Acta Botanica Neerlandica **8** (1959) 292–303

A PRELIMINARY NOTE ON THE PLACENTA OF STELLARIA MEDIA (L.) VILL. AND STELLARIA GRAMINEA L. A POSSIBLE AXIAL ORIGIN OF OVULA?

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(received March 31th, 1959)

Introduction

The different types of gynoecia can be explained by those, who consider the carpel as an infolded foliage leaf, which develops ovula at the margins. This typo-morphological conception is supported by most botanists. This theory, also called the appendicular theory, goes back to A. P. de Candolle.

In fact the appendicular theory leans on the vascular anatomy, a method, founded by Van Tieghem (1868; 1875) and employed with much success by Eames and his school, for the interpretation of the flower. In this theory, the central placenta is a much discussed subject, which caused a good deal of research. In many cases the central placenta of the Primulaceae has been the motive. All this work centered upon the question whether the central placenta is wholly or partly formed by carpellary tissue. In a well documented article Puri (1951) states, that "the central region of the column is axial, while its peripheral region which bears the ovules is carpellary".

Typologically the Primulaceae gynoecium may be derived from the Caryophyllaceae by further reduction of its septa, since we can state that in several genera of this family the septa may vanish in later stages of its ontogenetical course. Moreover, this opinion is supported by the facts, known from vascular anatomy. (Douglas 1936; Dickson 1936; Thomson 1942).

Eckhardt (1954; 1955) states in his work on the Centrospermae with basal ovules, that these are formed by the carpels, namely as a product of the "querzône", where also the vascular anatomy had to supply the evidence.

Starting from the idea of the infolded foliage leaf, Leinfellner (1950) states that the Caryophyllaceae placenta is formed by the basal and marginal parts of the carpels; in his terminology: by means of the symplicate and synascidiate parts of the syncarpous gynoecium. This opinion however, is not the same as that of Schäfer's (1890), who thought that in the more-seeded Caryophyllaceae gynoecium the basal part of the placenta is not formed by the basal part of the carpels but by the carpel-margins. In Troll's terminology: the carpel may be epeltate.

On the contrary, the other opinion states, that the ovules are not a product of the carpel-margins, but just axial products.

PAYER (1875) thought this to be sound for all ovules. In her work on the vascular anatomy of the Primulaceae, DOUGLAS (1936) has published a wellwritten review of the authors supporting the axial nature of the ovules. These authors willingly admit that the placental column is partly formed by carpel-margins or -bases, but insist on the axial origin of the ovules. Especially those investigators working with fossil material and several historical-orientated workers are likely to held this opinion.

Recently this controversion gave birth to a renewed vivid discussion, caused by a series of publications by LAM (1947–1955). The paleobotanical idea of axial and folial sporangien was adapted by Lam for his conception concerning the phylogeny of the cormophyta. Lam suggested, that the angiosperms could be derived from two stocks, namely the phyllo- and stachyospore plants. The Centrosperms could well have been of stachyosporous origin.

Lam's publications have aroused much opposition, because his ideas are controversial to the classical idea of the carpel and the probable origin of the angiosperms. (EAMES 1951; ECKHARDT 1954; 1955).

From an investigation into the ontogeny of flower phylloms in some Stellaria species, I was struck by the way the placental column is formed. This investigation might probably be a small contribution for a further discussion concerning the nature of the problem I stated in my introduction to this article.

MATERIALS, METHODS AND OBSERVATIONS

The floral diagram and the position of the symmetrical plane of Stellaria species has long been misunderstood. The carpel orientation with respect to the sepals is presented in different ways, to begin with WYDLER (1851). In 1932 MATZKE published an elaborate study about *Stellaria media*, in which he stated, that an equal number of flowers with sepals originated in clockwise sequence as well as in counterclockwise sequence. This phenomenon is reflected in the carpel orientation.

Contrary to the other authors Matzke demonstrated that the symmetrical plane goes through sepal number 4 and between sepals number 3 and 5. (Fig. 1).

Although I haven't used as many flowers as Matzke had in his investigations, I agree with his findings.

1ST METHOD. Flower buds of different age, put into diluted glycerine, are examined through a binocular microscope. This method has been excellently employed by PAYER (1857), and as to Caryophyllaceae tribus Alsinae, especially with regard to the placenta, by LISTER (1883).

After the sepals have been formed in a quincunx, clockwise or counterclockwise, the episepal anthers are formed. Then the epipetal anthers are formed. When these latter primordia have formed hill-like shapes, there still is left a dome-shaped column, the future placenta. Meanwhile at the base of the column emerges a ringwall: the carpels.

