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

III. THE GYNAECIUM OF *SALIX CINEREA*

BY

O. HAGERUP

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PREFACE

The material for the present work has been collected on *Salix cinerea* individuals growing wild at Brede near Copenhagen. The most important developmental stages of the flowers have been fixed in Carnoy's liquid in July—August whereupon they have been cut into continuous microtome series 6—12 μ thick. These stain well in Saphranin or Haematoxylin.

My manuscript has been read through by Professors K. JESSEN and O. PAULSEN of Copenhagen, besides by Professor J. McLEAN THOMPSON of Liverpool, who has also revised the translation. I owe a heavy debt of gratitude to these three gentlemen and specially to Professor J. McLEAN THOMPSON for many valuable critical hints.

To the trustees of the CARLSBERG Foundation, who have rendered possible my studies for a number of years, I tender respectful thanks.

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I. The Problems.

The present work is a direct continuation of my earlier phylogenetic studies, which have aimed at a revision of the current view of the morphology of the gynaecium. For it may be considered that through enquiry in this direction an understanding can be reached of the manner in which the dominant vegetation of the present day has evolved upon our globe; on which subject little is, in fact, known.

We have already examined in earlier publications numerous gynaecia with central placentae, and have shown in each case that the placenta is the apex of the floral axis, and that the ovules seated thereon are complete independent "leaves" which may be called macrosporophylls. In addition, it has been shown that the carpels surrounding the placentae do not bear the ovules on their edges, but form merely an involucre of barren leaves.

It is among the remaining forms of gynaecium that the classical carpellary theory might be expected to find its strongest support, especially in such cases as those in which the carpels remain free from each other. But in these also the Cycadean homologies which have previously been proposed are invalid, and even in the Leguminosae J. M. Thompson has shown that the ovules arise on the apex of the floral axis, being formed like young leaves upon it. It is true that the apices of the carpels may be formed, as

in *Acacia* (NEWMAN, 1936), as lateral outgrowths immediately beneath the tips of the floral axes. But as THOMPSON has fully shown, using NEWMAN's own figures of floral development in two Australian species of *Acacia*, intercalary growth occurs so that certain parts of the apex are soon involved in carpellary organisation.

From among the remaining common forms of gynaecium we shall now consider an example of an ovary with parietal placentation, supplementing in this way our earlier enquiries. In this case also one might expect to find whatever confirmation is possible for the classical carpellary theory. For this theory would be readily understandable on the facts as they stand if, for example, an ovary such as is shown in Figs. 1 and 2 were composed of two carpels, the swollen edges of which were united and so formed the two placentae. Nevertheless, as is shown in detail below, a thorough organogenetic and teratological research renders the classical interpretation untenable.

Salix has been chosen as a subject well suited to investigation for the simple reason that there may be found in this genus diverse and unusually valuable abnormalities, occurring in such large numbers as to make possible an important teratological analyses not only of the carpels but also of the ovules. Our investigation will, however, begin with an account of the earliest ontogenetic stages of the normal gynaecium, a special attempt being made to determine whether the placentae originate and are formed upon the carpels, as is maintained on the Cycadean hypothesis, or on the apex of the stem and between the carpels.

The adult structure of the flower of *Salix* is so well known that it may here suffice to give but a brief account of it, referring the reader to the accompanying Figs. 1 and 2.
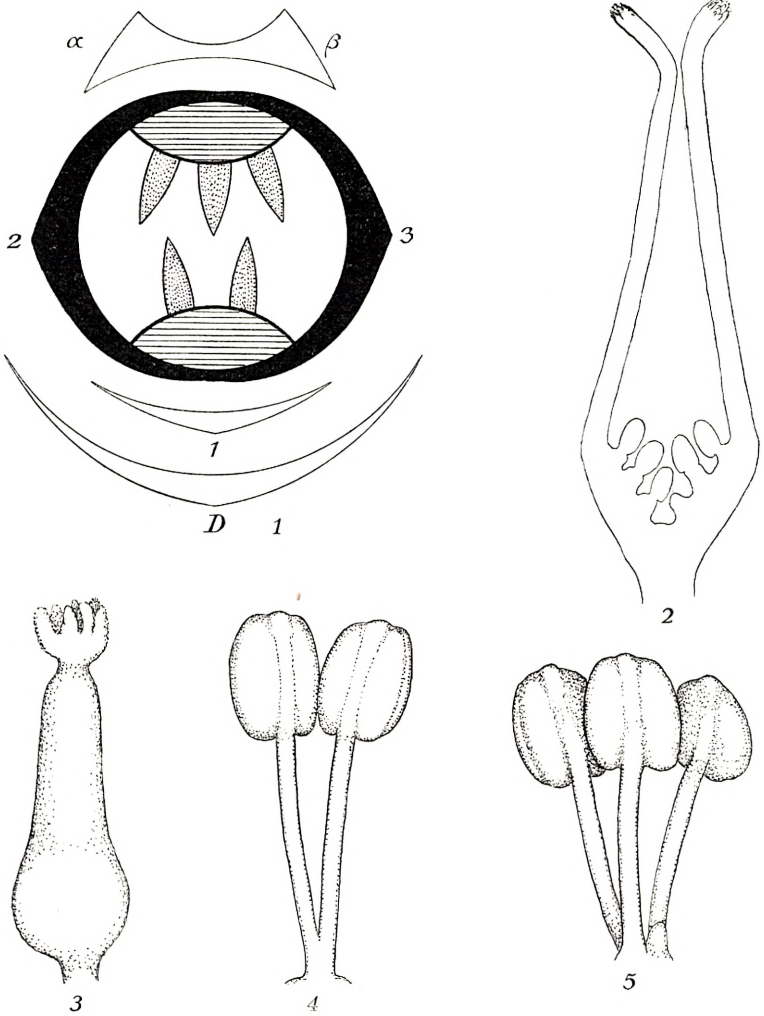
Fig. 1. Diagram of a normal female flower. D, bract; α and β, bracteoles; 1, perianth; 2 and 3, carpels; the floral axis (placenta) horizontally shaded; ovules (macrosporophylls) dotted. — Fig. 2. Longitudinal section of a normal gynaecium. × 20. — Fig. 3. Normal gynaecium. × 12. — Fig. 4. Normal male flower. × 12. — Fig. 5. Male flower with 3 stamens, corresponding to leaves 1, 2 and 3 in Fig. 1. × 12.

Velenovský has already shown that the gland situated behind the gynaecium is the union-product of the bracteoles (a and β). The abaxial leaf, 1, is generally rudimentary in *S. cinerea*, but occasionally and rarely it may be developed as a stamen (Fig. 5): or in other species it may mature as a gland. Leaves 2 and 3 are placed laterally: they mature as carpels in the female flower; in the male flower they mature as stamens (Fig. 4). In *S. cinerea* the placentae stand on the lines of coalescence of the carpellary margins as is required by and is in accordance with the classical theory. But the validity of the latter becomes immediately doubtful once the fact is considered that in many other species (cf. Eichler) the placentae are developed along the mid-lines of the carpels.

II. The Organogenesis of the Gynaecium.

In a series of publications Grégoire has shown that the growing point of a floral axis may be built on quite a different plan from that of a vegetative shoot. These differences are so definite that in referring to a floral axis, Grégoire has spoken of it as an organ "sui generis". Doubtless the use of such a term in this connection may be carrying matters to too great an extreme as is shown, for instance, by such malformations as those in which the gynaecium is replaced by a leaf-bearing stem. Some of Grégoire's observations are, however, of great value; and, indeed, we shall find that they are confirmed by *Salix* in which the histological conditions furnish much fresh information and throw an unexpected light on the morphological nature of the placentae.

