THE MORPHOLOGY AND BIOLOGY
OF THE *CORYLUS*-FRUIT

BY

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CONTENTS

Preface.

My manuscript has been read through by Professors K. Jessen and O. Paulsen of Copenhagen, and I owe a debt of gratitude to these gentlemen for 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.

The translation from the Danish has been done by Miss Annie I. Fausbøll M. A.
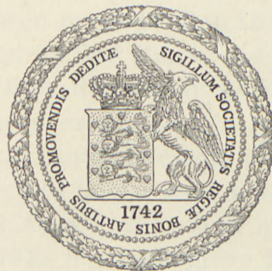
1. Introduction. The Problems.

An attempt to make clear the structure of the fruit of *Corylus* by means of the available literature will soon show that—on close consideration—surprisingly little is known about this common object, though in most lessons in botany it is used to exemplify the structure of a nut, or serves to illustrate the definition of this conception itself. It was in order to remove this uncertainty that I first began to study the organogeny of the fruit.

One of the most admirable investigations of the flower of *Corylus* has already been made by Baillon. In 1875 he followed the organogenesis from its first stages, but owing to the primitive technical aids of his time there were several of the finer details which he was unable to examine.

Later morphological contributions to the understanding of the structure of the catkin and flower were made by Eichler (1878), Trotter (1929), and Abbe (1935), and a comprehensive list of the literature before 1913 has been given by Büsgen. It appears from this, however, that the few available observations are often contradictory, while several are incorrect. It was for these reasons that I started the investigations here presented. They are based on fresh material, gathered near Lyngby, north of Copenhagen.

The specimens were collected at intervals of a few days and at all seasons of the year. For the investigation of histological problems the objects were fixed and afterwards cut into series of thin sections with a microtome.

For the present study *Corylus avellana* was almost the only species used, and only on rare occasions *C. maxima* for comparison, these two species being almost similar in the features dealt with below. The fruit of *C. maxima*, however, differs in its involucre which remains, enveloping the nut, because the two leaves of which it is formed are concrescent and, in addition, have only very small swelling bodies at their base.

2. Organogeny.

BAILLON found the first delicate primordium of the female flower already on June 15th the year before the flowering. About a month later the styles begin to form and already in August the female flower terminates its development for the year. Growth is not resumed until the next spring (March) when the well-known red styles are found exserted from the catkin and soon able to receive pollen.

On a closer inspection of the female flower in the pollination stage it is difficult to see anything resembling the full-grown fruit that develops later on. Thus during the flowering (March) no ovary has as yet been evolved; the gynaecium merely consists of the two long styles which are so close together that there is only a quite narrow space between them. The ovules, too, do not appear till a couple of months later (May). The subjoined figures show a longitudinal section (fig. 1) and a transverse section (fig. 2) of female flowers gathered on the 5th May. The two styles (G) enclose a narrow fissure, at the bottom of which there is a quite young ovule (F) on its placenta. Outside the styles there is a circle of small scales (B) which constitute the perianth; how many leaves these represent altogether is unknown; but this may perhaps be decided by examining the first developmental stages of the perianth which are found in July (the year before the flowering).

The above-described remarkable recently pollinated flower which, as already stated, lacks an ovary with ovules, remains in

its undeveloped state for a couple of months. Not until about the close of April and the beginning of May is growth resumed; and this then happens in a characteristic way. A narrow intercalary growing zone (*V—V* in fig. 1) arises which extends right across the apex of the floral axis near the place where the styles are attached.
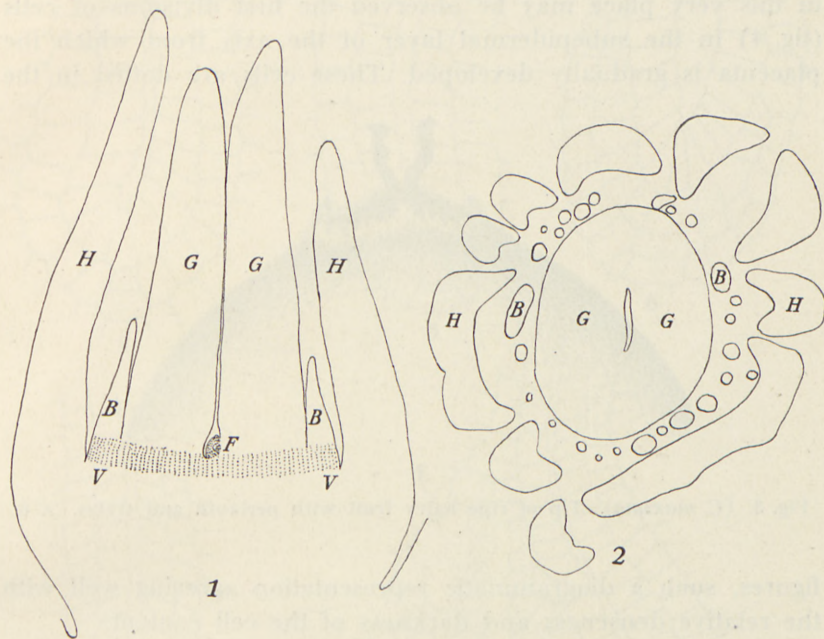

Figs. 1 and 2. Longitudinal (Fig. 1) and transverse (Fig. 2) sections of a flower. *H*, involucre; *B*, perianth; *G*, style; *F*, young placenta and ovule; *V—V*, intercalary growing zone (dotted). 5. May, × 50.

By the action of this intercalary growing zone the perianth and the styles are then gradually raised to the apex of the emerging ovary, whereas the bracteoles (*H*) remain below the fruit because the zone of growth is situated above the point where they are attached but below the perianth.

Special interest attaches to the development of the placenta, which is also one of the results of the activity of the aforementioned growing zone. And since the literature has no description of this remarkable process, it is illustrated by the appended figures (4—8), which show part of the region around the bottom

of the cavity between the styles; it is seen as a vertical fissure—
clothed with epidermis—through the central part of all the
sections shown.

To understand the morphology of the placenta it is important
to keep in mind that the tissue under the bottom of the stylar
fissure belongs to the floral axis which carries the styles; and
in this very place may be observed the first divisions of cells
(fig. 4) in the subepidermal layer of the axis from which the
placenta is gradually developed. These cells are dotted in the
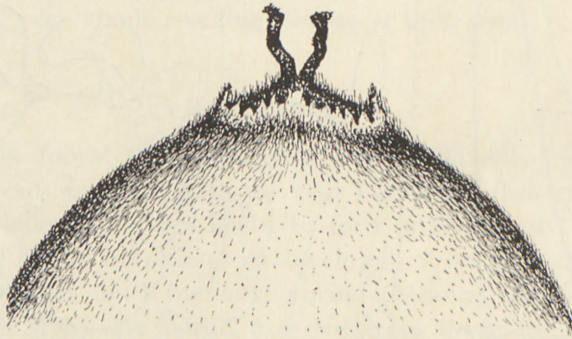
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Fig. 3. (*C. maxima*). Tip of ripe hairy fruit with perianth and styles. × 6.

figures, such a diagrammatic representation agreeing well with
the relative denseness and darkness of the cell content.

Fig. 4 shows the very first inception of the placenta in the
tip of the axis below the cavity between the styles. Here a sub-
epidermal cell has divided by means of a horizontal wall, and
the two daughter cells continue their development, two sub-
epidermal layers of cells arising from them (fig. 5). By similar
continual horizontal division more and more layers gradually
arise (figs. 6 and 7) from the original single subepidermal layer.
In addition numerous vertical walls appear and by the con-
tinued activity of the intercalary zone of growth the young placental
tissue soon extends upward too, along the inner side of the cavity
of the young ovary (figs. 6—7).

Thus the originally basal young placenta, which belonged to
the axis, gradually becomes parietal.