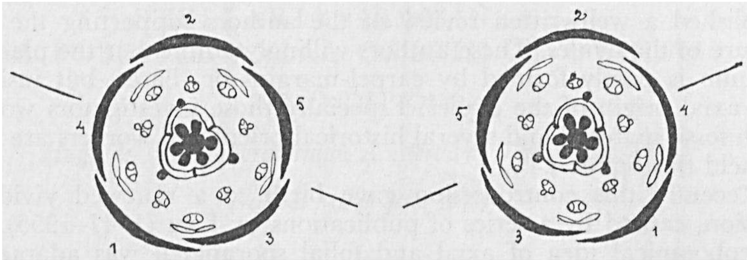


Fig. 1. Floral diagram of Stellaria media. The clockwise and the counterclockwise form; showing the symmetrical plane of the flower (after MATZKE).

In a later stage of the growth of the carpels, I detected small and delicate ridges pointing upwards the ringwall into the direction of the top of the column: the future septa. Only then the situation named by Lister in her article is achieved.

According to BAUM (1950) we may have here the forming of congenital fused carpels, quite in contradiction to Lister. When these carpels have grown half the height of the column, the ovules are formed; starting at the top these ovules are situated next and apart from the septa.

Before the forming of the first ovules the petals emerge from an own primordium as small transparant protrusions directly behind and at the base of the epipetal anthers, provided they exist; since *Stellaria media* frequently has less than ten anthers. The fast growing sepals quickly envelop the other floral phylloms.

From these observations concerning gynoecia, the following questions can be raised:

1. When the carpels from their primordia are formed and still there is a dome-shaped column mass, could it be possible that this column tissue is partly formed by carpel tissue in its peripheral zone, or could this be a direct prolongation of the stem?
2. When the ovules are formed whilst the carpels are not yet fully developed, (that is, when the ringwall has not yet reached the height of the column), and where the septa are hardly detectable, could they be able to form the ovules in the manner as the classical theory states?

To give an answer for above mentioned questions, I had to use normal microtome technics, since the first used method can only be applied for examining the outer sides of the floral phylloms.

2ND METHOD. Dichasia from *Stellaria media* and *Stellaria graminea* were embedded in paraffine, sectioned serially at 10 microns, stained in Delafield haematoxyline (for plasma staining) and in haematoxyline according to Regaud + saffranin. Complete series were studied, transverse and longitudinal.

In this manner series of different flower stages could be obtained. The histogenetical pattern of cells of the flower phylloms were studied. The same sequence of ontogenetical development is observed as before with the first method by using a binocular microscope.

On account of recent histogenetical research concerning the flower, to begin with GREGOIRE (1937) and especially by the newest findings of PHILIPSON (1947), BUVAT (1952) and BERSILLON (1955) and others, the conception considering the forming of the flower has changed. For an insight into this matter I refer to the publications of the authors mentioned above.

The opinion of Buvat and his followers with respect to the forming of the flowers, I can agree with. Namely, that the flower apex consists of a cap of two layers. The cells of these layers are big and darkly stained in my microscopical slides; proméristème sporogène — (Buvat).

Here beneath lies a core formed by cells which divide principally anticlinically = proméristème receptaculaire (Buvat). The subepidermic layer is active in forming the floral phyllomes, except the sepals. I will go in details in an other paper in respect to this problem.

Photograph 1. Gives a longitudinal view of a flower bud. Here we see a detail of the gynoecium of a young flower of *Stellaria graminea.* On the left and on the right hand side of the picture are anthers. In this section a petal primordium is slightly cut up which can be noticed at the base of the right hand anther. Between the anthers is situated the flower apex, the future placental column, which for convenience' sake we will call just "column". At both sides of the column's base we see carpels. The left one is nearly cut in the midst. In this part we can see the active topcell which divides peri- and anticlinically. The two outer layers of the column are dark stained while the rest of the column tissue is made up by ribmeristem.

Figure no 2 is a drawing of a detail of a longitudinally cut young gynoecium of *Stellaria graminea.* On the left side, a carpel is cut through the septum. On the right side a carpel is cut through about the midst.

Figure no 3 is a drawing of a longitudinally cut young flower of *Stellaria graminea* in a later stage of growth. In this drawing, the left carpel is cut through about the midst, while the right carpel is cut through the septum. This figure is a transection through the symmetrical plane of the flower, because we see on the left side a petal primordium with its epipetal anther and on the right side we see an anther which is bigger than the other one: an episepal anther. From the floral diagram as it is given by Matzke and agreed upon by me, it is clear, that a plane as described above can only be the symmetrical plane.

When we look at a series of details of this young gynoecium reprcsented by photographs 2–7, from which photograph no. 2 corresponds with Fig. 4, photograph no. 5 corresponds with Fig. 5 (which is a

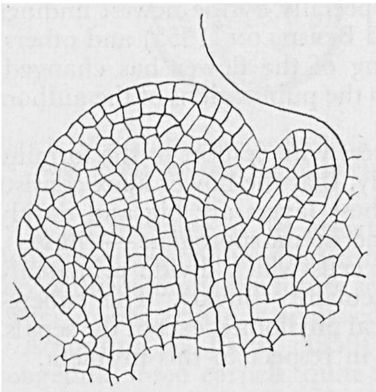


Fig. 2.