For purposes of comparison we will begin our study by

examining the apex of an ordinary vegetative shoot of
S. cinerea (Fig. 6). In no single respect does it differ in
principle of organisation from, for instance, such branch
tips as are figured as typical in our common text books,
such as the vegetative tip of *Hippuris*. The cells are arranged
in regular and almost parallel layers. The central cell rows
of the medulla—which are drawn with firm outlines in
Figs. 6—13[1]— are of special interest. For it will be seen
that these rows do not extend to the epidermis but are
separated from the latter by several layers of cells. In
addition, Fig. 6 shows that a vegetative leaf is initiated in
the sub-epidermal layer, and that, at an early stage, other
cells immediately beneath the dividing cells of the sub-
epidermal layer are also involved in leaf-formation.

The apex of the axis of an inflorescence is constructed
on a similar plan (Fig. 7); but the component cells are not
arranged so regularly as in the apical cone of a vegetative
shoot (Fig. 6).

On the other hand, an examination of the growing apex
of a floral axis prior to carpel formation (Fig. 8) may
afford some cause for surprise. For there is here a striking
difference in organisation from that observed in the apex
of a vegetative shoot (Fig. 6); and, in fact, the condition
shown in Fig. 8 is particularly reminiscent of that which
maintains in certain Algae, as for instance, *Furcellaria*. For
the floral apex is traversed by a longitudinal, narrow, and
almost cylindrical core of cell rows which are continued

[1] It should be emphasised that the walls of the medullary cells are
all thin as are all other walls of the meristem. The thickening of the
outlines of the medullary cells is therefore a subjective matter which
should not escape the notice and criticism of the reader. For the choice
of the outer limits whereby the medulla may be defined is a somewhat
arbitrary matter.
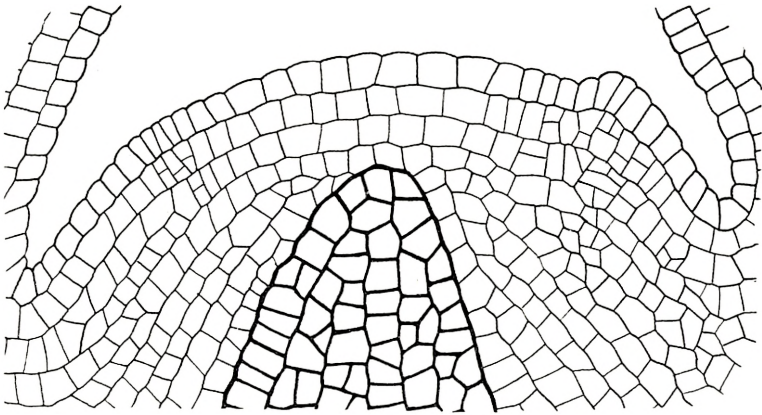
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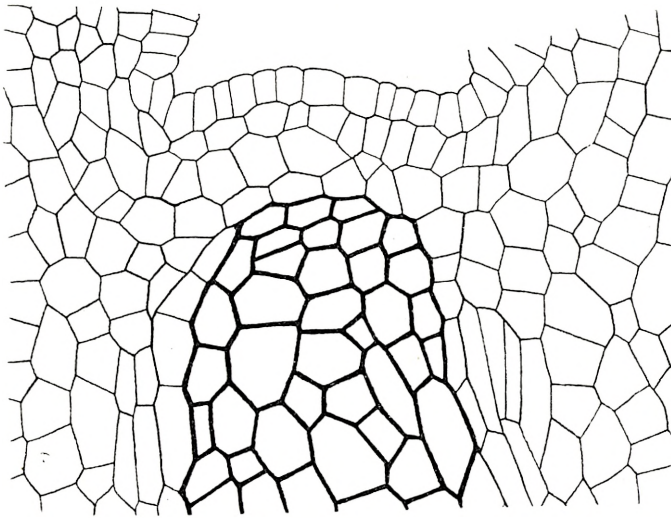
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Fig. 6. Growing point of vegetative shoot. Walls of the central medullary cells shown in firm outline. × 500. — Fig. 7. Growing point at tip of axis in a young catkin. × 500.

upwards just to the epidermis clothing the very apex. These rows are emphasised by a firm tracing of the walls in Fig. 8. Investing this core there is, in longitudinal section, a fan-like radiation of other cell rows directed almost at right

angles to the epidermis, and with divisions effected in such a way that the rows may appear to bifurcate as they are followed outwards. The number of these peripheral cell rows may be increased by new initials, arising as mother-cells for additional rows, wherever anticlinal division occurs in sub-epidermal cells. It will be noted, further, that once this state of organisation has been reached there is no longer a distinct and continuous sub-epidermal layer in the apex of the young flower stem (Fig. 8), the newly formed cells being arranged in quite another way from that which characterises the earlier stages of floral stem development (Fig. 7 a).

So that some understanding may be reached of the manner in which the remarkable condition of organisation of the cone of the young floral axis shown in Fig. 8 has been reached, we may now consider two younger stages in floral development. Thus in Fig. 7 a there is shown a longitudinal section of a floral primordium which is so young that nothing more than the base of the flower stalk is defined as a tiny cone. The latter is constructed on a plan which is almost identical with that of an ordinary vegetative stem apex, with several continuous cell layers beneath the epidermis and parallel to it (Fig. 6). When cell division occurs in these layers, the newly formed cell walls are placed as a rule at right angles to the epidermis. This arrangement of the outer tissues of the young flower stem is soon disturbed by dividing walls formed in the sub-epidermal layer, and which are parallel to the epidermis or periclinal. Two such walls may already be observed in the early stage of floral ontogeny shown in Fig. 7 a. Fig. 7 b shows a somewhat older flower stalk in longitudinal section and in the core of which the original arrangement of cells
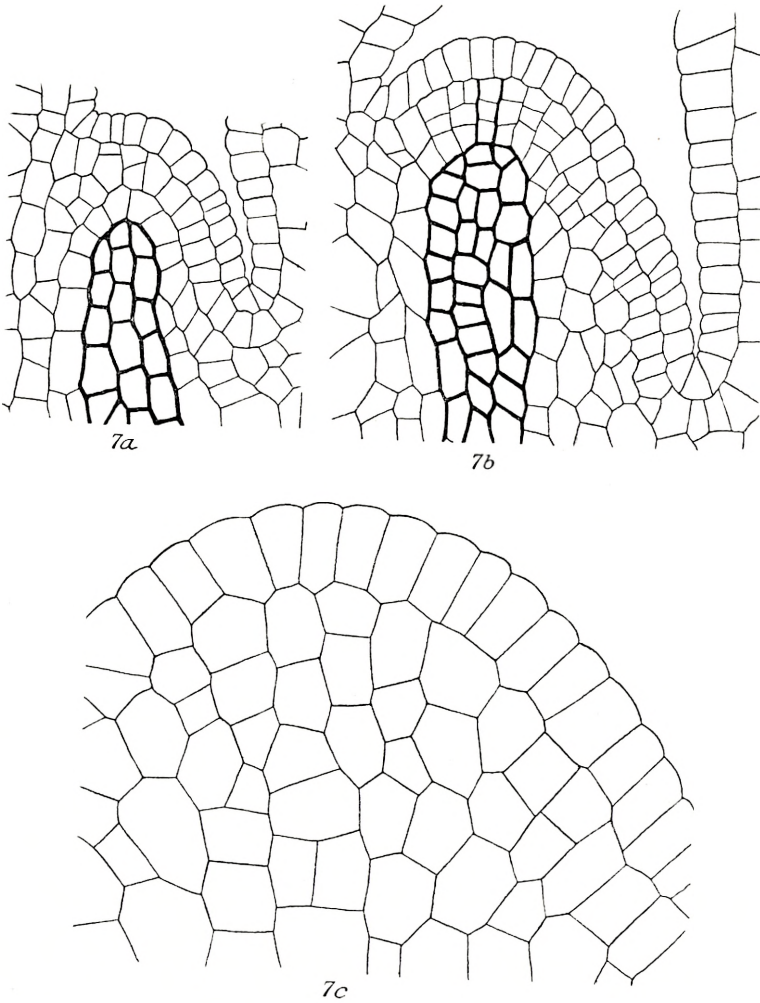
Fig. 7a. Young primordium of flower stalk with typical growing point (cp. Figs. 6—7). × 500. — Fig. 7b. Somewhat older stage with young initials of the cell rows arranged like a fan (cp. Fig. 8). × 500. — Fig. 7c. Growing point of a flower at a slightly older stage than that shown in Fig. 7b. × 1000.