During the continued growth the cells below the subepidermal
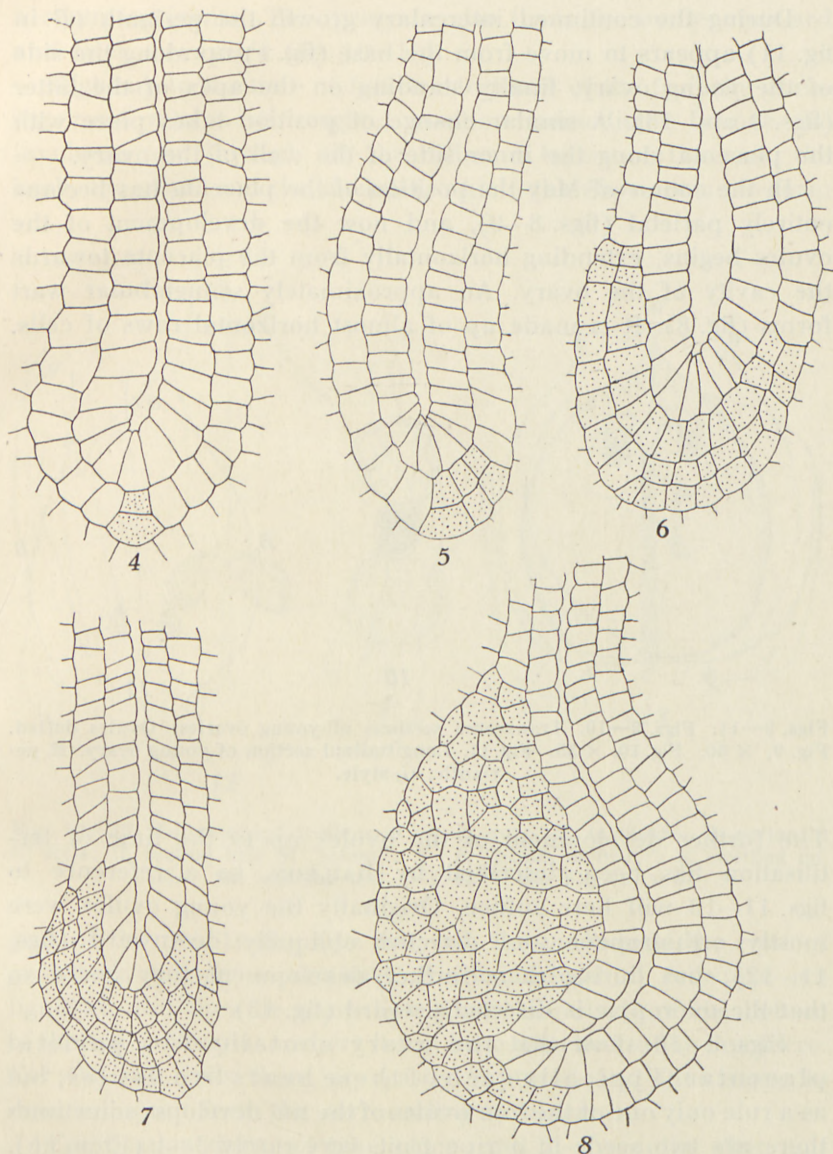
Figs. 4—8. The placenta (dotted) beginning to develop at the tip of the stem below the bottom of the ovarial cavity (in the middle of the figures). × 500. 5. May. See also text.

layer also divide—the greater part vertically—so that the originally fairly regular arrangement of the cells is obliterated.

During the continued intercalary growth the perianth (*B* in fig. 11) appears to move from the base (fig. 1) up along the side of the young ovary, finally standing on the apex of the latter (figs. 3 and 13). A similar change of position takes place with the placenta along the inner side of the wall of the ovary.

In the course of May the position of the placenta has become entirely parietal (figs. 8—9), and now the development of the ovules begins, extending horizontally from the placenta towards the cavity of the ovary. An approximately semiglobular wart forms (fig. 8). It is made up of almost horizontal rows of cells.
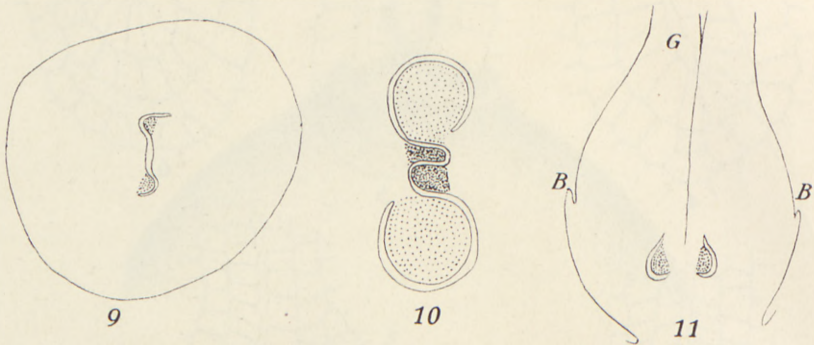
Figs. 9—11. Figs. 9—10. Transverse sections of young ovaries. Ovules dotted. Fig. 9, × 60. Fig. 10, × 35. Fig. 11. Longitudinal section of young ovary. *B*, perianth; *G*, style.

The further development of the ovules up to the time of fertilisation has been described by BAILLON, so a reference to figs. 11—13 will here suffice. Originally the young ovules were mostly orthotropous and directed obliquely downward (figs. 11—12); but during their further development they curve so that the micropyle is directed upward (fig. 13).

Figs. 9—10 show that the ovary contains two parietal placentae. Typically each of these bears two ovules, but as a rule only one of the four ovules of the nut develops; sometimes there are two seeds in a ripe fruit, very rarely 3—4 (EICHLER).

Owing to incorrect statements in the literature it should here be emphasised that the ovary has only one locule: but later the placentae are pressed so close together that only a very narrow and sinuous cavity remains between them (fig. 10); and this may make the ovary look as if it contained a septum and

a central placenta. This pressure also turns the ovules outward
and later downward (fig. 10—13).

Right up to the time of full development of the fruit the grow-
ing zone retains its original position immediately above the
involucre and through all the different layers of the axis, the
bark, the wood and the medulla, which, therefore, come to form
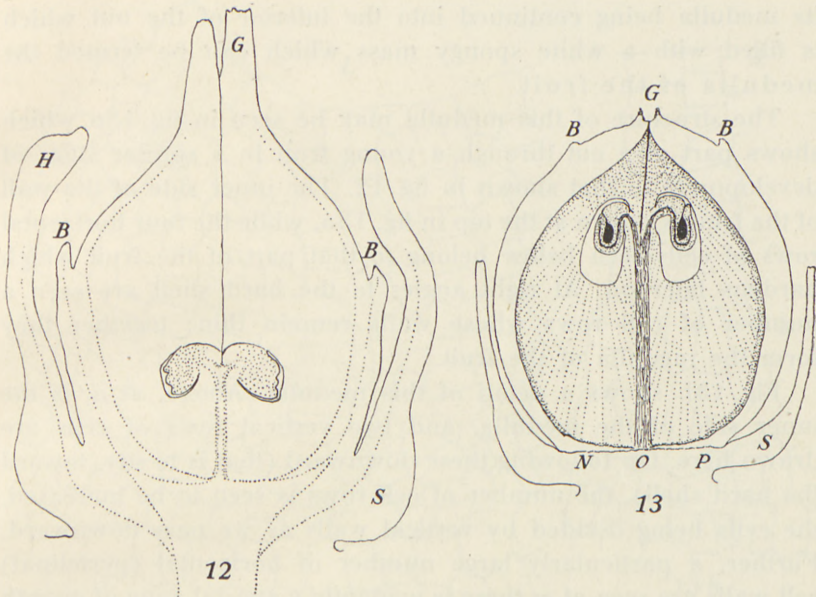
Figs. 12—13. Longitudinal sections of young nuts. *H*, involucre; *B*, perianth;
G, style; *O*, central hole of "hilum"; *N—P*, "hilum of fruit"; *S*, swelling bo-
dies. See also the text. Fig. 12, × 20; Fig. 13, × 6.

part of the nut. In the ripe nut, too, the position of the zone of
growth is readily ascertained, for its individual cells are not
lignified, and they lie immediately on the outside of the bottom
of the nut in the place where it has been attached to the involucre.
For the soft cells there are easily ruptured and thus serve to
detach the nut from the surrounding involucre.

Fertilisation does not take place until 2—3 months after pol-
lination (in July); and only then does the fruit begin to increase
appreciably in size. But in spite of this another month or two
will pass before the seeds commence to grow in earnest. This
does not happen until the nut is fully developed and begins to
lignify at the apex (at the close of July).

