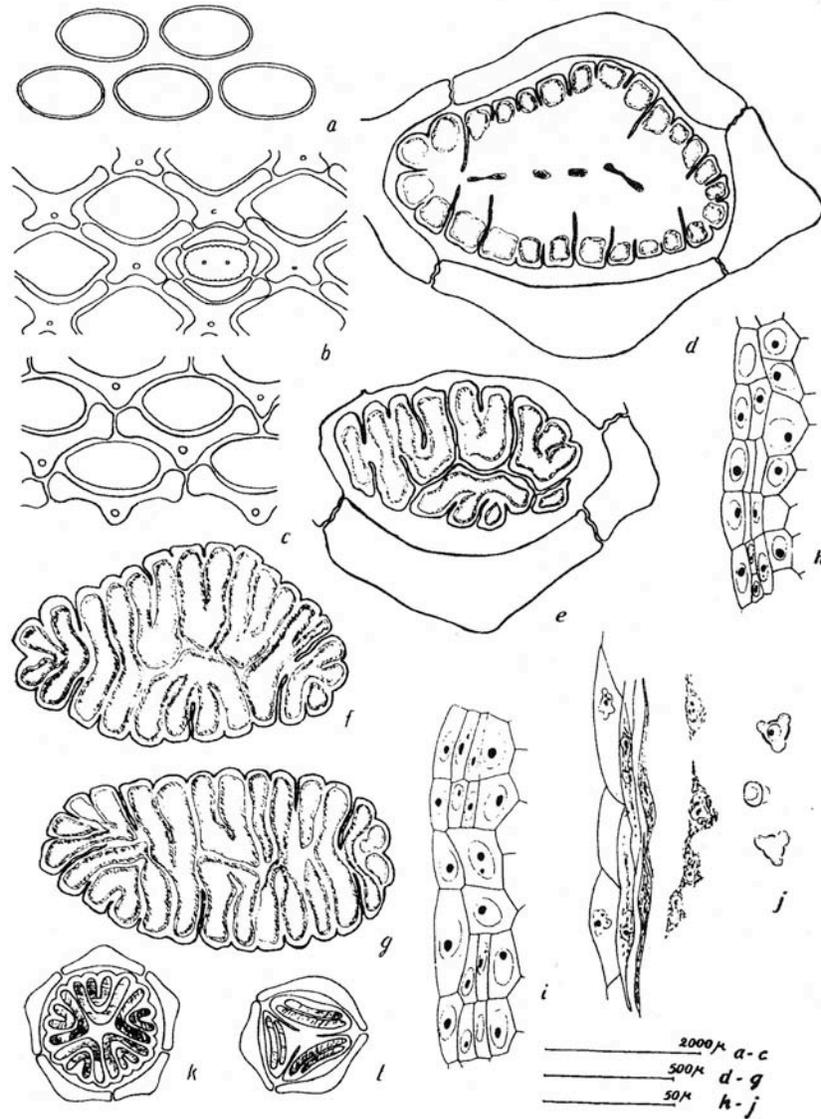


Fig. 1. *a—j. Balanophora elongata*. *a—c*. Cross sections of male flowers and corresponding scales at different levels. *d*. Median cross section of a male flower. *e*. Cross section at the apical part of the male flower *f—g*. The anther lobe system of the male floral spheridium, projected on one level. *h—j*. arrangement and exploded view of the anther lobe walls. *k*. Schematic picture of the construction of the male flower of *Balanophorotypus*. *l*. Same with *Balania*.

