The Embryo-Sac of *Peperomia*.

BY

DOUGLAS HOUGHTON CAMPBELL,

Professor of Botany in the Stanford University, California, U.S.A.

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With Plate VI.
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DURING the summer of 1899 the writer collected at the Royal Botanic Gardens at Kew several species of *Peperomia*, with a view to investigating the development of the embryo-sac and embryo. A preliminary study was made soon after, the more important results of which were afterwards published ¹.

Since the writer's account appeared, the same species has been investigated by Dr. D. S. Johnson ², who has confirmed the most important discovery brought out in the former paper—namely, the presence of sixteen nuclei in the unfertilized embryo-sac; but he at the same time called attention to an error in the interpretation of the structures found in the older embryo-sac.

¹ Die Entwicklung des Embryosackes von *Peperomia pellucida*. Ber. der Deutschen Botanischen Gesellschaft, Bd. xvii, Heft 10, 1899. A preliminary note appeared in the Annals of Botany for December, 1899.

² On the Endosperm and Embryo of *Peperomia pellucida*; Bot. Gazette, xxx, No. 1, July, 1900.

It seemed desirable, therefore, to examine the subject again, and a number of new preparations were made, to supply certain stages which were lacking in the series of slides made for the preliminary examination. In preparing these, Flemming's triple stain was employed, which gave much better results than the simpler aniline-water safranine, which had been used before. From a study of these new preparations it was soon evident that Johnson's conclusions were substantially correct, although there were one or two minor points with which the writer's results do not agree.

In the former paper, the writer asserted that no endosperm was formed, and that in the ripe seed the embryo filled the whole embryo-sac. The error arose from a failure to find the stages between the very young embryo, and the stage where the embryo apparently filled the whole sac. The embryo is small, and its cells closely resemble those of the large-celled endosperm. As Johnson has shown, certain of the nuclei take no part in the endosperm-formation, and these being seen crowded against the walls of the embryo-sac by the globular mass of large-celled endosperm, the latter was mistaken for an embryo, which had filled up the embryo-sac, without any endosperm being formed.

THE FLOWER.

The flower in *Peperomia* is exceedingly simple, the gynoeceum consisting of a single carpel with a solitary erect ovule, having but a single integument. Two stamens are present, and the flowers, which are set on thick spadix-like spikes, are each subtended by a peltate bract.

The development of the flower is easily followed in longitudinal sections of the young spike, and it was found to agree with the account given by Schmitz ¹.

The ovule develops a single large archesporial cell ², from which a single tapetal cell is cut off, which undergoes repeated

¹ Die Blütenentwicklung der Piperaceen; Hanstein, Bot. Abhandl., ii, 1, 1872.

² Campbell, loc. cit., Figs. 1, 2.

division, and gives rise to several (3-4) layers of cells between the apex of the embryo-sac and the epidermal layer of the nucellus (Fig. 1, *t*).

The inner archesporial cell becomes at once the mother-cell of the embryo-sac.

THE EMBRYO-SAC.

The most remarkable fact brought out in the study of the development of the embryo-sac was the behaviour of the nuclei, which differ remarkably from those of other Angiosperms. The marked polarity of the typical embryo-sac was found to be entirely wanting, and the nuclei were uniformly distributed. Most important of all was the further division, unique so far as is at present known among Angiosperms, of each of the eight nuclei, so that there are normally sixteen nuclei in the unfertilized embryo-sac (Pl. VI, Fig. 1).

The sixteen nuclei are at first entirely similar, and equally distributed in the rather thick cytoplasmic layer which surrounds the large central vacuole. As the embryo-sac develops, a certain number of the nuclei, usually but not always eight, approach, and about them there is an accumulation of cytoplasm (Figs. 2, 3, *E. n*). This group of nuclei is often placed at the chalazal end of the embryo-sac, and much resembles a group of antipodal cells, although, as we shall see, they are not the homologues of the antipodals of the typical Angiosperm embryo-sac.

At the micropylar end there may be found two or three, or occasionally more, nuclei, while the remainder are arranged without definite order about the wall of the embryo-sac. Of the nuclei at the upper end of the sac, one soon becomes somewhat larger than the others, and there is an accumulation of cytoplasm about it, which is bounded by a more or less evident protoplasmic membrane (Figs. 3, 4, *o*); but this is not so evident, nor is the egg-cell thus formed so large, as Johnson describes for his preparations. This, together with some other slight variations, suggested that perhaps his plant

was not the same as the one cultivated under the same name at Kew.