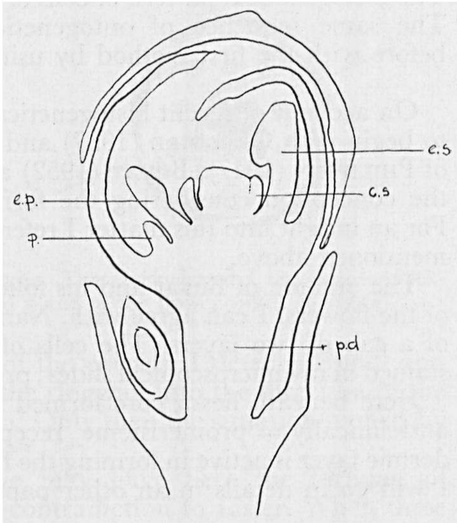


Fig. 3.

Fig. 2. Stellaria graminea. Longitudinal section through a young gynoecium. At the left side of the column, the section goes through the margin of a carpel primordium. In this place the future septum will be formed. At the right side of the column, a carpel is cut through the midst.

Fig. 3. Stellaria graminea. A drawing of a longitudinal cutting of a flower, through the symmetrical plane. (see text). Left carpel is cut through the midst, the right one through its septum. ep = epipetal anther; es = episepal anther; p = petal; cs = carpel septum; pd = peduncle.

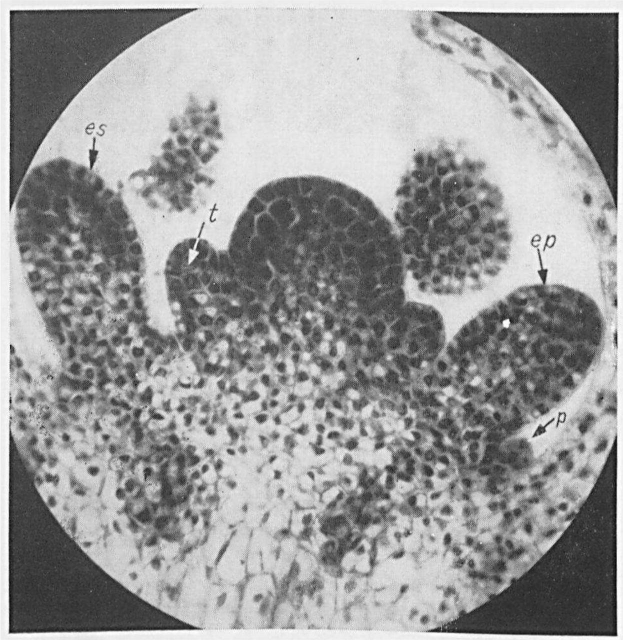
detail of Fig. 3) and photograph no. 6 corresponds with Fig. 6, we observe on this series the following facts:

We see the caesura between column and right hand carpel reduce, which means, that the cuttings are approaching the septum. In photograph 4 and 5 the septum is reached and in photograph 6 and 7 we have entered the next locus, which is to be seen on the growing caesura. On the contrary the caesura between column and left septum is deepening, this indicates that we are going into the direction of the middle of the carpel.

In Fig. 4 we see that the column is flattened at the top, a beginning of the forming of the ovules has started, while at the leftside base of the column the forming of the ovules is yet about to begin.

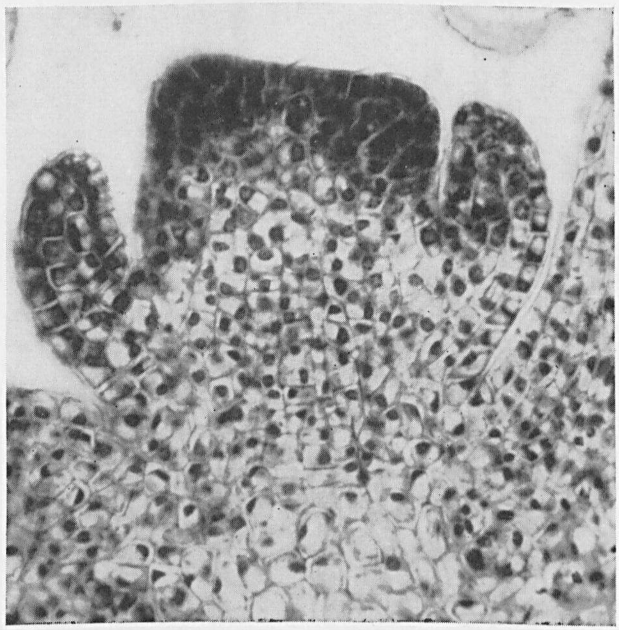
This younger phase of ovule forming on the left side of the column can be better seen on photograph no. 3.