During the activity of the growing zone the ovules also seem to change their place in the ovary. Originally their position was basal (fig. 11) but they are soon lifted upward (fig. 12), and finally stand near the apex of the fully developed fruit (fig. 13).

The hard outer layer of the fruit forms a direct continuation of the bark and wood of the axis beneath the growing zone, its medulla being continued into the interior of the nut which is filled with a white spongy mass which can be termed the medulla of the fruit.

The structure of this medulla may be seen in fig. 13a which shows part of a cut through a young fruit in a similar stage of development to that shown in fig. 12. The inner side of the wall of the fruit is shown at the top in fig. 13a, while the four horizontal rows of cells seen below belong to that part of the fruit which hardens later on. At right angles to the hard shell are seen a number of cell rows whose walls remain thin; together they form the medulla of the fruit.

Fig. 13b shows a detail of this medulla. Above, at *d*, is the inner side of the medulla, and two vertical rows of cells are drawn here. On following these downward (that is to say, toward the hard shell), the number of cell rows is seen to be increased, the cells being divided by vertical walls as we pass downward. Further, a particularly large number of horizontal (periclinal) cell walls are seen at *c*; there is evidently a special zone of growth (a cambium) here, where the medullary layer increases in thickness. On the stretch *b—a* below this part, the medullary cells are more irregularly placed, until at *a*, and below, they are arranged in rows at right angles to the vertical columns of the medulla. These horizontal rows of cells (fig. 13a) lignify later and become part of the hard outer portion of the nut shell.

Finally fig. 13 shows in detail how the cell-rows of the medulla, which are indicated by dotted lines, exhibit a fan-like or almost radial arrangement with the cavity of the ovary in the centre.

On the stretch *N—P* in fig. 13 lies one of the intercalary growing zones. Here the nut grows fast in thickness (breadth), the cell-rows of the medulla being at the same time pressed sideways. But in addition the longitudinal growth of the fruit likewise takes place near its base, some few layers of cells above the zone *N—P* (at *c* in fig. 13b).

In accordance with its original position at the tip of the floral axis the placenta receives a vascular bundle from this stalk which, in spite of subsequent changes of position retains its original central position, as seen in the sections shown in figs. 12—13 and 25.
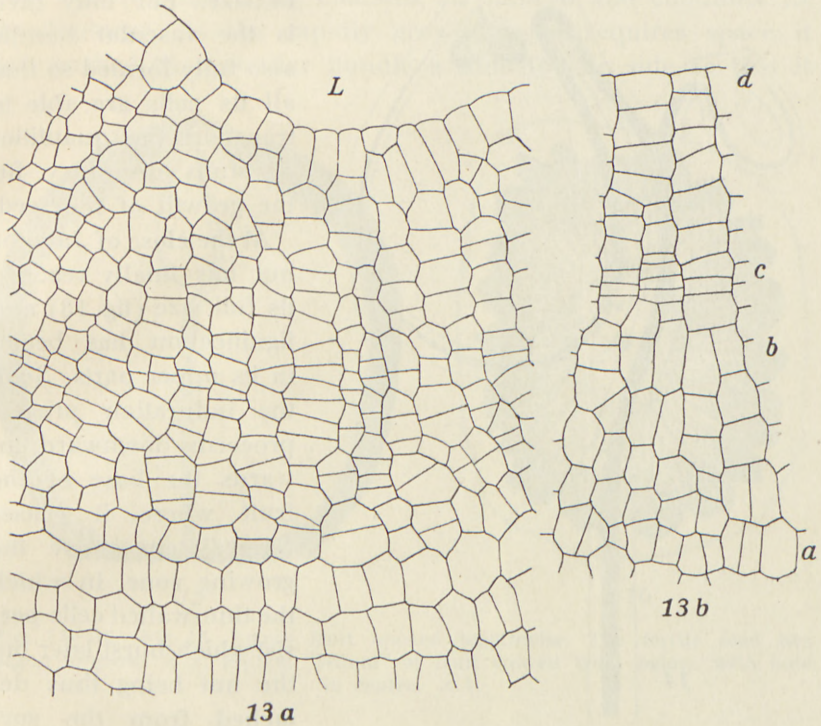
Figs. 13 a and 13 b. Part of transverse sections through "hilum" of young ovary. L, cavity of ovary. Innermost (above in figures) vertical columns of medullary cells; outermost (below in figures) horizontal rows of young sclerenchyma cells. × 500. See also text.

The young nut has thus an axillary medullary vascular bundle. This phenomenon is rare; it is found now and then in the axis of other plants (e. g. in the *Burseraceae*), but it does not occur in the vegetative branches of *Corylus*.

Fig. 13 shows that the axillary vascular bundle of the nut runs through the centre (O) of the intercalary growing zone (N—P). From this it again follows that the vascular bundle must take a share in the longitudinal growth of the nut and that right

through the base of the bundle there is a zone of embryonal
cells which can only in very slight degree function as the cells
in a fully developed vascular bundle. This is perhaps one of
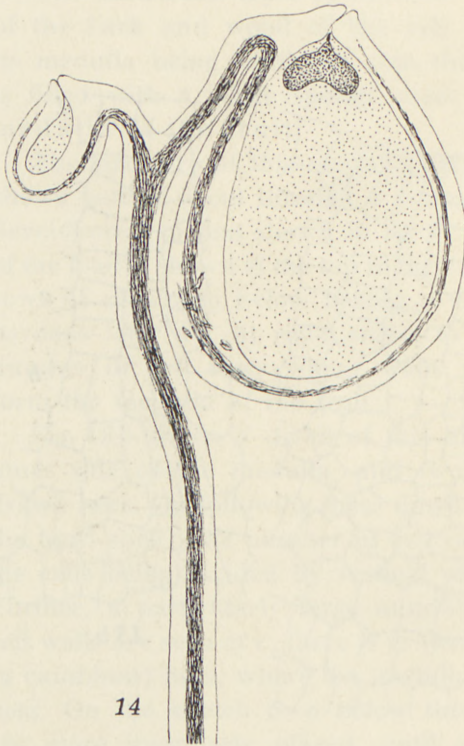the reasons why the seed does not begin to grow till the whole
fruit is fully developed
in size. For only then
is the vascular bundle
also fully formed so that
all its cells are able to
transport the quantities
of stuffs necessary for
the growth of the seed.

At the close of July the
nut has finally reached
its full size (fig. 13) and
lignification has begun
in its upper parts. Soon
the induration process
proceeds downward to-
wards the base of the
fruit where it ceases
immediately above the
growing zone, in which
the thin-walled cells per-
sist which burst later on,
the nut being thus de-
tached from the sur-
rounding involucre.

Fig. 14. The central vascular bundle carries
one abortive (left) and one fertile ovule at its
tip. × 18.

Thus the apex of the
nut with the perianth
and styles is a little more than a year older than its base.

When the fruit has attained its full size at the close of July
a new phase in its development begins. Now at last the seed
also grows with astonishing rapidity, and in the course of about
one month only it can fill up nearly the whole cavity in its hard
shell. But, as will appear from the subjoined figures, this growth
of the seed takes place in a very peculiar way.

Of the 2—4 young ovules there is generally only one which
continues its growth; the rest are suppressed, and one of these

is nearly always found as a desiccated remnant at the upper end of the fully developed seed (fig. 15).

Fig. 14 shows that the central vascular bundle in a fruit (collected August 1st) gives off two branches at the top which are connected by a short funicle each with its ovule, of which only one (on the right) contains an embryo and continues its development. As the rapidly growing seed requires space it has pushed the vascular bundle a little to one side so that it
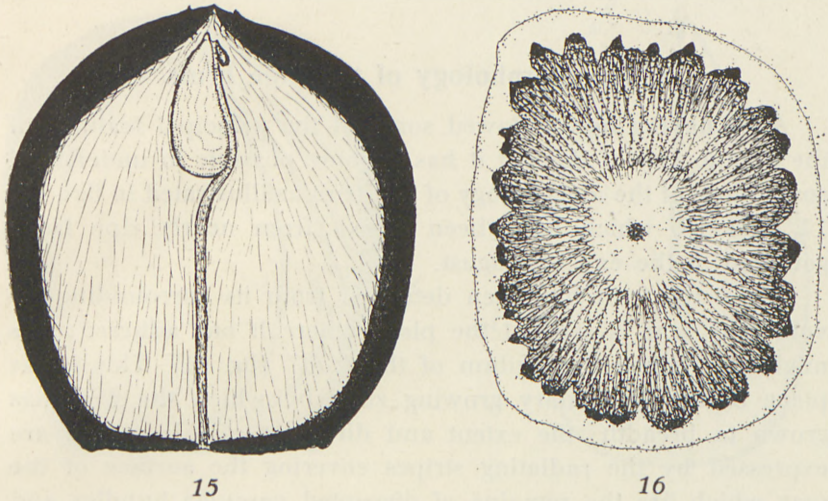
15   *16*

Figs. 15—16. Fig. 15. Young fruit opened lengthwise. The fertile seed has begun to grow. × 5. Fig. 16. "Hilum" of fruit viewed from below, with hole in centre. × 4.

forms a curve. During the continued growth of the seed the vascular bundle is pushed more and more sideways (fig. 15). In the ripe nut it has been forced away from its original axillary position, right over towards the inner side of the hard shell.