may still be faintly observed (cf. Fig. 7a). But several cells of the sub-epidermal layer have now been divided by periclinal walls. The daughter-cells thus formed divide again by periclinal walls, and division continuing in

this way, shorter or longer rows of cells are formed at right angles to the epidermis (cf. Fig. 8). The number of these rows may be increased wherever anticlinal walls are also formed. It is in this way that the young floral cone shown in section in Fig. 7 c and 8 is soon produced with its distinctive features of organisation. The latter can, in large measure, be traced in origin to the balance struck between the alternative planes of division in the sub-epidermal layer of the young conical flower stalk.

There is thus in a phanerogam a unique type of generative cone (Fig. 8); and it is easily understandable that no ordinary shoot can be developed from it. And, in fact, the growth product of this stem apex is the mysterious gynaecium with its sequence of ontogenetic changes presenting still further surprises, as will be shown by the figures which follow.

But before we proceed to consider the ontogeny of the carpels, it is important to note the initial form of the floral apex (Fig. 8). For if we carry with us a picture of this form so as to be able to compare it with those given in the succeeding figures, we shall have a sufficiently accurate means for deciding the approximate limit between leaf and stem. And this despite the fact—which is not of decisive importance—that there will always be some cells which cannot be classified in this way.

It will be observed that in Fig. 9 the cells immediately beneath the epidermis are now arranged with a sufficient regularity to warrant the description of a sub-epidermal layer. It is this layer which plays an important part in giving an understanding of the further development of the gynaecium. For the carpels are initiated in this layer (Fig. 9) in a manner identical to that in which ordinary
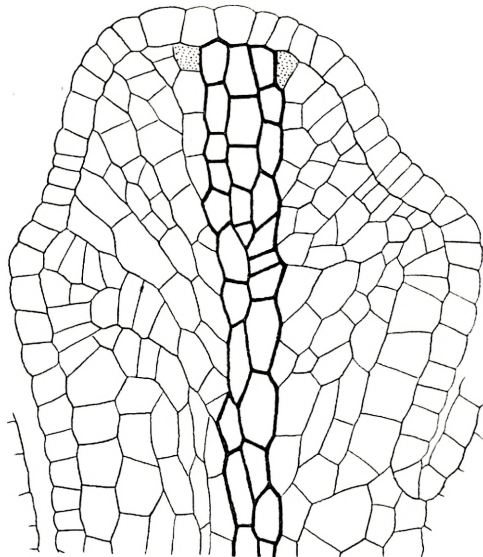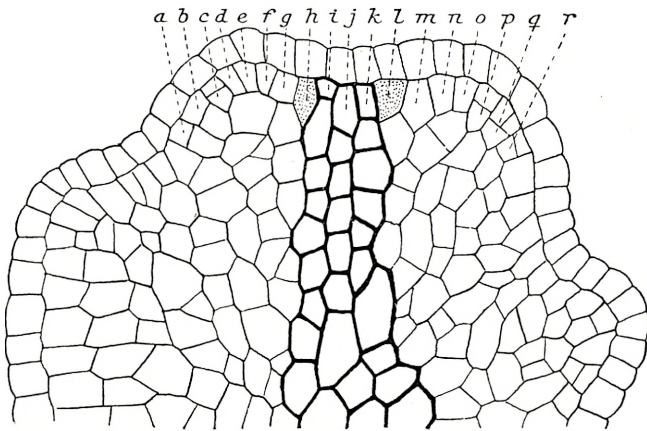
Fig. 8. Growing point of the tip of the floral axis just before the carpels are formed. × 700. — Fig. 9. First primordia for the carpels (a, b, c) and (p, q, r). × 700. Central rows of medullary cells (with heavily out-lined walls) reaching upwards to the epidermis. Dotted cells are mother cells of the placentae. Cp. further the text.

vegetative leaves are formed (Fig. 6). Thus a carpel is
initiated by the continuous periclinal division of such cells
as are lettered a, b and c in Fig. 9. These cells become
the mother-cells of long rows which compose the internal
tissue of the carpels (Figs. 10—13), and which, as it were,
lift the epidermis locally from its original position on the
stem surface.

The gynaecium comes to be furnished with a
central cavity due to the simple fact that such
cells as i, j and k, Fig. 9.— and which are in cen-
tral positions towards the summit of the grow-
ing apex — cease almost entirely to grow and
form rows, while the surrounding tissue con-
tinues in upward growth.

Between the two carpel primordia indicated by a—b—c
and p—q—r, Fig. 9, there lies a complete row of cells which
are lettered d—o. These cells belong to the stem and are
not involved in the carpel primordia. Thus the initial cone
has not been "used up" in carpel initiation, nor has it
ceased to grow except in its central portion which marked
its prior summit (i—k, Fig. 9). But the stem cells, such as
d—h and l—o — and which lie between the carpel pri-
mordia and the central meristematic cells i—k — divide
once more at later stages, their progeny coming to be
raised somewhat from the original and almost horizontal
position. These further products of growth and division
thus come to form downward continuations of the adaxial
sub-epidermal layers of the young carpels (Figs. 10 and 11).
In this way the floor of the ovary is partially
composed of the almost crateriform apex of the
floral axis.

If we now seek to probe into the nature of the placentae,
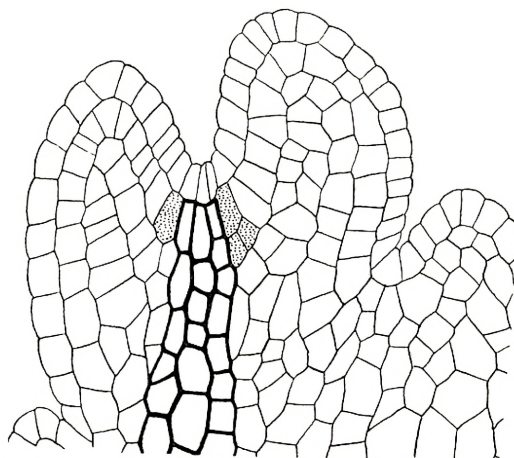
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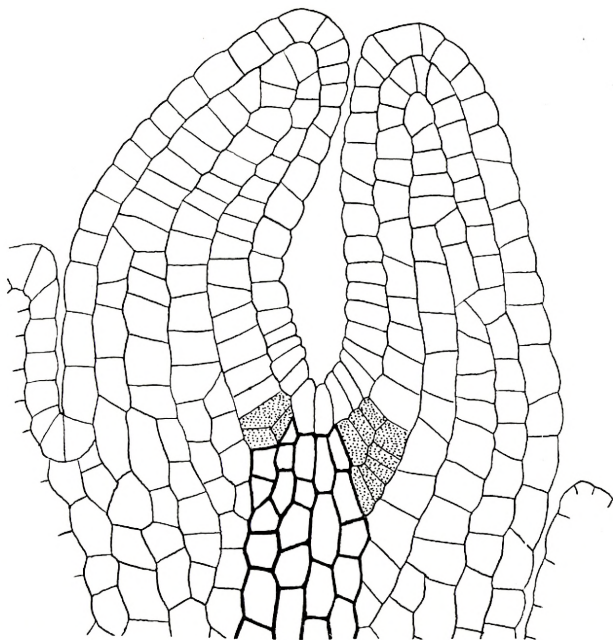
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Figs. 10—11. The first divisions of the mother cells of the placentae (dotted). The ovarial cavity is formed over the central medullary cells the growth of which ceases. × 750. Cp. also the text.

