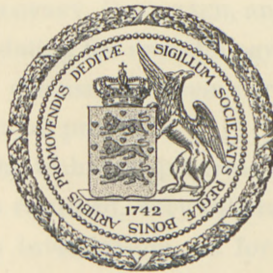# ON THE ORIGIN OF SOME ANGIOSPERMS THROUGH THE *GNETALES* AND THE *CONIFERAE*

IV. THE GYNAECIUM OF *PERSONATAE*

BY

O. HAGERUP

I. Introduction.

In my earlier phylogenetic works rather primitive phanerogams only were examined. In the present investigation, however, which is a direct continuation of the preceding ones, an attempt will be made to demonstrate that the results previously gained may be generalised so as to apply also to such a highly developed group of phanerogams as the *Personatae*. In this demonstration teratological features will be given special weight, which, again, is due to my having received from Dr. A. LEVAN a very valuable material of *Petunia*, for which I here beg Dr. LEVAN to accept my cordial thanks.

Owing to the primitive technique of earlier times the great morphologists of the last century, EICHLER, PAYER, VAN TIEGHEM, ČELAKOVSKÝ, PEYRITSCH, and many others, did not succeed in elucidating the morphology of the gynaecium. And the animated discussions then carried on gradually ebbed out for want of proofs.

However, with the technical progress of recent years the discussion has been resumed, very different views being set forth by numerous investigators, as for instance MCLEAN THOMPSON, GRÉGOIRE, TROLL, KOZO-POLJANSKI, JUHNKE and WINKLER, PARKIN, EAMES, SAUNDERS, HENNING, HUNT, STEFANOFF, RISCHKOV, THOMAS, HAGERUP, and several others. A good summary of the results of this debate will

be found for instance in Grégoire's comprehensive treat-
ment of the literature, to which work it will suffice here to
refer the reader.

It should merely be noted that there are, in particular,
two different opinions sharply opposed to each other, whose
main points may be briefly characterised as follows:

1) The gynaecium consists almost exclusively of leaves
(carpels). This "classical theory", which originates from
the last century (Goethe), especially has its adherents
among German scientists.

2) The gynaecium further includes larger or smaller
parts of the floral axis.

For the purpose of forming an opinion on the greatly
diverging views two methods especially will be adopted in
the present work, viz. the histological and the teratological
method.

It was during my study of the gynaecium of *Salix* that
I realised the value of the histological examination of the
various developmental stages of the gynaecium. In the
present work this method has therefore been employed on
a number of selected objects within the *Personatae*, which
I have collected partly on various journeys in the Indies
and Africa, partly under natural conditions in Denmark and
in the Botanical Garden of the University of Copenhagen.
The young flowers were cut into series of thin sections.

The *Personatae* are valuable as objects of investigation,
because the gynaecia of the different families are very
differently built. Thus in most of them the placenta is cen-
tral, while in *Gesneriaceae* and *Orobanchaceae* the placenta is
parietal. In most families the ovary contains septa; how-
ever, as is well known, a unilocular gynaecium is found
in the *Lentibulariaceae* and the *Gesneriaceae*. Some selected

types of gynaecia will be examined below, special attention being given to the placenta and ovules, as I consider the "classical" interpretation of these organs incorrect. On the other hand, there is hardly any reason to doubt that an essential part of the carpels has been formed of leaves; this appears distinctly from their organogeny, as is especially shown in TROLL's most recent works (1939).

II. The Organogeny of the Gynaecium.

Among the various forms of gynaecia found within the *Personatae*, it is easiest to examine and understand such as have a central placenta; and among these, again, we first select a unilocular gynaecium, and in the first example will confine ourselves—for the sake of clarity—to outline drawings of a series of developmental stages (Figs. 1—6).
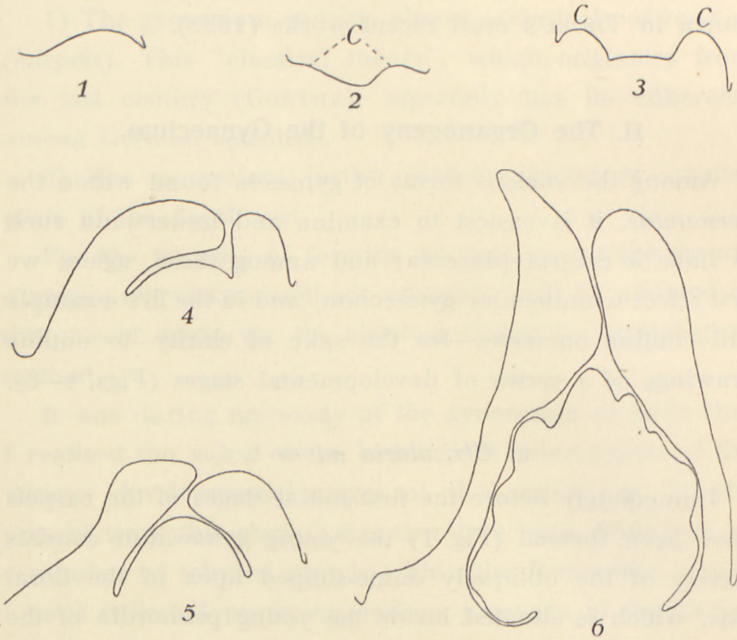
a. *Utricularia minor* L.

Immediately before the first initial stages of the carpels have been formed (Fig. 1) the young gynaecium consists merely of the obliquely dome-shaped apex of the floral axis, which is situated inside the young primordia of the stamens. Figs. 2 and 3 show very young initial stages of the carpels (C); they do not cover the whole apex of the stem, of which a distinct remnant is left; this remnant will continue to grow, increasing both in length and breadth (Fig. 4—5), to develop finally (Fig. 6) into the placenta. Accordingly the young placenta is the oldest part of the gynaecium, and the carpels begin as lateral leaves on the placenta.

In the following will be given, as a supplement, a histological analysis of the organogeny of some other gynaecia

which behave in the main like *Utricularia* and are provided
with a central placenta.

b. *Plantago major L.*

Fig. 7 represents a median longitudinal section through
the growing point of a quite young flower stalk; nearly

Figs. 1—6. *Utricularia minor* L. The organogeny of the gynaecium in
median longitudinal sections. × 200. C, carpels. Cf. further the text.

three mantle-shaped cell layers are seen, one outside the
other and parallel to the epidermis. The innermost central
cell-rows do not reach the epidermis; and on the whole
this growing point is built in a similar way to other stem
apices in phanerogams.

However, during the further development of the young
flower something happens which morphologically is very
curious: the typical apical growth shown in Fig. 7, as it

were ceases, the newly formed cells being situated in a
way different from the usual one. This feature is shown
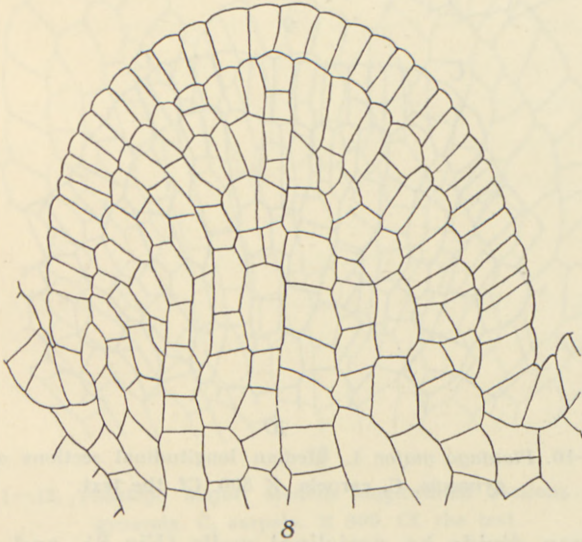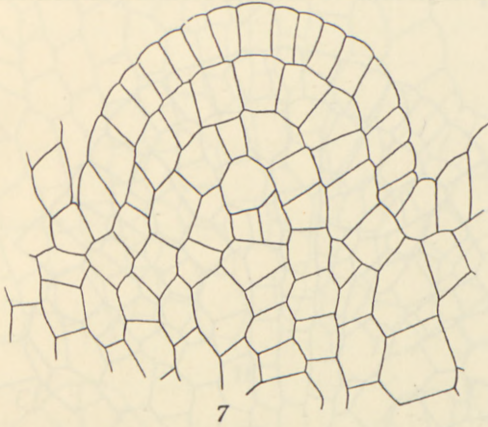
Figs. 7—8. *Plantago major* L. Median longitudinal sections of very young
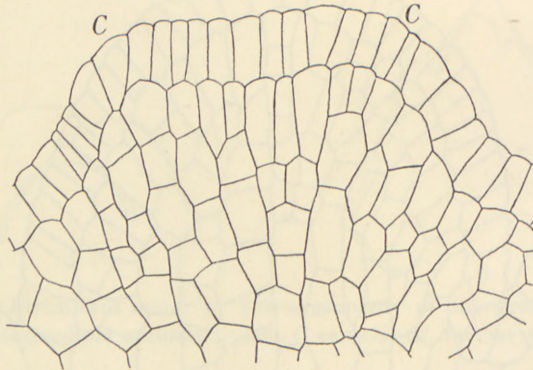flowers. × 800. Cf. the text.