An inspection of figs. 12 and 13 will show that the cavity of the young fruit is remarkably small and at any rate not big enough by far to hold the rapidly growing seed, subsequently so voluminous, which fills up the entire interior of the hard shell. But the space is enlarged in a peculiar way. During its continued growth the one seed which develops presses together the medullary cells below, so that they are killed. Further and

further the seed pushes its way down in the axis, and finally there is nothing left of the medulla but the dried up cell walls which, like a whole layer of brown fibres, lie squeezed in between the seed and the hard shell. So, morphologically, this medullary layer belongs to the inner part of the wall of the ovary (not to the testa).

If the nut is split some of the dead medulla-fibres will often remain on the outside of the seed, whereas the rest will adhere to the inside of the hard shell.

3. The Morphology of the Ripe Fruit.

After having now followed some of the principal features of the organogeny of the nut it has become possible to understand some more of the morphology of this fruit as illustrated in figs. 16, 17, and 18, which have been drawn from nearly ripe fruits gathered at the end of August.

When the fruit has been detached from its surrounding involucre a scar is seen at the place where it has adhered; this might be termed the "hilum of the fruit" (fig. 16). This is the place of the intercalary growing zone by which the fruit has grown in breadth: the extent and direction of this growth are expressed by the radiating stripes covering the surface of the scar which are the remains of disrupted vascular bundles and parenchyma.

In the centre of the "hilum" (fig. 16) is seen a more or less distinct, small, dark mark; it is most easily distinguished if the surface of the hilum is smoothed with a file or a sharp knife. And if you insert a fine needle into the above-mentioned mark it turns out that in this place there is a very fine hole right through the hard nut-shell. If the nut is split into its two halves, the crack will as a rule run through this very hole, and it is then easily observed (fig. 17) that the vascular bundle of the seed passes through the hard shell and enters the soft interior of the fruit through this little hole.

From the centre of the "hilum" (O in fig. 17) the long vascular bundle passes up along the seed, generally following the raphe. The vascular bundle is not, as sometimes stated, the remnant of a septum, for the fruit of *Corylus* has no septum but is uni-

locular (figs. 9—10). The seed is attached at the upper end of the vascular bundle, and there is a fairly distinct real hilum (*N* in fig. 18) and next to it a sterile ovule. Just above the hilum there is an indistinct micropyle with the embryonal root hidden under it (*R* in fig. 18).

A distinct raphe issues from the hilum, running only about halfway down one side of the seed to the chalaza (*C* in fig. 18).
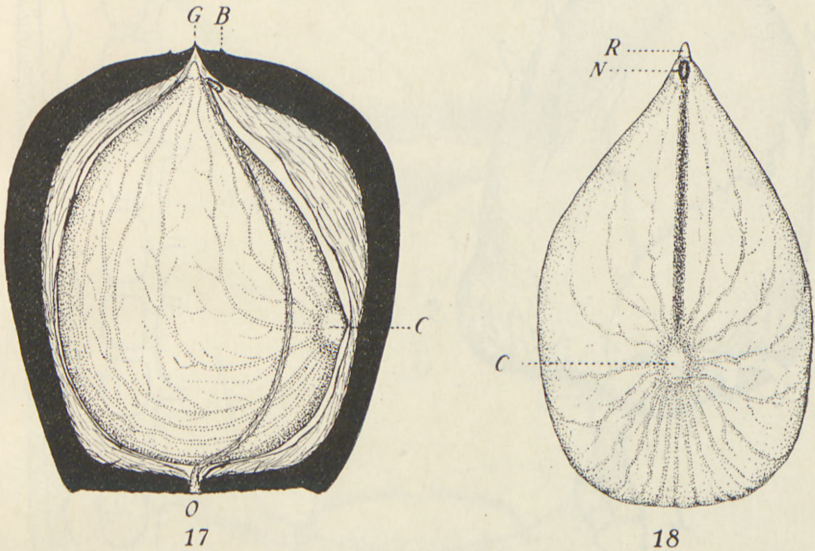

Figs. 17—18. Fig. 17. Nearly ripe fruit in longitudinal section. Shell black. *G*, style; *B*, perianth; *C*, chalaza; the vascular bundle passes through the hole, *O*, in the centre of the "hilum", and carries two hanging seeds at its tip. × 4. Fig. 18. Scarcely ripe seed viewed from the back. *R*, the place of the embryonal root; *C*, chalaza; *N*, hilum. × 4.

Often the raphe lies in a groove which has arisen owing to pressure from the squeezed in vascular bundle. The chalaza gives off numerous vigorous branched vascular bundles which are distributed over the whole of the testa like the nerves in a leaf (figs. 17, 18).

Hence the seed is plainly campylotropous but it is not so curved as for instance the seed of *Phaseolus*. In addition the embryo is straight as in anatropous ovules. Thus the seed in *Corylus* is intermediate between a campylotropous and an anatropous seed.

4. Dispersion of the Fruits.

When finally, at the close of August, the embryo is fully developed the fruit will normally remain on the tree for yet
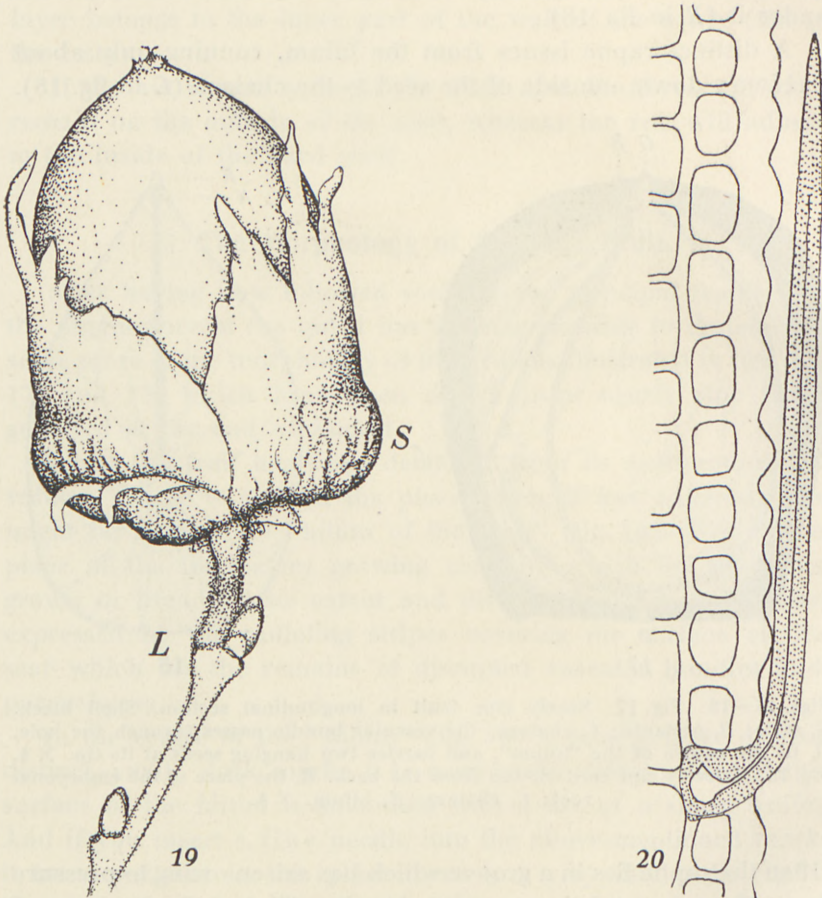
Figs. 19—20. Fig. 19. Ripe fruit with involucre. S, water tissue; L, joint where the stem breaks. × 2. Fig. 20. Hair from surface of fruit. × 600.

another month and no great external changes can be seen in it. But in the course of September the nut will gradually detach itself and it can then without difficulty be picked out of its involucre.

