Flower morphological and embryological studies on the viscoids ***Korthalsella Opuntia*** **Merr. And *Ginalloa linearis* Dans.**

By Alfred Rutishauser.

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I. Introduction.

The viscoids, like all other Loranthaceae, are distinguished by the simple construction of their flowers. Complete absence, or at least strong reductions in the structure of the sperm plants are characteristic for all representatives of the family. In general these simplifications are considered as secondary phenomena, reconstructions. In an earlier work (A. Rutishauser, 1934) I have attempted to show that the reductions only affect the sporophyte, but not the gametophyte, the latter is rather conservative, its form, position and inner construction, despite the changes that the sporophyte undergoes.

Through the transfer and mediation of new research material by Prof. Dr. A. Ernst, it has become possible for me to confirm the above conclusion with new observations. Mr. Prof. Dr. A. Ernst had the goodness to give me the material of *Korthalsella Opuntia* Merr. And through his mediation I received from the collections of the botanical museum in Buitenzorq, Java, fixed material of *Ginalloa linearis* Dans.

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1 Outcome of subsidies by the Julius Klaus Foundation for Inheritance Research, Social Anthropology and Racial Hygiene and the Foundation for Scientific Research at the University of Zurich by Professor Dr. Alfred Ernst and Dr. Marthe Ernst - Schwarzenbach, conducted an IndoMalay research trip (July 28, 1930-16 April 1931), No. 8.

Korthalsella Opuntia Merr. is an east Asian viscoid. Its hosts belong to the genera *Adinandra, Eurya, Ilex*, and other deciduous genera. Morphologically, the species is not fully known. H. Lecomte (1916) described the fruits of a viscoid which he described as *Korthalsella moniliformis*, which, according to B. H. Danser, is identical with *K. Opuntia* Merr. Whether Lecome's description of the synandium of the male flower, which he published some time later, is also based on *K. moniliformis*, *K. Opuntia* Merr. is not clear. For this reason, I have at least briefly reproduced the results of my own investigations on this point, in spite of a great agreement with H. Lecomte. This is also because B. Hayata (1915, 1916), who probably also dealt with the same species, came to such deviant results with regard to the construction of the androeceum that it even caused him to set up a new genus. While H. Lecomte (1916) assumes that the fused anthers are in front of the perigone leaves, B. Hayata, on account of his investigations carried out on microtome sections, leads to the assumption of alternation between the perigone leaves and the anthers.

The genus *Ginalloa* is from Korthals (1839) has become known from the description of the west Indian species *G. Arnottiana* Korth. by Ph. Van Tieghem (1895, p. 646), with the embryo sac being described for the first time. Unfortunately, it is no longer possible to determine the manner in which Ph. Van Tieghem carried out his observations. However, it can be inferred from the fact that it was not a question of *Ginalloa linearis*, which means that, despite the fact that it is largely in line, it will again be necessary to revert to the points which Ph. Van Tieghem has already taken into account.

I was able to carry out investigations into the present work in the years 1935/1936, using the facilities of the Institute of General Botany, University of Zurich, for which I thank the Head of the Institute, Professor Dr. A. Ernst, to whom I am greatly indebted. Thanks also to Dr. Dr. F. Steindl for the production of the microphotographs.

II. Materials and technology.

The material of *Korthalsella Opuntia* Merr. comes from Ceylon, where it was collected by Mr. and Mrs. Prof. Ernst - Schwarzenbach on 25 August 1930 by way of Nuwara Eliya to Hakgalla. Only 95% alcohol was used as fixing and preserving liquid. The fixation was sufficient to study flower morphology and embryology, but the material was not very suitable for finer cytology. After all, it was nevertheless possible to obtain some cytological data, at least roughly. Staining was carried out with iron hematoxylin according to Heidenhain and Feulgen's nuclear reaction.

My efforts to obtain fixed material from *Ginalloa* had not been very successful despite various requests. Mr. Prof. Dr. BH Danser gave us the friendly message that in the collections of the herbarium in Buitenzorg, alcohol material collected by Miss B. Polak in Mador, near Poentianak, Borneo, and by himself a viscoid as *G. linearis* nov. spec., is present. At the request of Prof. Dr. A. Ernst was given this material by Professor Dr. C. G. G. J. van Steenis for the collection of suitable samples. It was, as it turned out, fortunately a large number of shoots. Unfortunately, in this case, the preservative (alcohol) proved not to be suitable for the investigation of embryo sac development, since the stages of the eight-nucleate embryo sac had shrunk considerably. This is also the reason why a more detailed description of the egg apparatus was not possible. The colorants used were the hematoxylin of Delafield and the hematoxylin of Heidenhain.

III. Investigations on *Korthalsella Opuntia* Merr.

1. The inflorescence.

All the shoots that were available to me were filled with flowers or fruits at the nodes. The flowering branches consist of flattened, oblong-oval segments, which can be up to 17 mm long and 5 mm wide. At the upper end of the internodes, the opposite leaf scales arise in a superposed arrangement. Ph. Van Tieghem (1896b, p. 165) already drew attention to this peculiar position, which is rare in the case of angiosperms. The leaves are fused at their lateral edges and form a ring containing the stem.

The flowers arise in the axils of the opposite scale leaves. A cross-section through young nodes shows the two fused leaf scales and in their axils first three flowers, of which the middle are male, the two lateral female. All other adventive flowers are female. Two flowers are always formed at a time, so that two of them have the same developmental state. They originate somewhat below and on the sides of the primary female flowers, in such a way that a second pair of female flowers comes to lie within the two first-formed flowers, and the third below the first pair. In this way, an inflorescence occurs consisting of 7-9 flowers, in which the female flowers are arranged in four rows below and on the side of the single male flower. The interspaces between them are filled with unbranched, multi-cellular hairs.

My observations on the arrangement of the flowers do not agree with the older Ph. Van Tieghem (1896 b, p. 162), the first worker on the genus *Korthalsella*, in two points. Regarding the developmental sequence of the flowers of *Korthalsella Remyana* which he examined, Ph. Van Tieghem states: "Il s'en fait d'abord une médiane vers le haut du massif de poils, puis une autre de chaque côté et un peu au-dessous, puis une nouvelle sous la médiane, puis deux nouvelles sous les Deux latérales et ainsi de suite. Les fleurs sont alors disposées en trois series longitudinales, dans chacune desquelles elles naissent de haut en bas." [First a median is made upwards of the hair mass, then another one on each side and a little below, then a new one under the median, then two new ones under the lateral two and so on. The flowers are then arranged in three longitudinal series, in each of which they are born from top to bottom.]