we may begin by examining the two sub-epidermal cells
h and l, Fig. 9, and which are immediately adjacent to
the core of medullary cells. These two sub-epidermal cells
(which are shaded in Figs. 8 and 9) gradually acquire
dense contents. They are especially capable of growth and
division and soon become the mother-cells of large tissue
masses. As is shown in subsequent figures, these tissue
masses gradually become the placentae.

It will be further evident that these mother-cells (h and
l, Fig. 9) belong to the floral stem, and not to the carpels,
since in the early ontogenetic stages shown in Figs. 8 and 9,
these mother-cells are in being before the carpels are
formed. And indeed, as is shown in Fig. 9, there are several
stem cells lying between such a mother-cell as h and the
carpel primordium lettered a, b, c.

Fig. 10 shows a median longitudinal section through a
somewhat older gynaecium. It will be seen from it that
all newly formed cells composing the carpels are in regular
rows, and that the sub-epidermal layers are particularly
distinct. Despite the fact that the carpels are now fairly
large, no placentae may yet be observed as prominences.
The carpels grow especially at their bases, their first formed
or older parts becoming the upper portions of the ovary
(cf. Fig. 2). On these upper portions neither placentae nor
ovules are formed.

It is not until the rather advanced stage in ontogeny
shown in Fig. 10 is reached that the mother-cells of the
placentae undergo their first divisions. The main directions
of the successive walls whereby these mother-cells are
divided are generally at right angles to each other. During
the earliest of these divisions the strictly localised mother-
cells are resolved by dominant anticlinal division into two

layers of cells (Fig. 11). It is in the o u t e r of these two cell
rows that growth and division is dominantly continued
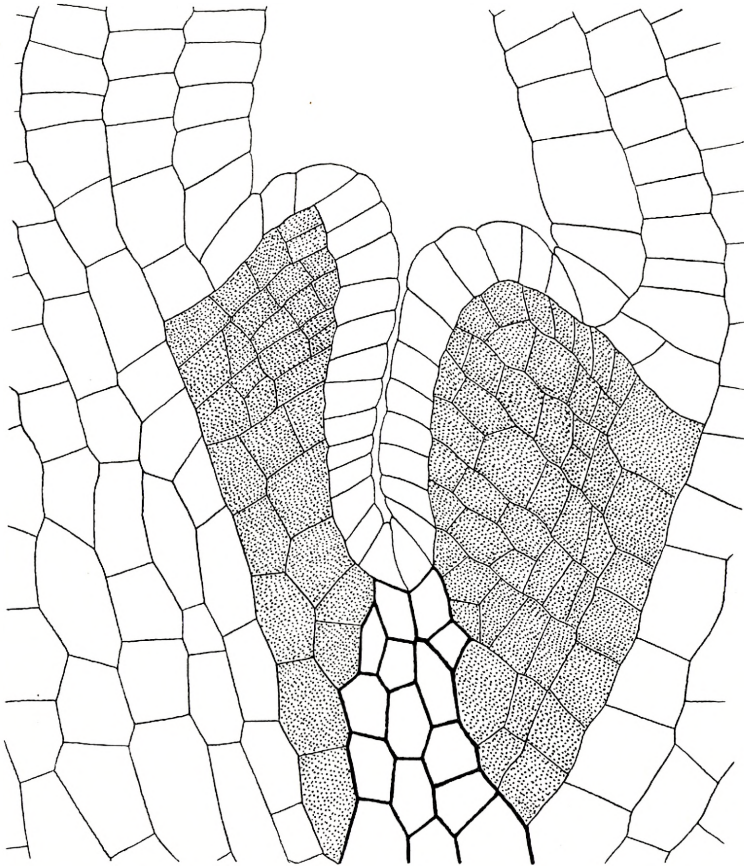
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Fig. 12. From the subepidermal layer of the tip of the axis are devel-
oped obliquely inward-directed cell rows (dotted) which form the pla-
centae. × 1000. (Cp. the text).

(Fig. 12), the individual cells being divided at first by walls
which are parallel to each other and to the inner surface
of the ovary. In this way moderately long and curved rows
of cells are formed directed obliquely upwards towards

the ovarial cavity (Fig. 13). The number of these rows is also increased by longitudinal walls which are placed anticlinally (Fig. 12).

In the older stages (e.g. Fig. 13), the original arrangement of the tissues of the axis and its appendages is so obscured that it is difficult of recognition. In the placentae, however, the bow-shaped and incurved rows of cells may still be observed, with clear indications of their origin from the stem apex at levels beneath the ovarial cavity. Taken by itself and judged by first appearances such an older stage as is shown in Fig. 13 seems to lend support to the suggestion that the classical theory is correct in maintaining that the placentae are essentially portions of the carpels. But the course of ontogeny shows that this is not a correct interpretation as has been demonstrated by the study of the changes in both the form and positions of the cells and their progeny shaded in Figs. 8—13. For the original blunt stem apex with its almost horizontal upper surface ceases to grow at the mid-point of its summit and continues in growth only along its margins which are raised almost in the form of a crater (J. M. Thompson), and along the inner faces of the carpels so as to constitute the placentae.

The form of the stem apex is not, however, that of a simple crater, for the crater rim is divided into two parts, which are the placentae, the division being evident almost to the crater floor, such as, for instance, the cupule of *Fagus* is subdivided into four portions. This subdivision is effected by inequalities in the rate of growth of the crater margin, growth being rapid along the mid-lines of the two placentae and being non-existent in the positions in which the clefts are formed.