In October most of the nuts come loose without any external action. Several biological peculiarities are associated with this

liberation process, among which especially the structure and function of the involucre will be discussed below.

As long as the fruit is not yet ripe the involucre is pressed
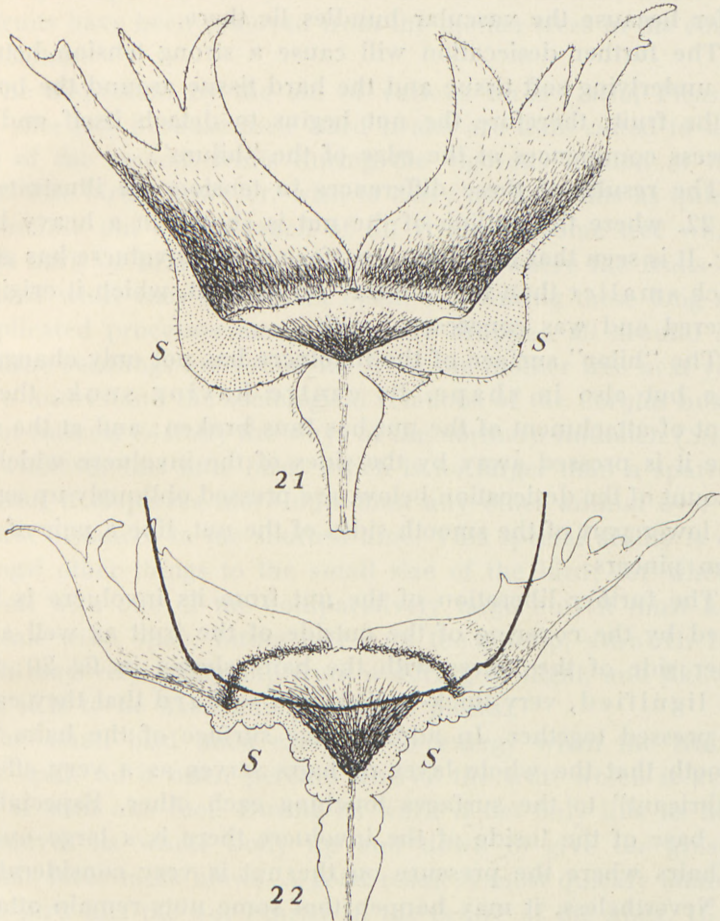
Figs. 21—22. Involucre. S, swelling bodies. The outline of the fruit drawn in a heavy black line. × 3. See also text.

close up against it. But in October when the nut detaches itself the tip of the involucre begins to bend outward. (fig. 21). This movement is due to the fact that nearly all the tissue surrounding the place at which the nut adheres (S, i figs. 19—21) is built up of large thin-walled cells filled with liquid. At the time of the leaf-fall the water supply stops and the water tissue (S) slowly

begins to dry, and at the same time it will also shrink consider-
ably. This reduction of volume is greatest on the outside of the
involucre where the desiccation is greatest, while the inside is
stiffer because the vascular bundles lie there.

The further desiccation will cause a strong tension between
the underlying soft tissue and the hard tissue around the bottom
of the fruit; therefore the nut begins to detach itself and this
process commences at the edge of the "hilum".

The results of these differences in tension are illustrated in
fig. 22, where the outline of the nut is shown in a heavy black
line. It is seen that the "hilar" surface of the involucre has grown
much smaller than the "hilum" of the fruit, which it originally
covered and was concrescent with.

The "hilar" surface of the involucre has not only changed in
size but also in shape. Its centre having sunk, the last
point of attachment of the nut has thus broken; and at the same
time it is pressed away by the sides of the involucre which, on
account of the desiccation below, are pressed obliquely up against
the lower part of the smooth sides of the nut, like a pair of wide
open pincers.

The further liberation of the nut from its involucre is facil-
itated by the covering of the outside of the fruit as well as the
inner side of the leaves with the hairs shown in fig. 20; these
are lignified, very thick-walled, and so hard that they cannot
be pressed together. In addition the surface of the hairs is so
smooth that the whole layer of hairs serves as a very effective
"lubricant" to the surfaces touching each other. Especially at
the base of the inside of the involucre there is a large number
of hairs where the pressure on the nut is very considerable.

Nevertheless, it may happen that some nuts remain attached
to the involucre; this may occur for instance in a very wet
autumn, when desiccation is slight. Fruits whose seeds have been
killed, for instance by the attacks of insects, also often remain
on the bushes because no detachment layer has been formed.

But when the autumn storms lash the trees nearly all the
fruits come off because their stalks break, a special detachment
layer having formed (L in fig. 19) right through the thin branch.

Thus the autumn storms fling the heavy fruit down among
the surrounding branches and thence to the ground where a

nut not free from its involucre is now rarely seen. Then the hunt for the nuts has long been in full swing, and so eagerly are they sought by many mammals and birds that nearly all the fruits have been removed from the mother trees in the course of October.

The dispersion by the aid of various birds (*Sitta, Picus*) is very effective, because their hard beaks are little suited to keep hold of the smooth fruits during the vigorous motion of their flight. The birds, however, wish to carry off the fruits as quickly as possible out of the reach of all rivals, to some tree with a rough bark or branches at suitable angles, where the fruits can be fixed while they split them open. But during these long and complicated processes many fruits are dropped all around and often the seedlings are found far from the mother tree next year.

To understand the sociological relations of the *Corylus* bushes it is of interest to study the ways of the northern nuthatch (*Sitta*). For wherever this little bird, which is no larger than a sparrow, is found it disperses more nuts than any other animal over the greatest distances in the shortest time. This special ability is due amongst other things to the small size of the bird; for when it flies off with one of the comparatively large nuts it must keep its beak wide open, biting hard on the plump, smooth fruit which may very easily slip from it during its flight, and likewise when it is to be fixed and pecked to pieces.

The small bird must exert all its energy when the fruit is to be split. So it often perches above the fruit which it keeps hold of with one foot. During its work it not only lifts its head but moves its whole body up and down to give the greatest possible force to its blows. A good result is most quickly attained if the bird hits the nut exactly in the centre of the apex. If, on the other hand, it hits the nut a little beside the apex its beak will glance off the oblique smooth sides of the nut and the fruit will easily slip and fall to the ground. Even if the bird tries to find the fruits that have been dropped many will be lost; and so the seeds for a hazel copse will be sown.

It is necessary, therefore, for the bird to find a particularly favourable tree in which to lodge the fruit. And if such a tree is not present near by it will fly a good distance with the fruit in its open beak. It has found itself a workshop beforehand,

the good quality of which is somewhat of a life condition for it. Young trees are as a rule useless because their bark is too smooth. For the same reason it also avoids *Fagus* and our other smooth-barked trees. Sometimes it will use *Ulmus* and *Fraxinus*, especially when these trees grow in avenues or gardens where they are allowed to grow old and form a thick bark with crevices.

Among our native trees there is none, however, which is so well suited for the purpose of the nuthatch as *Quercus*. Notably where there are old and solitary specimens one is generally sure to find traces of the activity of the nuthatch. For here there are as a rule both good places for nests in holes, for instance in old gnarls. And outside the breeding period the bird may pass the night there or use the nest as a storing place for the greater or smaller number of nuts collected. Further *Sitta* is also satisfied with the fruits of *Quercus*, just as it will feed on the fruits of *Fagus*, *Cerasus*, *Acer*, *Coniferae* and others.

The fruits of *Quercus*, too, are most effectively dispersed by the nuthatch (*Sitta*); and in Sweden, for instance, the northern limit of the oak and *Sitta* almost coincide. It may also be noted that *Corylus* and *Quercus* came into Denmark at about the same time (IVERSEN).

