

The Structure and Development of *Triglochin maritimum*, L.

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With Plates VI and VII.
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TRIGLOCHIN has been somewhat neglected by botanists up to the present time, very little work indeed having been done upon it. The material upon which this investigation was carried out was collected at Yarmouth, in the Isle of Wight, by Prof. Farmer, and at Tilbury, in Essex, where it grows in abundance on the banks of the Thames.

The genus contains about twelve species, many of which are Australian, and is distributed throughout the Temperate regions of the Earth.

Triglochin maritimum, L., grows in salt marshes along the coast and estuaries of temperate climates. It possesses a rhizome of a fair thickness, bearing at its apex a dense tuft of leaves, which are generally half-cylindrical in shape, and may attain quite a considerable length. The inflorescence is a raceme; the flowers are very numerous, and borne upon very short pedicels.

The fruit consists of six carpels, which separate one from

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another when maturity is reached. The fruits of this plant are much stouter and shorter than are those of *Triglochin palustre*, L.

ANATOMY.

The existing accounts of the anatomy of *Triglochin maritimum* are very scanty. The only descriptions which have been found relating to the anatomy, taken as a whole, are embodied in an account by Chatin (3), which was published in 1862, and in a paper by Van Tieghem, published in 1870 (14 a), the latter being mainly concerned with the structure of the root. These two papers are the principal sources of our information of the structure of the plant, and they leave much to be desired in the matter of completeness. Chatin, in the paper just referred to, gives a very short account of the general anatomy of *Triglochin maritimum*, and adds a few remarks on that of *Triglochin palustre*. He gives very few details, and merely describes the general disposition of the tissues, briefly noting a few characters of each. In speaking of the root, he correctly states that spiral vessels are absent.

Van Tieghem (14 a), in discussing the structure of the roots, states that the xylem-strands do not meet in the centre of the root, but are separated by parenchymatous cells; the pericycle is described as a continuous layer, with the sieve-tube of each phloem-group abutting on it, and the companion-cell does not appear to have been noticed. These statements have not been verified in this investigation. Van Tieghem also calls attention to the fact that the lacunae in the inner cortex show signs of lysigenous development.

THE RHIZOME.

This organ may attain a considerable length; how long, it is impossible to say exactly, for the rhizomes are very brittle, and the plant grows in a very heavy soil, so that it is extremely difficult to clear away the earth without breaking them; pieces of rhizome, however, have been found as long as 7 cm. The root-stock is not very thick; the older portions have a diameter

of 4 mm., while in the more apical regions a diameter of 8 mm. is quite common in well-grown plants ; the reason of this lies in the fact that here the cells are younger, and consequently more turgid.

The younger parts of the rhizome are covered, especially around and just below the apex, with the persistent bases of old leaves, which are quite chaffy in character. The rhizome frequently forks into two branches, each end bearing a crown of leaves and possibly flowers.

A transverse section of an old rhizome shows a structure such as is diagrammatically figured in Pl. VI, Fig. 1. From this figure it may be seen that the underground stem is bounded by a mass of brown cells, to the inside of which succeeds a layer of sclerotic elements, which are lignified and extremely hard. These cells are much pitted with simple branched pits. It will also be observed that these strongly lignified cells occur in various other places, the more central regions of the axis of the older parts of the rhizome being always occupied by cells of this character.

The cortex consists of rounded cells loosely arranged in a somewhat radial manner, with numerous intercellular air-spaces (Fig. 2). The cells of the cortex of plants collected in the winter and spring are densely packed with starch-granules, and so also are the parenchymatous cells of the central cylinder.

The endodermis is represented in Figs. 2 and 3, Pl. VI : in the older parts of the rhizome it is extremely well marked, forming a continuous ring of cells much thickened on their radial and inner walls ; this layer, in fact, is remarkably similar to the endodermis such as is met with in the roots of *Dracaena* or *Iris*.

The endodermis in the younger parts of the rhizome is not easy to make out in the ordinary stained microscopic preparations, but its presence can easily be demonstrated by means of the usual test of iodine and sulphuric acid.

The central cylinder has a large number of vascular bundles, which, when fully developed, resemble those of the concentric

type (excepting that here the xylem is interrupted by parenchymatous passage-cells, see Fig. 2), the xylem surrounding the phloem, as 'occurs in the lower ends of the leaf-trace bundles of many, but not of all, rhizomes of Monocotyledons, where they lie at the periphery of the bundle-cylinder in the stem, e. g. *Iris germanica*, *Cyperus aureus*, *Papyrus*, *Carex arenaria* (but not, for example, *C. disticha* and *C. hirta*), *Acorus calamus*, and *A. gramineus*¹.'

A transverse section of a fully formed bundle is represented in Fig. 2, Pl. VI. The xylem consists of tracheides, which are, comparatively speaking, of great length and frequently branched; sliding growth has gone on to a great extent, so that these elements are much interwoven; hence it is extremely difficult to isolate them.

The protoxylem consists of a few elements thickened in the usual manner; it is generally placed towards the centre of the axis, although cases have been observed in which the protoxylem occupies a more lateral position.

The ring of xylem in such a concentric bundle is not, as already stated, complete, but is separated into masses by parenchymatous passage-cells; five such passage-cells are frequently present.

The phloem is exceedingly well marked and regular, the sieve-tubes (*s. t.*) and companion-cells (*comp. c.*) being very distinct; the former are apparently void of contents, and the latter filled with protoplasm, with a large and well-defined nucleus.

The parenchyma surrounding a bundle may sometimes be thickened in various places; such a case is shown in Fig. 2 (*th. par.*).

The ground-tissue in which the bundles are embedded is made up of parenchymatous cells, generally rounded in shape, but often elongated between two adjacent vascular bundles.