The ovules are later initiated upon the placentae as local
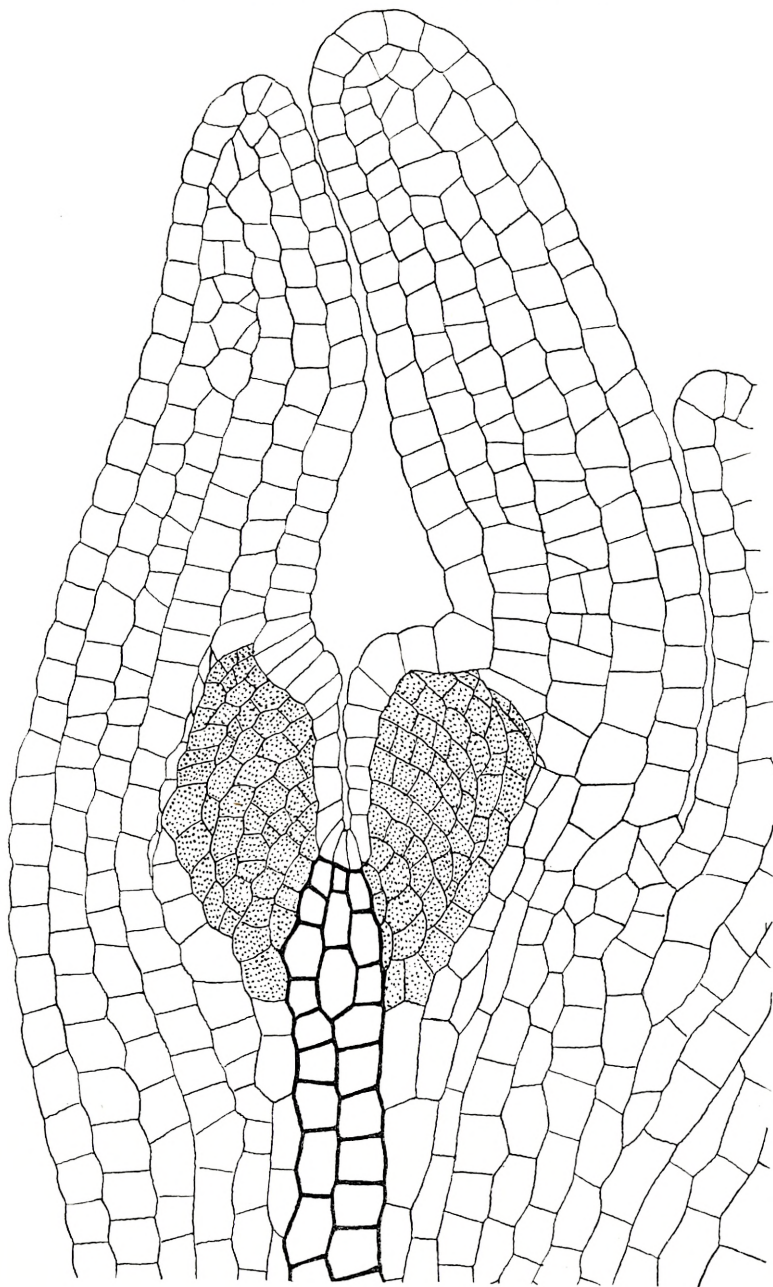
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Fig. 13. Older gynaecium before the forming of the ovules. The placentae
form the crateriform tip of the floral axis. × 700. Cp. the text and
Figs. 8—12.

growing points in the sub-epidermal and the underlying cells which are soon differentiated. They arise on the placentae in a manner similar to that in which foliage leaves and carpels are formed. This point is, however, so well known as to call for no emphasis here. It may suffice to state that on the evidence the ovules are inserted on those portions of the stem which are developed as placentae, and that they are completely dorsiventral and lateral organs like most other forms of leaves.

From the point of view of morphology there can then be no reasonable objection to regarding the ovules as individual, complete, and independent organs of foliar form. And it is to the abundant support of this interpretation that the consideration of the monstrosities illustrated below is directed.

But before these matters are considered, the results of our ontogenetic study may be presented in simple and clear diagrams such as Figs. 1 and 45.

It should, however, be kept clearly in mind that an histological analysis such as has been given above carries the drawback that it is not always possible to fix definitely the boundary between stem and leaf; and this in relation to the fact that these organs are phylogenetically of common origin and are interchangeable. The illustrations considered above are therefore open to other interpretations than those which I have proposed. And hence, so that there shall be no undue doubt on my reading of the facts of morphology, we shall now approach the matter from a different angle, namely that which is presented by the facts of teratology. In this way an opportunity may be given to check the conclusions of our histological study and to discover whether the results of teratological enquiry run

counter to our analysis, or the two methods of approach give compatible results.

III. Teratology.

During the past century many and varied malformations have been described among the flowers of numerous species of *Salix*. A good idea of the extensive literature on this subject has already been given in the long list of references provided by RAINIO and in the summaries of PENZIG. Many illustrations of anomalous flowers are available, and among those worthy of special mention are CHAMBERLAIN's figures of "ovules" replaced by stamens. I think, therefore, that it may suffice to add to these illustrations Figs. 14—44. For they serve to confirm what has already been made known in the literature and warrant a generalisation which is founded on observation. And in particular, these additional figures provide a means of checking the histological features described and discussed above in relation to organogenesis.

Figs. 14—19 show longitudinal sections of a number of gynaecia taken from one and the same tree of *Salix cinerea*. It will be observed from these figures that the form, stature and fertility of the placentae may vary considerably. For comparison of the conditions shown, the reader is referred to Fig. 2 in which the normal placentae and their fertility are depicted. Fig. 15 shows, however, a flower with only one parietal placenta. Or again, the single placenta may be central, as in Fig. 19, in which case it forms a distinct prolongation of the floral axis as is habitual in the *Centrospermae*. And further, Fig. 18 shows that in one and the same flower the placenta may be central, with, at the same time, parietal portions as in the normal flower. In the light

of the ontogeny of the latter it seems reasonable to conclude
that both the parietal and the central portions of the placenta
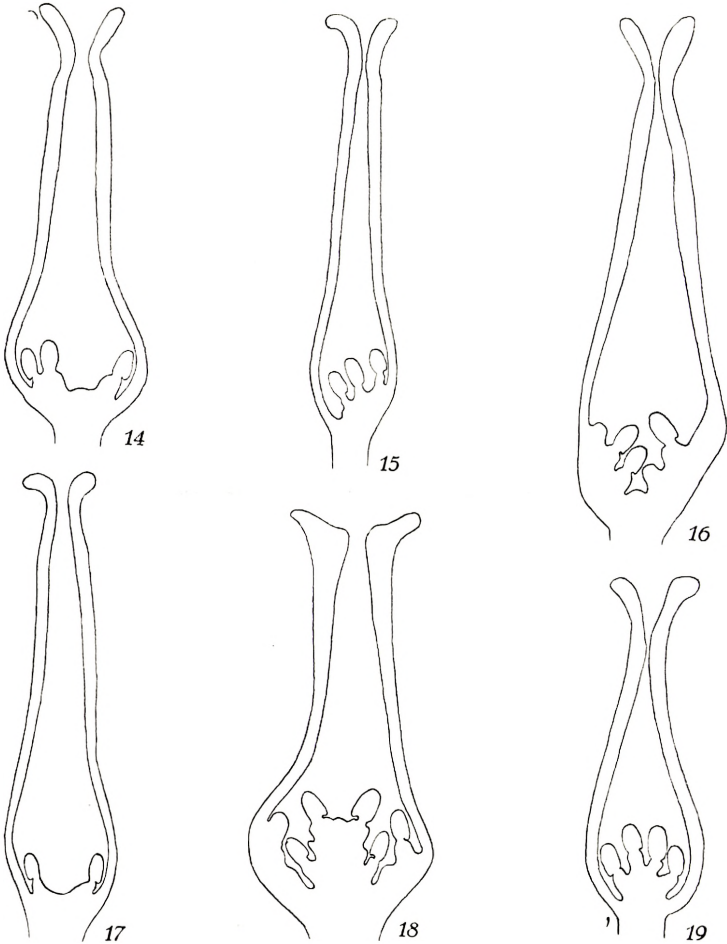
Figs. 14—19. Longitudinal sections of gynaecia showing that the pla-
centae may be both parietal and central. × 20.

are here products of the stem apex. Finally, Fig. 17 shows
a crateriform depression of the apex of a central placenta.