in Fig. 8: in the innermost and lowermost parts of the
section figured the primary arrangement of the cells as

shown in Fig. 7 is still plainly distinguished. However, the
cells of the subepidermal layer (Fig. 7) have elongated in a
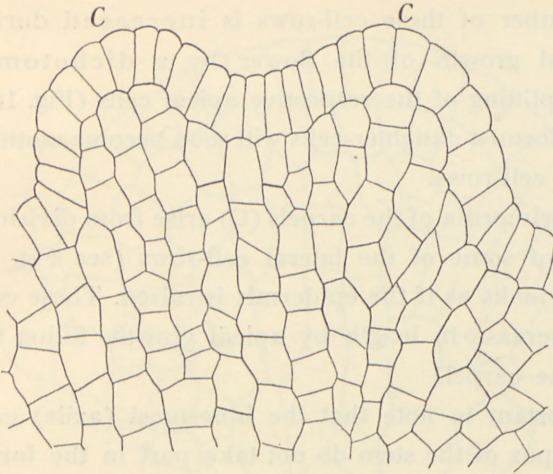direction perpendicular to the epidermis (anticlinal); these
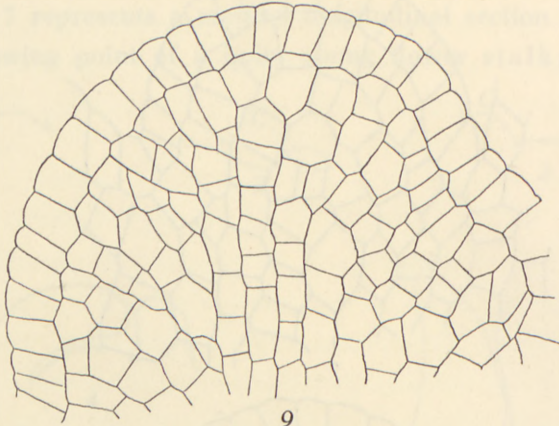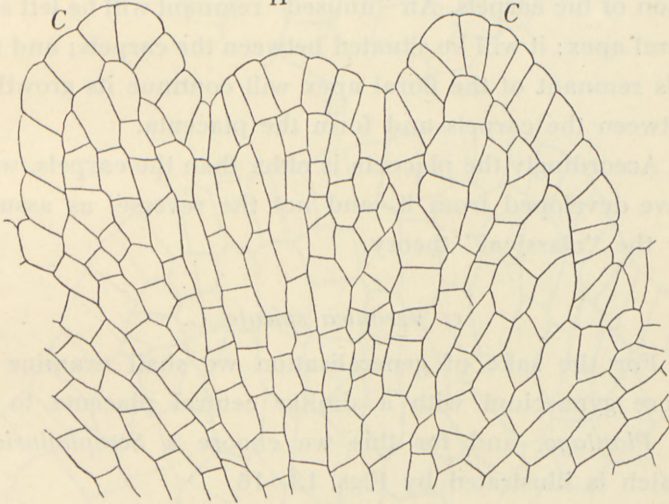

Figs. 9—10. *Plantago major* L. Median longitudinal sections of young
gynaecia. C, carpels. × 800. Cf. the text.

cells soon divide by periclinal walls (Fig. 8), and during
the continued growth (Figs. 9—12) the subepidermal cells
(Fig. 7) will become mother cells of veritable cell-rows,
which expand sideways as in a fan and are perpendicular
to the epidermis.

Figs. 11—12. *Plantago major*. Median longitudinal sections of young
gynaecia. C, carpels. × 800. Cf. the text.

In the succeeding developmental stages (Fig. 9—12) no
cell layer parallel to the epidermis is found, all cells being
arranged in rows perpendicular to the epidermis, as
in the growing points of certain algae (e. g. *Furcellaria*).

And the number of these cell-rows is increased during the continued growth of the flower by a dichotomal (anticlinal) splitting of the respective apical cells (Fig. 10); and the new-formed daughter-cells will soon become mother-cells of new cell-rows.

The first primordia of the carpels (C) arise from divisions at the apex of some of the lateral cell-rows (see Fig. 10, right), and it looks as if the epidermis is raised. These cell-rows soon increase in length by apical growth, filling the interior of the carpel.

It is important to note that the innermost (axile) cell-rows of the apex of the stem do not take part in the form-ation of the carpels. An "unused" remnant will be left at the floral apex; it will be situated between the carpels; and soon this remnant of the floral apex will continue its growth up between the carpels and form the placenta.

Accordingly the placenta is older than the carpels, which have developed from it—and not the reverse, as assumed by the "classical" theory.
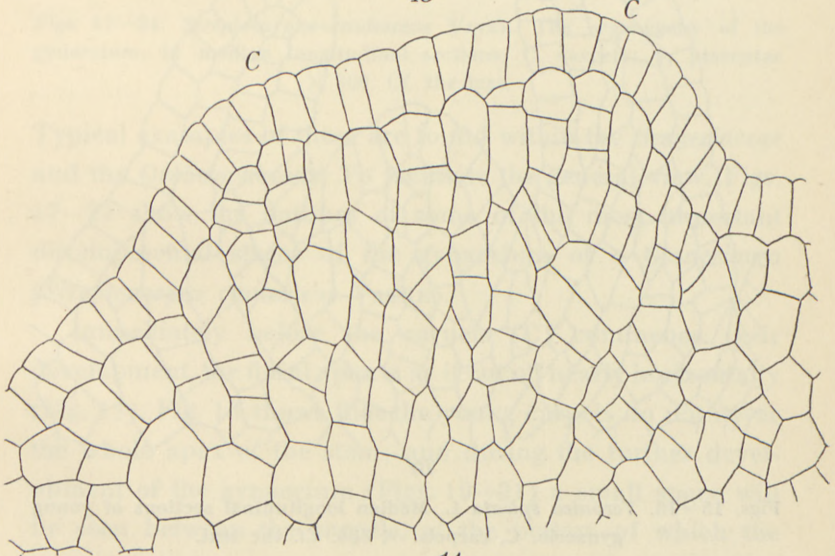
c. *Veronica spicata* L.

For the sake of generalisation we shall examine one more gynaecium with a similar central placenta to that of *Plantago*, and for this we choose a *Scrophulariacea*, which is illustrated by Figs. 13—16.