The behaviour of the other nuclei, at the apex of the sac, is not always the same. In some cases observed, where there were two of these, they were arranged with reference to the egg-cell in such a manner as to suggest the typical angiospermous egg-apparatus. Johnson¹ states that he always found a single conspicuous synergid, which after fertilization developed a cell-wall and persisted until the embryo was nearly full-grown. The writer found, in a good many cases, preparations which showed an appearance not unlike that described, but it was impossible to see in what essential respect the so-called synergid was different from the other nuclei which do not form part of the group already referred to.

These also develop a membrane about them, and are often quite as conspicuous as the alleged synergid (Fig. 6, *B*, *x*) which we are inclined to think is nothing more than one of these nuclei with its accompanying cytoplasm, which simply is close to the egg. As there may be two, or even three of these cells in the upper part of the embryo-sac, and they take no part in the conduction of the generative nucleus to the egg, it is very questionable whether they can be properly spoken of as synergids.

At the time the pollen-tube reaches the embryo-sac, the egg-cell, which may be slightly pushed to one side, appears as a flattened body, and close to it there are from one to three nuclei, with a more or less definite aggregation of cytoplasm about them, and perhaps to be considered as the morphological equivalents of the synergidae of the typical embryo-sac. They take no part, however, in the process of fecundation.

The group of (usually) eight nuclei already referred to (Figs. 2, 3), may at the time of fertilization occupy the base of the sac, or these nuclei may be aggregated at a point on one side, or even close to the egg-cell. These, as Johnson has

¹ loc. cit., p. 2.

shown, are the homologues of the two polar nuclei of the ordinary Angiosperms.

The remaining nuclei, which lie close to the wall of the embryo-sac, are more or less flattened, and subsequently develop a cell-wall about the deeply stained cytoplasm, forming a lenticular cell which projects into the cavity of the embryo-sac (Figs. 5, 7, *x*).

THE POLLEN.

The small, globular pollen-spores (Fig. 8) have a roughened membrane, and contain when ripe two relatively large nuclei. The larger of these, which stains much less deeply than the other, and has a more conspicuous nucleolus, is the vegetative nucleus. The other, which stains very strongly, is the generative nucleus. In no case was a division of the latter observed in the ungerminated spore.

Pollination is effected some time before the embryo-sac is mature. Nothing unusual was noted in regard to the growth of the pollen-tube through the pistil. It penetrates as usual through the micropyle, and on reaching the apex of the nucellus pushes apart the large epidermal cells, and then crowds between the tapetal cells, which are not, however, destroyed, and finally comes into direct contact with the egg (Fig. 3).

POLLINATION.

In one case (Fig. 4) two similar, deeply stained nuclei were seen within the end of the pollen-tube which had just reached the embryo-sac. These were, with little question, the two generative nuclei, which were the result of the division of the single generative nucleus of the ripe pollen-spore. The vegetative nucleus of the pollen-spore could not be certainly detected in any instance within the pollen-tube, although in one case a body that looked as if it might be the disorganized remains of a nucleus was seen within the tube, above the generative nuclei.

FERTILIZATION.

Although repeated search was made, it was not possible to determine the fate of the second generative nucleus. One enters the egg directly from the pollen-tube, but what becomes of the other is not clear. The nuclei of the cells immediately surrounding the embryo-sac appear contracted and deeply stained in the preparation, and although in several cases a nucleus was seen which looked as if it might be the second generative nucleus, it was not possible to be certain whether this did not belong to one of the disorganized cells of the inner nucellar tissue.

In the specimen shown in Fig. 3, the generative nucleus had apparently just entered the egg-cell. The nuclear membrane appeared indistinct, and the chromatin formed an irregular mass, somewhat suggestive in form of a spermatozoid; but as no others were found in this stage, it must remain undecided at present, how far this is a normal appearance. Later, as Johnson has shown, the male nucleus assumes a form closely resembling that of the egg-nucleus, except that it is somewhat smaller; but it is always decidedly larger than the generative nucleus of the pollen-spore (Figs. 5, 10).

The fusion of the two nuclei does not usually occur at once, but there seems to be a good deal of difference in the time in different instances. In one case observed, the fusion of the nuclei was completed, and the first division of the embryo ensued, before any division of the endosperm took place; but usually the fusion of the sexual nuclei is not accomplished until after the completed fusion of the endosperm nuclei.

