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ON THE STRUCTURE OF THE FEMALE FLOWER OF SOME BALANOPHORACEAE

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Gentlemen,

If I may for a while call your attention to the family Balanophoraceae, it's not that I claim to expose the complete and definitive outcome of investigations. Far from it, my paper will deal only with some parts of the subject; but as it deals with issues still little known, and that it may throw some light on them, I hope to ask this learned assembly, considering the interest that these curious plants offer, to lend me their kind attention and give me all their indulgence.

Despite the beautiful and recent research by Mr. J.-D. Hooker, Weddell and Hofmeister (1), it is in the natural history of Balanophoraceae, a point on which there is still some darkness: the morphological structure and composition of the female flower. Allow me, neglecting the old views that could only be very imperfect, because of the inadequacy of the method and means of investigations, immediately throw a glance on the current state of science regarding this topic.

In the simplest case, the female flower consists of a naked pistil: this is the organization of *Balanophora* and *Sarcophyte* (f. 1). In other genera, there is a perigone adjoining the pistil and adherent to it, and mostly over it as a few distinct limbs (f. 3, 5-9). Sometimes entire, dentate or crenate (f. 3, 5, 8), the limb only affects *Mystropetalum* in the form of a pronounced and regularly lobed perianth (f. 10). This formation progresses in *Cynomorium* whose perigone consists of several petals, whose number ranges from 1 to 8, which are not fused together (f. 11), and often adhere to the pistil at its bottom. It is still the only genus in which it is sometimes found in the female flower the rudiment of a stamen (f. 11). This body is lacking, in fact, in the female flowers of other family members.

The pistil has this characteristic difference in that each is provided with one style (f. 1, 3, 10, 11), in others with two (f. 5, 7, 8). It is from this difference that the family Balanophoraceae was divided into two groups: Monostyli and Distyli; and that it was thought that only one carpel [exists] in the first and two in the second.

According to observers, including the just-mentioned research, the ovary usually contains only one ovule, erect in each and inclined in the others. In preparations of Hélosidées (2), there is both atropic and orthotropic or without integuments, sessile at the wide base at the bottom of the ovary, and adherent to the ovary wall everywhere: it is a ovoid or oblong parenchyma mass, embedded with an embryo sac located in the center near the top (6 f.). But, according to Mr. Hofmeister, *Scybalium* present a remarkable exception in that it has two extra-axillary and symmetrically opposite embryo sacs (3) (f. 7).

The inclined ovule is specific to the groups Lophophytées and Monostyli. On Lophophytées, we do not have no recent indications as Mr. Weddell (4), which imply a naked and anatropous nucellus, freely pendant from the summit of the ovarian cavity (f. 9). But this contradicts descriptions from the data, which have been there already more than thirty years, by Mr. Poeppig for *Ombrophytum*, and Messrs. Schott and Endlicher for *Lophophytum* (5). According to these descriptions, whose seniority prevented that we would give them much importance, the ovary contains two ovules in two locules.

In the tribes Sarcophytées and Langsdorffiées the ovule is made, according to M. Hofmeister, from a single cell that is freely hanging from a likewise unicellular funiculus (f. 4 f), near the top of the ovarian cavity (f . 4). The situation of the embryonic vesicles, located in the vicinity of the funiculus (f. Ls v), shows that this ovule is anatropous, despite the simplicity of its structure (6).

The group of Balanophoraceae proper, which consists only of the genus *Balanophora*, has a simple ovule, yet composed of a few cells. It is, however, like the previous one, devoid of an integument, anatropous, and attached by a unicellular suspensor at the top of the ovarian cavity, where it hangs freely (f. 2).

Finally, in Cynomoriées and Mystropétalées, we find the most developed ovule of those families: it consists of a multicellular nucellus, dressed in a plain integument, but also composed of several layers of cells (8) (f .12). Hemitropous in *Cynomorium* (f. 12), it is in *Mystropetalum* perfectly anatropous, however, in both genera, it hangs freely from the top of the ovary by a short funiculus, or it is immediately attached to its chalaza (f. 12).

These are the principle modifications that occur in the structure of the female flower of Balanophoraceae. These are very significant differences in appearance that would be encountered only very rarely, perhaps never, in another order of the plant kingdom, and can in no way be reduced to a common type. This is especially from those differences that we tried, firstly, to divide the family in groups, secondly, to determine the systematic position. In respect to their affinity, the Balanophoraceae today are generally placed in the vicinity of Haloragaceae, especially on the authority of Mr. J.-D. Hooker and Hofmeister. To characterize this report, Mr. Hooker is based mainly on the external structure, Mr. Hofmeister more on reasons drawn from embryology, Dr. Hooker reads in part:

> "The epigynous upper tepal and stamen of *Cynomorium* (that genus should decide the issue, since it is the most developed of the order) would classify Balanophoraceae among epigynous Calyciflores; and it would obviously be the genus *Hippuris* that by its single stamen, by its monocarpellate pistil and single style and its unique inclined ovule, would represent the most approximate shape of *Cynomorium*. On the other hand, for the Distyli, it would be the genus *Gunnera* also of the order Haloragaceae (broad sense), which proves the affinity of the two families. For the pistil of *Gunnera* (subgenus *Misandra*), with its two styles, its only ovule inclined, its perigone adherent, is almost similar to the female flower of *Lophophytum*; the male flower of both genera, by its perigone composed of two petals and two alternate stamens, also denotes closer affinity".

Mr. Hofmeister confirmed this view, not only because the very exceptional ovule for Balanophoraceae, reduced to a completely naked nucellus, is found in *Hippuris*, but because the endosperm is formed in both genera in an identical and equally outstanding manner, the complete partition of the whole embryo sac, and not, as in most genera, by free cells. - Among the many hypotheses made on the affinity of Balanophoraceae, that of Mr. Hooker f. and Hofmeister is definitely the best substantiated; however, he errs in that he provides only incomplete reports, because the authors have neglected the erect ovule forms, which have no analogues among Haloragaceae.