My observations show that, after the first female pair, not one, but two other female flowers are formed at the same time, which do not arise directly under the first male flower, but below and on both sides, so that four rows of female flowers are created. This observation is of some importance because it shows that the flower arrangement within a leaf axil is similar to that of *K. Dacrydii*, but also that of *Phoradendron*. According to K. Goebel (1931, p. 137), the inflorescence of *Phoradendron polygonum* consists of four-edged shoots with likewise opposing, reduced scale leaves. The male flowers above the leafy scales are the internodes, the many female flowers the four edges of the same. Two of the four rows of female flowers belong to a male flower and together can be viewed as inflorescences. There are, therefore, two inflorescences at each internode, the individual flowers of which are raised above the cover by an intercalary growth zone. The difference with *K. Opuntia* seems to me to be that there is no intercalary growth zone in this intercalar zone, or effectively at least only a little, so that the flowers are more crowded.

Ph. Van Tieghem (1896a, p. 84) writes about the numerical ratio of the male and female flowers: "Chaque groupe renferme des fleures mâles et des fleurs femelles, mélangées sans ordre bien marqué, les premières plus nombreuses que les secondes." [Each group contains male flowers and female flowers, mixed in no clear order, the first more numerous than the second].

The distribution of the male and female flowers is much more regular in the plants I have examined, since the first flowering is always male, but all the others are female. In contrast to Ph. Van Tieghem's observation, the female flowers are much more numerous than the male ones. The number of male and female flowers is 1: 6 or 1: 8 for the individual inflorescences.

2. The male flower.

The developmental history of male as well as female flowers is the same in the first stages as I described them for *K. Dacrydii* (A. Rutishauser, 1934). It is therefore unnecessary to go into it. Only in the later stages of the synandrial development do some differences become apparent which lead to a somewhat different construction.

The male flower consists of two leaf whorls, the three perigone leaves and the synandrium containing six pollen sacs. The number and position of the anthers which synthesize the synandrium can not be directly determined, since no vascular bundles are present. There are also completely identical transverse walls between the pollen sacks arranged in the circle (Fig. 1 a, b). Hence, from the anatomical structure of these, neither conclusions can be drawn as to the anther number nor to the original position of the individual anthers relative to the periogone leaves. In my opinion, however, the assumption that the synandium is composed of three anthers lying in front of the perigone leaves is, in my opinion, scarcely absent, since the nearest relatives of our species are distinguished by such a development of the androecium.

A circumstance seemed, however, against this conception. In cross sections, the canal, enclosed by the synandium, appeared regularly in the form of a triangle with long drawn out corners, each of which had two pollen sacs surrounded by the extended corners, and consequently is to be regarded as wholly belonging together. The idea that two such pollen sacs correspond to one of the three anthers was obvious. Since, however, the extended corners of the central canal ran exactly against the center of the perigone leaves, it would also have to be assumed that the three anthers were between the perigone leaves.

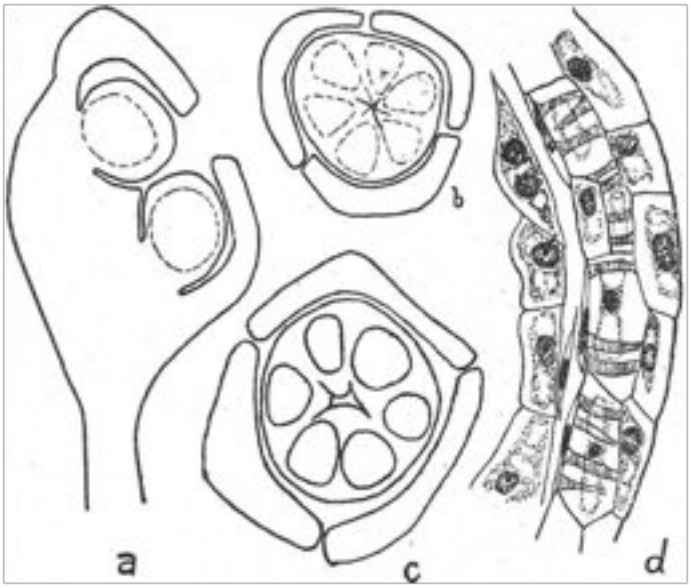

Fig. 1. Morphology of the male flower of *Korthalsella Opuntia*. A Median longitudinal section, b and c cross sections. D cross section through the anther wall. (Magnification ac 1: 40, d 1: 300).

B. Hayata (1915, 1916) already made a similar observation to the present one, and drew from it the conclusions which we have just given. He consequently goes so far as to extract the plant from the genus *Korthalsella* and to establish for it a new genus, *Pseudixus*. However, I do not believe that the above-mentioned observation is of any importance to me, and I agree with the view of J. C. Mekel (1935), who refuses to interpret the observation of Hayatas as he does. The similarity of *K. Opuntia* with the species of the genus *Ginalloa*, where the three dubious anthers are in front of the perigone leaves, is too great for the species of the two genera to differ in such an important feature. But then the construction of the central canal of the synandium, which gives rise to these differences, is not always the same, so that no such great weight should be placed on this feature. In a cross section series through a mature male flower, I found a central canal, drawn out into *four* points, by which a quite irregular grouping of the pollensacs came about, so that groups of two pollen sacs separated by no incisions stood opposite individual pollen sacs (Figure 1 c). There is, therefore, no reason to conclude from the position of the anthers alternating with the perigone leaves from the probably occasional triangular central canal. The species can therefore be kept easily in the genus *Korthalsella*.

The external anther wall of the synandium is composed of four cell layers (Fig. 1d). An epidermis, which has a thickened exterior membrane, closes off the antheric ring bulge. This is followed by a well-formed endothecium. The third layer consists initially of narrow elongated cells, which are almost completely compressed and degenerated in the course of anther development. The binucleate tapetum is attached to it. In contrast to *K. Dacrydi*, *K. Opuntia* has a perfectly normal anther wall.

The vascular bundle system is very simple. It consists of three vascular bundles running through the pedicel, which feed the perigone leaves. Branches, such as at the base of the synandrium, have not been observed. The anthers therefore have no vascular bundles.