Fig. 13 shows the growing point of the apex of the axis of a flower so young that the primordia of the carpels have not yet been formed. It will be seen that here, too, the stem apex is built up of dichotomally branched cell-rows spread-ing sideways like fans. The carpels arise (Fig. 14) from the apex of some of the lateral cell-rows growing obliquely upwards, raising the epidermis from its original position.
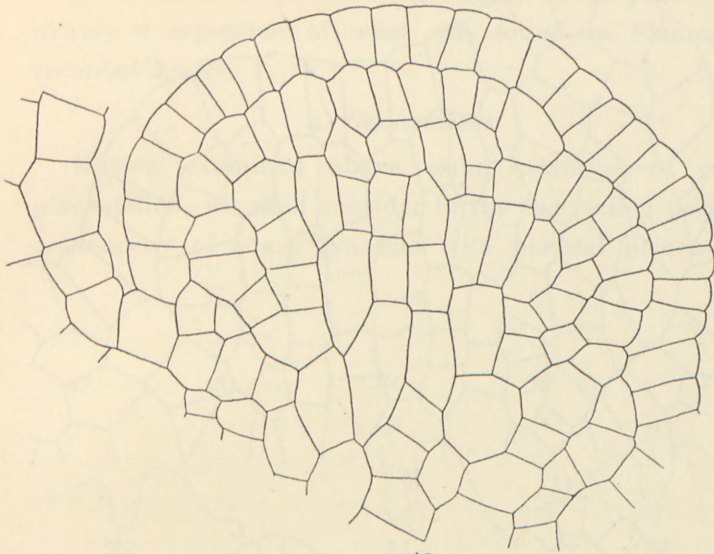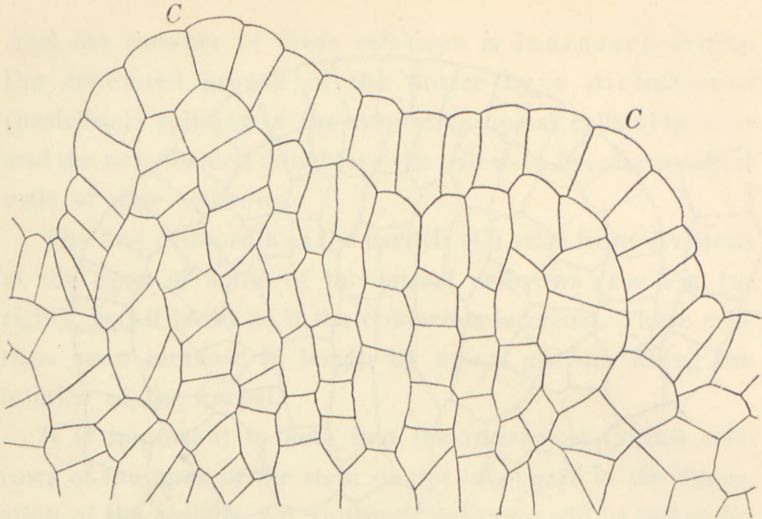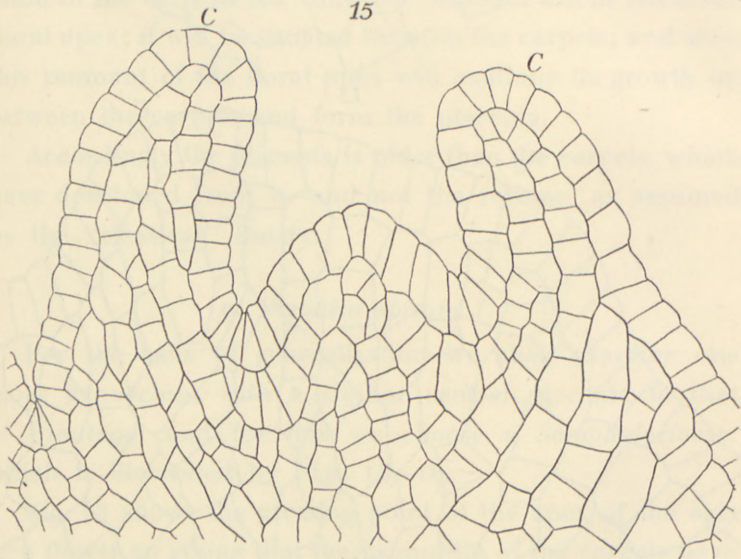
Figs. 13—14. *Veronica spicata* L. Median longitudinal sections of very young gynaecia. C, carpels. × 800. Cf. the text.

Figs. 15—16. *Veronica spicata* L. Median longitudinal sections of young
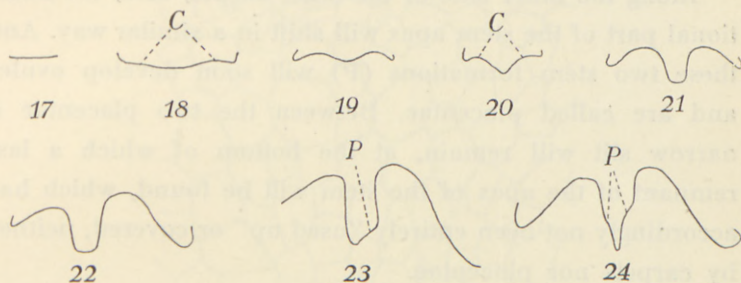gynaecia. C, carpels. × 800. Cf. the text.

Soon that part of the stem apex which is situated between
the carpels will grow up between the latter, forming the
placenta (Figs. 15—16).

In the main features the organogeny of this plant is thus merely a repetition of what was found in *Plantago* as recorded above.

d. *Gesneriaceae*.

Having examined above some examples of central placentation, we shall consider in the succeeding pages the organogeny of some gynaecia with parietal placentation.

Figs. 17—24. *Streptocarpus caulescens* VATKE. The organogeny of the gynaecium, in median longitudinal sections. C, carpels; P, placentae × 200. Cf. the text.

Typical examples of these are found within the *Gesneriaceae* and the *Orobanchaceae*. To facilitate the general view, Figs. 17—24 show the outlines of some of the most important developmental stages of the gynaecium of a *Gesneriacea* (*Streptocarpus caulescens* VATKE).

Immediately before the carpels (C) commence their development, the floral apex is as if cut off nearly horizontally (Fig. 17). Fig. 18 shows that the young carpels do not cover the whole apex of the stem; and during the further development of the gynaecium (Figs. 19—21) a small space will be seen between the carpels, at the bottom of which the remnant of the growing apex of the stem is found.

If we compare Figs. 22 and 23, it will be seen that the apex of the stem enclosed between the carpels has become

oblique because it has grown a little upwards on its right side. This peculiar growth will constantly continue, and since at the same time the carpels grow by an intercalary zone across their base, the result will be that the afore-mentioned oblique part of the apex of the stem will be shifted upwards along the inner side of the carpel, so that the characteristic parietal position will result.

Along the inner side of the other carpel, also, an additional part of the stem apex will shift in a similar way. And these two stem formations (P) will soon develop ovules and are called placentae. Between the two placentae a narrow slit will remain, at the bottom of which a last remnant of the apex of the stem will be found, which has accordingly not been entirely "used up" or covered, neither by carpels nor placentae.

However, after these introductory remarks we shall give below a more detailed histological analysis of the peculiar organogenetic phenomena, and for this purpose we select the same species.

Fig. 25 represents a median longitudinal section through a flower, so young that only the first tiny primordia of the stamens (S) are distinguishable. From the portion of the stem apex situated between them the gynaecium will later develop.

In the middle lower part of Fig. 25 some vertical cell-rows are seen which show part of the original arrangement of the tissue of the young flower stalk. However, it appears from the uppermost left part of the phase figured here that below the epidermis cell-rows in fan-shaped arrangement are present, similar to those characteristic also of the young gynaecia with central placentae described above.

Now the apex of the floral axis increases in thickness

(Fig. 26), which causes fresh alterations in the arrangement
of the tissue; i. a. there gradually develop some more or

S   S

C   25   C

26
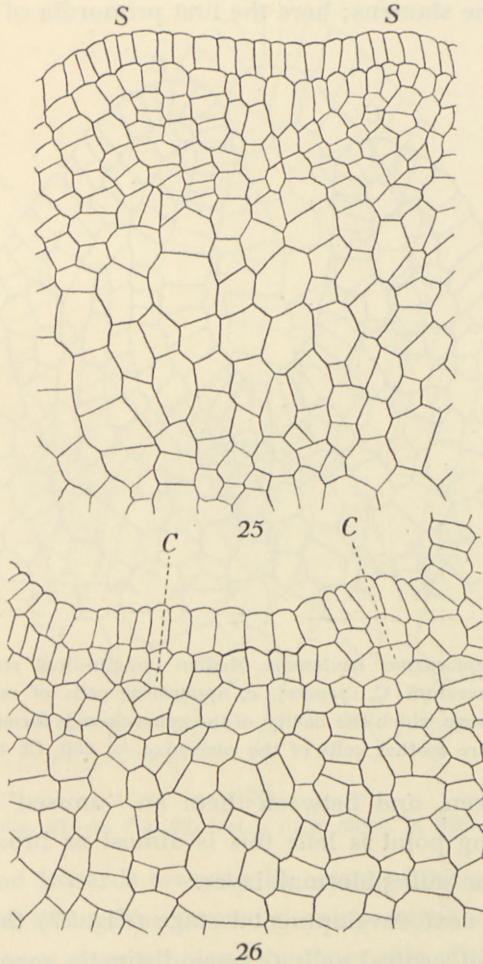
Figs. 25—26. *Streptocarpus caulescens*. Median longitudinal sections through
the apex of young flowers. S, stamens; C, carpels. × 600. Cf. the text.

less distinct cell-rows which are parallel to the epidermis;
this applies especially to the subepidermal layer, in which

the other organs of the gynaecium are initiated, as will
be seen in the following figures.