I will now ask the congregation permission to exhibit my own research, and I first choose as the most favorable for the clarity of the beginning, the female flower *Lophophytum*, especially *L. mirabile*.

The materials that were used in this research consists of a beautiful series of specimens preserved in alcohol and collected in the vicinity of Canta Gallo, Rio de Janeiro province, by the Honourable Dr. Theodore Peckolt. These samples are part of Mr. Martius' collections; they were put to me by this illustrious scientist with the greatest kindness. I eagerly seize this opportunity to publicly express to Dr. Martius my sincere and deep thanks. I am also extremely grateful for the communication of precious materials, Mr. Naegeli, Director of the Botanical Museum of Munich, Mr. Al. Braun and Garcke who sent the Balanophoraceae from the Royal Herbarium Berlin, to M. Fenzl, to whom I owe those of the Imperial and Royal Herbarium of Vienna, Mr. Wigand (Marburg) at MJ-D. Hooker and Mr. Weddell.

Observed from the exterior, the flower of *Lophophytum mirabile* has the shape of a hexagonal cone, inverted, elongate, slightly compressed, somewhat narrowed in the middle, and completed at its top, by a crater-shaped depression which emerge two short and divergent styles (f. 8). Except at its base, this flower has a hard consistency, almost boney towards the top, and of a yellowish color; it has a length of 4.5 mm. To facilitate the understanding of its internal structure, which can not explain in a few words, it will be good to get right into the organogenic examination.

The flowers of *L. mirabile* born immediately below the top of the inflorescence axis, which are united with the female flowers, and which form when young a broad hump, but relatively low, in the form of a hemispherical nipple, in which there is no trace of bracts (9) (f. 13a). The nipple then lengthens into a short cylinder or a claviform body, without further change (f 13 b.); then begins another phase. The cells situated immediately below the summit enlarge, divide and subdivide, and form two opposite projections that point to the left and right of the anthodium axis (f. 13 c). By increasing rapidly, these projections will soon take the form of a flared spoon (f. 14) that are inclined toward each other, bending at the top, and ending up together from the base (f. 14, 15). By doing this, they constitute an ovoid-shaped cavity, compressed, which is first in communication with the outside through a channel located at its top, and which persist long enough in this state (f. 15). The union of the edges, moreover, is so perfect that we do not find any trace in the developed flower. It should, furthermore, be noted that the two organs (which are other than carpels, as we shall see more clearly later this exhibition) share first, internally, in two layers consisting of a single row of cells originally. One of them, the outer, does not increase by vertical partitions in its surface, and is therefore, in this direction, always composed of a single row of cells. Later, they expand, mainly towards the top, and they acquire thick, porous, hard and whitish walls; the content becomes clear and disappears, and everything finally turns into a well pronounced epidermis (f. 15-18) (10). The inner layer, however, being increased by divisions in all directions, is soon made of several rows of cells that continually increase and differ very much from the epidermal cells by their thin walls and by their plasmatic and grainy cytoplasmic content (f. 15-18). It is, therefore, this layer that formed the largest mass, the body, so to speak of the flower, and it is in this part that subsequently operate most of the phases of development.

The top of the primitive nipple, which gave birth to the carpels, and is therefore the floral axis, during the beginning of development I have just described, is hidden between the carpels at the base of the flower, where it forms a barely visible hemispherical hump (f. 15 a). But it soon rises, goes into a free cone in the ovarian cavity and laterally produces two new organs, namely, two very small areolar mamelons, that are each located opposite a carpel. They grow, and as they are gradually lowered to the base, all soon takes the form of a column, the top of which hang two ovoid bodies (f. 16 ov), which are the ovules in their first phase of development.

During this, the carpels that were left open at the top, are united, and the ovarian cavity is closed on all sides (f. 16). The styles with closed tops are born immediately (f. 16). This is the outer layer (which plays the role of an ovarian epidermis) giving birth and their development due to a secondary development. But it would be of great interest to enter into the details of this development, and I think also neglect the description of the structure of styles. Let me just point out that each of them is exactly in the center line of carpel which it belongs, and that, therefore, they are both oriented, as are the ovules; left and right of the center of the anthodium.

As for changes in the interior of the carpels during the birth of ovules, there are only two that should be noted. First we see a parenchymal area, located around the top of the ovarian cavity, turn into a ring of very thick walled sclerenchymatous cells; porous and whitish, formed by superimposed layers, the content of which eventually disappears (f. 16 sc). This ring, very thin at first, gradually increases by adding neighboring cells that turn into sclerenchyma cells, and comes to represent a thick bell-shaped coat, open at the top allowing the thin tissue that leads styles (f. 17 sc). We still encounter in a degree of further development, structure of cells scattered in small groups over the ring in the vicinity of the summit (f. 17 sc'). - At the same time begins the formation of vascular bundles. They enter, originally two in the floral axis; they are located one on the left, one on the right, and thus correspond to the two carpels; but slightly above the base, each of them giving rise to a branch which curves toward the center of the flower, one in front and one in rear, so that, on the horizontal section, we find four arranged crosswise (f. 18 f), because these amount to four fascicles that maintain their respective positions until they end abruptly at the sclerenchymatous coat of the outer surface (f. 17 f).

The axile column and the two young ovules attached to it, continuing to rise, eventually filling the ovarian cavity completely; the column expands so in the direction of the center line, it touches the walls in front and back. So the whole system is mingled with ovarian walls, so that the whole flower represents a solid body. It is obvious that this is the column that thus forms a complete partition between the two ovules (f. 17-18).

So the flower reached a stage of development that can look almost as definitive. It even underwent some changes to its perfect development; but only to complete the formation of parts already established and not to create completely new bodies.