But in the cold season its favourite food is above all the fruit of *Corylus*, of which it consumes as much as it can on the spot, while, as already stated, any surplus is stored, the nuts being either buried singly in the ground, or several are collected in crevices under bark, under roofs, in the cracks of walls, between stones etc. The whole store is not collected in the same place, however, as the animal might then risk being robbed of its whole supply at once, for instance by a squirrel or other larger animal attacking it.

The nuthatch (*Sitta*) may stay hour by hour and day after day near the same old oak trunk to which it returns again and again after its forays in the neighbourhood. From this starting point it gradually strays in all directions and often it is from comparatively long distances that it returns with nuts. Some of them are dropped and disappear under withered leaves or in the grass where they will perhaps be buried by other animals so that they can germinate next spring.

In close growths of *Fagus*, *Corylus* does not occur; it will

not tolerate the deep shade, and the smooth stems offer little opportunity for dispersion by *Sitta*. More frequently hazel is found under old specimens of *Fraxinus* and *Ulmus* with cracked bark.

The mixed forest of big oaks with a luxuriant undergrowth of hazel known in so many countries has no doubt in great part grown up and obtained its characteristic composition as a result of the activities of the nuthatch and other nut-feeders as dispersers of seeds. The term symbiosis might perhaps with some justice be employed about the interrelationship between the oak and hazel community and the nuthatch, the constant companion and disperser of the nut.

Mice, too, disperse a great many nuts. Not only do they thoroughly search the ground under the trees, but in the night they climb the trees and search the branches. I have often found the stomach of *Hypudaeus glareola* filled with gnawed male catkins which chiefly in the winter constitute a very important food stuff for a particularly numerous stock of mice living under *Corylus*, especially where this shrub grows in abundance. The fruits, too, are well suited for being stored as winter food, and they are gathered together in the well-known underground burrows where they are kept under suitable conditions of moisture (and are exceedingly tasty). In the evening all through the autumn you may hear the rustling of the mice among the fallen leaves under the hazel-bushes. And even if snow falls the work with the nuts is still continued with great energy below the sheltering cover, where the mice now move about more hidden, and so in less danger of being attacked. The underground stores may also harbour male catkins which give evidence of the nocturnal activity of the animals in the treetops.

Many nuts are consumed at the place where they are found. Here the empty shells may then be seen with holes gnawed in them which are different for the different species of mammals. This has been more closely investigated by DEGERBØL who has kept the animals in captivity to study their different working methods when nuts are fed to them.

The rivalry of the pugnacious mice during the gathering and transport of the comparatively large smooth fruits will hardly

proceed without fighting and the consequent loss of nuts on the
way. At any rate nearly all the fruits are quickly removed from
their original position under the trees and are soon dispersed
far and wide.

As many mice are consumed by other animals in the course
of the winter not a few subterranean stores will be left without
owners. And then with the advent of spring the many nuts
gathered together will germinate in the same spot, and a dense
growth of seedlings will emerge from the ground. The finding
of such abandoned stores has provided a rich material of the
remarkable seedlings which will be dealt with in more detail
below.

In the course of the summer all the weaker seedlings that
have come up from the subterranean stores of mice die off,
and one or two vigorous plants remain which—thanks to the
mice—have been sown under favourable conditions in the
ground.

To ensure successful germination it is probably necessary
for the fruits to be buried in the soil. At any rate, I have never
found germinating nuts above ground, but always under ground.
How the fruits are sown remains an enigma.

It has been shown above, however, that mice can bury them
effectively, and something similar can be done by squirrels
(*Sciurus*) and *Sitta*.

When the nuts ripen this means that a great amount of food
has suddenly become available; and this also happens at a time
of year when it is very important both for many birds and for
mammals to have a store to draw upon in the coming unfavour-
able season. However, the season for gathering them in is very
short, and perhaps the animals know that the chances of finding
nuts in larger quantities will only last a few weeks.

So rival collectors flock to the place from all directions, each
of them merely trying to carry off as many fruits as possible
in the shortest possible time. But since the nuts can be kept
concealed, it is not necessary that this spoil—as so many other
kinds—should be eaten at once.

Therefore the lucky finders hurry off as quickly as possible
in all directions to hide their spoil from their rivals, afterwards
hastening back as fast as they can, hardly allowing themselves

time to eat. According to oral information, M. DEGERBØL has seen squirrels work in this way; one by one the fruits were carried off, buried not very deeply, and covered with mould. Some of them were indeed later found by woodpeckers (*Picus*) and devoured; but a number of the nuts buried singly will easily be forgotten, even though the competitors prey very much on the stores so hurriedly laid down by the others.

While mice laboriously gnaw a hole at the top of the nuts, the squirrel can quickly open them by splitting them length-wise into two halves. It bites off the tip and bores down its teeth where the nut anatomically has its weakest point (DEGERBØL).

The strong beak of the woodpeckers (*Picus*), too, is re-markably well suited for opening the hard fruits. On the other hand, the beak of the titmouse (*Parus*) is usually too weak to bring about any very successful results; these birds, however, also try their luck.

Among our common indigenous birds it is, however, the Northern Nuthatch (*Sitta*) which helps most to spread the nuts; often it is seen flying off with one in its beak and it will also bury the fruits one at a time, if it cannot consume the whole harvest at the same time.

The dispersion and burying of the *Corylus* fruit is thus very effective; it takes place both by day and by night and especially in one short period of the year (October). It is true that the great majority of the fruits are consumed by animals, but the growth of seedlings in their natural habitats shows that several of the hard smooth fruits either slip from the animals or are forgotten where they were buried, under good conditions for germination, at a shorter or longer distance from the mother plant.

5. Germination.

At germination the embryo must first overcome the difficulties due to the fact that its tenderest parts are imprisoned in a very hard shell. And as a matter of fact it turns out that some remark-able features in the structure are designed for this purpose and serve to break the shell so that the embryonal root can emerge.

If the tip of the fruit is removed by a transverse cut near the place where the perianth is attached, a cutting surface is

obtained similar to that shown in fig. 23. In the lengthwise direction of the section the dark line (*T*) is plainly seen which is well known to any one who tries to open a nut by sticking the point of a knife into this very line. As already mentioned, it is here that the squirrel bores its teeth into the nut with a successful result (DEGERBØL), and *Sitta*, too, can break open the nut by a vigorous vertical thrust into the apex of the nut. More rarely the little bird splits open the hard fruit by pecking at the side.
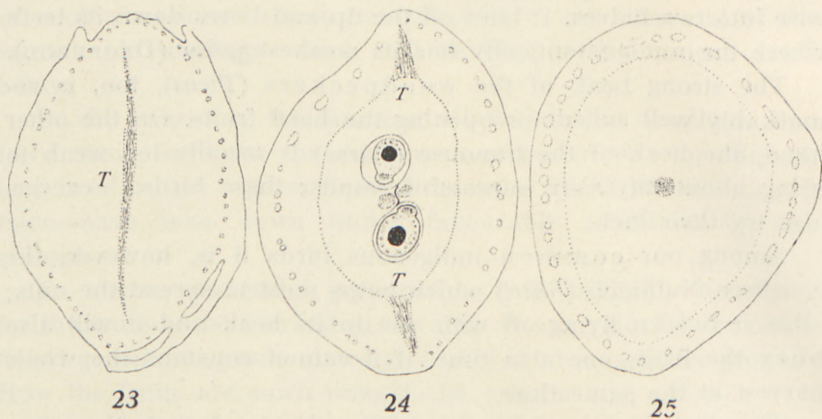
Figs. 23—25. Fig. 23. Transverse section through apex of fruit. *T*, soft tissue in a fissure in the hard surrounding shell. × 50. Fig. 24. Transverse section striking the ovules. *T*, groove in shell. × 15. Fig. 25. Transverse section through middle of nut; in the centre the vascular bundle. × 10. See also text.