As the rhizome increases in age the central parenchymatous cell-walls of the vascular cylinder thicken up and become

¹ De Bary, *Comp. Anat. of the Phanerogams and Ferns*, Eng. ed., 1884, p. 339.

lignified to such an extent that the lumina become almost obliterated ; in this manner the extremely hard sclerotic cells already referred to become differentiated.

The course of the leaf-trace bundles in the rhizome calls for no special comment, inasmuch as it somewhat resembles the type exemplified by the Palms, that is to say, the bundles, after coming in from the leaves, travel obliquely through the cortex to the central cylinder, where they curve towards the centre and then pass out to the periphery. In *Triglochin* the course of these bundles is very complicated, inasmuch as numerous branchings and anastomoses take place.

A transverse section of the rhizome shows numerous small bundles arranged in the peripheral part of the central cylinder. These are connected by horizontal commissures to form a *réseau radicifère* such as obtains in many Monocotyledons. These peripheral bundles run roughly in a longitudinal direction ; but in the region of insertion of a root they are united transversely, so that a root may be connected with at least one-half of the total number of bundles, of which there may be as many as twenty-five to thirty.

One feature of interest connected with the anatomy of the plant under consideration lies in the occurrence of occasional cell-divisions recalling those of a cambium. These cambia were not at all common ; the best example seen is represented in Fig. 3, Pl. VI. From this figure it will be seen that the cambium is well marked and has been formed from the pericycle ; it is situated opposite a young bundle on its outer side. The other examples seen were cambial divisions in single pericyclic cells ; they were not sufficiently developed, however, to throw much light upon the subject.

The part of the rhizome from which the section containing this cambium (Fig. 3) was cut was not by any means young, as is seen by the greatly thickened endodermis ; unfortunately it cannot be said exactly how old this part of the rhizome was, inasmuch as the portion was an isolated piece of stem. There were no indications of the cambium being due to pathological effects, the cells around being, as far as could be judged from

their appearance, quite healthy and normal. It may perhaps be argued that in *Triglochin maritimum* we have a case of incipient secondary thickening which is found developed to a much greater extent in Monocotyledons like *Aristea*, *Dracaena*, *Yucca*, &c., and in this respect it is interesting to recall remarks by Dr. Scott and Mr. Brebner¹. Writing of *Aristea corymbosa*, Benth., they state their opinion that the secondary thickening 'has originated *de novo* probably at a comparatively recent period.' And again, 'it is very probable that the first origin of secondary growth may be taking place in some of the Monocotyledons at the present day.'

Petersen² expresses much the same opinion in his paper on secondary thickening in Monocotyledons; he says: 'En examinant un nombre assez grand de tiges de plantes monocotylédones je me suis pourtant convaincu de ce qu'il se trouve une transition plus graduelle de ces tiges, où l'on n'a point du tout pu démontrer une formation méristématique, jusqu'aux phénomènes que nous connaissons chez le *Dracaena*.'

Triglochin palustre, the rhizome of which is much smaller than that of *T. maritimum*, has been examined for cambium, but so far without success. It is quite possible, however, that some of the other species of *Triglochin*, especially those with a well-developed rhizome, may be found to show a more advanced secondary thickening.

Unfortunately it was not possible to obtain fresh material of other species of *Triglochin* for this investigation, although a small quantity of herbarium material was obtained of the following species: *T. triandrum*, Mich., *T. procerum*, R. Br., *T. Maundii*, F. Muell., and *T. montevidense*, Spreng.; but this material was very unsatisfactory to work with, and it was not possible to obtain reliable evidence either way.

¹ Scott, D. H., and Brebner, G., on the Secondary Tissues in certain Monocotyledons. *Annals of Botany*, Vol. vii, 1893.

² Petersen, O. G., Remarques sur la croissance en épaisseur et sur les régions anatomiques de la tige monocotylédone; French résumé. *Botanisk Tidsskrift*, Vol. xviii, 1892, p. 125.

THE FLOWERING STEM.

Fig. 4, Pl. VI, illustrates in a diagrammatic manner a transverse section of a flowering stem.

The epidermis is well marked, consisting in young specimens of thin-walled oval cells, as seen in transverse section; in the older specimens a cuticle is developed, which is longitudinally ridged in much the same way as in the leaf to be described later. Stomata occur in the epidermis, but they are not very numerous; the guard-cells are sunk a little below the general surface of the stalk, and are very similar to those of the leaf. The cortical cells immediately within the epidermis contain chlorophyll-corpuscles.

In the cortex of the lower regions of the stalk a large number of air-spaces occur, recalling the arrangement met with in the spongy mesophyll of an ordinary leaf. These air-spaces are more regular in the younger regions of the stem, where their appearance is very similar to that of the air-spaces in the stem and petiole of purely aquatic plants.

The structure of the vascular bundles, which are here of the collateral type, is illustrated by Figs. 5 and 6, Pl. VI. The phloem, as is usual with Monocotyledons, is very regular and well marked. In some bundles, more especially in the older ones, a few elements in the phloem-parenchyma become lignified; such a case is shown in Fig. 6. In Fig. 5, illustrating the structure of a younger bundle, it may be seen that primary meristem, between the phloem and xylem, persists for some time before passing over into permanent tissue: this is of some interest, inasmuch as the same persistence of meristematic tissue is found in many plants belonging to the Ranunculaceae. This cambial arrangement is not so well marked in older bundles, for, of course, the elements have been transformed into permanent tissue.

The xylem calls for no special comment.

As the flower-stalk grows older the cells of the ground-tissue surrounding the separate bundles form a lignified sheath,

so that in quite old stems there is a ring of strongly lignified tissue, the cells of which often exhibit well-marked simple pits.