These subsequent changes, we must first mention the development of embryo sacs. This form, as usual, one in each ovule; developed in the flower, the sac is an elongated extraaxile utricle, located in the vicinity of the partition, containing two embryonic vesicles at its upper end and two antipodal vesicles at opposite points (f. 19). One can conclude from this that the development of the ovule followed the anatropous type and (in the words of MJ-G. Agardh) apotropous, we even had to assume it already by the configuration that had taken tissue in earlier phases. The rest of the tissue of the sac surrounding the ovule is transformed by repeated divisions in a very tight regular parenchyma, filled with a cloudy and opaque cytoplasm, by which it is very clearly distinguished from the tissue of the ovary wall and the wall, which remains much clearer (f. 17-19). It should, however, be noted that the top of the partition is developed in the same manner as ovular tissue, so that the two ovules eventually appear mingled, above the partition (f. 17). Moreover, it is hardly necessary to state that these ovules are completely devoid of an integument, as this result is obvious from the figures.

The last phase of development that I have yet to mention is that we see a proliferation of cells at the base of the wall and the innermost layer of the ovary wall, around the time the ovules are mingled with it. This multiplication ceases only when the flower has reached perfection. As the cells thus formed are much smaller than those around them, is formed in this way a special parenchymal coat that surrounds all the ovular system and tapers towards the tapering styles (f. 17-19 m). This is a layer of this part which turns into the sclerenchymatous layer of the fruit (11).

It is here that ends the development of the female flower, therefore adapted to receive the impregnation. Later phases belong to the fruit.

After the exposition, the morphological explanation of the floral organ of *Lophophytum* offers more difficulties. The primordial mamelon is the axis; the two lateral organs that are born and which give rise to the styles are the carpels. The whole flower is therefore only a naked pistil. The median septum, resulting in the development of the primarily free and central ovuliferous column, must be regarded as a placenta, and a placenta as a direct continuation of the floral axis; finally, the rest is self-evident. I just have to point out that the morphological significance of the ovules have the character of a transformed bud rather than a leaf (12).

I have considered the flower as a naked pistil; authors who have preceded me have, it is true, attributed a perigone to what they took for such a crateriform edge that crowns the top of the flower. But it is obvious that this interpretation is unfounded. Indeed, this edge, this so-called limbus, must, as we have seen, give rise to carpels; and what best proves how impossible it is to bespeak of perigone, in the constitution of the flower, if only a single layer of cells, the tissue that emits styles and which therefore undoubtedly belongs to the carpel forms the outermost part, that is to say, the epidermis of the flower. We find, moreover, many analagous examples to follow carpel around the base of styles, especially among gynobasic pistils, etc.

The structure of the female flower of *Lophophytum* and reveals a form entirely new and unexpected in the family of Balanophoraceae; in addition, it allows us not only to explain previous indications of Messrs. Schott and Endlicher (13) that so shocked modern botanists, but also to correct taxonomic views based on the structure of this genus. But let me, gentlemen, give up about this for a while, which I will return later.

The male flower *Lophophytum* looks great, on the whole, as the female flower of the same genus; it also consists of only two leafy organs: two stamens supported by a very shortened axis and located as carpels, left and right of the center of the anthodium on which the flowers are still joined. Botanists have granted it a perigone, considering as such some fleshy scales that are between the stamens, but these are only aborted ovaries. There are similar bodies intertwined with the *Langsdorffia* male flowers and other plants of this order (14).

The structure we have just described is not unique to the one genus *Lophophytum*: it is still found in some others, and first in *Ombrophytum*.

Thereof is extremely similar to the previous. The female flowers, regardless of the size of the parts and some minor details are barely distinguishable from those of *Lophophytum*. What I am saying here confirms the accuracy of the description previously traced by Mr. Poeppig (15), who attributed to this plant two ovules separated by a partition; and nothing will change in the morphological interpretation. The same conformity exists between the male flowers of both genera.

Another genus enters this type: *Scybalium*. It would take too long to describe the structure; I merely give (Pl. II, f. 20), a figure that will be enough if we refer to the explanation of the plates, to demonstrate the perfect analogy between *Scybalium* and *Lophophytum*. By analogy to explain not only the old descriptions (16) which gives *Scybalium* two ovules separated by a partition, but the latest indication of Mr. Hofmeister (17) which grants it one ovule with two embryo sacs. This is due to what Mr. Hofmeister did not realize were the two nucelles, he confused the cells with the surrounding ovarian tissue.

If we found in the previous three genera, all of which are American, always two carpels and two ovules, on the contrary *Sarcophyte*, a genus of Southern Africa, presents these bodies three in number, without altering any of the main types of the previous organization. However, as the materials I could have were not clean, the delicate examination required by organogenic education, I can safely transmit this assertion; I can only say that Mr. Hofmeister's description (18), which assigns *Sarcophyte* a unicellular inclined ovule (or sometimes two by exception) is not accurate, and that I always found myself three ovules, with a multicellular nucellus, separated by as many septa that join on the axis, and adherent, from all sides, to the septa and ovarian walls (pl. II, f. 21 and 22). I do not know if the ovules are erect or inclined, anatropous or orthotropous, and I do not know more, in this genus, the nature of development of the partitions; but, considering the undeniable affinity of *Sarcophyte* with Lophophytées, and recognizing how they are near [each other], by the totality of its floral structure, genera of this tribe, one can conclude that this structure differs only in the number of organs. I am willing to believe that the flower of *Sarcophyte* is also a naked pistil (as is the opinion of all the botanists), it consists of three carpels, first it provides a free axile placenta, with three descendant ovules attached to its top, which eventually become anatropous and apotropous, a placenta that widens, subsequently forming the partitions between the ovules, and finally merges with the latter and with the ovary wall into a solid body.

The male flowers have a perigone in *Sarcophyte* and in *Scybalium*. This can not change anything in the explanation we have given of the female flower; especially as in all other genera of Balanophoraceae, except only *Lophophytum* and *Ombrophytum* there is no point of similarity between the flowers of both sexes, with respect to their morphological composition.

In the group Hélosidées we will find structure and development quite different from the previous (I excluded *Scybalium* already described). I will use this new type of examination of the genus *Helosis*; putting down, to be brief, I will report on the main features, returning for the rest to the Flora brasiliensis and memory already cited several times by Mr. Hofmeister, whose Hélosidées-related investigations seem to me, with few exceptions, to provide highly accurate results.