    The peculiar apex of a floral axis may thus assume
diverse forms and varied fertility. But the variations in

form, position, stature and fertility of the placentae do not entail differences of principle since one and the same organ is involved in their production. Conditions similar to these here discussed have already been recorded for *Mesembryanthemum* (HAGERUP, 1936) in which the placenta of some species is central, while in others it is parietal.

It suffices to make an analysis of the steps in organogenesis in order to establish the point, shown in Figs. 46—48, that the top of the gynaecium is composed of two lateral carpels. In the maturing flower such as is shown in Fig. 20, these two leaves are normally free from each other from a level at or above the upper limits of the placentae. The ovary here shown is reminiscent of the gynaecium in families in which the carpels are more or less independent, as, for example, the *Rosales* and the *Leguminosae.* It is in such families that one might expect to find support for the Cycadean homologies; but in point of fact it has been from these very affinities that the testimony on gynaecial organisation has caused the classical theory to be doubted (J. M. THOMPSON).

It will be seen, further, from Figs. 21—28; 36—44; and from Fig. 49 that either one or both of the normal carpels may be replaced by a stamen or by an anther-bearing organ. If then stamens are to be viewed as microsporophylls, the carpels of the normal flower must be considered homologous with such leaves. But in several of the flowers depicted it will be noted further that the stamen connective is prolonged as a stigmatic style, as is shown, for example, in Figs. 22 and 28, and, in lesser degree in Figs. 33 and 34: hence the stigmatic style and the connective may be considered homologous. In addition, two stylar branches may be formed as upward extensions of a single anther (Fig. 32).
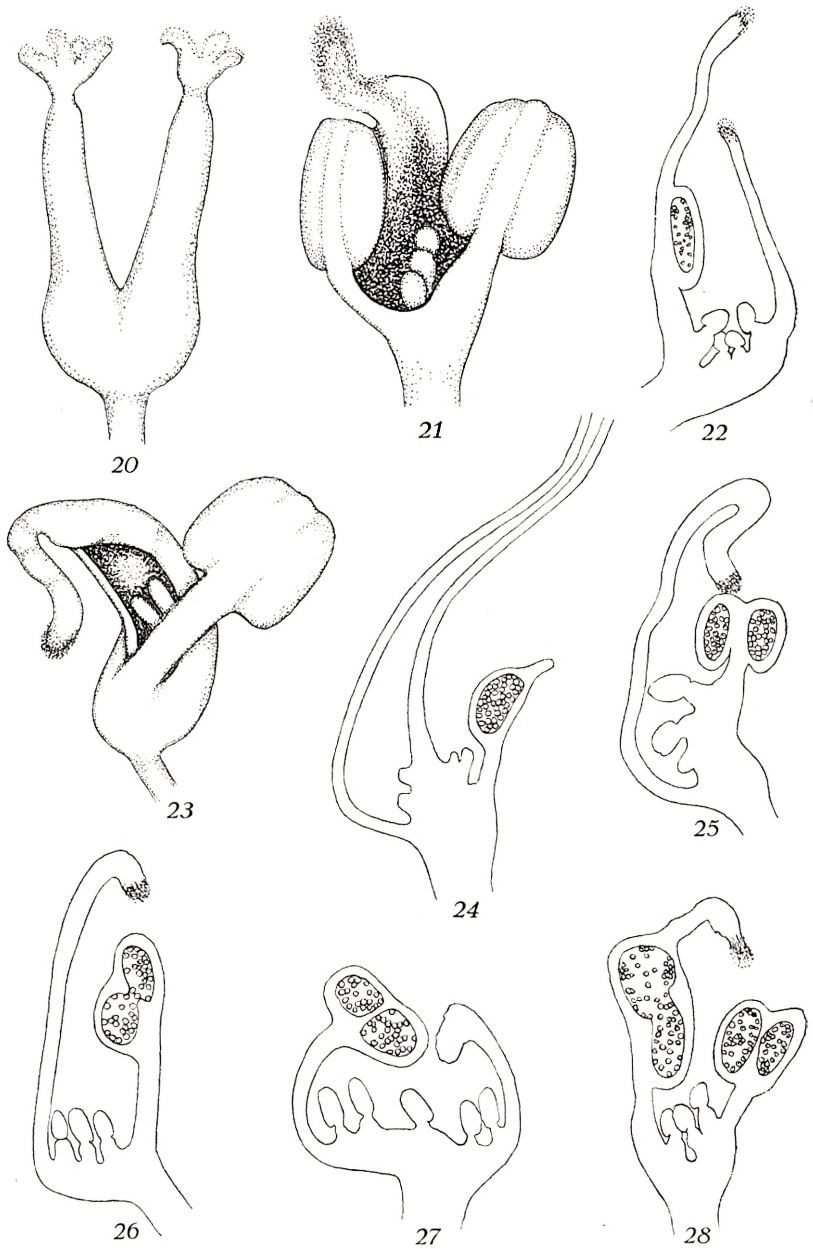
Figs. 20—28. Abnormal female flowers showing the homology of a carpel
with a stamen. × 12. Cp. also the text.

The abnormalities here considered are very common, and their equivalents have frequently been figured.

To the left of Fig. 21 is an organ one half of which is matured as a half anther while the remaining portion is carpellate with an ovule-bearing placenta at its base.

It is, however, of special interest to note that throughout such variations the placenta may persist as if possessed of a definite morphological independence, irrespective of whether or not either or both of the carpels may be replaced by an organ which can no longer function in the normal way. Thus in the flowers shown in Figs. 28 and 49 the organs surmounting the gynaecium must be described as stamens rather than otherwise, despite the fact that in one instance the connective is replaced by a stigmatic style. And throughout all these variations it will be noted particularly that the ovarial base in each of these peculiar "male flowers" is female and is the bearer of several ovules.

The morphological explanation of this interesting condition may reasonably be taken to be that the placenta is the crateriform apex of the floral axis, and that along the rim of this "crater" (J. M. THOMPSON) are placed the "carpels" which are interchangeable with stamens and which may be replaced in part or in whole thereby. Reverting in this connection to Fig. 21 it will be noted that the ovules are inserted at the base of the crater, and it may be added that the condition here shown is one of the commonest in the abnormal flowers. Still further, it is most common to find flowers one of whose "carpels" is male while the other is normal in both form and function. And in such cases — as is shown in Fig. 25 — the ovules may be inserted immediately beneath the stamen upon their
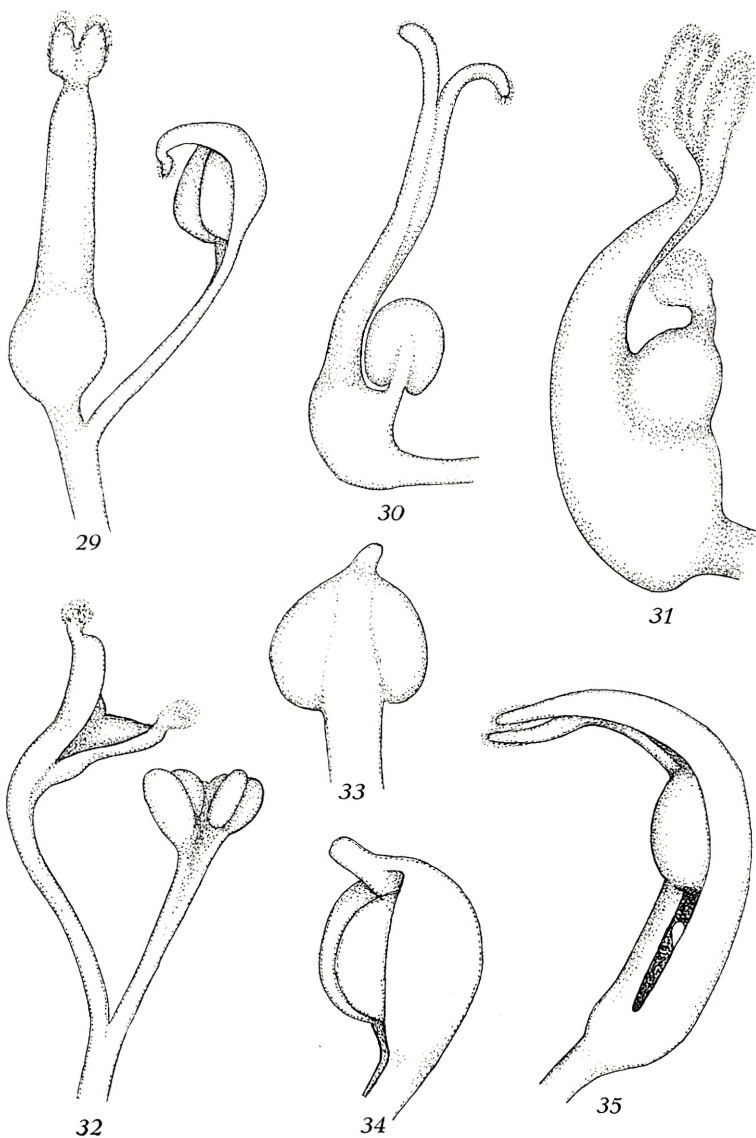
Figs. 29—35. Malformations of female flowers. × 15. Cp. also the text.