The medulla of the young flowering stems has a large number of air-spaces developed in it; these air-spaces are arranged in a very regular manner, and their appearance recalls that which is generally associated with aquatic plants. The older scapes are frequently hollow, this being due to the inequality of growth of the outer and the more central regions of the stem.

THE LEAF.

The leaves of *Triglochin* are acicular in shape, with a sheathing base, and are arranged in an equitant manner. In transverse section they are generally semicircular in outline. They may attain a length of 15–16 cm.; the breadth of course varies in the different regions of the leaf. The greater diameter of a half-cylindrical leaf was 3 mm., and the lesser $1\frac{1}{2}$ mm., measured across the middle region.

The structure of the leaves is illustrated by Figs. 7 and 8. Fig. 7 shows the general structure in a diagrammatic manner. Surrounding the two younger leaves the sheathing base of an older one is seen; from this figure it is also apparent that air-spaces, which are schizogenous in origin, are largely developed, especially in the more central regions. Embedded in the ground-tissue are numerous collateral vascular bundles, the larger ones lying nearer to the median plane of the leaf (see Fig. 45, Pl. VII). These bundles are very similar in structure to those already described for the peduncle, and hardly call for a detailed account here.

On comparing the positions of the separate bundles, in the sheathing and upper regions respectively, of a leaf, it will be seen that as the bundles pass from the base towards the apex they alter very much as regards their relative positions; hence it was desirable to trace out their course in some detail.

Several bundles pass up from the rhizome to each leaf, e.g. all those represented in diagram *A*, Fig. 45, Pl. VII, were found to run into the stem as separate leaf-traces.

Fig. 45 illustrates the positions of the bundles in the upper and lower regions of the leaf.

A transverse section of a leaf, just above its junction with the stem, shows the general arrangement of the bundles, the largest one (1) being in the centre. Intercalated between the larger bundles are smaller ones, sometimes consisting of quite a few elements; these small bundles may completely disappear higher up in the leaf. The diagram *A* in Fig. 45, Pl. VII, shows the bundles in the upper regions of the sheathing leaf-base; all the bundles here represented are to be found in the higher portions of the leaf, although their relative positions are different. In order that this may be followed more easily the bundles have been numbered, those having the same number in the two diagrams being identical.

As the bundles pass up the leaf the first changes in position noticed are: 2 and 11 in the sheathing base move towards the convex side, and the bundles of the horns of the crescent gradually travel obliquely up towards bundle 1.

The large bundle 1 remains in practically the same central position.

The bundles 3 and 10 travel in such a way as to retain their relative position with regard to bundle 1. Passing upwards from the sheathing base, the bundle 9 moves towards the plane (ventral) surface of the leaf, taking up a position below and a little to the right of 1; bundle 4 does likewise, taking up a similar position on the left side of 1. Before the bundles 4 and 9 have taken up their final position (shown in *B*), it was found that three new bundles arose near the periphery of the convex (dorsal) side of the leaf, and almost opposite to the bundles 1, 3, and 10; they are indicated by the letters *a*, *b*, and *c* in diagram *B*.

All the bundles have now left the sheath; a branch is then given off from 6 and joins up with 4, and subsequently a branch from 7 unites with 9. Bundle 6 now gives off another branch (6'), which runs up the leaf in a position between the two first-named bundles. Bundle *e*, which occupies a similar position to 6' in the opposite side of the leaf, was found not to be

a branch from 7, but to arise independently¹. It seems very probable that this may be a special anomalous case, as in other respects the behaviour of the bundles is similar on the two sides of the leaf; so that one would expect a branch from 7 to occupy the position filled in this particular leaf by the bundle *e*.

There is a certain amount of variation as to the course of the bundles in different leaves; for example, it was found that in another leaf the bundle corresponding to 1 gave off a branch, which finally occupied a position similar to that of 9 in the leaf described above. Then, again, the adjacent bundles of some leaves, especially the larger ones, anastomose somewhat freely in the transitional regions between the sheath and the blade. The main points, however, expressed above are typical.

The structure of the assimilatory region of the leaf is illustrated in Fig. 8. The epidermis is well marked and, in the older parts of the leaf, is covered with a cuticle of fair thickness. This cuticle, like that of the flowering stem, is longitudinally ridged, there being from three to five ridges to each epidermal cell. The stomata are numerous, showing a typical structure, and are placed slightly below the general level of the epidermis. The palisade-parenchyma is several layers in thickness, and is made up of oval-shaped cells with small air-spaces between them.

Glandular bodies are developed in the axils of the leaves; in shape they are triangular and flattened, and very frequently quite numerous, as many as seventeen having been counted in one leaf-axil: they are sessile and made up of parenchymatous cells, with dense contents and well-marked nuclei, somewhat larger than are found in the non-glandular vegetative parts of the plant.

Irmisch (10) was the first to call attention to these glands in the leaf-axils of *Triglochin maritimum*.

¹ No definite connexions were to be made out between these and the adjacent bundles; this may be due to the fact that the leaf was quite a young one, and still retained its merismatic condition. It might also be noted that these bundles, *a*, *b*, and *c*, are not found in all leaves.

In the paper referred to he describes their form and arrangement. Similar structures occur in other natural orders, e. g. Hydrocharidaceae and Callitrichaceae (see Caspary, 2, and Hegelmaier, 9.)

At the base of each glandular body there is seen, in longitudinal section (Figs. 10 and 11), a layer of cells, thickened in much the same manner as an endodermis. This layer of endodermoid cells is continuous across the plane of attachment of the gland, and is not found elsewhere.

The thickenings are somewhat difficult to make out in the very young glands, but with advancing age the thickenings increase considerably until they are as represented in Fig. 11; so that when the gland is no longer necessary to the plant and drops off, the part of the cortex with which it was in contact is fully protected. This very interesting fact does not appear to have been noticed by earlier observers.