The flower of *Helosis* is born, like that of *Lophophytum*, as an areolar mamelon representing the floral axis. This produces two opposite projections (f. 23), increasing rapidly and joining the edges, soon forming a bag, overcoming the axis and carrying two elongated spikes that meet the peaks of the primary projections (f . 24-26). Since these two points are transformed later into styles, organs that produced them, that is to say, the two projections, should be considered as carpels. However the floral axis increases along the carpels without further change (f. 24-26); and when they eventually collect at the top and also by forming the ovarian cavity, they completely fill the cavity, and merges on all sides with the walls. While it results in a very intimate union, a suture remains quite visible from the difference in the juxtaposed cells, a suture that very clearly indicates where the axis begins and where the end of the carpels are (f. 27). Finally, a cell located slightly below the top of the axis, is transformed into an embryo sac and provided at its upper end with two vesicles; nearby tissue is randomly filled out with disorderly thick cytoplasm; Briefly, the top of the shaft is transformed directly into an ovule (f. 27). As for the subsequent changes occurring in the carpels, they offer nothing very interesting; I also omit, but without neglecting to note that the top of the carpel rises almost as in the *Lophophytum*, around the base of the styles in a short limb, thin and irregular, which crowns the top of the ovary (f. 25-27). It therefore has no limbus the value of a perigone, we always recognized value it; this is just a simple extension of carpels.

The flower of *Helosis* is reduced to a naked pistil, like the previous ones, and consists, like *Lophophytum*, of two carpels; but here's the important difference that characterizes it: the floral axis which developed in the preceding into a placenta on which the ovules were born as lateral organs, in *Helosis* immediately becomes the ovule itself; the result is a single ovule erect and orthotropic, while in Lophophytées and related genera it was derived anatropous ovules, and as many as carpels.

The structure of *Helosis* is common to all genera of the known tribe Hélosidées; although we do not know the development of any of them, we can infer from the preceding observations and this analogy, they all develop as *Helosis*.

I am inclined to believe that this is still the same in Langsdorffiées. Indeed, if these plants differ from Hélosidées in a few notable points, mainly in that they have only one terminal style, at least, by the structure of their ovaries and their ovule, then they seem very similar. My investigations have in fact demonstrated that the ovule of *Langsdorffia* does not consist, as Mr. Hofmeister said (19) of a single anatropous cell, downward and free; it, instead, consists of a very large number of cells, upright, orthotropic and everywhere adherent to the ovary. It is easy to be convinced of the correctness of my assertions by consulting Figures 28 and 29 attached to this work. The rest of the structures of the flower *Langsdorffia*, this flower is, in my opinion, like that of all previous genera, devoid of perigone and consisting of only a naked pistil; I do not see, in fact, sufficient grounds to assume the role of a perigone, like the authors, the short limb which crowns this flower. This limb, according to its anatomical structure, has the same meaning as that of Hélosidées and other genera already examined; this is just a simple extension of the edges of the ovary itself; but it would take too long to explain here the details of this structure. As to whether the pistil of *Langsdorffia* consists, such as in Hélosidées, of two carpels whose styles are coalesced, or reduced by one abortion, or if instead the pistil consists only of a single carpel thought of as a simple style, this is a question that I can not decide; materials of my studies are too insufficient and would not allow it, and this should be reserved for further investigation. Moreover, for the moment, it is not of great importance; in fact, all we have found is that the flower of *Langsdorffia* is a naked pistil, with a single, erect ovule, and devoid of orthotropic integuments, which, as we conclude by analogy, is the same origin as in Hélosidées, in that it represents the transformed floral axis.

For the genus *Balanophora*, I am able to observe the accuracy of the researches of M. Hofmeister (20). The result of his investigations were that the female flower of this genus also consists of a naked pistil and a single style, it has only one ovule, consisting of very few cells, anatropous and hanging down freely from the top of the ovarian cavity (f. 1, 2). It is likely, however, that in this kind of pistil only of a single carpel is formed.

Now if we take a retrospective look at the forms he just discussed, we find that all the female flower always consists of a naked pistil and the ovules are there without integuments. The two genera that remain to be examined, *Cynomorium* and *Mystropetalum,* are not under the same conditions; they not only have a well acknowledged perigone (f. 10, 11), but also an ovule with an integument (f. 12). There it joins some other differences, the most notable is perhaps the one I'm going to outline. All Balanophoraceae, except for only the two genera, the inflorescences are born in the manner of adventitious buds: that is to say they are formed in the interior of the vegetative organ which is in this case a kind of rhizome. They remain there long enough, and force their growth through the tissue of the rhizome that expands to provide them an envelope; Finally, in stretching they suddenly break and go beyond the envelope, which persists at the base of the stalk as a sheath or sometimes inconspicuous epicalyx (*Phyllocoryne*), but more often conspicuous (*Langsdorffia*) and in some cases truly huge (*Ombrophytum*). In contrast, in *Cynomorium* and *Mystropetalum*, we do not find this strange development, reminiscent in some way to the fruiting *Agaricus*; inflorescences there form a continuation of the rhizome branches.

I am inclined to believe that these differences, of the floral and vegetative structure, are sufficient reasons to separate these two genera of Balanophoraceae. They form the family Cynomoriées. It will give me at least, even if one does not agree with me on this separation, that the Cynomoriées have less affinity with Balanophoraceae than do the members of the latter group. Besides, considering how the genera of Balanophoraceae as we define them, are congruent with the characters of their fruiting and vegetation, mentioned above, it seems clear that this order can not be divided further.

I tried to establish on the basis of this study a systematic arrangement of Balanophoraceae that I have reason to believe is natural. The resulting groups coincide with most of those offered by Mr. Hooker. I naturally excluded Cynomoriées.