evident placenta which may now justifiably be considered
a portion of the axis.

Among the many curious malformations which have

been observed there are some of outstanding interest in
that the ovules may be replaced by organs of distinct and
well defined morphological category. Such malformations
have already been brought to our notice by HENRY, MAR-
QUART and CHAMBERLAIN, the observations of the latter on
American Salices being in marked agreement with those
now recorded in Figs. 36—44 from our Danish *Salix cinerea*.
One may therefore venture to believe that the facts here
presented do not merely represent chance and localised
occurrences in the genus but may help to express valid
rules of variation and of interchange between the floral
organs.

Fig. 41 shows a flower with the usual ovuliferous crater
as its base and with two lateral "carpels" forming the
margin of the crater. By far the larger of these marginal
organs is a short stamen with expanded filament: the smaller
is an ovule. In Fig. 37 is shown a longitudinal section of a
somewhat similar flower in which there is an ovule in place
of a normal carpel. It may be suggested that this solitary
ovule is borne on the rim of the crateriform receptacle
because the carpel to which it should be related has been
greatly reduced, though still persisting as the rim upon
which the ovule is raised. But against this possible view
stands the fact that neither in this instance nor in any
other which has been examined histologically has any
trace been found of a residual sporophyll. It seems more
reasonable to assume that the "solitary ovule" here con-
sidered is equivalent to a "carpel" and has replaced the
latter in a manner comparable to that in which a stamen
may be substituted.

The condition here considered is in direct opposition to
the suggestions of the classical theory according to which
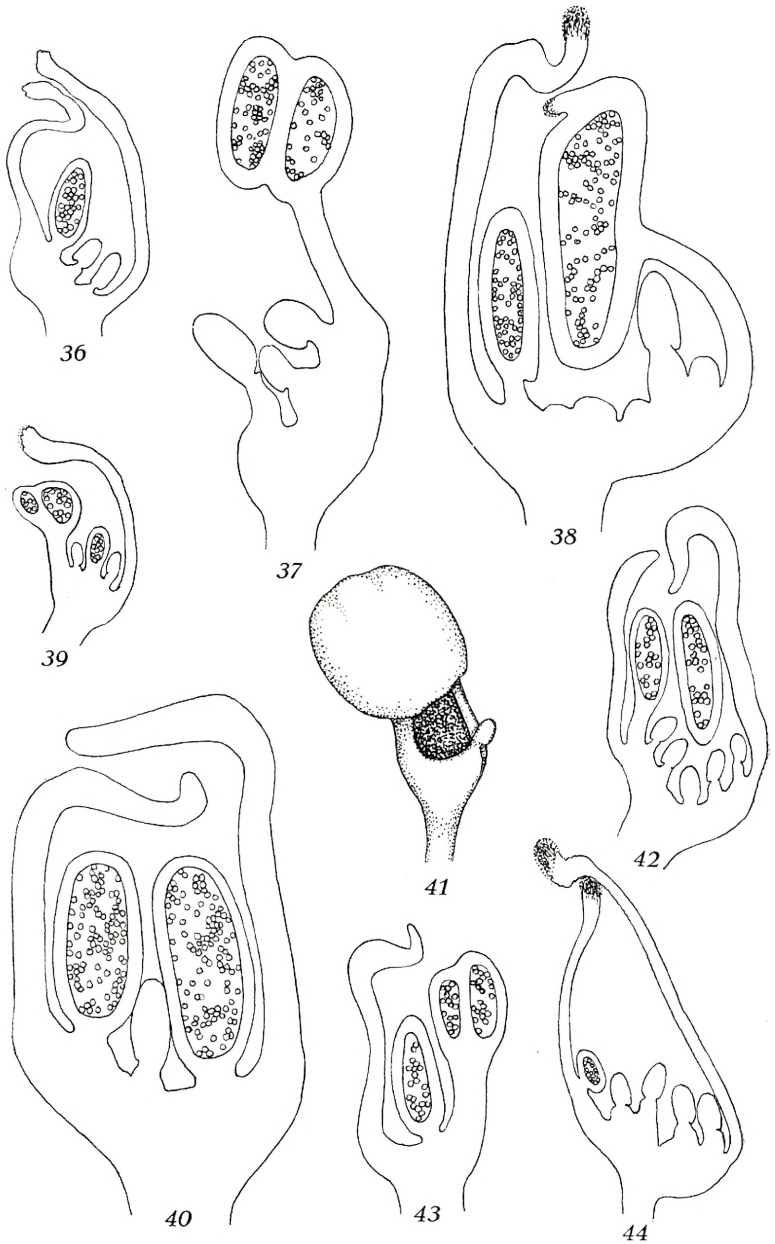
Figs. 36—44. Abnormal gynaecia showing that an ovule may be replaced
by (and may be enquivalent to) a stamen. Figs. 37 and 41 show a
„carpel" replaced by an ovule. × 15. Cp. also the text.
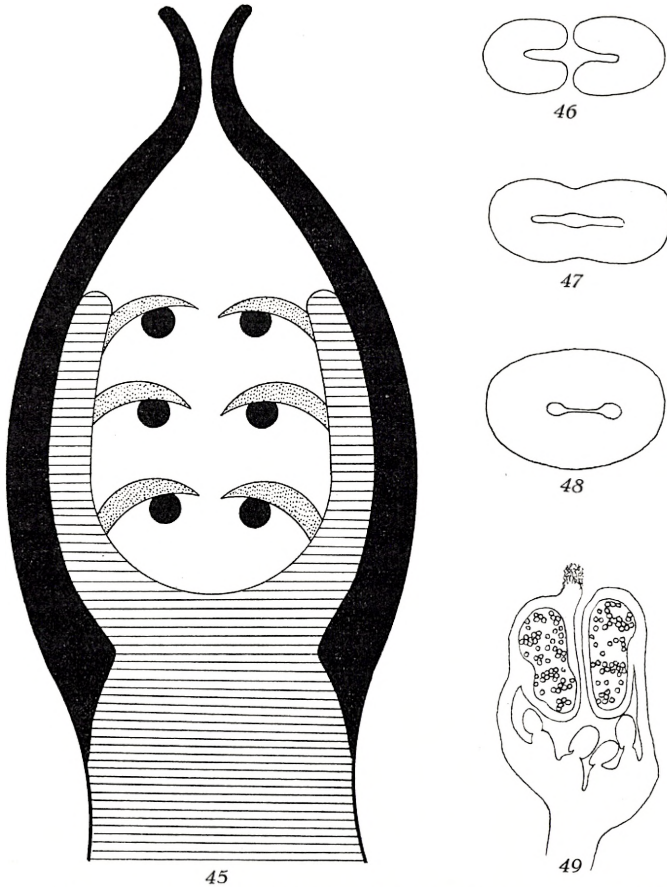
Fig. 45. Diagram of the morphology of the gynaecium (cp. Fig. 1). Carpels black; the placentae are prolongations of the floral axis (horizontally shaded) whose leaves (macrosporophylls) are developed as ovules (dotted and in black). Cp. also the text. — Figs. 46—48. Transverse sections of young gynaecia. The carpellary edges do not curve inward (Fig. 46) and do not swell (Fig. 47). × 160. — Fig. 49. Longitudinal section of a "gynaecium" whose "carpels" are replaced by stamens. × 12.