Fig. 26 represents the part of the stem apex that is found
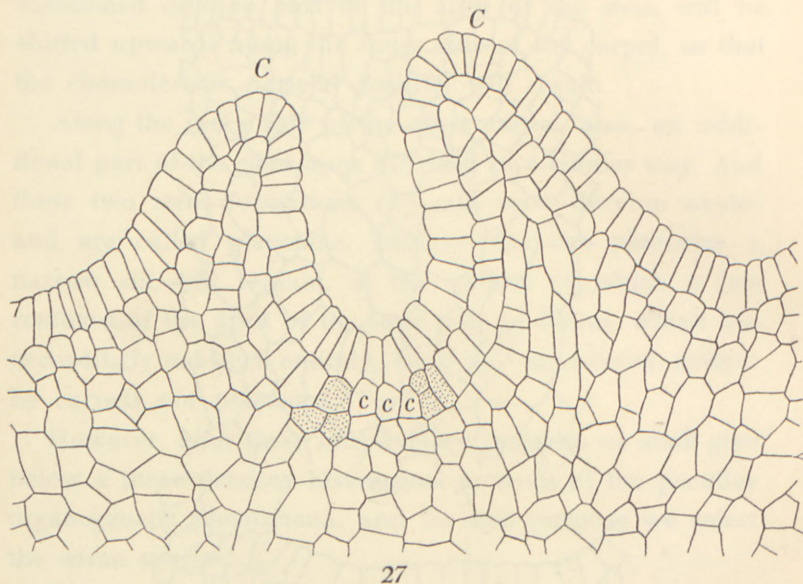between the stamens; here the first primordia of the carpels

27

Fig. 27. *Streptocarpus caulescens*. Median Longitudinal section through
a young gynaecium. C, carpels; c, uppermost cells of median vertical
cell-rows, above which the cavity of the gynaecium is formed. The dotted
cells are mother cells of the placentae. × 600. Cf. the text.

(C) are seen, and between them an "unused" portion of
the growing point is left; this is almost as broad as seven
cells of the subepidermal layer.

In the next developmental stage (Fig. 27) three vertical
cell-rows of central cells (c) are distinctly seen, extending
upwards to the epidermis and continuing downwards into
the axile rows of medullary cells of the flower stalk. The
cells of the subepidermal layer situated nearest to the said
axile cell-rows are dotted in the next figures, and it soon

becomes evident (Figs. 27—29) that these (dotted) cells
divide rapidly by periclinal walls so as to become the
mother-cells of cell-rows which are directed obliquely
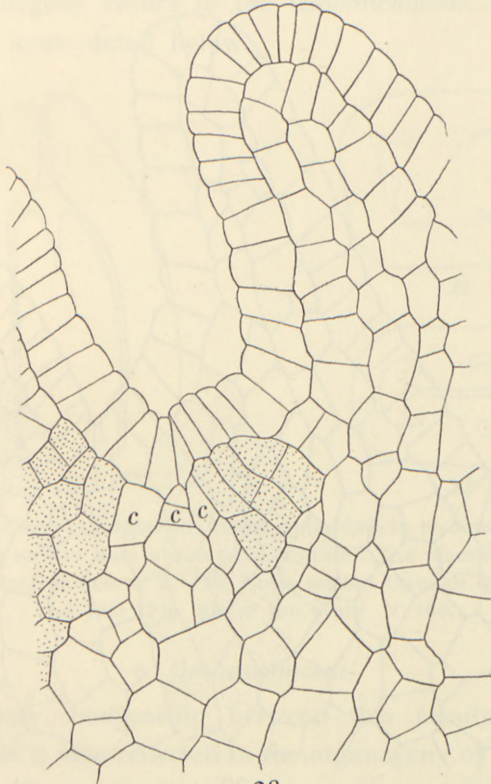
28

Fig. 28. As Fig. 27, but a little older. × 800.

upwards and inwards towards the cavity of the gynaecium.
The mass of tissue thus formed develops into the placenta,
which will soon grow up along the inner side of the carpels.
The divisions in the placentae continue, and new cell-rows
are initiated by anticlinal divisions in the subepidermal layer.

The axile cell-rows also (c) continue to divide for some
time yet, though at a s l o w e r rate than in the surrounding

tissue (dotted in the figures). As a consequence of this
peculiar unequal growth the apex of the stem will be cleaved,
as shown in Fig. 30. This, again, is distinctly seen in cross

29

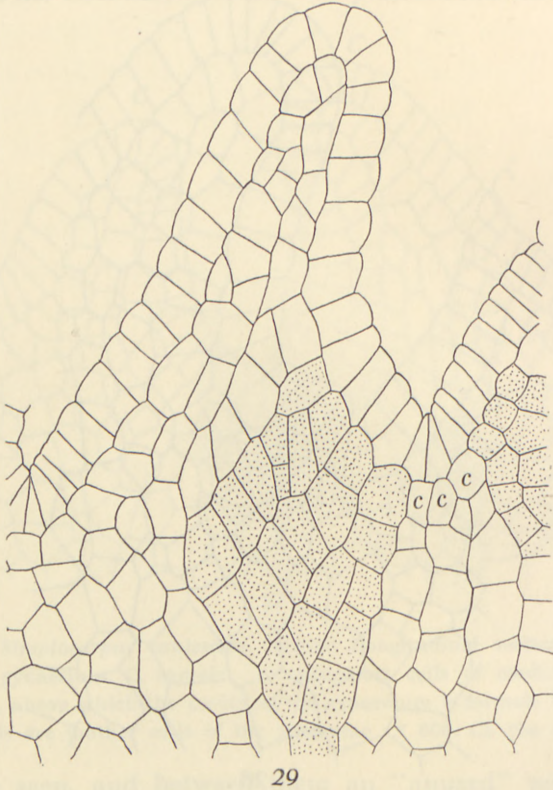Fig. 29. As Fig. 27, but somewhat older. × 800.

sections, which show that in the upper part of the ovary
the placentation is parietal (Fig. 32); but in the lower part
there is a central placenta as in most other *Personatae*
(Fig. 31).

For the sake of generalisation we show in Figs. 33—35
and Figs. 36—38 some of the most important develop-
mental stages of the gynaecium of two other *Gesneriaceae*.

And it will be seen that the carpels (C) and the placenta (P) are developed in a way which corresponds in the main features to that found above in *Streptocarpus* (Figs. 17—24). This organogeny recurs in the *Orobanchaceae*, as will be shown in more detail below.
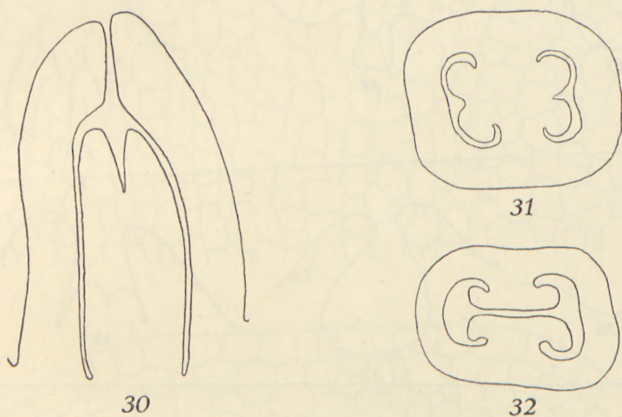

Fig. 30. *Streptocarpus caulescens*. Young gynaecium in median longitudinal section. (The section does not cut the septum). The placenta is parietal above, but central below. × 150. Cross section through apex (Fig. 32) and base (Fig. 31) of the ovary. × 100.

e. *Orobanchaceae.*

The close relationship between this family and the *Gesneriaceae* is also reflected in the organogeny of the gynaecium, as will appear from a comparison of Figs. 33—42. Of these, Figs. 39—42 have been drawn from sections through young gynaecia of *Orobanche lucorum*.