Balanophoraceae

Trib. 1. Eubalanophoreae.
♀. Style 1; ovule 1, pendant, free, anatropous.
Balanophora Forst.
Trib. II. Langsdorffieae.
♀. Style 1; ovule 1, orthotropous, adherent to the ovary.
Langsdorffia Mart., *Thonningia* Vahl (*Dactylanthus* Hook. f.?).
Trib. III. Helosideae.
♀. Styles 2; ovule 1, orthotropic, adherent to the ovary. -- ♂ A perigone, 3 stamens. - Clavate hairs interspersed with flowers.
Helosis Rich, *Corynaea* Hook. f., *Rhopalocnemis* Jungh., *Phyllocoryne* Hook. st., Sphaerorrhizon Hook. f.
Trib. IV. Scybalieae.
♀. Styles 2; ovules 2 pendant from the top of an axile placenta processed partition, anatropous, adhering to the wall and to the ovary. -- ♂. A perigone; 3 stamens. - Clavate hairs interspersed with flowers.
Trib. V. Lophophyteae.
♀. Styles and ovules as in Scybalieae. -- ♂. No perigone; 2 stamens. - Course of hair between the flowers.
Lophophytum Schott and Endl, *Ombrophytum* Poepp.
Trib. VI. *Sarcophyte*ae.
♀. Ovary composed of 3 carpels; sessile stigma; ovules 3, hanging from the top of a axile placenta extended partitions between ovules, anatropous, adhering to the walls and the ovary. -- ♂. A perigone; 3 stamens. - Course of hair between the flowers.
Sarcophyte Sparrm.

Allow me, gentlemen, two words on the taxonomic status of the order Balanophoraceae, thus formed. If we agree to exclude *Cynomorium* and *Mystropetalum*, from my example, there is no need to assign affinity with the genus *Hippuris* based only on *Cynomorium*. As we have found that *Lophophytum* has neither a perigone or single ovule, affinity with the *Misandra*, supposed by J.-D. Hooker also falls. Thus, any analogy between Balanophoraceae and

Haloragaceae disappears. The view is doing the contrary in a very different direction; and this is the *Myzodendron* we recognize as the most similar shape to a part of our genera. Indeed the female flower of *Myzodendron* also consists of a naked pistil formed, like *Sarcophyte*, of three carpels; and its floral axis extends into a central placenta which carries three eggs, each located in front of each carpel, pendant, anatropous and without integuments, as are those of Lophophytées, *Scybalium* and *Sarcophyte*. It is true that in *Myzodendron* the placenta does not expand at the point of the partition, and that the ovules do not adhere to the ovary. But this difference may not raise serious objections; because not we see only in *Lophophytum* placentas and originally free ovules (so the *Myzodendron* somehow represents a younger phase of *Lophophytum*) but still we find in some very related genera of *Myzodendron* developed placental partitions, and sometimes, at least in the result, adhesion between the seed and the ovary (21). I have to point out that the male flowers are also almost identical in *Lophophytum* and *Myzodendron*; they consist, in fact, in the latter genus, as two or three stamens without a perigone. In a word, the analogy of two types is as perfect as can be desired.

As for Hélosidées and Langsdorfliées, in a single ovule, erect, orthotropous and adherent to the ovary, we find a striking analogy among Viscacées and Loranthées. Because according to the research of M. Hofmeister (22), ovary and ovule of the two groups were formed following the same mode, and the ovule is devoid of an integument. It is true that Viscacées and Loranthées feature a perigone, an organ which, as we have seen, is completely lacking in female flowers of Balanophoraceae. We believe, however, that for many reasons Balanophoraceae should go directly into the large class M. Baillon has made for Viscacées, Loranthées, Santalaceae (including *Myzodendron*), Olacinées, etc., and he named the class Loranthaceae. Indeed, the difference provided by the presence of a perigone is erased by transitions linking the various types of this class; if *Myzodendron* still has open flowers, related genera have a single or double perigone and this development is also revealed in some way in Balanophoraceae, knowledge of their male flower, which is naked in Lophophytées and provided with a perigone in other types. The Balanophoraceae, in the class of Loranthaceae, constitute the lower group, the least developed organization, organization that, through Myzodendrées and Viscacées, would connect the forms of Santalaceae, Loranthées and Olacinées that represent the highest evolution of the same type.

But there is a difficulty which continues to oppose this systematic arrangement; it is presented by the genus *Balanophora* whose ovule attaches to the ovary wall, not from an axile placenta or constituting the top of the axis itself, for has no analogue among Loranthaceae. However, it is possible to conjecture that the story of the evolution of this genus, we do not yet know, we may show that there is in *Balanophora* originally an axile placenta that fused with the ovary wall and at the top of which would hang the ovule: arbitrary conjecture no doubt, but not without probability. If this assumption was justified, it is Lophophytées that *Balanophora* is the closest to; it would be inserted very naturally with them in the common type of the class Loranthaceae. If to the contrary, it would be that Balanophoraceae would still have affinities with other levels within Loranthaceae. It would be the same if we kept Cynomoriées among them, then they would contain some very different types, which would connect to very distant orders. The affinity indicated by Cynomoriées of concern remains *Hippuris* and Haloragaceae, as I readily grant to Mr. Hooker.

MJ-E. Planchon has the following comments:

The reports on Santalaceae, Olacinées and Loranthaceae were sketched by R. Brown, Mr. Decaisne and myself, long before the works of M. Baillon. It could well be that we had to assimilate with each other vegetative types which, however, differ in the presence or absence of an ovular integument or even a perianth. Perhaps *Cynomorium* is simply a Balanophorée that accomplished a superior organization [compared] to the incomplete types from the same family. We know that there Piperaceae with an incomplete perianth that are more acknowledged in Saururées, and according to Mr. Eichler himself, one can not separate *Myzodendron* from Loranthaceae.

Mr. Eichler replied that Balanophoraceae, as he sees them, are very logically connected in a single group by the lack of ovular integuments and the uniqueness of their buds.