ovule formation necessitates the presence of a megasporophyll beneath the solitary ovule to the left of Fig. 37. And further — so that the homologies proposed by this theory may be maintained — it would be necessary to hold that the stamen to the right of Fig. 37 is an equivalent micro-

sporophyll without which anther formation should not be possible. But if an homology is to be sought on the evidence as it stands it would seem more natural to propose that the ovule and the stamen are equivalent organs.

From such abnormalities as are shown in Figs. 37 and 41 the conclusion may be drawn that an ovule is a complete and independent organ. And by reason of its axial origin I have preferred to designate it a leaf. But, however, it may be named, the conclusion offered on this matter by the facts of ontogeny of the normal flower supports this interpretation which is in harmony with the abnormalities figured above. For in the flowers shown in Figs. 36—44 one or several ovules have been replaced by larger or smaller stamens with filaments of varied form and stature. And in this interplay — as has been held by J. M. Thompson — the anther is homologous with the nucellus and the filament with the funicle.

Further to this matter, I have examined in detail the flowering of a species of *Populus*, namely, *P. canescens*, and have found that the ontogeny of its gynaecium resembles so closely that of *Salix cinerea* that its description here would involve merely unnecessary repetition. It may then be held that *Salix cinerea* offers a general and representative picture of the events of gynaecial organisation in the *Salicaceae* as a whole.

IV. Summary.

1. The observations here detailed have been made and discussed so that, for the purposes of phylogeny, the classical carpellary theory may be put to the test for a genus possessing a gynaecium with parietal placentation. To this end, the ovary of *Salix cinerea* has been analysed in both its

normal ontogeny and in its teratological states at and towards maturity.

2. The ontogeny has shown (1) that the margins of the carpels do not curve inwards (Fig. 46); (2) that they do not swell (Fig. 47); and (3) that they do not form the placentae. This is in accordance with the facts disclosed by J. M. Thompson for a long series of Scitaminean plants.

3. The carpels form merely an involucre of coalescing and barren leaves. They do not bear the ovules but merely enclose them, thus producing the state of angiospermy.

4. The facts of ontogeny shown in Figs. 8—13 harmonise with the view that the placentae are prolongations of the floral axis, displaced, as growth proceeds, so as to be extended along the carpel bases.

5. The ovules are held to be complete and independent organs, which, in the absence of a more appropriate term by which they may be designated, I have called leaves. And this for the following reasons:—

a. They are inserted on the stem which comprises the placentae.

b. They are dorsiventral and they are lateral to the placentae.

c. When malformation occurs they may be replaced by independent organs of other categories, such as stamens (Figs. 36—44); or an ovule may completely replace a carpel (Figs. 37, 41).

6. The funicle is held to correspond to the stamen filament, and the anther to be homologous with the nucellus and its integuments.

7. Thus the classical Cycadean homologies are con-

sidered invalid in the case of *Salix* as has already been shown for many other genera, for example, by J. M. THOMPSON and O. HAGERUP.

8. The main points of interpretation of the floral structure of *Salix* offered in the text are expressed in Figs. 1 and 45.

9. According to this interpretation an ovule is a monosporangiate macrosporophyll. On this view it may even be assumed that a phylogenetic connection is possible between some Angiosperms and the *Lycopodiales*, the *Gnetales* and *Coniferae* lying on the lines of descent. The reader is referred to earlier phylogenetic work for the evidence on which this thesis has been made to stand (cf. HAGERUP).

V. Bibliography.

AUBERT, P. L. (1873—1876): Organogenie de la fleur dans le genre *Salix*. Adan. 11, p. 183—186.

CHAMBERLAIN, C. J. (1897): Contribution to the Life History of *Salix*. Bot. Gazette. 23 p. 147.

FISHER, M. J. (1928): The Morphology and Anatomy of the Flowers of the *Salicaceae*. Am. Journ. Bot. Vol. 15, p. 307 and 372.

GREGOIRE, V. (1931): La valeur morphologique des carpelles dans les angiospermes. Bull. Acad. Roy. Belgique, Cl. Sci. Sér. 5, Nr. 17.

GREGOIRE, V. (1935): Sporophylles et organes floraux, tige et axe floral. Rec. trav. bot. néerlandais. XXXII, 2, p. 453.

HAGERUP, O. (1933): Zur Organogenie und Phylogenie den Koniferen-Zapfen. Kgl. Danske Vidensk. Selsk. Biol. Medd. X, 7.

HAGERUP, O. (1934): Zur Abstammung einiger Angiospermen durch *Gnetales* und *Coniferae*. Kgl. Danske Vidensk. Selsk. Biolog. Medd. XI, 4.

HAGERUP, O. (1936): Zur Abstammung einiger Angiospermen durch *Gnetales* und *Coniferae*. II. *Centrospermae*. Kgl. Danske Vidensk. Selsk. Biolog. Medd. XIII, 6.

HENRY, A. und MARQUART, CL. (1841): Über abnorme Bildungen des Fruchtknotens bei *Salix cinerea* L. Jahresber. d. nat. Ver. d. Prov. Rheinl. und Westph. zu Bonn. II.

NEWMAN, J. V. (1936): Studies in Australian Acacias. VI. Proc. Linn. Soc. of New South Wales. LXI, 1—2, p. 56.

PENZIG, O. (1922): Pflanzen-Teratologie. Berlin.

RAINIO, A. J. (1927): Über die Intersexualität d. Gattg. *Salix*. Ann. Soc. Zool.-Bot. Fenn., Bd. 5, p. 166.

THOMPSON, J. M. (1932): The Theory of the Leguminous Strobilus. Proc. Linn. Soc., 144.

THOMPSON, J. M. (1933): The Theory of Scitaminean Flowering. Pub. Hartley Bot. Lab., No. 11.

Thompson, J. M. (1934): The State of Flowering known as Angiospermy. Pub. Hartley Bot. Lab. No. 12.

Thompson, J. M. (1936): On the Gynoecial Apex of *Acacia* etc. Publ. Hartley Bot. Lab., Nr. 13.

Thompson, J. M. (1937): On the Place of Ontogeny in Floral Enquiry. Publ. Hartley Bot. Lab. No. 17.

Velenovský, J. (1904): Vergleichende Studien über die *Salix*-Blüte. Beih. Bot. Zentralbl. XVII, S. 123.

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