As usual in Angiosperms, the two sexual nuclei become closely appressed (Figs. 5, 10); and finally the cavities of the two are thrown together, and a single nucleus results.

THE ENDOSPERM.

As we have seen, the eight endosperm-nuclei lie close together, often actually in contact, and surrounded by a mass of cytoplasm which is much thicker than the layer lining the

embryo-sac at other places. This group of endosperm-nuclei may be either at the base of the sac, or at the side, even close to the fertilized egg. Shortly after fertilization is completed, the cytoplasm within the embryo-sac increases greatly in amount, and the central vacuole disappears. At this stage (Fig. 6) the cytoplasm is usually densest in the centre of the sac, and surrounding this central mass are numerous smaller vacuoles separated by thick layers of granular cytoplasm. The group of endosperm-nuclei usually occupies the central part of the cytoplasm (Fig. 6).

The fusion of the group of endosperm-nuclei, to form the definitive nucleus, which has been followed in detail by Johnson¹, could only be found in its earlier phases (Fig. 7); but there seems no reason to doubt the accuracy of his observations, as the single endosperm-nucleus resulting from the fusion of the group was found, and its division observed. According to Johnson's account, two of the nuclei first fuse, and this is followed by the gradual absorption of the whole group into one very large nucleus, in which the nucleoli are more or less completely fused.

Fig. 9 shows the large endosperm-nucleus, apparently in the early prophase of division. The form was somewhat irregular, showing evidences of its compound structure. The nucleoli had quite disappeared, and the very numerous chromosomes were plainly evident and showed an almost complete separation into two groups, almost suggesting a direct division of the nucleus. It is certain, however, that a typical mitosis occurs in some cases, and it is not likely that a direct division of the primary endosperm-nucleus ever takes place, although the possibility of such a division is not to be denied.

The first division-wall in the endosperm is usually vertical (Fig. 10), but it may be more or less inclined, or even almost horizontal. The resting nuclei after the first division (Fig. 10) are very large and contain numerous nucleoli, each of which, in stained specimens, shows a clear area about it: they have

¹ loc. cit., pp. 4, 5.

very much the appearance of being made up of several fused nuclei.

The dense cytoplasm of these cells shows the coarse, vacuolate appearance seen in the undivided embryo-sac. The subsequent division-walls are mostly radial, so that the young embryo is surrounded by a single layer of very large endosperm-cells. The contents of these cells become more uniformly granular as they grow older, and the vacuoles mostly disappear. Later, there may be formed a small number of periclinal divisions; but even in the ripe seed many of the endosperm-cells extend from the embryo to the periphery of the embryo-sac. Johnson states that there may be forty or more endosperm-cells in the ripe seed.

THE ACCESSORY NUCLEI.

The nuclei which do not fuse to form the endosperm-nucleus are usually closely appressed to the wall of the embryo-sac, but this is not always the case. In Fig. 6, *B*, is shown one of these nuclei which has remained very like the endosperm-nuclei, and has surrounded itself with a cell-wall, forming a very conspicuous cell projecting into the embryo-sac. In this case there was a similar conspicuous cell occupying the position corresponding to the single synergid described by Johnson; and, as the accessory nuclei regularly develop a cell-wall, become filled with deeply stained cytoplasm, and are very similar to the supposed synergid, it is probable they are homologous with it.

While the group of unfused endosperm-nuclei, with the surrounding cytoplasm, often occupies the antipodal end of the embryo-sac and looks very much like a group of antipodal cells, their subsequent behaviour shows that they are not the equivalents of the antipodals of the typical angiospermous embryo-sac. These must be sought in the separated cells, developed about the accessory nuclei, which here are not united in a group, but are distributed singly about the periphery of the embryo-sac. While they can hardly be spoken

of as 'antipodal' cells, they must be regarded as their equivalents, being those nuclei which are not directly concerned in the production of the egg-apparatus or endosperm.

THE EMBRYO.

The embryo remains very slightly developed, even in the ripe seed. The fusion of the two pro-nuclei is often not complete until the endosperm-nuclei have been fused. The fertilized egg-cell has grown somewhat and become almost globular. The first division is longitudinal, and is followed by a second longitudinal wall in each of the two cells. Transverse walls then form, but the embryo increases but little in size, nor is there much enlargement of the embryo-sac after the endosperm begins to develop. In *Peperomia*, as in all the Piperaceae, the nutritive function of the endosperm is assumed by the perisperm, developed from the nucellar tissue, whose cells become filled with starch.