In Fig. 4 we see again the two layers of dark stained cells forming the cap of the column, while the rest of the column tissue is made up



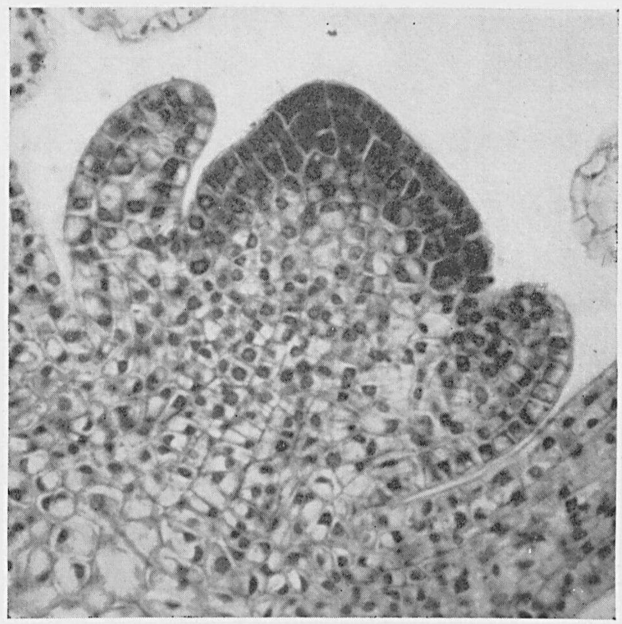
Photograph no 1 *Photo: F. J. Smith*

Stellaria graminea (L.) Longitudinal section through a young gynoecium. es = episepal anther; ep = epipetal anther; p = petal primordium, just slightly cut; t = topcel of carpel primordium. The two-celled tunica layer is dark stained and bigger than the other cells. Stained with Delafield's haematoxyline.



Photograph no 2 *Photo: F. J. Smith*

Stellaria graminea. The photographs 2–7 are details of a series of cuttings through a young gynoecium. Photograph no 2 presents at both sides of the top the differentiation of the ovules (→).

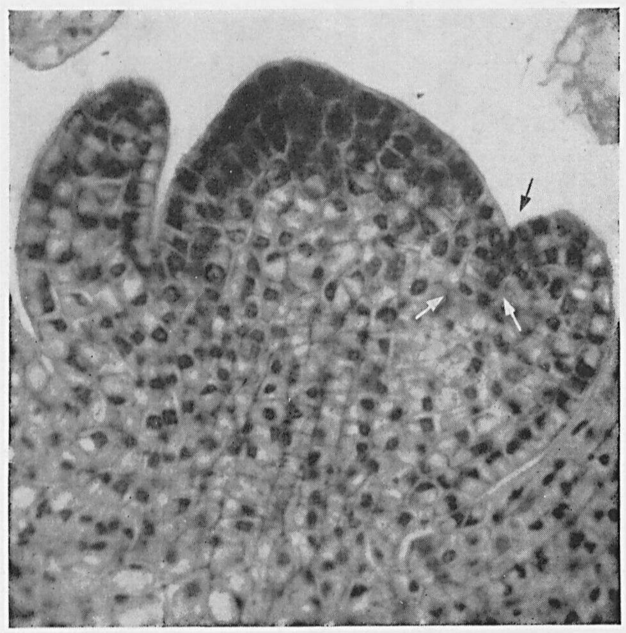


Photograph no 3 *Photo: F. J. Smith*

Stellaria graminea. At the left side of the column we can see the differentiation of a basal ovule. The right side carpel is fused with the column, higher than in the preceding photograph.

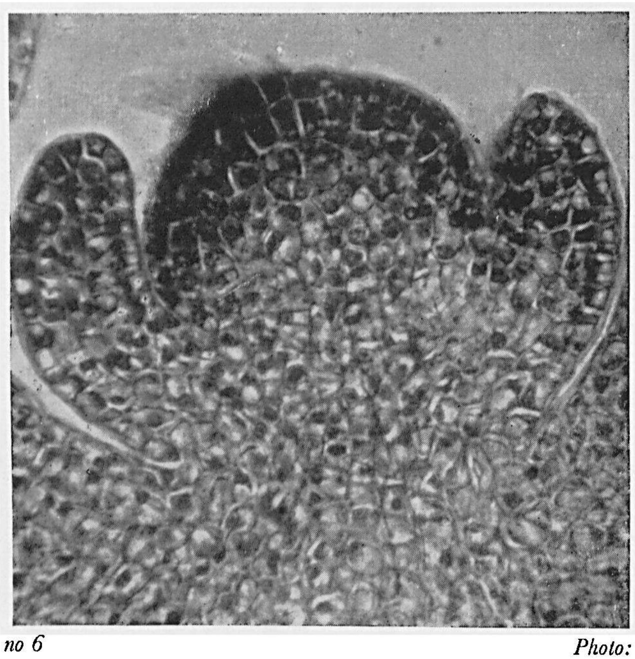
Photograph no 4 *Photo: F. J. Smith*

Stellaria graminea. Photograph no 4 and no 5 are details of Fig. 3 Photograph no. 4. The cutting is through the symmetrical plane. Here we notice, that carpel margin tissue is just slightly penetrating the column tissue.