The pollen development is similar to that of *K. Dacrydii*. The chromosome numbers of the nuclei I could not determine exactly. They may not differ materially from those found in *K. Dacrydii*. Differences to *K. Dacrydii*, on the other hand, arise with regard to the finished pollen grains, since the vegetative nucleus of *K. Opuntia* is spherical, and in the cytoplasm a marked degree of starch can be demonstrated.

3. The female flower.

The spadiceous female flower consists of three perigone and - probably - two carpel leaves. At least the two-lobed stima and the inner construction of the ovary can be traced back to the two-pointed carpel tissue. The carpels are fused, but the growth is not complete. There is always a narrow, slit-shaped stylar channel, which extends downwards to the ovary cavity filled by a central placenta (Fig. 2 a). Against the stylar canal, the carpels are provided with a fine cuticle, as is the placenta. The latter has the form of a cone flattened in the median plane of the carpel, on which no bulges are present. So ovules are not developed.

The vascular bundle system consists of three vascular bundles, which, as in the case of the male flower, extend through the pedicel and end in the three perigone leaves. The young carpel tissues do not yet have any vascular bundles.

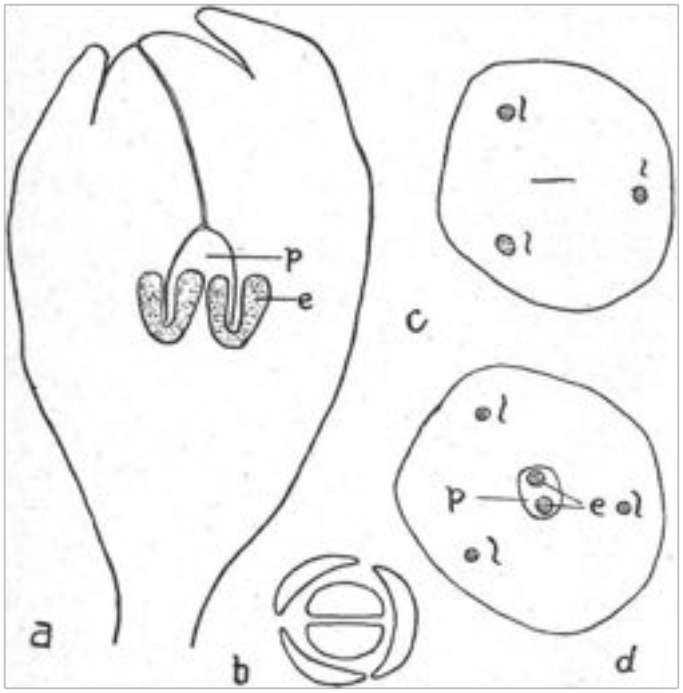

Fig. 2. Morphology of the female flower of *Korthalsella Opuntia*. A Median longitudinal section. b-d Cross-sections of the young female flower. e Embryo sac. l Vascular bundles. p Placenta. (Magnification a, 1: 70, b-d, 1: 40).

The position of the carpel to the perigone leaves has been developed from cross sectional series. The following pictures appear first from the top downwards: The first three periogone leaves, then the two stigmatic lobes, whose longitudinal gap is directed exactly perpendicularly to one of the perigone leaves (Fig. 2b). At the height of the stylar canal, the position of the perigonal leaves can be determined from the position of the three vascular bundles, while the position of the carpel can be determined by the direction of the slit-shaped stylar canal, which points to one of the vascular bundles (Fig. 2 c). Further down, the center of the flower is filled by the oval placenta whose longitudinal axis is perpendicular to the stylar canal in the median plane of the two carpels. Depending on the developmental stage of the flower, it contains the archespore or stages of development of the embryo sac (Figure 2 d). Even at this height, only the three vascular bundles of the perigone are visible.
The gametophyte originates in the tissue of the placenta. In the young placenta two subepidermal cells are differentiated by further growth and enlargement of the nucleus into archesporial cells. They lie in the median plane of the carpel and are separated by two to three cell layers. From these, the embryo sac mother cells are produced without further division (Fig. 3 a). I could not keep track of the tetrad divisions that were beginning. However, it can be concluded from the existing stages that, after the first division, a transverse wall is formed through which the embryo sac mother cell is divided into two superimposed cells, the upper embryo sac cell and the degenerating lower sister cell. From the second reduction division, which is also the first of embryo sac formation, the two-nucleate embryo sac (Fig. 3 b) results. After the next synchronous nucleation step, which leads to the formation of the four-nucleate embryo sac (Fig. 3 c), a period of rest occurs at least with respect to the growth and division processes. On the other hand starch is stored during this stage in large quantities. The number of the 4-5µ large starch granules disintegrated into two to three partial grains is finally so

large that the cytoplasm gets a brittle structure. Starch storage also continues at the beginning of the next growth period. In the course of the later stages of embryo development, the starch disappears almost completely. The fertilized embryo sac contains only a few starch grains.