Immediately before the carpels are initiated (Fig. 39), the growing point of the flower is only slightly convex. This stem apex is not entirely covered by the young carpels (Fig. 41), but a portion of the central part of the growing apex will remain at the bottom of the cavity of the gynaecium. This portion of the stem will increase somewhat in

2*

thickness, and soon it will also grow in length and "move upwards" along the inner side of the carpels. This young placenta will be deeply cleaved because some few of the axile cell-rows of the floral axis cease to grow (cf. Fig. 46).
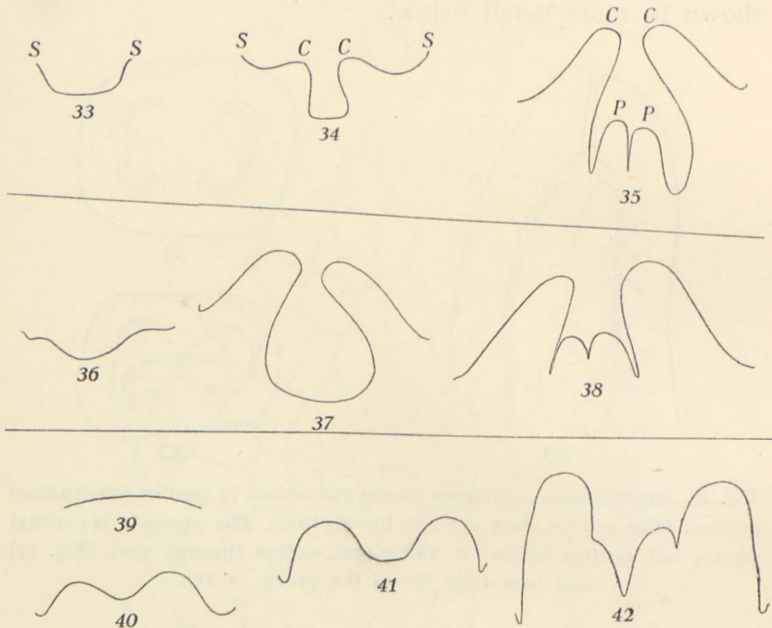
Figs. 33—35. The organogeny of the gynaecium in *Achimenes candida* LINDL. in median longitudinal sections. S, stamens; C, carpels; P, placentae. × 160. — Figs. 36—38. *Smithiantha zebrina* (PAXT.). × 160. — Figs. 39—42. *Orobanche lucorum* A. BR. × 80.

Figs. 43—47 give histological details of some of the most important developmental stages of another *Orobanchacea* (*Aeginetia indica*) which I brought home from the Indies (Sumatra).

It will be seen that immediately before the corolla is initiated (Fig. 43) the cells of the growing point are not arranged in layers parallel to the epidermis, as in the growing points of ordinary vegetative stems. In the lower

middle part of the figure, however, some short vertical cell-rows are seen which were formed at the time the
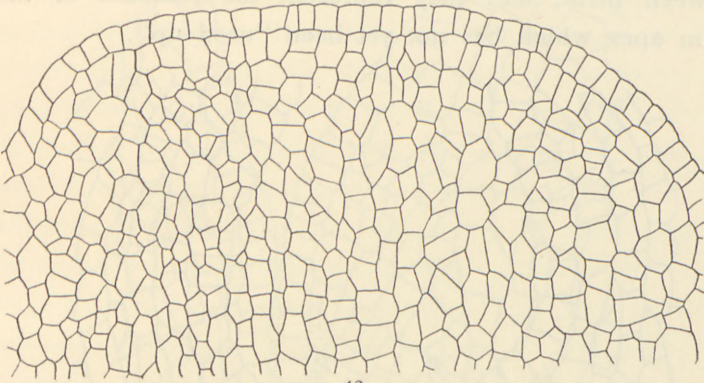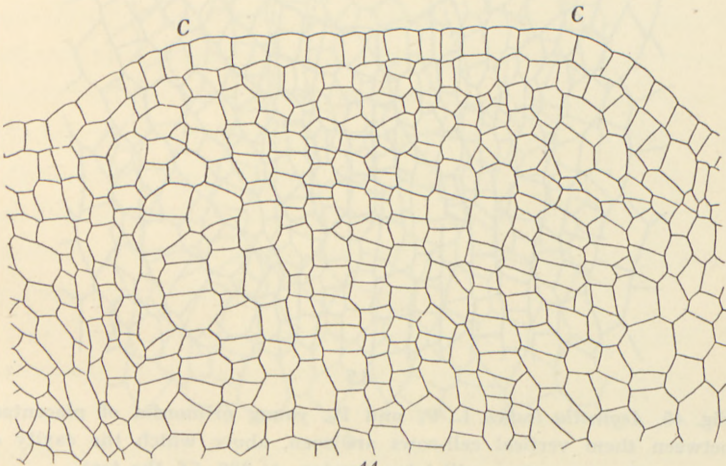
Figs. 43—44. *Aeginetia indica* L. Median longitudinal sections through young flowers, Fig. 43 immediately before the corolla is initiated. C, carpels. × 240. Cf. the text.

flower stalk was growing by a typical vegetative growing point. The cells subsequently formed (Fig. 43, top) are arranged in irregular fan-shaped cell-rows almost per- pendicular to the epidermis.

The carpels (C in Fig. 44) arise in a distinctly lateral
position; many (about 6—8) vertical cell rows are situated
between them, and they represent the remnant of the
stem apex which has not yet been "used up".

45
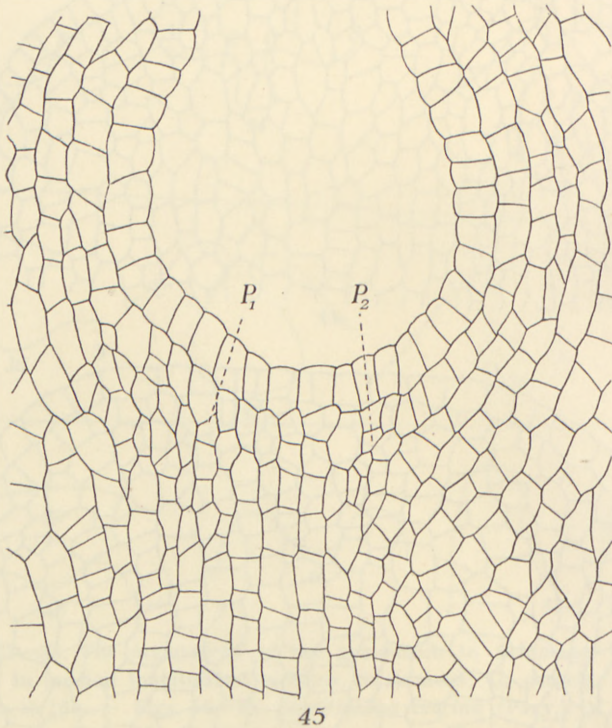
Fig. 45. *Aeginetia indica* L. P_1 and P_2, young primordia of placentae;
between them vertical cell-rows are seen, above which the cavity of
the gynaecium will later develop. × 300. Cf. the text.

Fig. 45 shows a still older stage, in which the axile
vertical cell-rows are distinctly seen; above they reach right
up to the epidermis at the bottom of the cavity of the gynae-
cium. And a microscopical examination of the whole section
(not drawn in Fig. 45) will show that these cell-rows con-
tinue downwards into the medulla of the flower stalk.
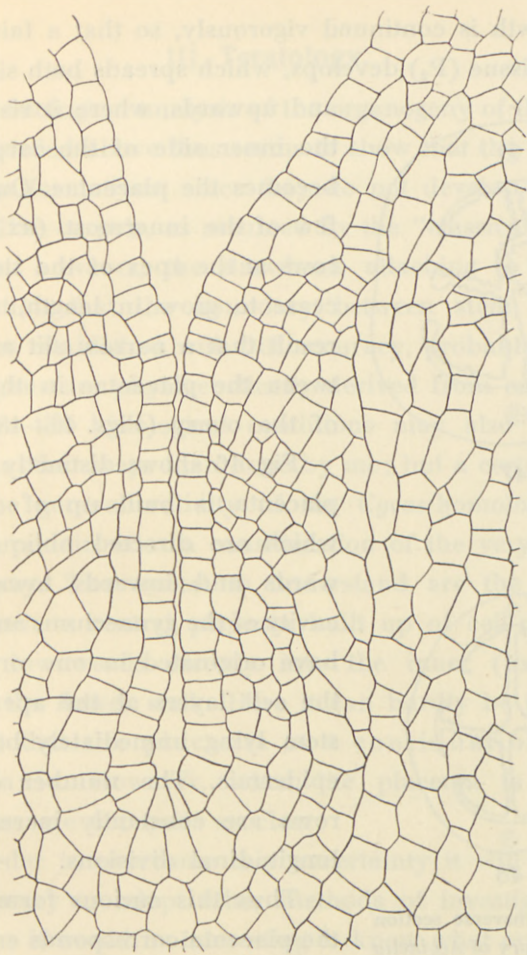
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Fig. 46. *Aeginetia indica* L. Longitudinal section through young placentae formed of cell-rows which are directed obliquely upwards and inwards. × 300.

It is of special interest to note the place where the placenta is originally initiated. It will be seen (at P_2 in Fig. 45) that several cell divisions have taken place in the outermost part of the remaining portion of the stem apex.