THE FRUIT.

The development of the fruit was not studied in detail, but as the writer's observations did not agree in all respects with those described by Johnson, a brief note of these differences will be given.

From the first, the ovule completely fills the ovarian cavity, and finally a sort of caryopsis is formed. The innermost layer of cells of the ovary-wall becomes very large, and upon their membranes are formed conspicuous reticulate thickenings¹, so that this layer forms a hard shell, covered with several layers of thin-walled cells. It is this inner layer of the carpel which constitutes the principal part of the hard portion of the fruit.

The cells forming the two layers of the integument become very dark-coloured, but this is mainly due to a change in the character of the wall. They stain so strongly as to appear quite opaque, but in thin sections it may sometimes be seen

¹ Johnson, loc. cit., Fig. 15.

that the cell-cavity is not closed, as Johnson describes (Fig. 13). The inner layer of integument-cells has the internal walls strongly undulated, so as to crowd and distort the outer layer of cells of the nucellus, which Johnson describes as belonging to the integument, supposing apparently that the darkly stained inner layer of cells of the integument was simply the much thickened cell-wall, belonging to what was really the outer nucellar layer¹. The real condition is readily seen in the younger fruits (see Figs. 12, 13).

SUMMARY OF RESULTS.

1. All species of *Peperomia* seem to agree in having regularly sixteen nuclei in the embryo-sac instead of the eight normally present in other Angiosperms. There is no trace of the marked polarity usually observed in Angiosperms.

2. One of the nuclei in the micropylar end enlarges somewhat, and there is an accumulation of cytoplasm about it to form the egg-cell. From one to three other nuclei are found near the egg-nucleus, and these may show a more or less evident aggregation of cytoplasm about them, and may perhaps be regarded as the equivalents of the synergidae of the ordinary egg-apparatus. They take no part in fertilization, and their synergidal character is open to question.

3. Several (usually eight) nuclei fuse to form the endosperm-nuclei, but must be considered as the homologues of the polar nuclei of the typical Angiosperms. The remaining nuclei are scattered, and each develops about it a cell-wall, much as do the antipodal cells of many Angiosperms.

4. The embryo remains very small, and shows no differentiation when the seed is ripe.

5. The divisions of the endosperm-nuclei are always accompanied by the formation of cell-walls.

6. The hard coat of the fruit is mainly formed from the innermost layer of cells of the pericarp.

¹ loc. cit., p. 7, Figs. 14, 15.

THEORETICAL CONSIDERATIONS.

The writer has already expressed his opinion that in *Peperomia* we have to do with the most primitive type of Angiosperm yet described. Johnson is inclined to differ from this conclusion, believing that the peculiarities are to be explained as secondary modifications. His reasoning is not, however, quite convincing. He says¹, 'I am inclined to believe that the peculiarities of the embryo-sac of *Peperomia* have been secondarily acquired, and are analogous to those found in Angiosperms of peculiar habit, e.g. many aquatic, parasitic and saprophytic forms.' Now the habit of *Peperomia*, so far as the writer is aware, conforms to none of the above categories, and is that of any normal green plant. Moreover the peculiarities of the embryo-sac are *not* reductions—unless we consider the embryo, which is not the question here; but consist rather in an increase in the number of parts, for which there is no parallel, so far as the writer is aware, as a result of the aforesaid peculiar habits.

Piper and *Heckeria* are undoubtedly related to *Peperomia*; but *Saururus* certainly cannot be considered a very near relative, as Engler thinks it sufficiently distinct from the Piperaceae to warrant the establishment of a separate family. Moreover the flowers, with their syncarpous gynoecium, are certainly much more specialized than the exceedingly simple unicarpellate flower of *Peperomia*. Just why the flower in *Peperomia* should be considered as a reduced form is not clear. From a study of many low types among the Monocotyledons, which cannot be readily derived from higher types, e.g. *Naias*, many Araceae, it seems more reasonable to consider the single carpel, with a single axial ovule, as the primitive type for the Angiosperms, and with this *Peperomia* agrees perfectly.