In connexion with the cutting off of these glands by the development of a special tissue, it is interesting to note that Miss E. Dale (5) has found that a somewhat analogous process obtains in the intumescences situated upon the stem of *Hibiscus vitifolius*, the outgrowths being there cut off by cork, which arises in the lowest row of daughter-cells derived from the original epidermis.

The secretion of these glands appears to be mucilaginous. They are stained pink with corallin-soda, and blue with aniline blue, although these reactions were not so well marked as those obtained with the glands of *Rumex*, which were tested at the same time and with the same reagents. Oils and tannin appear to be absent, for no reactions took place when they were treated with osmic acid, chromic acid, potassium bichromate, and ferrous sulphate and nitric acid.

THE ROOT.

The roots of *Triglochin* are adventitious, and arise acropetally from the rhizome; they are very numerous, and may attain a length of 10 to 11 cm., with a diameter of about 1 mm.

The structure of these organs is illustrated by Figs. 12, 13, and 14, Pl. VII.

The piliferous layer is well marked, the cells being generally oblong in shape, whilst those which have grown out into root-hairs are nearly square. This layer may become lignified in old roots. The root-hairs, on becoming functionless, do not necessarily die off, but may become thickened and persist. According to Van Tieghem (14*b*), the root-hairs are sometimes formed very near the end of the root, just behind the calyptra.

Immediately beneath the piliferous layer is a well-marked exodermis (Fig. 12 *exo*), normally one cell in thickness, but here and there forming a double layer.

Beneath the exodermis are two or three layers of rounded thickened cells, with no intercellular spaces; these, however, occur between the innermost row and the subjacent cortical layers.

The cells of the inner cortex are arranged in a very regular radial manner, especially in the younger regions of the roots. They are rounded in shape, with lozenge-shaped schizogenous air-spaces between them; these cells and their accompanying air-spaces gradually grow smaller in passing from the periphery to the central cylinder.

The endodermis is extremely well marked, having much the same appearance as the endodermis of the rhizome, the radial and inner walls being very strongly thickened (Fig. 13).

In the older regions of the roots large lacunae are found in the outer parts of the inner cortex; these air-containing spaces show some signs of lysigenous development. Van Tieghem draws attention to this.

The vascular cylinder may be pentarch, hexarch, or heptarch. Van Tieghem (14*a*) states that the radiating vascular strands do not meet in the centre, being separated by parenchymatous cells; the material examined did not bear out this statement, for it was found that in every case the xylem-strands did meet in the centre.

In common with the roots of many other Monocotyledons, e.g. *Aponogeton* and *Potamogeton lucens*, according to Van Tieghem (14 a), each phloem-group in the roots of *Triglochin maritimum* is reduced to one sieve-tube with its companion-cell.

In the very young regions of the roots the mother-cell of the sieve-tube and companion-cell is seen as a six-sided element, somewhat larger than its neighbours. As it increases in age a periclinal wall arises, dividing the cell into an outer cell, which is the sieve-tube, and an inner segment, which is the companion-cell. The sieve-tube abuts directly on the endodermis, thus interrupting the pericycle at this point.

It is somewhat difficult to demonstrate the presence of the sieve-plate; not one was clearly seen in the younger parts of the root; Fig. 14 illustrates these structures as they were found in the oldest part of a root embedded in the cortex of the rhizome. From this figure it may be seen that the sieve-tube is undoubtedly next the endodermis, and in this case the sieve-plates are typical and of the simple type of structure.

Van Tieghem figures and describes the pericycle as a continuous layer, with the sieve-tube abutting on it, and he does not appear to have noticed the companion-cell. In all cases the sieve-tube is in contact with the endodermis and interrupts the pericycle, and the companion-cell is easily recognized¹.

In longitudinal section the protoxylem is seen to be composed generally of annular elements.

The apex of the root of *Triglochin maritimum* so closely resembles that of *Zea Mais* that it hardly calls for an extended description.

The roots do not frequently branch, so that preparations showing the first origin of lateral roots were not obtained. From young lateral roots, still embedded in the cortex of the mother root, it appears that they arise from the pericycle opposite the protoxylem-groups.

¹ It would perhaps be as well to note here that Figs. 33 and 35 in Van Tieghem's paper appear to be wrongly numbered. Fig. 33 seems to refer to *Aponogeton*, and Fig. 35 to *Triglochin*, instead of vice versa.

INFLORESCENCE AND FLOWERS.

The inflorescence of *Triglochin maritimum* consists of a raceme, the flowers being attached by very short pedicels to the peduncle. The flowers in each inflorescence are very numerous, and are especially crowded at the apex of the flowering stem.

An interesting fact, which has already been recorded in connexion with the inflorescence of this plant by Van Tieghem (14*b*) and other observers, is that the apex of the flowering stem is very frequently occupied by a flower.

The individual mature flowers, which have no bracts, are greenish in colour, although they sometimes have a very decided purple hue.

The perianth consists of six segments arranged in two alternating whorls of three lobes, the segments of the outer ring being somewhat larger than those of the inner. The stamens are six in number, arranged in two whorls, alternating with those of the perianth.

The ovary is made up of six carpels which, early in life, become attached to one another, separating when the seeds are ripe. Each carpel has a single feathery stigma, and contains one seed. The fruit of *Triglochin maritimum* is not nearly so long as the fruit of *Triglochin palustre*, but is very much broader.

FLOWER-DEVELOPMENT.

Cordemoy (4) worked out the floral development of *Triglochin palustre*, and his account, which unfortunately is not illustrated, closely corresponds to what has been found to obtain in *Triglochin maritimum*, excepting, of course, the fact that in *Triglochin palustre* one whorl of carpels is suppressed.