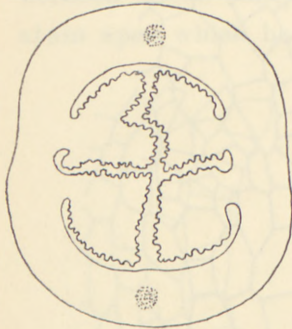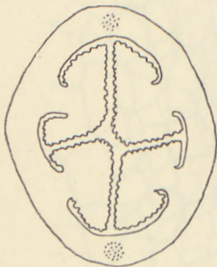This growth is continued vigorously, so that a fairly large mass of tissue (P_2) develops, which spreads both sidewards and upwards, where it rises along the inner side of the carpels and becomes the placentae. Only some few of the innermost (axile) cell-rows at the apex of the stem soon cease to grow in length, with the result that a narrow slit arises between the placentae in the centre of the ovary (Figs. 46—48).

Fig. 46 shows distinctly that the placenta is built up of cell-rows which are directed obliquely upwards and inwards towards the cavity of the gynaecium, and which have originated in one or two of the cell layers at the apex of the stem lying immediately below the epidermis. The number of these rows are constantly increased by longitudinal divisions.

Thus this curious formation of the placenta corresponds entirely to that found above in the *Gesneriaceae*, except that in *Aeginetia* (Fig. 47) there are f o u r placentae, and they are not situated on the place where the edges of the carpels are joined together, but some distance out on the l a m i n a. This is even more distinct in *Cistanche* (Fig. 48)—which shows that the placentae are n o t formed of the margins of the carpels.

Fig. 47. Transverse section of young ovary of *Aeginetia indica*. × 20. — Fig. 48. *Cistanche lutea* Lk. et Hoffm. Transverse section of young ovary, showing four parietal placentae on the lamina of the two carpels. × 20.

III. **Teratology.**

The histological analysis of the organogeny of the gynae-
cium recorded above thus seems to show that the placentae
are stem formations, since they do not develop from the
edges of the carpels, as assumed by the "classical" theory.
There is, however, the drawback attaching to such an
investigation that the boundary between stem and leaf
cannot be established with full accuracy, probably because
these organs are phylogenetically derived from each other.
Therefore the histological conditions may also be inter-
preted in other ways than done by me; but a certain doubt
as to the general validity of the *Cycas*-homologies may
possibly remain after a consideration of the very peculiar
organogeny. The easiest to understand are the gynaecia
which have a central placenta built up of cell-rows con-
tinuing downwards directly into the inner (axile) cell-
rows of the flower stalk. Here it can hardly be justifiable
to doubt that the placenta is a continuation of the
floral axis. However, when the placenta is parietal,
conditions are not quite so clear.

In order to overcome this uncertainty it will therefore
be necessary to adopt other methods of investigation. In
particular it would be interesting to know what organs may
develop from the placenta. Unfortunately the morpholog-
ical value of the ovules has not been definitely recognised.
But could they be found transformed into other organs of
known morphological value, we should obtain a valuable
body of evidence. That such a possibility is within the
bounds of probability cannot reasonably be doubted if for
instance we utilise PENZIG's ample information about
"oolysis". Personally I have previously (1938) described

numerous examples showing that ovules (in *Salix*) may be
transformed into stamens; and similar observations have
been made within the *Personatae* (Rischkow), for instance
in *Petunia*.

That the c a r p e l s are homologous with leaves, has been
doubted by Grégoire; but that this doubt is unfounded
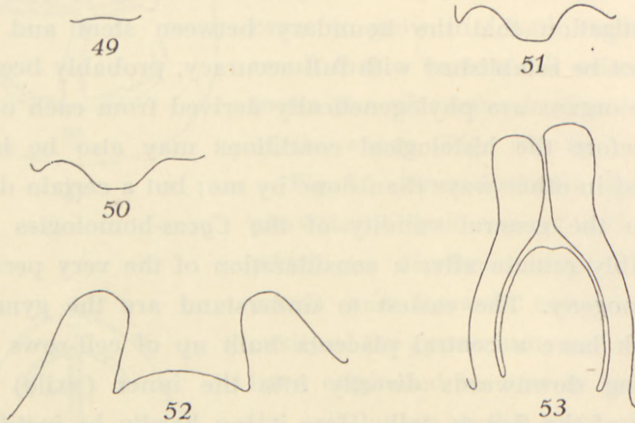
Figs. 49—53. The organogeny of the gynaecium in a normal *Petunia
nyctaginiflora* Juss. Figs. 49—52, × 200. Fig. 53, × 60. The placenta is
slightly parietal at the apex, otherwise central.

has recently been shown by Troll and his school, who
by a histological analysis of the various developmental
stages of the carpels found good agreement with the general
organogeny of the leaves. We will therefore in the following
pages attempt to throw light on the morphological nature
of the carpels and ovules. And for this purpose we shall
employ Levan's valuable teratological material of *Petunia*
and his work on it, to which the following considerations
are merely to be regarded as a supplement.

However, we shall begin the teratological examination
of *Petunia* by tracing the organogeny of a normal gynaecium

(Figs. 49—53) in order to show that in the main features the development is the same as was found above in *Perso-natae* that have a central placenta: At the apex of the floral axis (Fig. 49) the carpels arise laterally (Figs. 50—51) so that an unused remnant of the apex of the stem will be left. This will later continue its growth (Fig. 52) so as to rise between the carpels, and will become the central placenta (Fig. 53).

It is a point of interest that LEVAN's teratological *Petunia* has not the character of something more or less casual and pathological, for the appearance of the plants is genetic-ally conditioned, so that they may be produced arbitrarily by the concurrence of certain genes. When such genetic conditions have then been fulfilled, all the flowers of the individual will be transformed. And in the individual flowers all the organs are transformed in a certain direction, so that they are reminiscent of the respective vegetative organs from which they are derived. This displacement in a vegetative direction is shown in the corolla by its turning greenish or whitish. Stamens (Fig. 56) and stigma (Fig. 55) also show their leaf-nature.

However, special interest attaches to the transformation of the gynaecium, which is very conspicuous in the later developmental stages of the flower, as will appear from LEVAN's photographs.

After flowering all the ovaries swell considerably although none of the ovules have been fertilised. The ovary will soon burst lengthwise, and numerous ovules will project (Fig. 54); they have a very peculiar appearance, as shown in Figs. 54 and 57—66. As each of the many ovaries of the plant contains several hundred seeds, it will be understood that an exceedingly rich teratological material may easily

be procured. This abundance is further augmented in that
the individual ovules of an ovary are transformed in very
different manners, so that all conceivable stages of transition
may easily be found between nearly normal ovules (Fig. 57)
and green leaves even (Fig. 66) with nerves and glandular
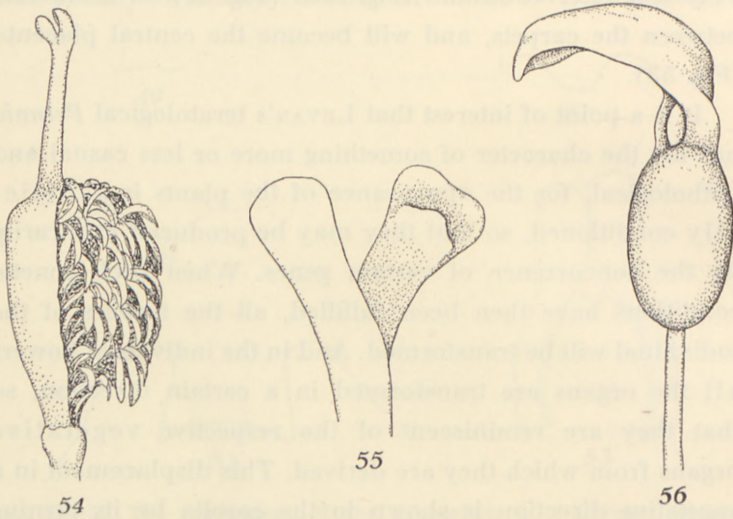
Figs. 54—56. Teratological *Petunia nyctaginiflora* Juss. — Fig. 54. The trans-
formed ovules have caused the ovary to burst. × 2. — Fig. 55. Transformed
stigma. × 5. — Fig. 56. Teratological anther with a large connective. × 5.

hairs and of an entirely similar appearance for instance
to that of normal sepals (Fig. 67), as to whose leaf-nature
there is hardly any reason to doubt.

All the ovules represented in Figs. 57—66 have been
dissected out from the same ovary and have been drawn
by means of a drawing apparatus at slight magnification.
Special attention should be given to the size of the micro-
pyle, which is indicated in the figures by heavy dotting.