Just inside the above-mentioned black line (*T* in fig. 23) the embryonal root lies concealed; this is the thinnest part of the shell, so this offers the best opportunity for the embryo to disengage itself from the shell. Microscopical examination shows that at the mark (*T*) there is a complete layer of soft thin-walled tissue in the middle of the hard shell. In transverse sections it can be observed that the parenchyma in question is continued in a groove downward along the inner side of the shell (fig. 24), which is thinnest at and along the two lines where the edges of the cotyledons lie. At the natural bursting of the shell—as at germination—the split runs through this parenchyma down to the "hilum" of the fruit, which often cracks through the above-mentioned central hole (*O* in fig. 13) through which the vascular bundle of the seed runs.
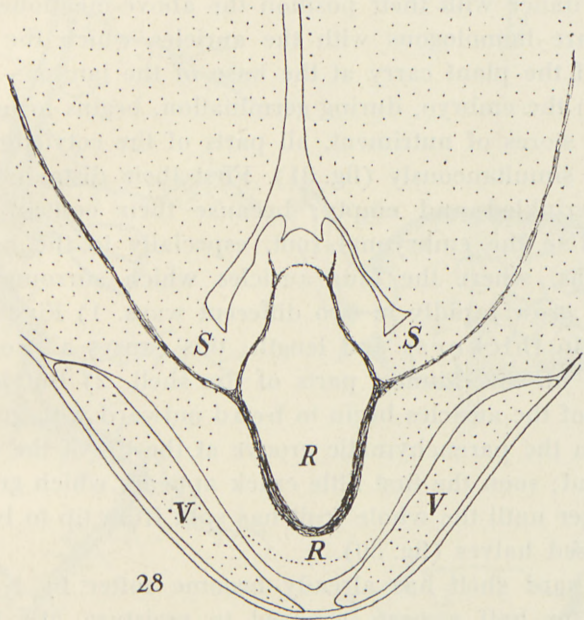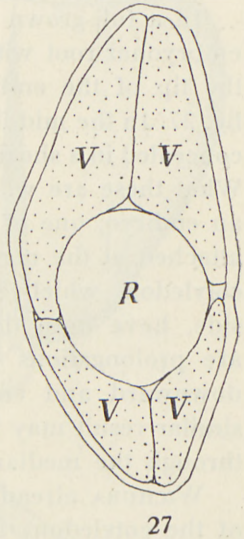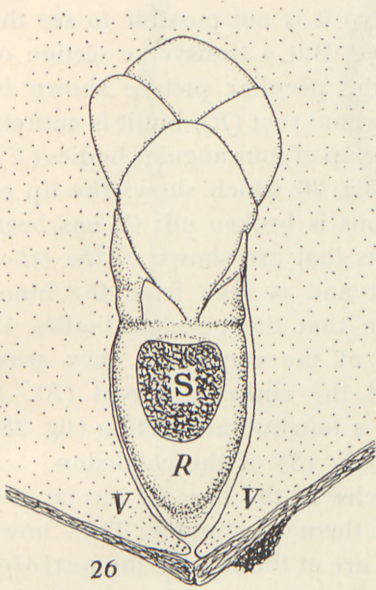
Figs. 26—28. Sections of ripe embryo showing appendages (V) of cotyledons
pointing downward. R, embryonal root; S, stalk of cotyledon. Cotyledon dotted.
× 25. Fig. 26. One cotyledon is broken off at S, the other is seen from the
inner side. Fig. 27. Transverse section through apex of embryo. Fig. 28. Lon-
gitudinal section striking both cotyledons medianly.

In a full-grown prepared embryo it is not possible to see the embryonal root with the naked eye. But a transverse section of the tip of the embryo provides the peculiar picture shown in fig. 27. In the middle lies the embryonal root (R), but it is entirely concealed in a sheath which is made up of four angular bodies (V). What these are will appear from fig. 26 which shows the tip of an embryo, one of whose cotyledons is broken off; (it has been attached at the mark S). The parts that are shown of the other cotyledon, which is still adherent and is seen from the inner side, have been dotted. It is seen that the peculiar bodies, V, are prolongations from the base of the cotyledon; they grow downward and entirely surround the embryonal root (R). A similar result may be obtained by a longitudinal section (fig. 28) through the median part of the stalk (S) of the cotyledon.

WICHURA already saw the auricles at the base of the lamina of the cotyledons and interpreted them as stipules. This, however, cannot be correct, as stipules are at the base of the petiole. In accordance with their position the above-mentioned peculiar organs are homologous with the auricles which the vegetative leaves of the plant carry at the base of the lamina.

When the embryo, during germination, begins to use some of its large stores of nutriment, all parts of the cotyledons are not emptied simultaneously (fig. 31). First their distal points begin to be wrinkled and empty; because their content has been removed to the embryonal root, especially to the base of the cotyledons, where the four auricles which surround the root begin to grow rapidly in two different ways. 1) First they grow quickly in thickness and length; this causes a strong inward pressure on the thinnest parts of the shell. 2) But in addition the tips of the auricles begin to bend outward with great vigour, and then the parenchymatic groove at the tip of the nut begins to expand; soon the first little crack appears which grows larger and larger until the whole fruit has split from tip to base in two equal-sized halves (fig. 30).

The hard shell has already become softer by lying in the ground for half a year, exposed to moisture, the inroads of fungi, and great variations in the climatic conditions.

Further, the water in the surrounding soil can penetrate directly through the shell in two places, namely through 1) the
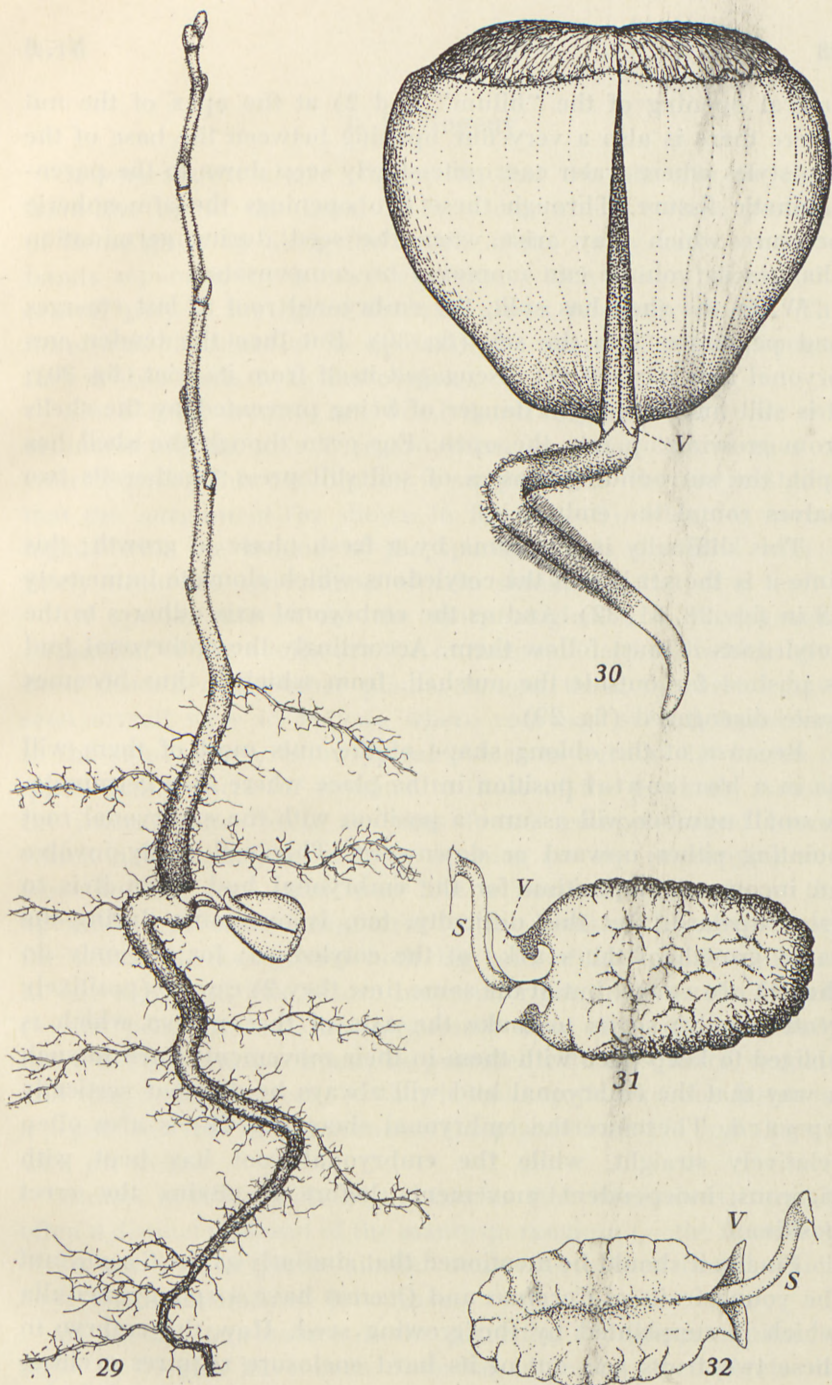
Figs. 29—32. Fig. 29. Seedling from October. × ²/₃. Fig. 30. Incipient germin-
ation. × 3. Fig. 31. Cotyledon viewed from the back, desiccated at tip but
still alive at base. October. × 3. Fig. 32. Cotyledon viewed from the inner
side. October. × 3. The cotyledons in all the figures with long stalks (S) and
auricles (V) at base of lamina. See also text.

central opening of the "hilum" and 2) at the apex of the nut where there is also a very fine opening between the base of the two styles where water can quite slowly seep down to the parenchymatic fissure. Through these two openings the atmospheric pressure which may arise when the seed during germination changes its volume can moreover be compensated.