The flower first arises as a spherical outgrowth, which is illustrated in Fig. 15.

The perianth is the first of the floral structures to arise, and, for the sake of clearness, the components of the outer

perianth whorl will be spoken of as the sepals, and the individual parts of the inner ring as the petals.

The individual whorls arise in acropetal succession from the first primordium.

Calyx. The anterior sepal arises first; it takes its origin from the basal part of the spherical primordium already referred to. The shape of this young sepal is somewhat crescentic, and of a fair thickness. Very soon after the first sepal has made its appearance the two lateral sepals arise, the left-hand one originating slightly before its fellow on the right-hand side (Figs. 15-18).

Corolla. After the sepals have grown slightly the petals commence to put in an appearance. They arise in positions alternate with those of the sepals, the posterior petal originating first; it does so as a small rounded outgrowth, which is more or less flattened. The shape of these young petals is not nearly so elongated as that of the young sepals; they are also very much smaller, and arise in a position situated higher up upon the original primordium. The other petals follow very quickly—indeed almost simultaneously—so that it is somewhat difficult to say which of the two lateral petals develops first: as far as can be made out, the petal which occupies a position between sepals 1 and 2 is the first to appear, and is very quickly followed by the other. It sometimes happens, however, that the first lateral petal to arise is that lying between sepals 1 and 3, so that a certain amount of variation may occur (Figs. 19 and 20).

The Androecium. As soon as the segments of the perianth have become differentiated, the stamens make their appearance.

The outer staminal ring, as already pointed out, is opposite the outer perianth whorl (sepals), and it arises before the inner ring of stamens as oval-shaped masses of tissue (Fig. 21). It seems very probable that the appearance of each stamen follows that of the perianth segment to which it is opposite, for it was observed that the stamen superposed on the first sepal was the first to originate. It was not seen which of the

two lateral stamens arose first, but, judging from their size, it seems extremely probable that the one opposite the second sepal arises slightly before the other, which follows it very quickly.

When the stamen has attained a certain size, increased lateral growth takes place, so that a two-lobed structure results, and in a short time the stamen becomes quite two-lobed, each lobe being slightly constricted, owing to the formation of the two loculi.

The inner staminal whorl arises after the first has been developed, the stamen opposite the posterior petal being the first to arise.

By the time the stamens are all developed, the sepals have increased very much in size, so that each one forms a hood, as it were, over the stamen opposite it (Figs. 21 and 22).

Gynoecium. As in the case of the stamens, the carpels also are arranged, though not quite so obviously, in two whorls. A carpel first arises as a somewhat flattened protuberance; growth gradually extends up the dome-shaped receptacle, so that a young carpel has a shape somewhat like that of a horse-shoe.

In the carpels the suture along which the coalescence of the two horns has taken place is indicated by a faint line (Fig. 25).

The walls of the carpel grow upwards, so that a hollow vessel, somewhat of the shape of a pear, results. After a time, the outer part of the wall of the carpel grows more quickly than its inner region; hence the aperture at the top becomes placed somewhat nearer the centre of the flower. In this way a hood-shaped structure is produced (Figs. 25 and 26). It is about this time that the hairy stigmatic surface arises.

The ovule originates as a dome-shaped mass of tissue, while the carpellary walls are still in a primitive state.

The ovule is basilar in origin, and anatropous in character.

THE EMBRYO-SAC.

Hofmeister (9) has described the embryo-sac, &c., of this plant. He draws attention to the anatropous ovule, and to the fact that the remains of the nucellus surrounding the embryo-sac are of some thickness.

Writing of the embryology he mentions that the oospore frequently increases in size before division takes place. In the segment-cell which immediately abuts on the end-cell of the proembryo, and which proves to be the mother-cell of the embryo, divisions take place in three directions of space.

He also draws attention to the endosperm, which, as a closed tissue, is quite suppressed in *Triglochin*, free nuclei only being formed, and then only in some cases.

The mature embryo-sac is oval in shape, and frequently contains the normal number of nuclei.

The chief interest of this structure lies in the fact that the antipodal cells exhibit a fairly considerable range of variation as regards the number which may be produced. Whilst in some instances the number may be as low as three, in others a tissue may be formed such as has been described as occurring in many of the lower Monocotyledons, e. g. Grasses (9 and 10), *Sparganium* (1 a and 1 b), *Lysichiton* (1 a), and some other Araceae (1 d). The number of antipodals thus formed is never so large as occurs, according to Campbell, in *Sparganium simplex*, in which plant 150 have been observed. As a matter of fact the largest number of antipodal cells counted in *Triglochin* was in the preparations illustrated by Figs. 28 and 29, and in this instance fourteen nuclei were made out. These numbers are similar to those obtained by Hofmeister (9) for the antipodals of Triticeae. It is an interesting fact that the embryo-sac which possessed fourteen antipodal cells also showed other peculiarities, for the number of cells observed at the micropylar end numbered five, and these cells were all of an equally large size, and similar in appearance (see Figs. 28-31, which represent preparations of the same embryo-

sac). Other embryo-sacs which showed a multiplication of the antipodal cells were quite normal as regards their egg-apparatus. Preparations showing the actual divisions of the antipodal cells were unfortunately not obtained, so that it is impossible to say whether they increase by fragmentation or by karyokinesis.

A considerable amount of time was spent in endeavouring to obtain preparations at the time of actual fertilization, in order to ascertain whether the same phenomena obtain in *Triglochin* as have been found in *Lilium* by Nawaschin (12) and Guignard (7). These efforts were unfortunately unsuccessful, and the failure may perhaps be at least partly due to the small size of the nuclei concerned.