Footnotes

(1) J.-D. Hooker, On, the structure and affinities of Balanophoraceae in the Transactions of the Linnean Society, vol. xii (1859). - Weddell Considerations female reproductive organ of Balanophoraceae and Rafflesiacees, in Ann. sc. nat. 111, 14, p. 166 ff. Submission on *Cynomorium coccineum* in Archives Museum, 1 x. - Hofmeister, Neue Beitraege zur Kenntniss Embryobildung der der Phanerogamen, p. 572 et seq.

(2) We tentatively follow the division proposed by J.-D. Hooker in the cited memory above.

(3) Hofmeister, l, c. p. 599. In this passage, the author suggests another explanation why: it is there in the *Scybalium* two ovules prepared and consistent.

(4) Ann. sc. nat., l. c., p. 184, 185, pl. 10. I must point out that the interpretation I exhibited was not given by Mr Weddell but is inferred from the figures of his memory.

(5) Poeppig and Endlicher, Nova Genera and Species Plant., t. II, p. 40, 155 lab.

(6) Schott and Endlicher, Meletemala botanica; p. 1, tab. 1.

(7) In the *Sarcophyte* often found, according to Mr. Hofmeister, two ovules separated by a partition. M. Hofmeister assumes that each belongs to one of the two carpels which consists of the pistil *Sarcophyte* and that the wall is formed by the ovary wall. We shall return to this point.

(8) In the *Mystropetalum* , we did not yet know the integument; it is however very distinct and easy to see. It forms on the seed a thin, membranous testa which adheres very closely to the endosperm.

(9) I note that Mr Weddell, who said bracts in this species (Ann. sc. nat., l. c. p. 185), was by eye not the real *L. mirabile* Scholl and Endl., but *Lophophytum* appointed by Leandro Archimedea, which is quite different from L. *mirabile* and constitue a new species which I will describe in the Flora brasiliensis by Mr. Martius under the name *L. Leandri*. In *L. mirabile* there are never bracts.

(10) This epidermis does not have stomatal organs known that the family of Balanophoraceae is usually private. (See JD Hooker, l. c.).

(11) It is the peripheral layer that undergoes this change. In fruits that abort, the coat turns entirely to sclerenchyma and thus forms a core with a small central cavity where are the remains of atrophied ovules.

(12) If I issue this hypothesis, it is because of the analogy that the organization of *Lophophytum* offers with that of Hélosidées and other tribes, in which the ovule is, as we shall see later, the

top of floral axis. However, I recognize that this interpretation suffers some difficulty, because in the development of *Lophophytum* ovule, lateral organs born on top of an axis better serves the birth of a leaf.

(13) Meletemata bot., l. c.

(14) I have observed transitional forms that link these scales with a well-developed ovary, but I can not stress here specifically on this point, which will be better, treated in the monograph of Balanophoraceae I prepare for the Flora brasiliensis by Mr. Martius.

(15) Poeppig and Endlicher, Nova Genera, SC

(16) Schott and Endlicher, bot- Meletemata., p. 3, Table 2.

(17) Neue Beitraege, l. c. p. 599.

(18) Neue Beitraege, 1. c., p. 581 ff. I must point out that the flowers examined by me are from the same sample as those described by M. Hofmeister. In the explanation of the plates, I tried as much as possible, to agree each other's observations.

(19) Neue Beitraege, loc. cit., p. 576. - Voy. also a memory of Mr. Karsten on this subject in Nova Acta Acad. Leop. - Carol. Curiosorum Naturae, t. XXVI, 2 pars.

(20) Loc. cit., p. 585 et seq.

(21) See Baillon, first and second Memoire on Loranthaceae in Adansonia 1861.

(22) Neue Beitraege, loc. cit., p. 539 et seq.

(23) Memoire sur les Loranthacées, loc. cit.

Plate I.

Fig. 1. *Balanophora polyandra* Griffith. - Female flower. (Magnification 20.)

Fig. 2. Ibidem - Longitudinal section of the female flower f, funiculus;. v, embryonic vesicles (according to Mr. Hofmeister, Neue Beitr. pl. 15, fig. 1). (Gross. 90.)

Fig. 3. *Langsdorffia* hypogaea Mart. - Isolated female flower. (Gross. 14.)

Fig. 4. Id - Longitudinal section of the female flower f, funiculus;. v, embryonic vesicles (according to Mr. Hofmeister, l. c. pl. 12, f. 4 except the addition of vesicles). (Gross. 175.)

Fig. 5. *Helosis guyanensis* Rich. - Female flower. (Gross. 10.)

Fig. 6. Id. - Schematic longitudinal section of the ovary, according to Mr. Hofmeister.

Fig. 7. *Scybalium fungiforme* Schott and Endl. - Schematic longitudinal section of the ovary, according to the ideas of Mr. Hofmeister.

Fig. 8. *Lophophytum mirabile* Schott and Endl. - Female flower. (Gross. 10.)

Fig. 9. Id. - Longitudinal section of the female flower, according to Mr. Weddell.

Fig. 10. *Mystropetalum thomii* Harv. - Fruit.

Fig. 11. *Cynomorium coccineum* L. - Half ripe fruit.

Fig. 12. Id. - Longitudinal section of the ovary (according to MM Weddell and Hofmeister.). (Gross. 15.)

Fig. 13. *Lophophytum mirabile* Schott and Endl. - Appearance of female flowers: a, b, c, successive degrees; c there arise in the carpels. (Gross. 40.)

Fig. 14. Id. - Flower a little older than the 13 c, the carpels have increased considerably. (Gross. 80.)

Fig. 15. Id - Longitudinal section of a flower a little older still, c, c, carpels; has top of the floral axis. (Gross. 65.)

Fig. 16. Id - Longitudinal section of the young flower at a more advanced stage of development where the ovarian cavity is closed, and where we now see the styles, the placenta and ovules:

pl column ovuliferous or placenta; ov, ovule; sc, transformed cells sclerenchyma; st, styles. (Gross. 30.)