While Johnson states that *Piper* and *Heckeria* have 'essentially typical' Angiospermous embryo-sacs, he gives no details or figures, so that it is impossible to judge whether

¹ loc. cit., p. 9.

there may not be some points in their structure which might be compared with some of the stages of development in *Peperomia*. That *Saururus*¹ should show a typical angiospermous embryo-sac is to be expected, as it does not exhibit any especially primitive features in the flowers, and is distinctly more specialized in this respect than are the Piperaceae.

As regards the significance of the fusion of the endosperm-nuclei, we agree with Johnson and Strasburger² that it is not a true fertilization, but has a nutritive significance only; and the whole endosperm, as well as the antipodal cells or their equivalents, represent gametophytic structures, and the endosperm is not to be considered as an embryo.

The behaviour of the endosperm-nuclei in *Peperomia* is a strong argument in favour of its primitive character, and is what might be expected from its other peculiarities. In harmony with the generalized character of the other structures of the embryo-sac, there occurs, instead of the two definite polar-nuclei of the other Angiosperms, a fusion of a somewhat variable number, which cannot be seen to bear any definite relation to any of the primary nuclei of the sac. With the reduction by half in the number of the embryo-sac nuclei, and the strongly marked polarity observed in most Angiosperms, the number of these nuclei becomes reduced to two, the polar nuclei, and the antipodal cells assume their characteristic position.

In regard to the homologies of the structures in the embryo-sac, the writer believes that the contents of the embryo-sac with the sixteen nuclei represent a prothallial tissue, and the nuclei are at first entirely similar. One of these becomes differentiated to form an archegonium, which is reduced to a single cell—the egg-cell. Whether the adjacent nuclei are to be considered as synergidal nuclei

¹ Johnson, D. S., On the Development of *Saururus cernuus*, L., Bull. of the Torrey Bot. Club, July 27, 1900.

² Einige Bemerkungen zur Frage nach der 'doppelten Befruchtung' bei den Angiospermen. Bot. Zeit., 1900, p. 293.

or not is doubtful, and the question whether the synergidae are, so to speak, sterile archegonia, or whether they are simply vegetative prothallial cells which become specialized for assistance in fertilization, cannot now be answered. The nearest approach to the structures found in *Peperomia* occurs in *Gnetum*¹, where no archegonium is formed, but the generative nucleus from the pollen-tube fuses with one of the free nuclei in the upper part of the embryo-sac.

That the fusion of the polar nuclei of the typical Angiosperms is in no sense a sexual process is borne out by the condition of affairs in *Peperomia*. The fusion of such a mass of nuclei is not conceivable as a sexual process, and is with little question, as already stated, a nutritive process, or perhaps a stimulus to active division in the endosperm-formation, or secondary growth of the prothallial tissue, which is to nourish the young embryo. This has no equivalent among either Archegoniates or Gymnosperms, and until further evidence is offered, may be assumed to have arisen among the lower Angiosperms, and to have become restricted to the special polar nuclei as the number of nuclei was reduced from sixteen to eight. The fusion of the second generative nucleus with the complex must also be assumed to be a special development. The second generative nucleus discharged into the embryo-sac, not having an egg with which to conjugate, might very naturally fuse with the only available nucleus, i. e. the endosperm-nucleus. That the tissue arising from this compound nucleus should show evidences of its hybrid character, where cross-pollination has taken place, is what would be expected, and by no means implies that the hybrid endosperm is in any proper sense of the word an embryo. The small cells developed individually about the nuclei which do not participate in the endosperm-formation in *Peperomia*, while they are not grouped together, must nevertheless be regarded as equivalent to the antipodal group of the typical Angiosperms, where the position of these cells

¹ Lotsy, Contributions to the Life-history of the Genus *Gnetum*. Ann. du Jar. Botanique, Buitenzörg, xvi, 1900, p. 46.

at the antipodal end is correlated with the marked polarity of the embryo-sac structures. In short, both antipodal cells and endosperm are equally of prothallial nature.

From a study of the condition of things in *Peperomia*, there is not the slightest evidence either that the antipodal group of the typical embryo-sac represents a second egg-apparatus, or that the polar nuclei are sexual in their nature.

THE SYSTEMATIC POSITION OF PEPEROMIA.

Through the kindness of Dr. D. H. Scott, several species of *Peperomia* were germinated at Kew, and an examination of these showed them to be true Dicotyledons—of which group *Peperomia* may be considered to be the most primitive type.