The polar nuclei, as far as could be ascertained without the actual stage of fertilization of the oosphere having been observed, do not appear to fuse till after fertilization, and, if this be correct, *Triglochin* in this respect would differ from *Sparganium simplex*, and would resemble *S. Greenii* as described by Campbell.

Examples of the fusion of these polar nuclei are illustrated in Figs. 30 and 32, Pl. VII.

EMBRYOLOGY.

The embryology of *Triglochin maritimum* in its chief features conforms to the type commonly met with amongst most Monocotyledons.

The chief peculiarities which distinguish *Triglochin* lie in the earlier divisions of the oospore.

The first division of the oospore takes place by means of a transverse wall cutting the original cell into a lower basal and a terminal embryo-cell (Fig. 34).

The terminal embryo-cell then divides by another transverse wall, thus giving rise to a three-celled structure (Fig. 35).

The next division which takes place was not actually observed, only the four-celled embryo which is thus produced being seen (Fig. 36), but judging from appearances it seems

extremely probable that the four-celled embryo is formed by a transverse division of the central cell of the previous three-celled stage.

The terminal cell next divides by a longitudinal wall which is frequently somewhat oblique; thus there is formed a five-celled embryo (Fig. 37).

Up to this point the divisions which have taken place in the oospore of *Triglochin* are identical with those which have been described as occurring in *Alisma Plantago* and *Sagittaria variabilis* by Schaffner (13 *a* and 13 *b*), and also with those of the oospore of *Sparganium* as described by Campbell (1 *b*).

The embryology of *Triglochin* differs from that of *Lilaea subulata*, H.B.K., as investigated by Campbell (1 *c*), inasmuch as in *Lilaea* the first longitudinal division occurs before the four superposed cells are formed.

The divisions which next occur may vary somewhat, as two distinct types were seen.

It sometimes happens that the two terminal cells of the embryo may again divide, before any other division takes place, by longitudinal walls, thus giving rise to a group of four terminal cells in the same plane. Such a case is illustrated in Fig. 38. When this is the case, the next division occurs in the cell immediately below the terminal ones, by means of a longitudinal wall (Fig. 38).

In the second type of division the cell directly below the terminal embryo-cell divides before any further divisions take place: this seems to be the commoner sequence, and when such is the case the next division is a longitudinal one occurring in one of the two terminal cells; this division is followed by a similar one in that cell which is diagonally opposite to the cell just divided in the tier above. Very frequently, however, and immediately before this takes place, it happens that the cell next above the basal cell divides by a transverse wall, so that a tier of five cells, including the basal cell, results (Fig. 39). Divisions now go on rapidly, resulting in the formation of an embryo such as that illustrated in Fig. 41, Pl. VII. Up to this stage it is possible to

distinguish the primary segment-walls, but in later stages this becomes increasingly difficult.

By subsequent growth in length the spherical embryo is converted into one of a more oval shape, as illustrated in Fig. 42. From this figure it may be seen that the basal cell is still attached to the embryo, and that there is a narrow chain of suspensor-cells.

The basal cell becomes detached from the embryo, but may be recognized for some time, until the embryo is well on its way to maturity. The stem-apex just arising is shown in Fig. 42, and from this it will be seen that, as in so many other Monocotyledons, the stem-apex arises laterally.

The mature embryo is straight, and not curved over, as is found in *Alisma Plantago*, and a second leaf is frequently differentiated while still in the seed.

THE FORMATION OF THE ENDOSPERM.

The first division of the definitive nucleus was observed in an embryo-sac in which the oosphere had been fertilized (Fig. 33); the two nuclei thus formed were found to be in a state of division when the embryo was a two-celled structure (Fig. 34).

The endosperm-nuclei formed are very distinct, each having a conspicuous and somewhat large nucleolus. These nuclei are not very numerous, considering the size of the embryo-sac, and they arrange themselves in the protoplasm which lines its walls. In no case were cell-walls observed between them, *Triglochin* thus differing from the endosperm of *Sparganium* and *Lysichiton*, and resembling that of *Lilaea subulata*.

SUMMARY.

Structure.

(a) *Rhizome.*

1. The endodermis is very similar to that of the roots of *Dracaena*, &c.
2. The vascular bundles are of the concentric type, with the xylem surrounding the phloem and broken up into separate masses by passage-cells. The protoxylem is placed towards the centre of the axis.
3. The course of the bundles is of the ordinary Palm-type, although a large number of anastomoses takes place. *Réseaux radicifères* are formed.
4. Cambium may be developed, which may be indicative of incipient secondary thickening.

(b) *Roots.*

1. The roots are adventitious, and arise acropetally.
2. A well-marked exodermis is formed.
3. The vascular cylinder may be pentarch, hexarch, or heptarch.
4. Each phloem-group is reduced to one sieve-tube, which borders directly upon the endodermis; the companion-cell is easily recognized.

(c) *Leaves.*

1. The vascular bundles are collateral.
2. In the axils of the leaves gland-like bodies are developed, and are finally cut off by a thickening of the cells across the base of each.

The glands seem to have a mucilaginous secretion.

(d) *Flowering-stem.*

1. The vascular bundles are of the collateral type, and when young have a structure remarkably similar to that of the same organs in several plants belonging to the Ranunculaceae.

Flower-development, &c.

1. The various parts of the flower are arranged in alternate whorls of three, which arise in acropetal succession. The anterior calyx-lobe is the first organ to arise.

The ovule is basilar in origin.

2. The embryo-sac often contains an increased number of antipodal cells, the number varying from three to fourteen, as far as has been seen.

3. The polar nuclei do not appear to fuse till after fertilization has taken place.

4. The embryology follows a normal course strongly resembling that of other Monocotyledons. A basal cell is developed, and it appears that this does not undergo division.