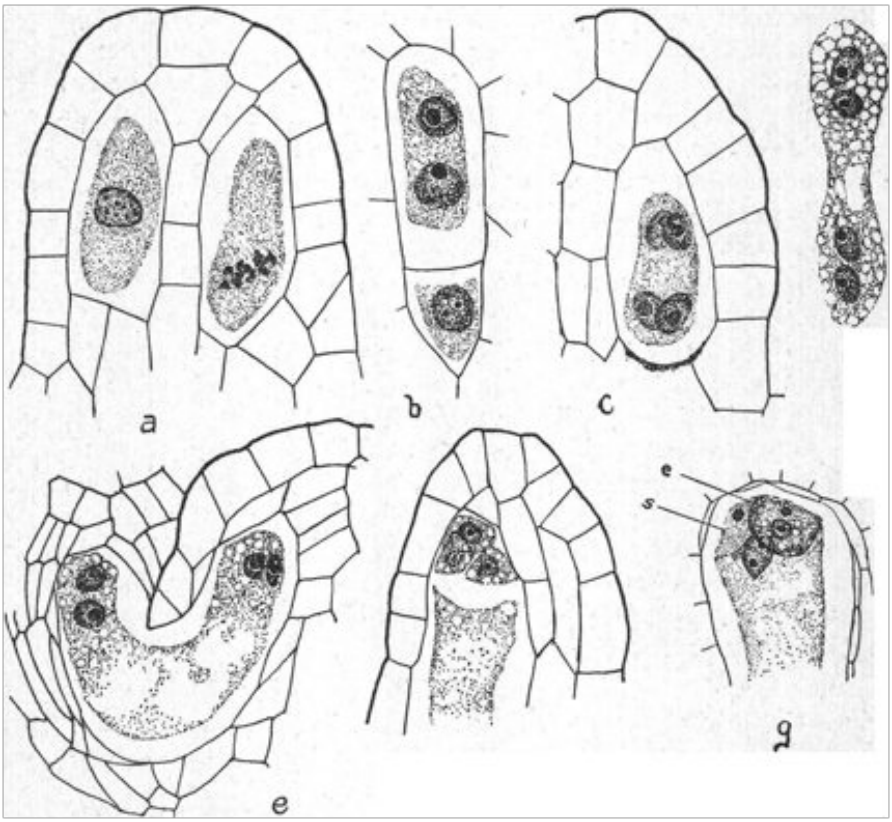

Fig. 3. The development of the embryo sac of *Korthalsella Opuntia*. a Embryo sac mother cells. b Two-nucleate embryo sac with sister cell. c Four-nucleate embryo sac. d and e growth stages of the four-nucleate embryo sac. f Antipodial end of the embryo sac. g egg apparatus. s Synergids. e egg cell. (Enlargement a-c 1: 950, d-g 1: 580.)

The embryo sac is the same as in the case of *K. Dacrydii*. The embryo sac first undergoes a longitudinal downward path, while no growth takes place upwards. The lower part of the four-nucleate embryo sac grows, laterally, out of the placenta, into the adjoining carpel tissue, displacing the vegetative cells of the carpel tissue (Fig. 3e). Turning upwards, it travels outside the placental epidermis but close to the placenta. Only after having adjusted its growth somewhat below it does the third division step of embryo sac formation take place.

The antipodial end of the embryo sac, which has become U-shaped as a result of these peculiar growth processes, is located in the placenta, and the egg apparatus is at the same level as the antipodals in the carpel tissue (Fig. 2a). The three antipodal cells are characterized by strongly vacuolated, starch-containing cytoplasm (Figure 3 g). The cells of the egg apparatus vary considerably in shape and behavior of the nucleus and cytoplasm (Figure 3 g). While the cytoplasm of the large nucleate egg is strongly vacuolated and filled with starch, the two synergids have small nuclei and fine-grained, starch-free cytoplasm. In the cytoplasm accumulation below the egg cell the two half-fused polar nuclei are embedded in the embryo sac core.

From what has been said, it can be seen that the embryo sac of *K. Opuntia* differs from the normal type in various points. For the formation of the embryo sac from the megaspore, only four division steps are necessary. The embryo sac development is thus based on the *Scilla* type. In addition, there are deviations in form and position, in that the embryo sac is not straight, but U-shaped, and the egg-apparatus is formed from the formerly lower end of the embryo sac, the latter thus behaving as if it belonged to a pendulous ovule.

The results of our embryological investigation coincide almost exactly with those obtained from *K. Dacrydii*. Regarding the location, development, shape and position of the embryos of the two species, no significant differences are to be found. Even the finer construction of the egg apparatus is almost exactly the same. We find the richly vaculate egg, the semicircular polar nuclei, and especially the synergids with fine-grained vacuole-free cytoplasm, both in *K. Dacrydii* and in *K. Opuntia*. The only difference seemed to be the occurrence of starch in the embryo sacs of *K. Opuntia*. A thorough examination of the corresponding stages of the embryo sac development in *K. Dacrydii* had the result, however, that even here, to a lesser degree, starch could be detected.

The great agreement in the construction of the embryos of the two species caused me to compare their dimensions. The number of measurements was very small according to the difficulty of obtaining whole U-shaped embryo sacs, but the results are sufficient to make at least a rough comparison of the sizes. The height of the U-shaped embryo sac from the bending point to the apex of the egg apparatus is between 110 and 120 μ in both species. Real differences can not be observed. I was able to find real differences in the diameter of the grains. The mean value for 50 measured pollen grains was 9.2 μ for *K. Dacrydii*, 8.2 μ for *K. Opuntia*.

The agreement in the size of the gametophytes is all the more striking since differences in size are evident. As can be seen from the following table, the flowers of *K. Opuntia* are by much larger than those of *K. Dacrydii*.

	K. Opuntia	*K. Dacrydii*
Length of female flower	0.97 mm	0.55 mm
Width of female flower	0.53 mm	0.35 mm
Length of male flower	0.97 mm	0.60 mm
Width of male flower	0.68 mm	0.42 mm

The flowers of the two species differ, however, not only in size. In contrast to the older authors, whose work does not reveal whether there are flower morphological differences within the species of the genus *Korthalsella*, my investigations on *K. Dacrydii* and *K. Opuntia* have led to the determination of both flower morphological and anatomical differences. Thus the stigmas of *K. Opuntia* are clearly two-lobed; between the two carpels, which are not completely fused with one another, a slit-shaped stylar canal is always kept out, and the ovarian locule is still detectable as a fine interspace between the carpels and the placenta. On the other hand, the carpels of the simple, stimatic *K. Dacrydii* are fused with one another at very early stages of development, so that their borders at the level of the style cannot be recognized at all at the level of the placenta, owing to the presence of a fine cuticle.

The fusion of organs, which occurs generally in the Loranthaceae and results in a simplified structure of the flowers, is therefore much more advanced in *K. Dacrydii* than in *K. Opuntia*, and also in *K. Remyana*, which, according to van Tieghem's description, best matches with *K.*

Opuntia. *K. Dacrydii*, therefore, appears to be phylogenetically the youngest of the three known species of *Korthalsella*.

The behavior of the vascular bundles also shows that differences in the structure of the flowers occur. At the time of the inflorescence there are two in *K. Dacrydii*, three in *K. Opuntia*, and in *K.* Remyana there is an external circle of three and one internal of two vascular bundles. Thus, *K. Dacrydii* is also reduced to a greater degree with respect to the vascular bundle system than the other two *Korthalsella* species.

In summary, we find that the species of the genus *Korthalsella*, to the extent that they are still embryologically studied, almost coincide with one another in the construction and development of the embryo sacs, but in the morphological structure of the flowers and the vegetative organs. Our assumption that the sporophytes are affected by the reduction alone, whereas the gametophyte is conservative, has recently been confirmed.