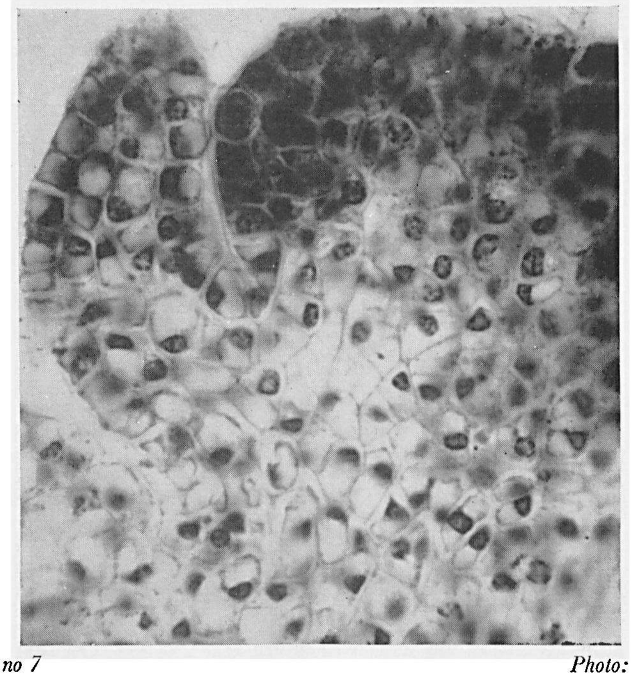
Photograph no 5 *Photo: F. J. Smith*

Stellaria graminea. Photograph of the same section as no 4, but taken with a focus deeper than that one. The borderline between column and carpel margin tissue is noticeable (Fig. 5).

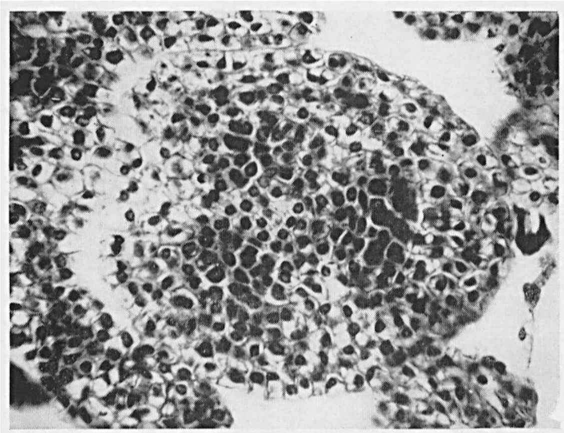


Photograph no 6 *Photo: F. J. Smith*

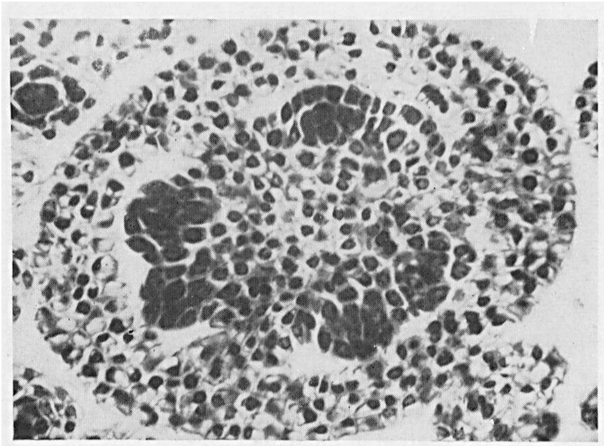
Stellaria graminea. The separation between right carpel and column tissue can here be noticed again; we have arrived into another locus. (Fig. 6). Taken with "phase contrast".



Photograph no 7 *Photo: F. J. Smith*



Photograph no 8 *Photo: F. J. Smith*



Photograph no 9 *Photo: F. J. Smith*

by the proméristème receptaculaire demonstrating a well outlined pattern of the cells of cambial nature. The growth of the carpels on the left and right side of the column doesn't interfere with column tissue.

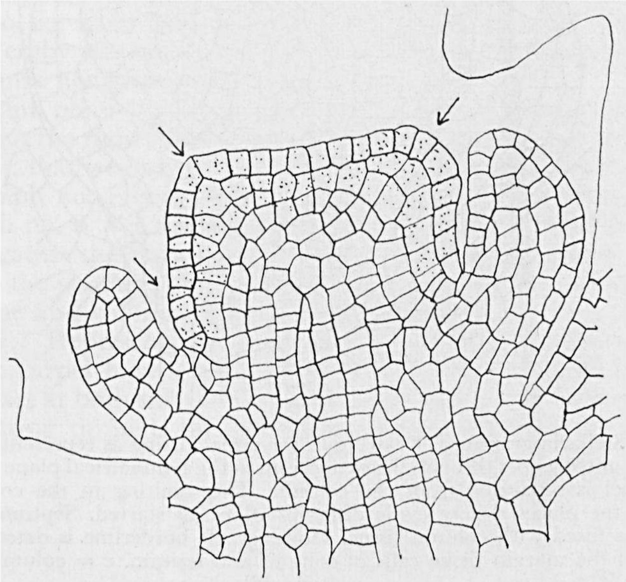


Fig. 4. Stellaria graminea. Drawing of the same cutting as represented in photograph. 2. A detail of a young gynoecium. Notice the flattened top of the column while at both sides ovula forming starts (→). Here too we see the regular pattern of anticlinally devided cells of the core (ribmeristem).