5. The embryo does not bend over, as in *Alisma*; the stem-apex is developed laterally.

6. An endosperm is formed, the nuclei of which are not separated by means of cell-walls; they are very distinct, lining the inner wall of the embryo-sac.

The greater part of this research was carried out in the botanical laboratories at the Royal College of Science, and I should like here to express my best thanks to Professor Farmer for the help and advice he has given me.

My thanks are also due to the Director of the Royal Gardens, Kew, and to Dr. Scott, Hon. Keeper of the Jodrell Laboratory, for allowing me to work in the Jodrell Laboratory during part of the summer vacation.

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EXPLANATION OF FIGURES IN PLATES
VI AND VII.Illustrating Mr. Hill's paper on *Triglochin maritimum*.

Abbreviations:—*antips.*, antipodal cells; *a. s.*, air-spaces of the medulla; *a. s.^l*, air-spaces of the cortex; *a. s. l.*, air-spaces of the leaf; *asm.*, assimilatory tissue; *b. c.*, basal cell; *camb.*, cambium; *carp.*, carpel; *c. c.*, central cavity; *co.*, cortex; *comp. c.*, companion-cell; *cot.*, cotyledon; *cu.*, cuticle; *d. n.*, definite nucleus; *emb.*, embryo; *end.*, endodermis; *exod.*, exodermal-like thickening; *g.*, glandular body; *g. c.*, guard-cell; *l.*, leaf; *l. b.*, leaf-base; *osp.*, oospore; *p.*, petal; *ph.*, phloem; *p. mer.*, primary meristem; *p. n.*, polar nucleus; *pxy.*, protoxylem; *rt.*, root; *s.*, sepal; *s. a.*, stem apex; *scl.*, sclerenchyma; *s. l.*, second leaf; *s. pl.*, sieve-plate; *s. t.*, sieve-tube; *sta.*, stamen; *syn.*, synergidae; *th. par.*, thickened parenchyma; *v. b.*, vascular bundle; *xy.*, xylem.

All the figures, excepting those relating to the flower-development, were outlined by means of an Abbe Camera lucida, the details being drawn by freehand. The lenses used were made by Zeiss.

Fig. 1. Diagram of a transverse section of an old rhizome. × 45.

Fig. 2. Transverse section of a rhizome, showing the vascular bundles. × 300.

Fig. 3. Transverse section of a rhizome, showing the cambium and a young bundle. × 250.

Fig. 4. Diagram of a transverse section of a peduncle. × 82.

Fig. 5. Transverse section of a peduncle, showing a young vascular bundle with primary meristem. × 650.

Fig. 6. Similar section, showing an older bundle with the surrounding tissue lignified. × 360.

Fig. 7. Transverse section of leaves; the sheathing base of the outermost one is shown; somewhat diagrammatic. × 45.

Fig. 8. Transverse section of a leaf, showing cortical structure. × 250.

Fig. 9. Longitudinal section of a glandular body. × 160.

Fig. 10. Similar section, showing the endodermoid markings at the base. × 360.

Fig. 11. Similar section of an older gland, showing the basal cells thickened to a much greater extent. × 650.

Fig. 12. Transverse section of a root, showing the exodermis and outer cortex. × 650.

Fig. 13. Transverse section of a root, showing the general structure. × 320.

Fig. 14. Longitudinal section of a root in the outer cortex of the rhizome, showing a sieve-tube and plates. × 680.

Fig. 15. First primordium of the flower, (*a*) in surface view; (*b*) from the side.

Fig. 16. Young flower, showing the first sepal and the second one just arising.

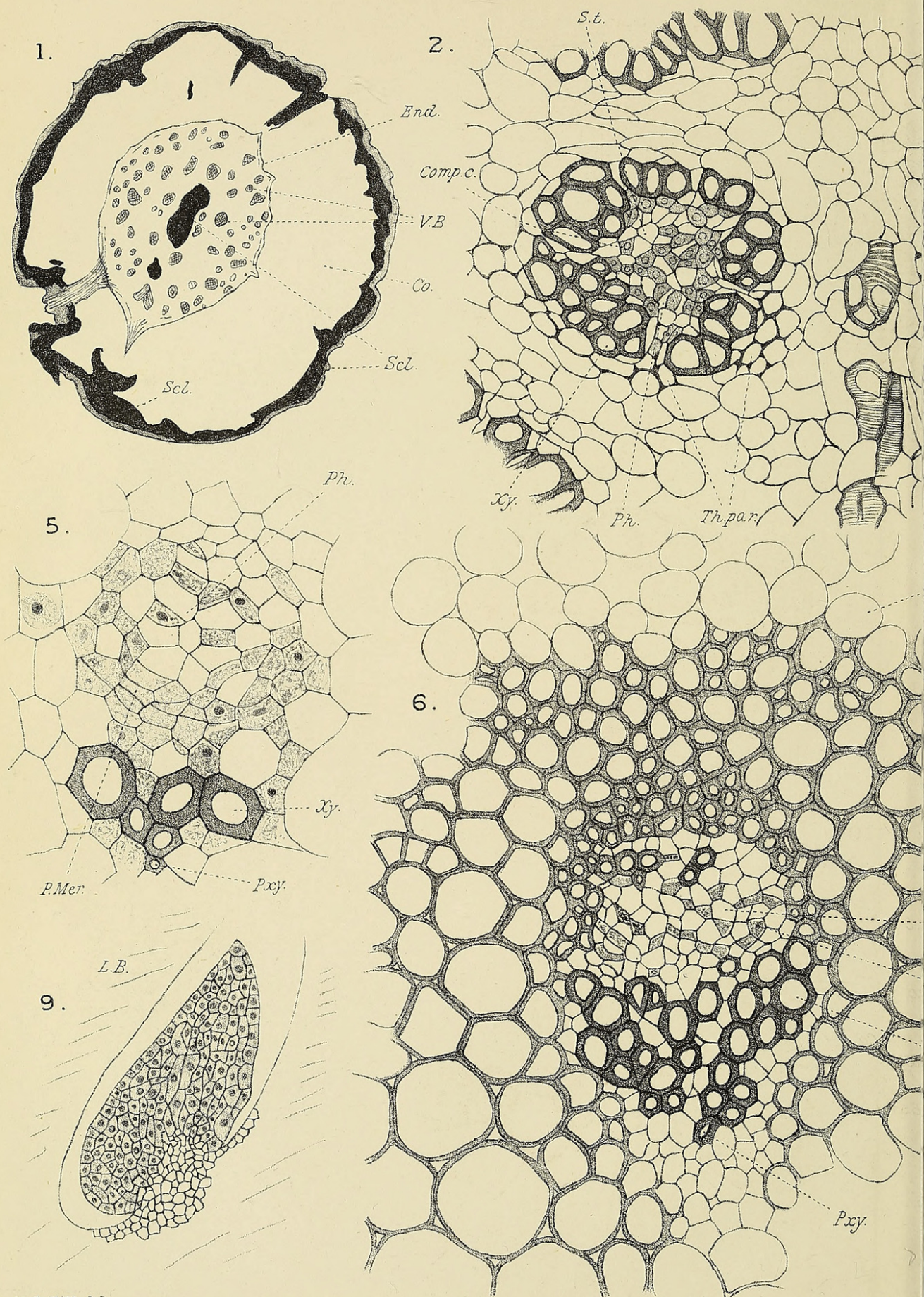
Fig. 17. Similar preparation of a slightly older flower seen from the side.