4. The fruit.

Unfortunately, I failed to observe stages of fertilization. On the other hand, it was possible to examine the first stages of endosperm development. The first division follows the formation of a transverse wall through which the embryo sac is divided into two unequal cells, a smaller upper and a lower cell occupying the whole remaining part of the embryo sac center. In the next observed stage, the endosperm consists of four transverse slices, of which the upper two are two-celled, the two lower one-celled. The further development is the same as with *K. Dacrydii*. It is, however, emphasized that in *K. Opuntia* the endosperm formation sometimes also extends into the antipodial arm of the U-shaped embryo sac.

Also with regard to the first stages of embryo formation, no significant differences are to be found between *K. Dacrydii*. The first partition wall is once again directed obliquely to the axis of the flower, a suspensor cell is not formed here either. It is only in the later stages of development that some differences can be observed, the lower end of the embryo being differentiated into two cotyledons and a long conical plumule (Fig. 4).

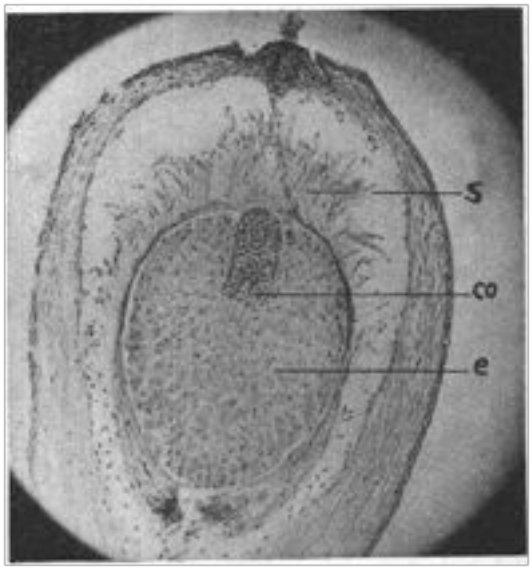

Fig. 4. Longitudinal section through the fruit of *Korthalsella Opuntia*. s viscin layer. e endosperm. co cotyledons of the embryo. (Magn. 1: 36). F. Steindl.

Studies on the reserves in the endosperm and embryo showed that the former is filled with starch granules, whereas the cells of the embryo contain little starch.

The construction of the other parts of the fruit has already been described by Lecomte (1916, p. 127). It is therefore unnecessary to go into it. There are only a few additions to the vascular system. As stated above, the fertilized flower has three vascular bundles extending into the perigone leaves. Two of them undergo a further development during embryo and endosperm development. A lateral branch is formed, which leads to the base of the carpel tissue and widens into a tissue of wide-lumina tracheids.

IV. Studies on *Ginalloa linearis* Dans.

1. The inflorescence.

The inflorescences, which are provided with very short internodes, have bracts that are arranged at the ends of the branches. The flowers are arranged in the axils of the bracts and they are arranged in such a way that a male flower is placed in the axils of the two to three upper bract pairs and a female flower in each of the lower ones. Never could I observe more than one flower in a leaf axil. My observations are contradictory to Danser's statements on this point. According to B. H. Danser (1931 b, p. 448), three flowers are to be found in each species of the genus *Ginalloa*, of which the middle is female, the two lateral are male. *Ginalloa linearis*, therefore, as regards the arrangement of the flowers, is essentially different from the other species of the genus.

2. The male flower.

The male flower is about ½ mm long. On a shortened stem is set a flat, central, raised conical receptacle from the edges of which arise the three perigone leaves. In front of the perigone leaves, the three anthers are triangular in cross-section (Fig. 5 a, b). Each of them contains two pollen sacs, so there are six pollen sacs in each flower. However, there are also exceptions.Thus I could observe in two flowers that one of the anthers formed only one pollen-sac, although it did not differ from the other anthers in the dimensions (Fig. 5b). This observation is, therefore, of some importance, because in the genus *Dendrophthora*, which is closely related to *Ginalloa*, perpetually only forms one pollen-sac.

According to the small size of the flower, its vascular bundle system is also very simple. On the other hand, only the three perigone leaves are not supplied with the anthers with vascular bundles.

The anatomical structure of the anther wall is normal. In particular, it should be noted that an endothecium is always clearly visible (Figure 5 c). The cells of the tapetum, unlike the *Korthalsella* species, are mononuclear.

The developmental history of the pollen grains could not be followed. The mature pollen grains are two-celled. Their starch content is striking. The starch appears in the form of composite, round or oval grains in such quantities that the nuclei only stand out as more darkly colored bodies from the environment (Figure 5 d).

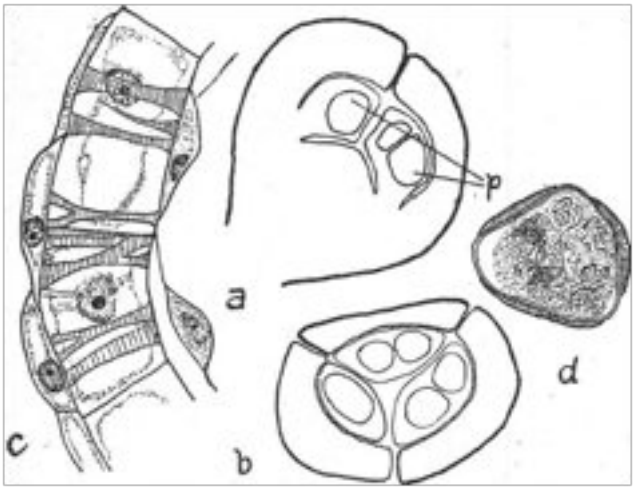

Fig. 5. Morphology of the male flower of *Ginalloa linearis*. a Median longitudinal section. b cross-section. c Section through the anther wall. d Two-nucleate pollen grain. (Magnification a, b, 1: 40, c, 1: .300, d, 1: 1150.)

It can be seen from the data given above that the male flower of *Ginalloa linearis* differs significantly from the *Korthalsella* flowers with a synandrium. On the other hand, it agrees well with the male flowers of the American genus *Phoradendron*. With the occasional emergence of simple anthers, the flowers of the American genus *Dendrophthora* also appear.

3. The female flower.

The female flower has three to four perigone leaves. The perigone lobes are very small and usually only ⅕ to ¼ of the total flowering length of 1.3 mm. The entire remaining part of the flower consists of a compact, slightly differentiated cell mass in the shape of a cylinder with an oval base. Since it was not possible to determine the number and position of the carpel tissue by examining the development history, it had to be developed from the construction of the vascular system. There are two whorls of vascular bundles, an inner one consisting of two and an outer, composed of eight to nine vascular bundles. We consider the inner two bundles as those belonging to the carpels, and believe from their number and position to conclude that the gynoecium consists of two carpels, the median plane of which lies in the plane of the greatest width of the flower.