Fig. 17. Id - Longitudinal section of the fully developed flower: f, vascular bundles;. m, very dense parenchyma coat, wrapping the ovular system and tapering towards the top in the tissue that leads styles: ov, ovule; if, embryo sac; cl, partition, resulting from transformation of the placenta; sc, sclerenchyma coat; thick, epidermis. (Gross. 25.)

Fig. 18. Id. - Horizontal section of the same flower, transverse of ovule. The letters have the same meaning as in Figure 17. (Gross. 45.)

Fic. 19. Id. - Portion of Figure 17, including an ovule, with a small portion of the septum and all external tissues of the ovule most highly magnified (65 times) to see the details of the embryo sac. Same meaning of the letters.

Plate II.

Fig. 20. *Scybalium fungiforme* Schott and End). - Longitudinal section of the ovary, through the two ovules. - Previously used letters are as defined in this figure and in the following, which enables to convince very easily from the structural identity of the female flowers in *Scybalium* and in *Lophophytum*. Indeed, we find here, with the exception of the vascular bundles, all parties that we see in the *Lophophytum* and all arranged the same. (Gross. 65.)

Fig. 21. *Sarcophyte sanguinea* Sparrm. - Longitudinal section of the female flower. (Gross. 65.)

Fig. 22. Id. - Longitudinal section of ovular system with its parenchymal envelope. We see from these figures that the flower does not have perigone, and has not developed styles; stigma (stg) whose buds are impaired by alcohol in which the duplicate was preserved, on the contrary sessile. The parenchyma of the ovary, arranged in radiating series is everywhere thin; missing here sclerenchyma cells of previous genera. There are three vascular bundles arranged in a triangle, each located in front of an ovule, and touching the surface of a special layer of tighter parenchyma m, which evidently represents the analogous mantle m Figure 17: analogy also supported on this fact, that the peripheral part of this layer is transformed, in the fruit of *Sarcophyte*, as in the *Lophophytum* in a sclerenchymatous shell (or the entire layer in fruits that abort). In the interior of this layer are seen the three ovules separated by as many partitions, which meet on the axis; although we can not recognize the details of their structure, it is clear that the organization is here similar general (apart from the difference in the number of organs) to that of *Lophophytum*. - The very different indications from the data provided by Mr. Hofmeister is probably what is learned by taking embryo sacs of the ovules, conjecture that, however, does not explain much of the diversity that Mr. Hofmeister and I have observed in the organs this flower. (Gross. 65.)

Fig. 23. *Helosis guyanensis* Rich. - Appearance of carpels cc on floral axis (75 Gross).

Fig. . 24. Id - Longitudinal section of a slightly more advanced flower: a, axis; st styles. (Gross. 40.)

Fig. 25. Flower a little older still. (Gross. 35.)

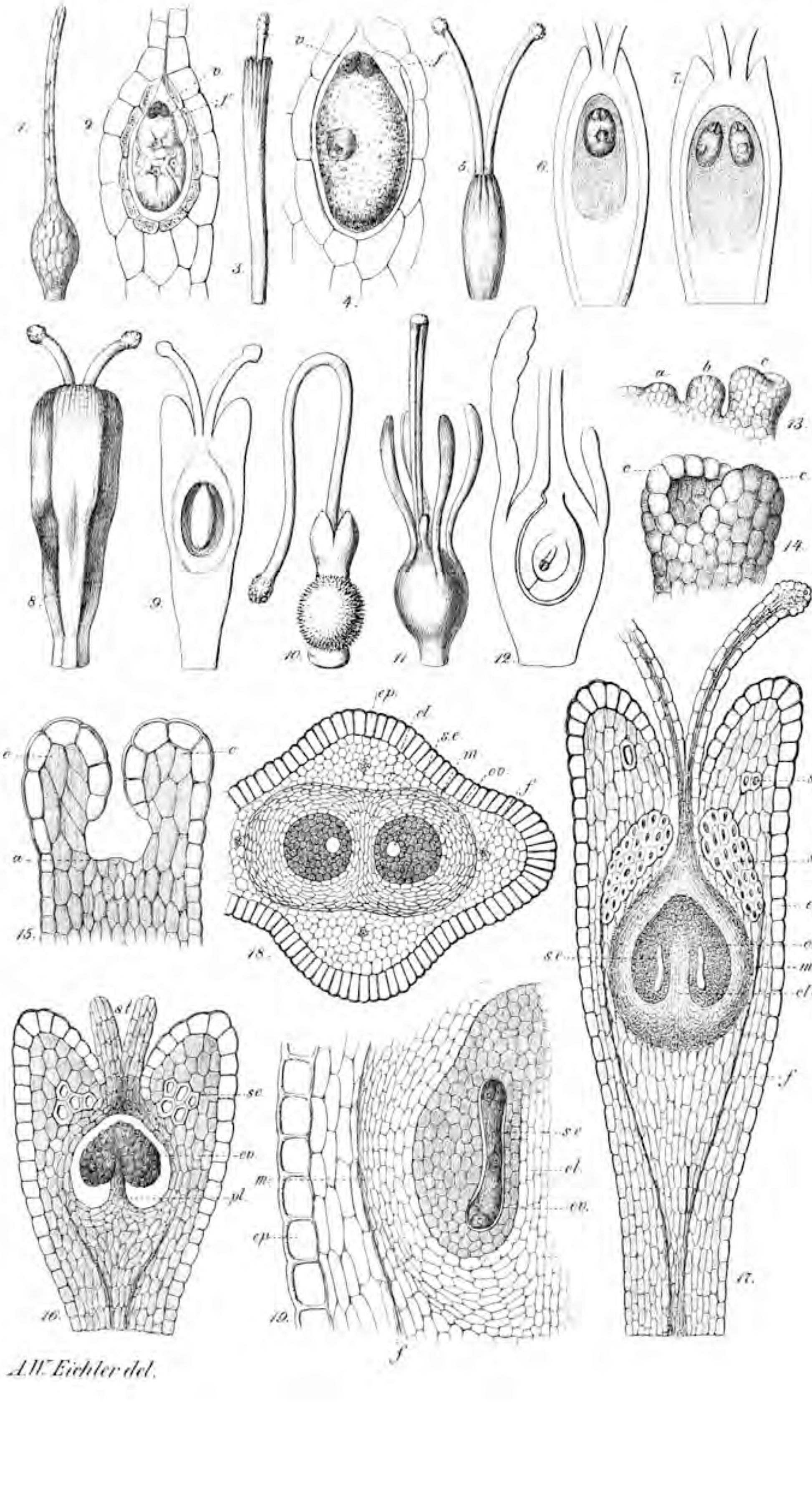
Fig. 26. Longitudinal section of the same: a, axis; st styles. (Gross. 50.)