Fig. 57 shows an almost normal ovule, whose micropyle
is relatively small and but slightly oblique. The following

figures show an increase of the size and obliquity of the
micropyle; and such ovules are present in the ovaries in
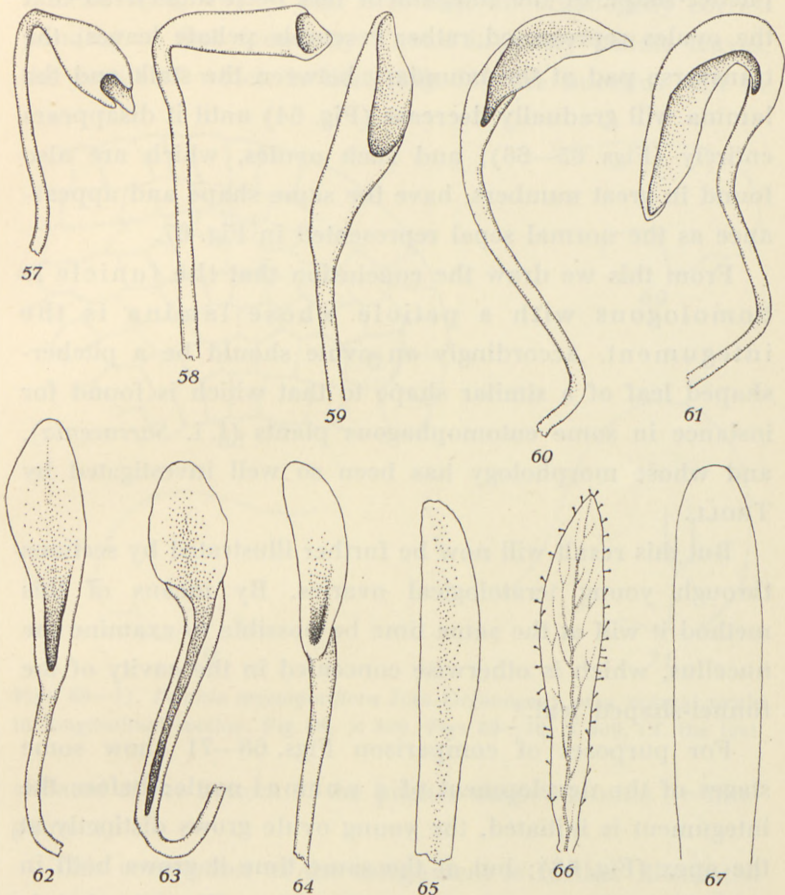
Figs. 57—66. *Petunia nyctaginiflora* Juss. Older teratological ovules showing
transitions from nearly normal ovules (Fig. 57) to leaf-like "ovules"
(Figs. 65—66). — Fig. 67, leaf of calyx. — Micropyle heavily dotted. × 8.
Cf. the text.

particularly large numbers. At the same time the funicle
becomes short, broad, and flat (Figs. 65—66), assuming the
character of a leaf stalk, while the micropyle attains such

a large size that the integument will assume the shape of a normal lamina. Figs. 62—64 will show that the original pitcher-shape of the integument has been altered so that the ovules represented rather resemble peltate leaves; the transverse pad at the boundary between the stalk and the lamina will gradually decrease (Fig. 64) until it disappears entirely (Figs. 65—66); and such ovules, which are also found in great numbers, have the same shape and appearance as the normal sepal represented in Fig. 67.

From this we draw the conclusion that the funicle is homologous with a petiole whose lamina is the integument. Accordingly an ovule should be a pitcher-shaped leaf of a similar shape to that which is found for instance in some entomophagous plants (f. i. *Sarracenia*), and whose morphology has been so well investigated by TROLL.

But this result will now be further illustrated by sections through young teratological ovaries. By means of this method it will at the same time be possible to examine the nucellus, which is otherwise concealed in the cavity of the funnel-shaped leaf.

For purposes of comparison Figs. 68—71 show some stages of the development of a normal ovule: before the integument is initiated, the young ovule grows distinctly at the apex (Fig. 68); but at the same time it grows both in thickness and breadth (along the edge, Fig. 88)—that is to say, in the same way as many vegetative leaves grow (cf. TROLL, 1939).

The cell which is dotted in Fig. 68 is the mother cell of the nucellus; but the young ovule constantly continues its apical growth (Fig. 69) beyond the nucellus, and the youngest apex of the lamina will soon bend up around it.

However, in addition a transverse pad will soon develop, which surrounds the proximal part of the base of the nucellus (Fig. 70) — that is to say, an organogeny corresponding to that found by TROLL in many peltate leaves, the result of which is that (Fig. 71) the nucellus will be

68

69

70   71
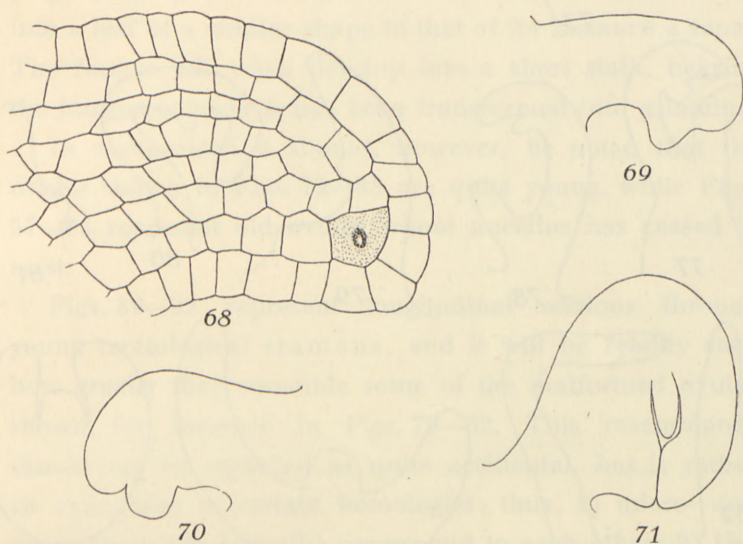
Figs. 68—71. *Petunia myctaginiflora* JUSS. Organogeny of a normal ovule in longitudinal section. Fig. 68, × 800. Figs. 69—70, × 300. Cf. the text.

situated at the bottom of the pitcher-shaped lamina (= integument).

This conception of the integument is further illustrated by the sections represented in Figs. 72—88, which show transitions from a nearly normal ovule to a leaf of an almost normal appearance (Fig. 83). In some cases both the nucellus and the integument are distinct. The latter may either be pitcher-shaped or more or less flat, or with a crescent-shaped transverse section; either the lamina is almost straight (Figs. 81—82), or it may (most frequently) be
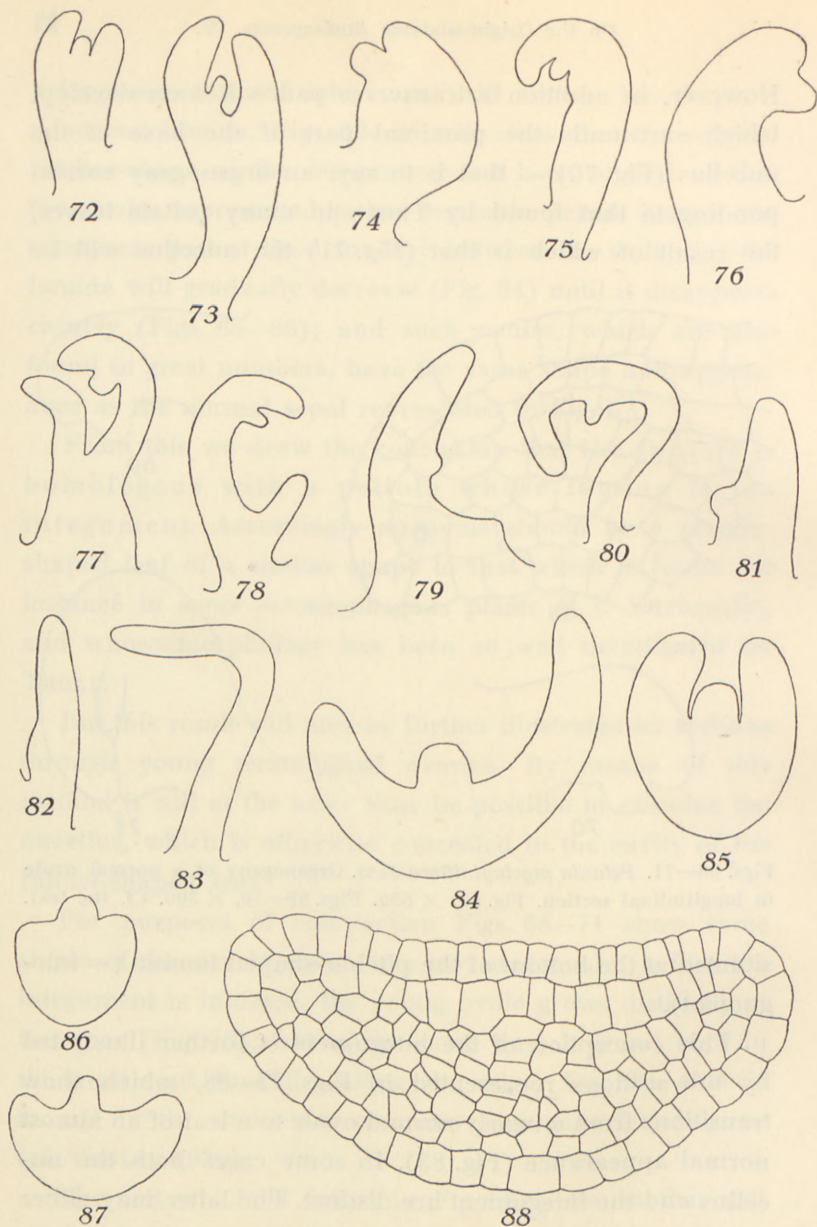
Figs. 72—88. *Petunia nyctaginiflora* Juss. Section of young teratological ovules. Figs. 72, 73, 75, 77, 78, 80, 82, × 100. Figs. 74, 76, 79, 84, 85, 86, 87, × 200. Fig. 88, × 600. Figs. 81 and 83, × 75. Above, slightly transformed ovules with small micropyles; below, ovules with nearly normal leaf-like shape. Cf. further Figs. 57—66 and the text.