As in the case of *K. Opuntia*, the two carpels in the center of the flower leave an ovarian cavity and a column-shaped stylar canal. The former is almost completely filled by the elongated, conical placenta. However, a fine interspace between the carpel side and the placenta can occasionally be observed as the last remnant of a free ovarian cavity. If this is not the case, the border between the placenta and the carpels is clearly recognizable, at least, by the formation of a cuticle. The placenta is closely below the apex with two small bulges lying in the median of the carpel. They are the embryos. Longitudinal sections, guided in this direction, showed in one case a very remarkable behavior of the placenta apex, in that it was divided into two lobes by a perpendicular slit in the upper quadrant (Fig. 6 a).

The examination of cross-section series and cuts perpendicular to the median plane of the carpel tissue in the longitudinal direction of the flower showed that the placenta is not of equal construction in the upper and lower half. The placenta appears first as an oval or almost

quadrangular structure in the transverse sections which follow one another from the top downwards, which is distinctly distinguished from the adjacent carpel tissue by the roundly well-developed cuticle (Fig. 6f). In deeper incisions, the cuticle disappears at the longitudinal sides of the placenta, and the carpel tissue passes over into the tissue of the placenta without a visible border. Only the width of the placenta lying in the median plane of the carpel is clearly distinguished from the carpels by the presence of a cuticle (Fig. 6g). According to the images found in these cross-sections, the placenta appears in the longitudinal sections perpendicular to the median plane of the carpel, from left to right as an elongated conical structure (Fig. 6b), which becomes shorter and shorter after the middle; has reached half the original size (Fig. 6c), in order to resume its original length in the following sections of the series. On the basis of our conception of the number and position of the carpel tissue, the peculiar structure of the placenta can best be explained by the assumption that the carpel margins are fused in the basal part of the placenta, with the result that the ovarian cavity is one-locular in the upper part, in the lower part, however, it becomes dubious. Similar observations have also been made by van Tieghem on the *Ginalloa* species he investigated.

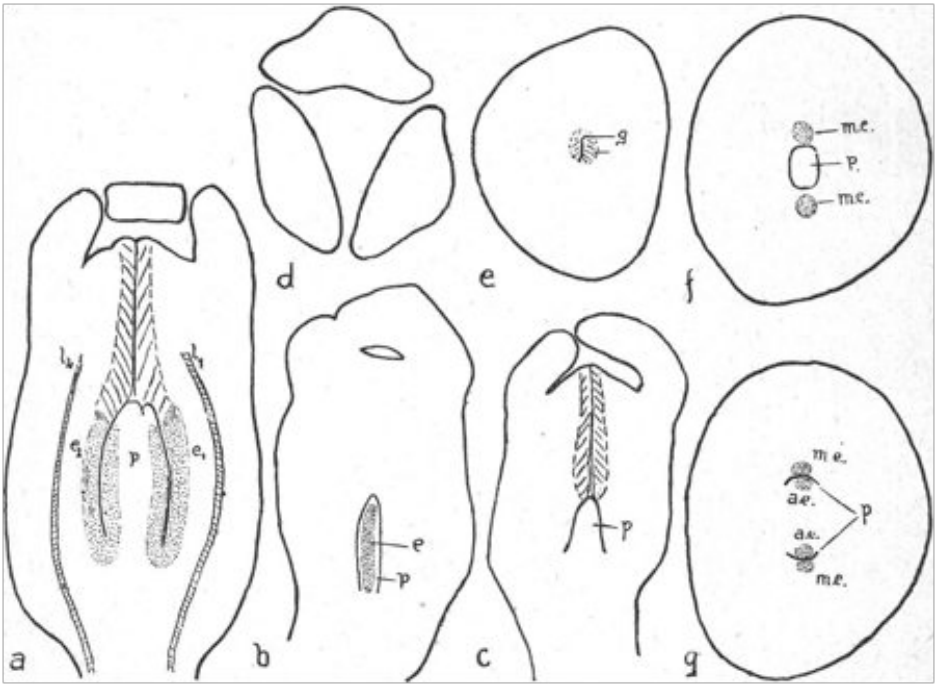

Fig. 6. Morphology of the female flower of *Ginalloa linearis*. a median longitudinal section through female flower. b-c Longitudinal sections guided perpendicular to the plane of the carpel tissue. b Median. c In the area of the placenta edge. d-g cross sections through fertilized mature female flower. e, e_1, e_2 embryo sac. m. e. Micropylar end of embryo sac. a. e. antipodal end of the embryo sac. g style. l_1 , l_2, vascular bundles. p placenta. (Magnification 1: 40).

It is remarkable that such a construction of the placenta occurs within the viscoids only in the genus *Ginalloa*. In the case of the Loranthaceae, however, a similar construction of the gynocium is widely used, but mainly in the Myzodendraceae and Olacaceae. The ovarian cavities of the last two families are in the basal part more, usually threefold, but in the upper one, however, one-fold. In contrast to *Ginalloa linearis*, however, the placenta at the tip always

carries hanging ovules, which are much less reduced than that of the species we are investigating.

Since there are no ovules in *G. linearis*, the embryos are formed in the placenta, as in the case of *Korthalsella* species. For reasons already mentioned, it was not possible for me to follow the embryo sac development more closely. However, the existing stages provide at least some of the most important questions. The two archespores arise at an early stage before the placenta is fully developed, in the two bulges situated below the apex (Fig. 7 a). They consist of a subepidermal cell, which is distinguished from the vegetative cells of the placenta tissue by fine-grained cytoplasm and large nuclei. They are separated by about seven to eight cells. The first reduction is performed in the basal part of the embryo sac mother cell, after a displacement of the nucleus has already taken place (Fig. 7 b). It is very probable that only one sister cell is discharged downwards, for I could observe in two cases that the two-nucleate embryo sac is limited by only one basal, already degenerationed sister cell (Figure 7c). The next stage already shows the growing four-nucleate embryonic sac (Fig. 7d, e). It lies close to the placenta epidermis and has reached the placenta base in the stage we have observed. In this state, the embryo sac is filled with such starch that almost nothing can be seen from the cytoplasm, and the nuclei are only more or less clearly distinguished by their intense coloration. The round or oval starch granules have decomposed into two or four partial grains and have a size of about 5-6 µ.