Photograp no. 4 and no. 5 (= detail of Fig. 3) are pictures of the same section, taken with different depth of focus. In these pictures the septum of the right side carpel is fused with the column tissue. Photograph no. 4 shows that the septum of the right side carpel is just slightly penetrating the column tissue, while photograph no. 5

Photograph no 7

Stellaria graminea. Detail of the left carpel of carpel, seen in a cutting next to the one presented in photograph 6. Carpel tissue lightly stained, column tissue dark, (see text).

Photograph no 8

Photo 8 and 9: Stellaria media. Details of transverse sections through a young gynoecium. Photo 8: The basal ovules are just differentiating, in the 3 loci, no vascular tissue is detectable.

Photograph no 9

Transverse section of the same gynoecium as in photo no 8, near the top of the column. The cutting goes through the older ovules. We see in each locule 2 ovules forming. No vascular tissue is detectable. Neither of both photographs shows the demarcation of carpel and column tissue.

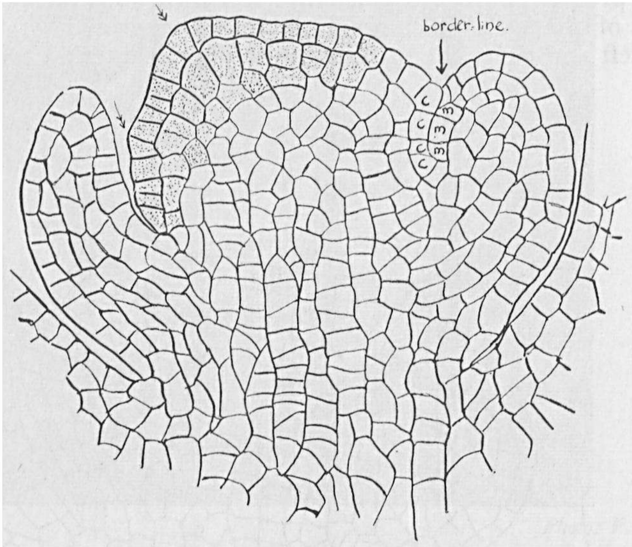


Fig. 5. Stellaria graminea. Drawing of the same cutting as represents photograph no 5. The cutting goes through the gynoecium in the symmetrical plane of the flower. Left carpel is separated from the column. The vaulting in the column (→→) indicates the places, where ovule differentiation has started. Septum of the right carpel has fused with column tissue. However, its borderline is detectable by the pattern of the margin tissue cells of column and septum. c = column cells; m = septum cells.

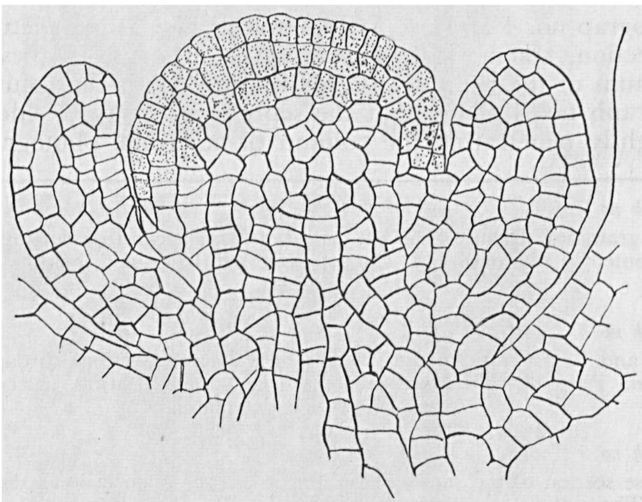


Fig. 6. Stellaria graminea. Drawing of the same cutting as represented in photograph 6. Explanation: see at that place.

shows that the outer cells of both column and septum are fused. This situation is drawn in Fig. 5. Although we can in that figure notice that the edges of column and septum tissue are fused, we still see in their histogenetical pattern (cells "c" = part of column tissue; cells "m" = marginal septum tissue) the borderline between septum and column. So we have here an apposition of the septum against the column. Hereby carpeltissue doesn't contribute to the peripheral zone of the column nor gives birth to the ovules.

Photograph no. 6 (= Fig. 6) represents a next cutting in the series. It shows that the right side carpel and the column are separated again. This means, that we have arrived from the septum into an other locus.