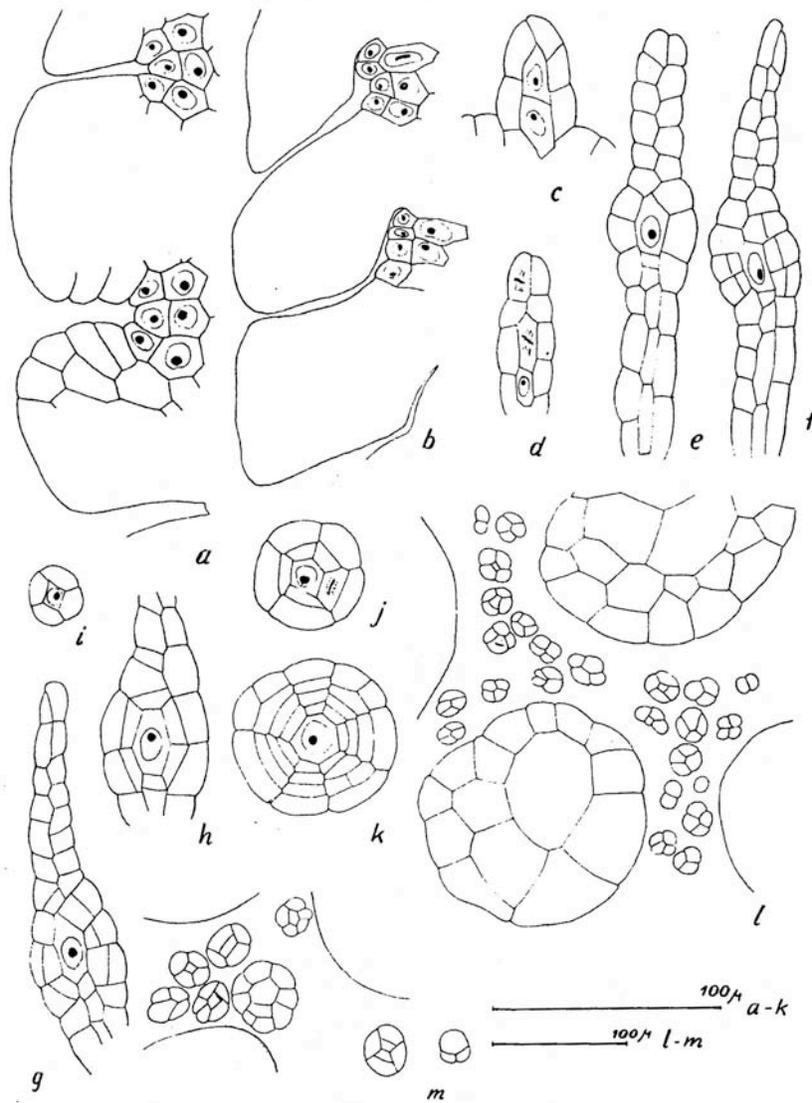


Fig. 2. *Balanophora elongata*. a—b. Scale of the female inflorescences with recent floral primordia in the “furrows”. c—k. Different development stages of the female flower. The sections are made centrally. l—m. tangential section through a female inflorescence, which shows a transverse section through the scales and female flowers. (Fig. m deeper than l).

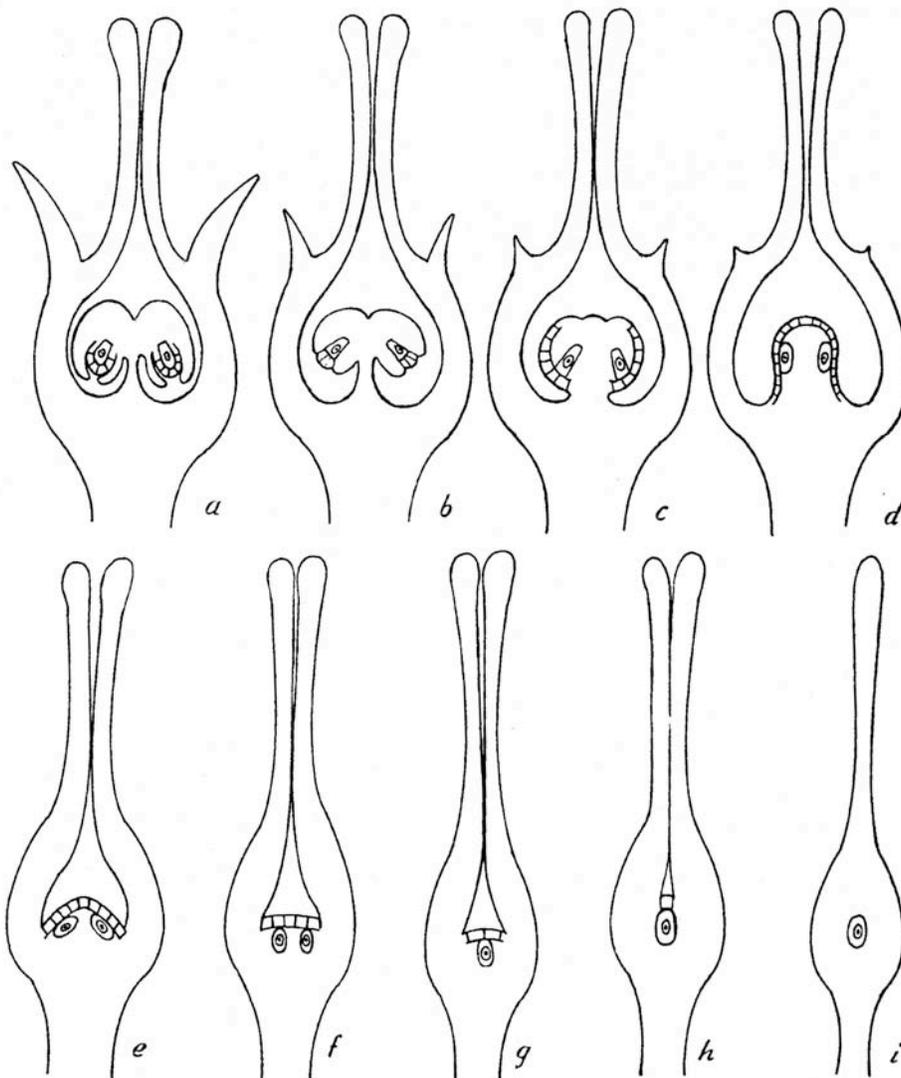


Fig. 3. Schematic representation of the derivation of the *Balanophora* flower (a shows normal ovary and placental conditions, b conditions with *Thesium*, c with *Osyris*, *Santalum* and *Myzodendron*, d with *Arceuthobium*, *Helosis*, etc., e with *Korthalsella*, f with *Viscum* and *Dendrophthoe*, g—h with *Scurrula* and i with *Balanophora*).