Similar observations on the starch content of the embryo sacs have been made in all Phoradendreae. H. H. York (1913) and F. H. Billings (1933) give starch to the embryo sacs of *Dendrophthora* and *Phoradendron*, the author has proved them for *K. Opuntia* and *K. Dacrydii*. According to Billings and my own observations, the starch appears only in the four-nucleate embryo sac, only York states he it has already seen starch in earlier stages of embryo development.

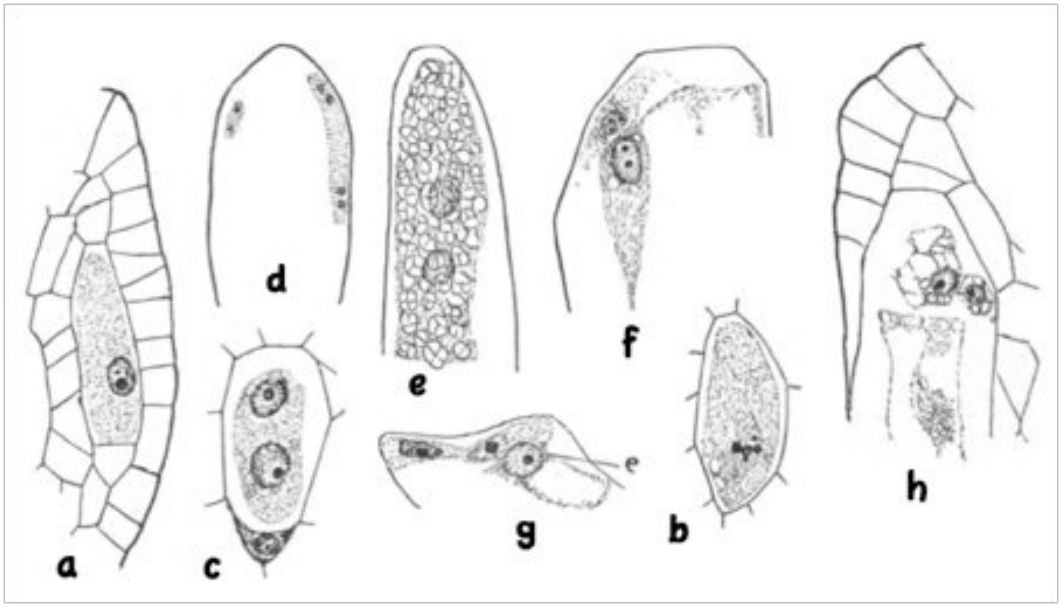

Fig. 7. The development of the embryo sac of *Ginalloa linearis*. a Embryo sac mother cell. b Embryo sac cell in division. c Two-nucleate embryo sac with sister cell. d placenta with two-nucleate and four-nucleate embryo sac. e Antipodal part of the four-nucleate embryo sac. f and g egg apparatus. h Antipodal end of the fertilized embryo sac. (Aug. 1: 580, d 1: 80)

The growth of the four-nucleate embryo sacs is similar to that of *K. Dacrydii*. The basal part of the embryo sac grows, after reaching the base of the placenta, into the carpel tissue, then makes a bend of 180 degrees, and penetrates along the cuticle of the placenta until it reaches approximately the same height as the non-bulging upper end. In this way, a U-shaped embryo sac is formed which is oriented in such a way that one limb lies in the placenta and the other lies in the carpel tissue (Fig. 6 a). The part remaining in the placenta carries the antipodals filled with starch at the upper end. Their number could not be determined exactly. In one case I saw only one nucleate, in a second two nucleate cells (Fig. 7h). Likewise, I was unable to obtain more accurate data on the construction of the egg apparatus. From the present observations it can be seen only that two synergids and one egg are most likely present (Figure 7g). The two fused polar nuclei have also been observed (Fig. 7- f).

The results of our embryological examination can be briefly summarized as follows: The two archespores are unicellular and arise as subepidermal cells just below the apex of the placenta. The development of embryos is most probably according to the *Scilla* type. With the appearance of the four-nucleate embryo sac, starch storage and growth begin. The latter results in a U-shaped embryo sac, the antipodals of which are located in the placenta, the egg-apparatus of which is in the carpel tissue. Since the egg apparatus originates from the formerly basal end of the embryo sac, we consider this end as the micropyle, and find that the embryo sac in its polarity behaves as if it were from a pendulous ovule.

A comparison between the female gametophytes of the two genus *Ginalloa* and *Korthalsella* therefore does not show any significant differences. In the construction of the archespore, in the development of embryo sacs, according to form and polarity, there is broad agreement. It is interesting in this context that the two species *G. linearis* and *K. Opuntia* coincide at the time of occurrence and in the form of the starch granules. Only in terms of quantity is a difference is there a difference in the quantity of starch granules from *G. linearis* through *K. Opuntia* to *K. Dacrydii*. Differences also arise with regard to the size of the embryo sacs. The embryo sacs of *K. Opuntia* and *K. Dacrydii* have a length of 110 to 120 µ, those of *G. linearis* of 380 µ.

The embryo sacs of the two genera agree, as can be seen from what has been said, apart from the magnitudes and the quantity of starch. It is also clear from the comparison between *Ginalloa* and *Korthalsella* that the sporophytes diverge to a greater degree than the gametophytes. The sporophytic parts of the gynoecium of *Ginalloa* prove the occurrence of a two part ovarian cavity and a pair of wholly composed vascular bundles less reduced than the gynoecium of the *Korthalsella* species.

4. The fruit.

The fruit of *G. linearis*, like that of all viscoids, is a false fruit, in that all the organs of the flower are involved in their structure. The formation of the fruit begins with the development of the endosperm. From the beginning it is cellular and progresses downwards from above, i.e., from the egg apparatus. By continuous transverse divisions, transverse slices are cut out of the micropylar branch of the embryo sac, in which longitudinal dissections occur later. A body is formed which is constricted from the top downwards, in the upper part of which the egg is later developed.