The reasons for this conclusion lie of course mainly in the character of the embryo-sac and the extremely simple flowers; but there are other features which point to this genus as a primitive generalized type. *Peperomia* shows several significant resemblances to the lower Monocotyledons, especially the Araceae, which themselves give evidence of being a very low type. The structure of the flowers, and their arrangement upon a thick spike, in many species quite like a true spadix, is noteworthy, while the habit of the plant, the form of the leaves, and the arrangement in the stem of the vascular bundles recalls very strongly the structure of the Araceae.

Moreover, the endosperm-formation is very similar in the two, being by direct division.

The relation of *Peperomia* to the other Piperaceae is unmistakable, and it is to be hoped that further investigations of members of this family may reveal some intermediate forms. The Saururaceae seem to represent a distinctly more specialized type than the Piperaceae, from which they have probably been derived. There seems no valid ground for supposing that the reverse is the case, as has been assumed by Engler¹,

¹ Engler, Piperaceae, Die nat. Pflanzenfamilien, iii. Th., 1. Abt., 1899.

who apparently regards the simple flower of the Piperaceae as reduced from the type found in the Saururaceae.

The question as to the relative antiquity of Monocotyledons and Dicotyledons is one which has not yet been answered, as the geological record is by no means complete. The close resemblances, however, between the Piperaceae and the lower series of Monocotyledons suggests that the divergence of the two divisions of the Angiosperms may have occurred very early; but much more evidence is necessary before it will be possible to decide this important question.

STANFORD UNIVERSITY, CALIFORNIA,
Jan., 1901.

EXPLANATION OF FIGURES IN PLATE VI.

Illustrating Prof. Campbell's paper on *Peperomia*.

All figures refer to *Peperomia pellucida*, Kunth, and were drawn with the camera lucida, Leitz oil im. $\frac{1}{16}$, oc. I. $\times$ about 600.

Fig. 1. Longitudinal section of an embryo-sac with sixteen nuclei, of which three are at the micropylar end. *t*, the tapetum.

Fig. 2. An older stage, in which the egg-cell, *o*, is differentiated, and the endosperm-nuclei, *E. n.*, are grouped together. A second large nucleus lay close to the egg, but there was no definite synergid.

Fig. 3. Embryo-sac just after the entrance of one of the generative nuclei, *Sp*, into the egg-cell, *o*; *p. t.*, the empty pollen-tube. The endosperm-nuclei, *E. n.*, are collected at the antipodal end of the embryo-sac. Two synergidae (?).

Fig. 4. *A*. Embryo-sac just before the entrance of the pollen-tube, *p. t.* The two generative nuclei can be seen near its extremity. Three synergidae (?); two shown in *B*.

Fig. 5. Fertilized embryo-sac, showing the two pro-nuclei, *Sp, o*, in process of fusion. The endosperm-nuclei were also beginning to fuse. *x*, one of the accessory nuclei, enclosed within its cell.

Fig. 6. *A* and *B*. Two sections of an older embryo-sac, in which the cytoplasm fills the cavity. The two pro-nuclei were still separate. Nine endosperm-nuclei occupied the centre of the sac. In *B* is shown an unusually large accessory nucleus, *x*, enclosed in a nearly globular cell.

Fig. 7. Beginning of the fusion of the endosperm-nuclei, *E. n.* *Em*, one-celled embryo. *x*, accessory nucleus.

Fig. 8. Section of a ripe pollen-spore, showing the two nuclei, *v* and *g*.

Fig. 9. Embryo-sac, shortly before the division of the fusion-nucleus, *E. n.* *Em*, embryo.

Fig. 10. Embryo-sac, after the first division of the endosperm. *Em*, embryo; the pro-nuclei in process of fusion.

Fig. 11. Older embryo-sac, containing a four-celled embryo, *Em*, and several endosperm-cells. *x*, accessory nucleus.

Figs. 12, 13. Longitudinal sections through the integument, *in.*, of the young seeds, showing the peculiar form assumed by the cells of the inner layer. The walls of these cells stain very strongly, but do not become noticeably thickened.

Fig. 1.

Fig. 2.

Fig. 5.

Fig. 6.

Fig. 11.

Fig. 10.

D.H. Campbell del.

Fig. 3.

Fig. 4.

Fig. 7.

Fig. 9.

Fig. 12.

Fig. 8.

Fig. 13.

Campbell, Douglas Houghton. 1901. "The embryo-sac of *Peperomia*." *Annals of botany* 15, 103–118. <https://doi.org/10.1093/oxfordjournals.aob.a088806>.

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