Photograph no. 7 is a detail of the left side of the cutting next to photograph no. 6. We see the left side carpel with its septum (lightly stained) against the dark column tissue. The septum seems to grow up against the column, but I think I have demonstrated already that carpel tissue and column tissue stay separated.

Figure 7. Represents the situation of a gynoecium which is a few older. The carpel have grown up higher, but the column too. This column bears at both sides of the figure two ovules. The figure is made from a cutting through the peripheral region of the column.

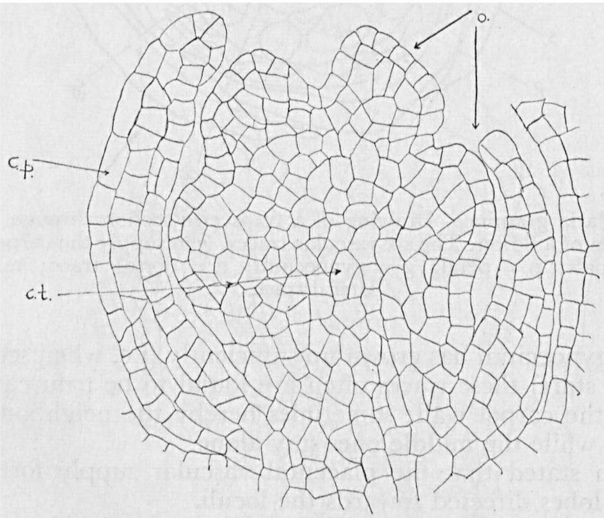


Fig. 7. Stellaria graminea. A detail of the longitudinal cutting through an older gynoecium than represented in the preceding figures. Carpels and column have grown up higher. (see text). Cp = carpel wall; ct = column tissue; o = ovule.

PLACENTATION

PURI (1952) has published a well written article on the placentation in Angiosperms. His interpretation on this subject centered upon the vascular anatomy. For the marginaxile (according to SACHS, 1882) or axile type of placentation of the other authors, the common placental type of the Caryophyllaceae, Puri states that the infolded carpel of this gynoecium have 5 traces, from which the ventrals are inversed.

THOMSON (1942) has already demonstrated that for some genera of this family, including *Stellaria* no inversed traces in the placental column are found.

I observed that at the base of the ovary the vascular tissue forms a hexagonal core with a lobe at each corner (Fig. 8). These six lobes give at different heights of the bottom of the gynoecium traces, namely the three dorsal medians and the three median laterals. These median lateral, according to the classical theory, are of a double nature.

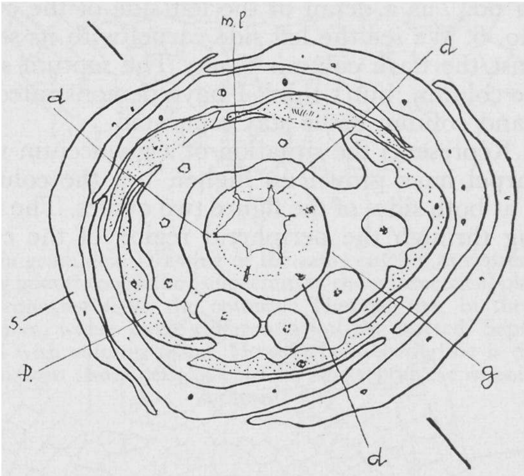


Fig. 8. Stellaria graminea. Drawing of a transverse section through the base of the gynoecium of a flower. The six vascular traces, who supply the carpels are to be seen. s = sepals; p = petal; g = gynoecium; d = dorsal trace; ml = median lateral trace.

When the gynoecium has grown up sufficiently (i.e. when seedforming is about to start) these traces often are found to be trifurcated at the bottom of the carpel wall; sometimes hereby the neighbouring side-traces fuse, while the middle ones stay alone.

Thomson stated that the placental vascular supply forms a core with three lobes directed towards the loculi.

Because most investigators on this subject are looking chiefly on transverse sections, and focus their attention to the vascular anatomy, they are not able to detect the separation of column tissue and carpel-tissue.

Photograph 8 and 9 give such a transection through a young gynoecium of *Stellaria media*. Photograph 8 gives a situation at the lower part of the column. Hereby, the younger ovules are not that much differentiated as the higher situated ones, visible in photograph 9. In both photographs we cannot see the borderline between septum and column tissue. I must agree, that there are some differences in outlook of the transverse section of *Stellaria media* and *Stellaria graminea* but there is no principal difference.

The vascular tissue develops rather slowly in the column tissue (photograph 8 and 9). The ovuleforming has started, but still no signs of any vascular development can be detected.

The vascular bundle development begins at the base and goes upwards in the already mentioned three edged core, starting at the corners. In the beginning more phloem is formed than xylem. The tissue between those three strands is differentiated afterwards into vascular tissue, so that at least the three-edged core is completed. Afterwards from these three corners the placental traces originate, and become fused with the ovules.