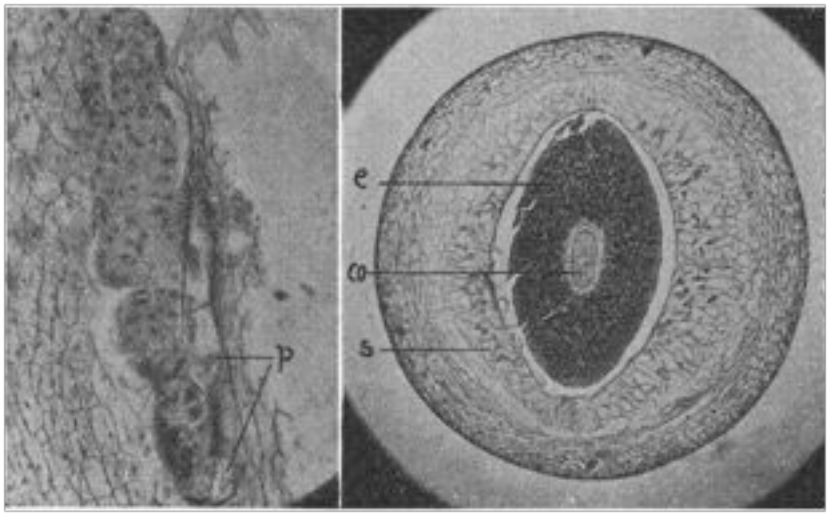

Fig. 8. The fruit of *Ginalloa linearis*. a development stage of the endosperm, at p, the endosperm formation also extends into the antipodial arm of the embryo sac. b cross section through the false fruit. s viscin layer. e endosperm. co cotyledons of the embryo. (Magnification a, 1: 100, b, 1: 18). F. Steindl.

The first stages of development are not essentially different from those found in *K. Dacrydii*. Later differences are noticeable. Cell formation, for example, in the lower part of the micropylar arm, but also encompasses the point of bending and ascends further into the chalazal arm. The endosperm is therefore temporarily U-shaped as is the finished embryonic sac (Fig. 8 a), with the difference, however, that the external, micropylar branch is considerably thicker than the inner antipodal branch. In the further development the two branches do not behave the same. The endosperm of the antipodal branch is single-rowed. The cells involved in its construction are provided with less cytoplasm than the endosperm of the micropylar branch. They no longer undergo further division, but are compressed and degenerated by the strong growth of the outer endosperm. Their walls, however, are still as long as those of the vegetative placenta cells.

The endosperm of the micropylar arm grows mainly in the direction of the greatest flower width, as well as in the direction of the longitudinal axis of the flower. The placenta is thereby increasingly compressed and pushed aside. It never disappears completely, but is still clearly visible in the ripe fruit.

The cells of the endosperm are already filled with starch at an early stage. During the first stages of development, the starch granules are small and rod-shaped; later they become larger, roundish to oval in shape, but neither in shape nor size of the starch which has appeared in the embryo sac before fertilization.

The embryo develops similarly to the *Korthalsella* species in such a way that a spherical cell body without a suspensor cell develops. It later undergoes a longitudinal extension, two cotyledons and the pointed conical plumule (Fig. 8b) differ from its lower end.

During the development of the endosperm and of the embryo, which together form a naked seed, the remaining tissues of the false fruit also undergo changes. The inner cell layers of the carpel stretch in the longitudinal direction and envelop the endosperm with a fine membrane containing small vascular bundles. The outer layers of the carpel tissue develop into the viscous layer. This consists of two crescent shaped lobes inclined inwards above the naked seed, which,

with their lateral supports, abut the two massive vascular bundles of the carpel tissue, and are thus separated in their entire extent.

V. Summary.

1. The present work provides some contributions to the flower morphology and embryology of the viscoids by examining *Korthalsella Opuntia* and *Ginalloa linearis*.

2. The flowers of the monoecious *K. Opuntia* sit in the axils of the opposite scale leaves. In each leaf axil, a male flower is first placed, and six to eight female flowers are placed in four rows.

3. The male flower, which is provided with three perigone leaves, is distinguished by a synadrium containing six pollen sacs. The anther walls are, in contrast to the findings of *K. Dacrydii*, provided with an endothecium. It is probable that the synandium is originally composed of three anthers, which are situated before the perigone leaves.

4. As with *K. Dacrydii*, the female flower of *K. Opuntia* also consists of three perigone and two fused carpel leaves, as well as a central placenta. However, there are differences between the two species, as *K. Opuntia* appears to be less reduced than *K. Dacrydii*, whose carpel is so fused with each other that there is no stylar canal, and no free ovarian cavity is present.

5. The embryo sac development proceeds according to the *Scilla* type. The subepidermal archesporial cells lie in the placenta. The four-nucleate embryo sac is characterized by proliferous starch storage and intensive growth. The growth process results in a U-shaped embryo sac, which is located in the carpel tissue while the antipodals remain in the placenta tissue. The embryo sac is oriented as if it were a hanging spermatozoa. It agrees in all features with that of *K. Dacrydii*. The fact that only the female gametophytes, but not the sporophytes, coincide with one another, is explained by the assumption that during the phylogenetic development only the sporophyte has undergone reductions.

6. Endosperm development is cellular and is similar to that of *K. Dacrydii*, as are the first stages of embryo development. In contrast to *K. Dacrydii*, the embryo forms two cotyledons in the later developmental stages.

7. *Ginalloa linearis* is monoecious. The flowers sit singly in the axils of decussed standing scale leaf, the upper two to three pairs are male, the lower female.

8. The male flowers consist of three perigone leaves and three free, anteriorly different anthers, sitting before the perigone leaves.

9. With regard to the morphological structure of the gynoecium, *G. linearis* deviates from all other viscoids. The two fused carpels of the female flower, which contains three to four perigone leaves, are fused in the basal part of the central placenta, so that the ovarian cavity becomes different at the bottom. In contrast to *K. Opuntia*, the two carpels have already two vascular bundles in the opening flower.

10. The embryo sac development is very likely to follow the *Scilla* type. The unicellular archespores arise as subepidermal cells close to the placenta apex. Only one sister cell is delivered downwards. The four-nucleate embryo sac stores large amounts of starch as in *K. Opuntia* and also becomes U-shaped. As the egg apparatus is formed in the formerly lower end of the four-nucleate embryo sac, the embryo sac is oriented as if it were a hanging ovule. A comparison between the female flowers of *Ginalloa linearis* and the investigated *Korthalsella* species shows that the sporophytic parts of the same are essentially different from each other. Gametophytes, however, largely coincide.

11. The endosperm development is cellular. During the first stages of development, endosperm is also formed in the chalazal arm of the embryo sac. Later, this part of the endosperm is displaced by the intensely developing endosperm of the micropylar arm of the embryo sac. The embryo development coincides with that of *K. Opuntia*.

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