Fig. 27. Longitudinal section of the ovary (with base styles st) fully developed. Same meaning of the letters in Figures 19 and 20. (Gross. 50.)

Fig. 28. *Langsdorffia hypogaea* Mart. - Longitudinal section of two adjacent flowers. These flowers stick together throughout their upper part, and are free at their base; the corners, cm,

are easy to distinguish from the top because the cells in this region adjoin the walls and contain highly cuticularized wax. At the base one perceives the ovule ov. (Gross. 20.)

Fig. 29. Portion of the basal part of the section shown in the previous figure, more highly magnified (100 times): se, embryo sac; v, embryonic vesicles; a antipodals, the well-defined layer of smaller cells than neighboring and filled with a thick plasma, must be regarded as the nucellus, as the embryo sac is free and therefore can alone represent the ovule. As, moreover, this layer has the same thickness throughout the periphery of embryo sac, this ovule can not be anatropous; rather it is atropous; and as ultimately the suspensor thread of the embryo is in the upper end of the seed (voy. Hofmeister, 1. c. pl. 12), one can not doubt that organs v are in reality vesicles and others, the antipodals. We must conclude from all this that the ovule of *Langsdorffia* is drawn up, orthotropic without an integument and, as seen in the figure, adheres to the ovarian walls. The letter p indicates a small portion of the parenchyma from the axis of the anthodium on which the flowers are united.



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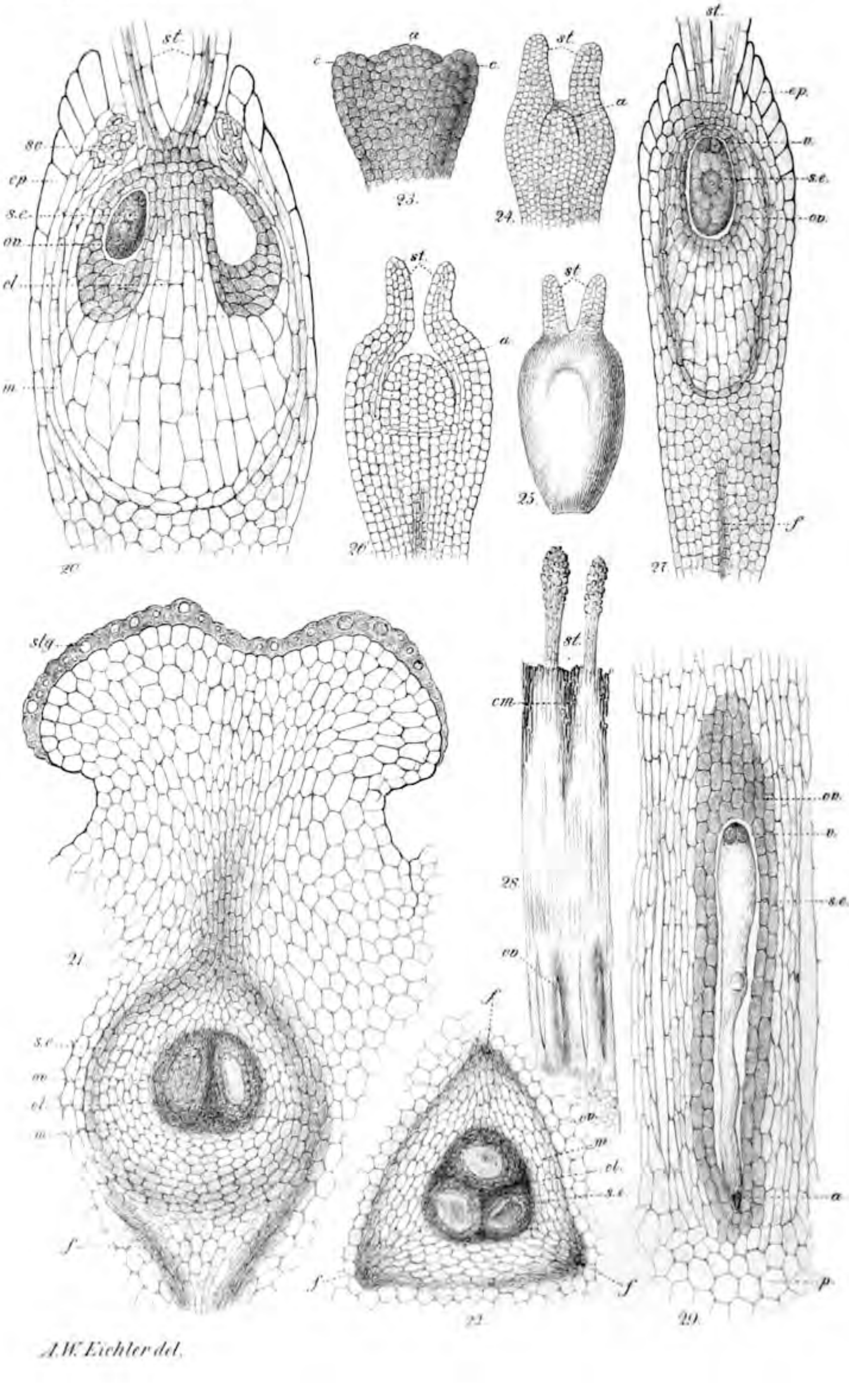

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