incurved at the apex in a similar way to that of a young fern-leaf.

The transverse pad which conditions the peltate shape of the young integument is in some cases large and distinct (Figs. 77—78), but often it is partially or entirely absent (Figs. 79—81), and if so, the ovule has been transformed into a leaf of a similar shape to that of for instance a sepal. The funicle will often develop into a short stalk, bearing the integument which has been transformed into a lamina.

In comparison it should, however, be noted that the ovules shown in Figs. 72—88 are quite young, while Figs. 57—66 represent old ovules whose nucellus has ceased to exist.

Figs. 89—92 represent longitudinal sections through young teratological stamens, and it will be readily seen how greatly they resemble some of the malformed ovules shown for instance in Figs. 79—82. This resemblance should not be regarded as quite accidental, but is rather an expression of certain homologies: thus, 1) micro- and macrosporangia (nucelli) correspond to each other; 2) the connective is homologous with an integument; and 3) the filament is homologous with the funicle. And as a whole an ovule is homologous with a microsporophyll and is itself a monosporangiate macrosporophyll.

PENZIG and RISCHKOW record many other malformations which create a presumption that the malformations described above do not illustrate conditions special to *Petunia*, but express morphological rules of general validity. Thus in *Datura stramonium* the ovules may be transformed into complete carpels, and in *Scrophularia vernalis* PENZIG has found handsome oolyses of a similar kind to those in *Petunia* described above. It is of special interest that in

Petunia the ovules may also be transformed into stamens, whose leaf-like nature there is hardly any reason to doubt. Similar transformations have previously been described by me in a plant which is placed in the system very far from *Petunia*, viz. *Salix*. Penzig further mentions similar oolyses in numerous other plants belonging to quite different groups,
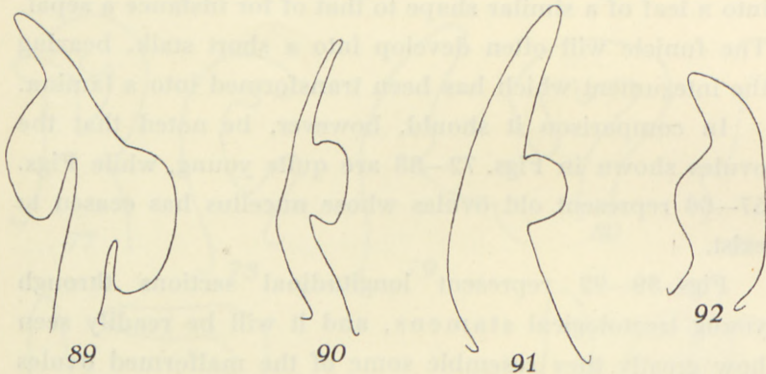

Figs. 89—92. *Petunia nyctaginiflora* Juss. Longitudinal section through tera-tological stamens, showing similarity to malformed ovules (Figs. 81—82). Slightly enlarged.

and showing that the ovules may often be transformed so as to resemble microsporophylls, calyx, corolla, or carpels.

The placenta also may in several plants be transformed into a shorter or longer axis whose leaves are more or less distinct ovules. Such malformations have been figured for instance by Peyritsch (1878) and especially distinctly by Rischkow, who has also examined i. a. many genera of the *Solanaceae*, in which he has produced experimentally very convincing malformations of ovaries: "In antholytic tomato-flowers the placenta acquires the character of a sprout, in the lower part of which there are leaflets, next come stamina, while above ovules are still present." (Rischkow, 1937, p. 131). Similar transformations were

found for instance in *Solanum, Datura, Atropa, Capsicum,*
Nicotiana, Physalis, Convolvulus, Allium, Brassica, etc.,
which warrants the assumption that the phenomena de-
scribed above in *Petunia* have a more universal validity.
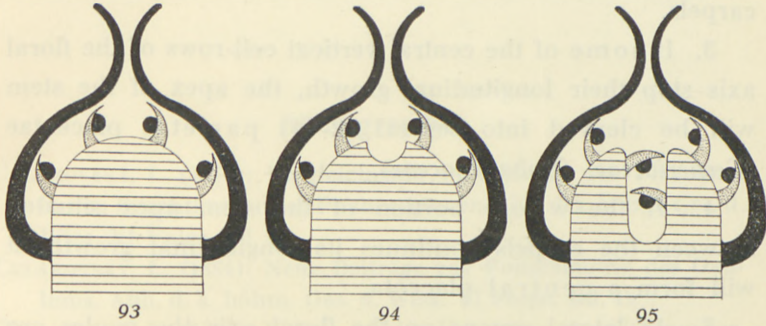
Figs. 93—95. Diagrams showing the morphology of the gynaecium. The
axial parts are horizontally ruled; the carpels are black; integument and
funicles dotted; nucelli black. Fig. 93, Central placenta (e. g. in *Solana-*
ceae). Fig. 94. Placenta parietal above, central below (e. g. in some
Gesneriaceae). Fig. 95. Placenta entirely parietal (*Orobanchaceae*). The
floral axis elongated and forming the placentae; it bears the following
leaves: 1) barren carpels, and 2) ovules which are monosporangiate macro-
sporophylls.

Thus both the organogeny of the gynaecium and the
teratological conditions seem to point in the same direction,
namely towards the view of the gynaecium which is ex-
pressed in the accompanying diagrammatic figures (93—95)
and in the subjoined summary.

IV. Summary.

The present work is an inquiry into the morphology of
the gynaecium in some selected types within the *Personatae.*
They were examined partly organogenetically, partly (*Pe-*
tunia) teratologically with the following results:

3*

1. The carpels are barren leaves, which do not bear ovules at their edges (as assumed by the "classical theory").

2. The placentae are direct continuations of the floral axis, whose cell-rows grow up between the carpels.

3. If some of the central vertical cell-rows of the floral axis stop their longitudinal growth, the apex of the stem will be cleaved into several (2—4) parietal placentae (*Gesneriaceae, Orobanchaceae*).

4. If the whole portion of the stem apex situated between the carpels continues its longitudinal growth, it will form a central placenta.

5. As lateral organs on the floral axis the ovules are homologous with leaves; they are monosporangiate macrosporophylls of a similar nature to those occurring in *Lycopodiales*.

6. The malformations show that the funicle is homologous with a leaf-stalk whose lamina is the pitcher-shaped integument.

7. In many *Solanaceae* Rischkow found the ovules to be transformed into: flat leaves, carpels, or stamina (i. e. organs homologous with leaves); and the placenta is often transformed into a sprout, which forms a direct continuation of the floral axis.

8. The view maintained in the present paper as to the morphology of the gynaecium is illustrated in Figs. 93—95, and in addition it is described at greater length in my previous works and in those of J. M. Thompson.

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