When the shell has split, the embryonal root at last emerges and penetrates into the soil (fig. 30). But then the tender embryonal axis has not yet disengaged itself from its coat (fig. 30); it is still imprisoned, in danger of being prevented by the shells from growing up into the open. For even though the shell has split, the surrounding masses of soil still press together its two halves round the embryo.

This difficulty is overcome by a fresh phase of growth; this time it is the stalks of the cotyledons which elongate immensely (S in figs. 28, 31, 32). And as the embryonal axis adheres to the cotyledons it must follow them. Accordingly the embryonal bud is pushed far outside the nutshell, from which it thus becomes quite disengaged (fig. 29).

Because of the oblong shape of the nuts most of them will lie in a horizontal position in the place where they germinate. A small number will assume a position with the embryonal root pointing either upward or downward. This will easily involve an inconvenient position for the embryonal bud when it is to grow upward. But this difficulty, too, is overcome during the rapid growth of the stalks of the cotyledons; for not only do they 1) elongate, but at the same time they 2) curve (positively geotropically) so as to make the axis of the embryo which is obliged to keep pace with them in their movements, turn in such a way that the embryonal bud will always be directed vertically upward. Therefore the embryonal shoot (fig. 29) is also often relatively straight, while the embryonal root has bent with vigorous independent movements before it attains the erect position.

Finally it should be mentioned that similarly as the *Corylus* nut the young fruits of *Carpinus* and *Quercus* have a spongy medulla which is supplanted by the growing seed. How the embryo in these two fruits gets out of its hard enclosure requires a closer investigation, and the same applies to many other hard fruits.

6. Phylogeny.

It was shown above (figs. 4—8) that the placenta develops from the tip of the floral axis, from which certain portions of tissue grow up along the inside of the ovary as two narrow bands separated by a narrow cavity, which arises because the central part of the tip of the axis grows relatively slowly. The floral axis therefore at its tip takes the shape of a two-pronged fork whose parts bear the ovules.

Since these ovules are dorsiventral organs which are co-ordinated on an axis I regard them as being homologues of entire leaves. This assumption is supported by the circumstance that the integument (as shown in figs. 17—18), which is homo-logous with the lamina of the sporophyll, is provided with a finely branched reticulation of ribs similar to that of a leaf.

Of special interest for the morphological and phylogenetic estimation of the ovules are the numerous "oolyses" which have been described for other plants. Among these the best I have seen myself were in *Petunia* where you may see all transitions in the same ovary, from typical ovules to normal flat leaves of quite similar form for instance to those of the perianth. Among the intermediate forms are thus found trumpet-shaped leaves which have sometimes a large opening (= the micropyle) and sometimes a very small one like a normal micropyle at the apex of an urceolate integument (= the lamina). In other ovules the micropyle has grown both big and oblique with a fissure at one side, and this fissure may run right down to the funicle (= the petiole). And the integument then often expands flatly like a normal lamina: it may be provided with ribs, hairs, stomata and may even be green, so that it looks quite like, for instance, a sepal. But this leaf is borne on the placenta and is homologous with an ovule.

Almost in the middle of the lamina (the integument) there is often a distinct remnant of the macrosporangium (= the nucellus).

In many other plants similar ovules have been found which have been transformed into leaves.

As to the stem-nature of the placenta, conditions similar to those in *Corylus* have been observed in many other plants. In this connection reference may be made to a series of investi-

gations by J. M. Thompson who even thinks that the revision
of the classic conception of the gynaecium should be extended
to the *Leguminosae*. I myself have found an organogenesis of
the parietal placenta similar to that of *Corylus* in *Mesembryan-
themum, Cactaceae, Gesneriaceae, Orobanchaceae*, and *Salix*.
Within the most nearly related species of several of the above-
mentioned groups of plants there are other plants (e. g. within
the *Personatae*) with a central placenta which is a direct
prolongation of the floral axis and not formed of the "con-
crescent edges of the carpels".

Further information and references to the literature con-
cerning the phylogenetic problems are found in Thompson's
and Hagerup's works. Here it should merely be noted that my
view—as indicated above—is that an ovule is a monospor-
angiate macrosporophyll of a similar type to those occurring
in the *Lycopodiales*.

This view opens up new perspectives for an elucidation of
the phylogeny of the angiosperms. And there seems to be a
phylogenetic line running down from certain angio-
sperms over *Gnetales* and *Coniferae* (especially *Juniperus*
and *Lebachia*) to the *Lycopodiales*.

7. Summary.

1. The various phases of the development of the female flower
occur approximately at the times given in the following example:

a. Styles and perianth begin to form: June-August 1941.
b. Resting period: August 1941—February 1942.
c. Pollination: March—April 1942.
d. Placenta and ovules begin to form: May 1942.
e. The fruit grows: May—July 1942.
f. Fertilisation: July 1942.
g. Seed begins to grow: The beginning of August 1942.
h. Termination of the growth of the seed: Close of August 1942.
i. Ripening of the fruit: September 1942.
j. Dispersion of fruit: October 1942.
k. Resting period for the fruit in the soil: October 1942—spring
   1943.
l. Germination: Spring 1943.

2. The organogeny and final aspect of the nut is characterised by the fact that soon after the flowering an intercalary growing zone develops right across the tip of the floral axis in the internode between the perianth and the involucre (fig. 1).

3. During the intercalary growth the hard shell of the nut develops as a direct continuation of the cortex and xylem of the floral axis; and the medulla of the latter is continued as a soft white tissue, filling the interior of the young nut.

4. During the growth of the seed the medulla of the fruit is compressed to such an extent that it is killed; and in the ripe fruit it lies as a brown scaly layer between the shell and the seed.

5. Through the centre (O) of the "hilum" of the fruit there is a hole (figs. 13, 16, 17) through which runs a vascular bundle carrying at its tip 2—4 hanging epitropic seeds. These are somewhat campylotropous, still with rather a long raphe (fig. 18). The funicle is very short. The central vascular bundle has erroneously been interpreted as a funicle or as "the remains of a septum". Originally, however, the fruit was unilocular with 2 parietal placentae.

6. The fruit is disengaged from its involucre as a consequence of desiccation and shrivelling of the water tissue in this sheath (figs. 21—22).

7. The fruits are especially dispersed and sown by birds (*Sitta*, *Picus*), but also by mice and squirrels.

8. As birds try to split open the fruits in crevices of the bark of trees, particularly *Quercus*, this tree will often be seen to have a vegetation of *Corylus* growing under it.

9. From the base of the lamina of the cotyledons issue four elongations (auricles) which entirely surround the embryonal root like a sheath (figs. 26—28). At germination these split the hard fruit, growing rapidly in length and thickness and also bending outward. The stalk of the cotyledons grows considerably in length (figs. 29, 31, 32) and thus pushes the embryonal bud right out of the shell.

10. The organogenesis shows that the two parietal placentae begin to form at the tip of the floral axis which soon assumes the form of a two-pronged fork (figs. 4—7).

11. As the ovules begin to form at the tip of a stem I consider them homologous with entire independent leaves. This view is explained in more detail on pp. 29—30 and in my earlier works.

12. Since the ovules are monosporangiate macrosporophylls I assume a phylogenetic connection with the *Lycopodiales*.

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PLATE I

Bark of *Quercus* in which *Sitta* has lodged two nuts. The lower nut is hacked at the tip and has begun to split lengthwise.