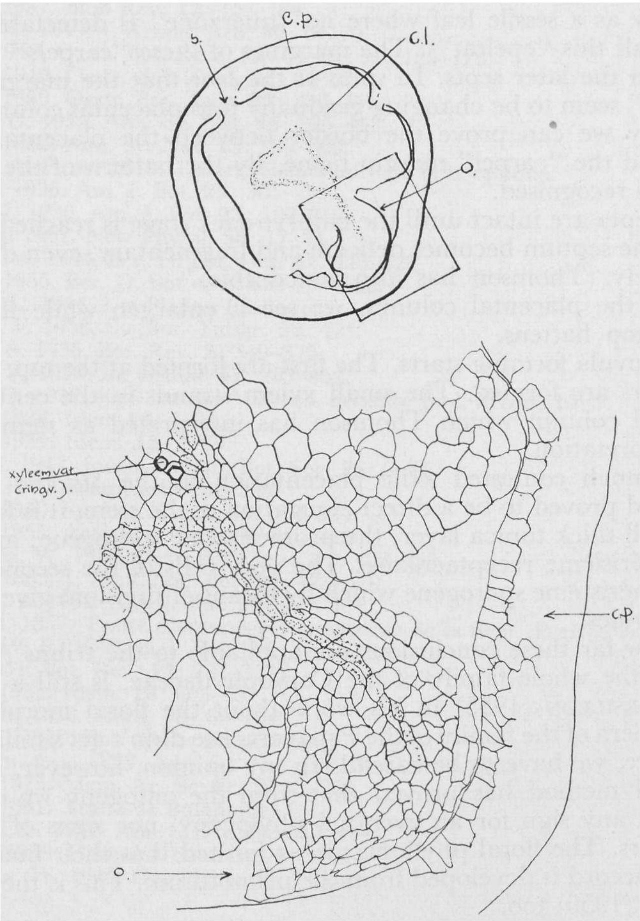


Fig. 9A and 9B. (Fig. 9B is a detail of 9A). Transverse section of the same flower of figure 7, through the base of the placental column, showing one ovule formed in a locus. Placental trace develops from column tissue (in drawing dotted). cp = carpel; s = carpel septum; cl = column tissue showing the three edged core of vascular tissue; o = ovule, differentiated from column tissue.

Figures no 9A and 9B (9B is a detail of 9A) show a differentiation of the columntissue into a trace from the ovule into the vascular core. This means that the placenta is also formed like the ovules from column tissue. In later stages the regular pattern of the vascular tissue in the column is disturbed by the growth of the different parts within the carpels, as e.g. is the case with the irregular number of ovules which set to seedforming.

Conclusions

The results, obtained by means of a histogenetic way of working, show that the idea of the placental column, partially or wholly covered with carpellary marginal tissue in which this very carpellary tissue bears the ovules, is contestable. The "carpels" are formed similarily as a sessile leaf where no "querzône" is detectable. (Troll would call this "epeltat"). The margines of these "carpels" are fused and form the later septs. In spite of the fact that the margins of the "carpels" seem to be changing gradually into placental column tissue, in reality we can prove the border between the placental column tissue and the "carpel" margin tissue. By the pattern of the cells this border is recognised.

The septa are intact until the embryo-sack stage is reached. In later stages, the septum becomes delicate and fragmentary, even disappears completely (Thomson has also stated this).

As to the placental column, we see it enlargen while the dome-shaped top flattens.

Then ovula forming starts. The first are formed at the top, hereafter the others are formed. The small xylem strands in the centre of the placental column which Thomson has interpreted as stemrests is a misinterpretation.

The much contested axile placentation in the *Stellaria* species I examined proved to be a direct elongation of the stem, it is formed by a two cell thick tunica layer, the proméristème sporogène; and a core of promérisième receptaculaire. The very cells of the second layer of the proméristème sporogène which by means of divisions give the birth to the ovules.

In how far these conclusions are appliable to the tribus Alsinae or even to the whole family of the Caryophyllaceae, is still a question, since Bersillon (1955) in his work about the floral morphology in some genera of the family of the Papaveraceae didn't get similar results. Therefore, we have to be careful. In my opinion, however, the histogenetical method has proved that from the ontogeny we cannot in fact find any sign for an eventual phylogeny, nor signs of primitive characters. The floral phylloms are so formed that their final form of its own accord is developed from the primordium. This is the meaning of Baum (1950) too.

It is quite alluring to consider the "carpel" in the classic meaning of the word now as a pseudocarpel Hagerup (1933), Lam (1947), Emberger (1944), Fagerlind (1958).

Since in present days the discussion about the subject is still very vivid, it seems wise to me, with the limited results I obtained, not to go into speculations about it. However, for the telom theory according to ZIMMERMANN (1949) the facts I found are not necessarily something extraordinary. For, according to this theory, leaf and axis are to be led back to "ground telomes" the flower as a whole being a complex of syntelomes.

Anyhow, it is clear, that those are right, who are pleading to broaden the conception of the carpel, as it is since the time of Goethe, defined by the typological way of consideration.

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