Fig. 18. A flower with all three sepals formed.

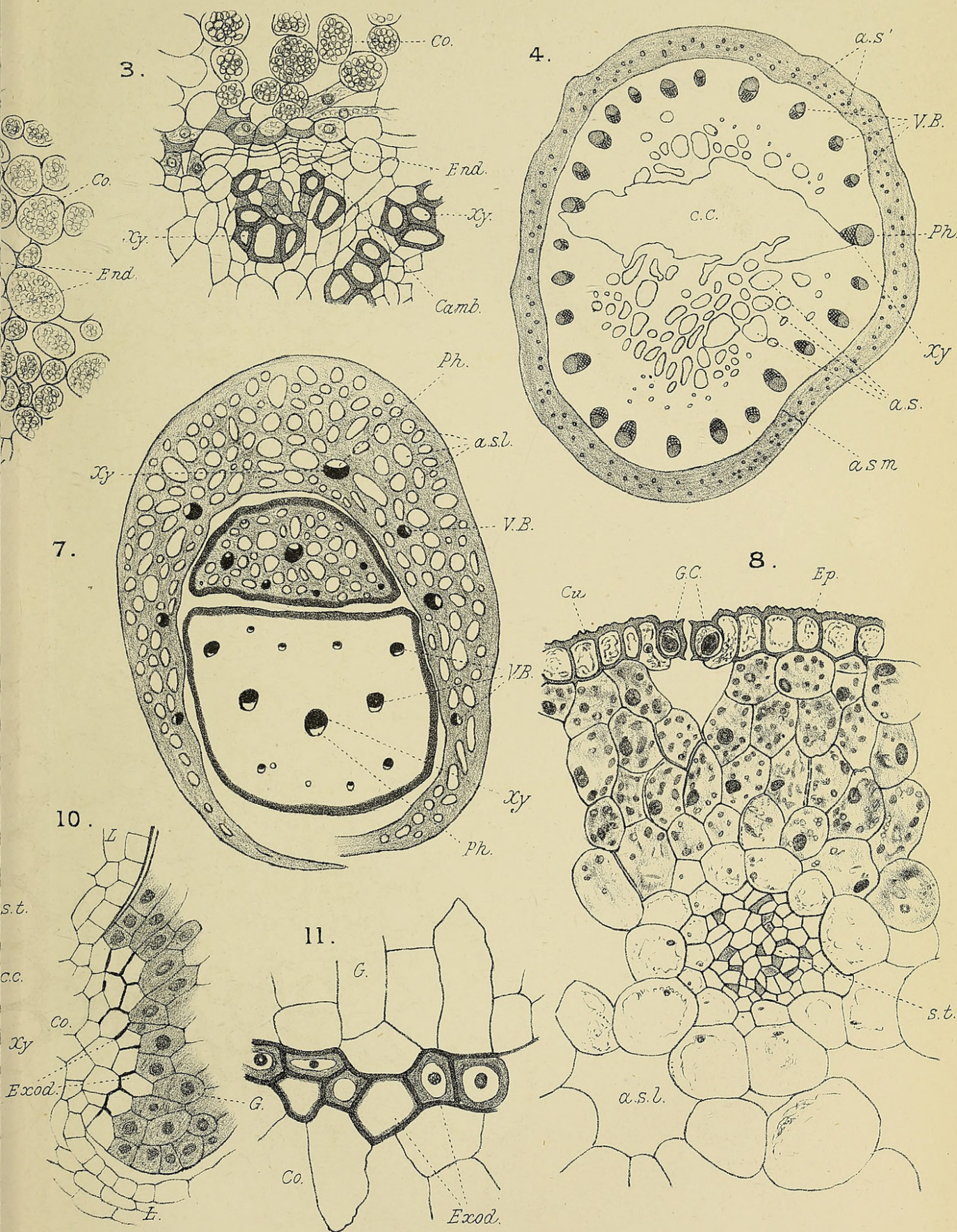
Fig. 19. A similar preparation of an older flower, showing the first two petals.

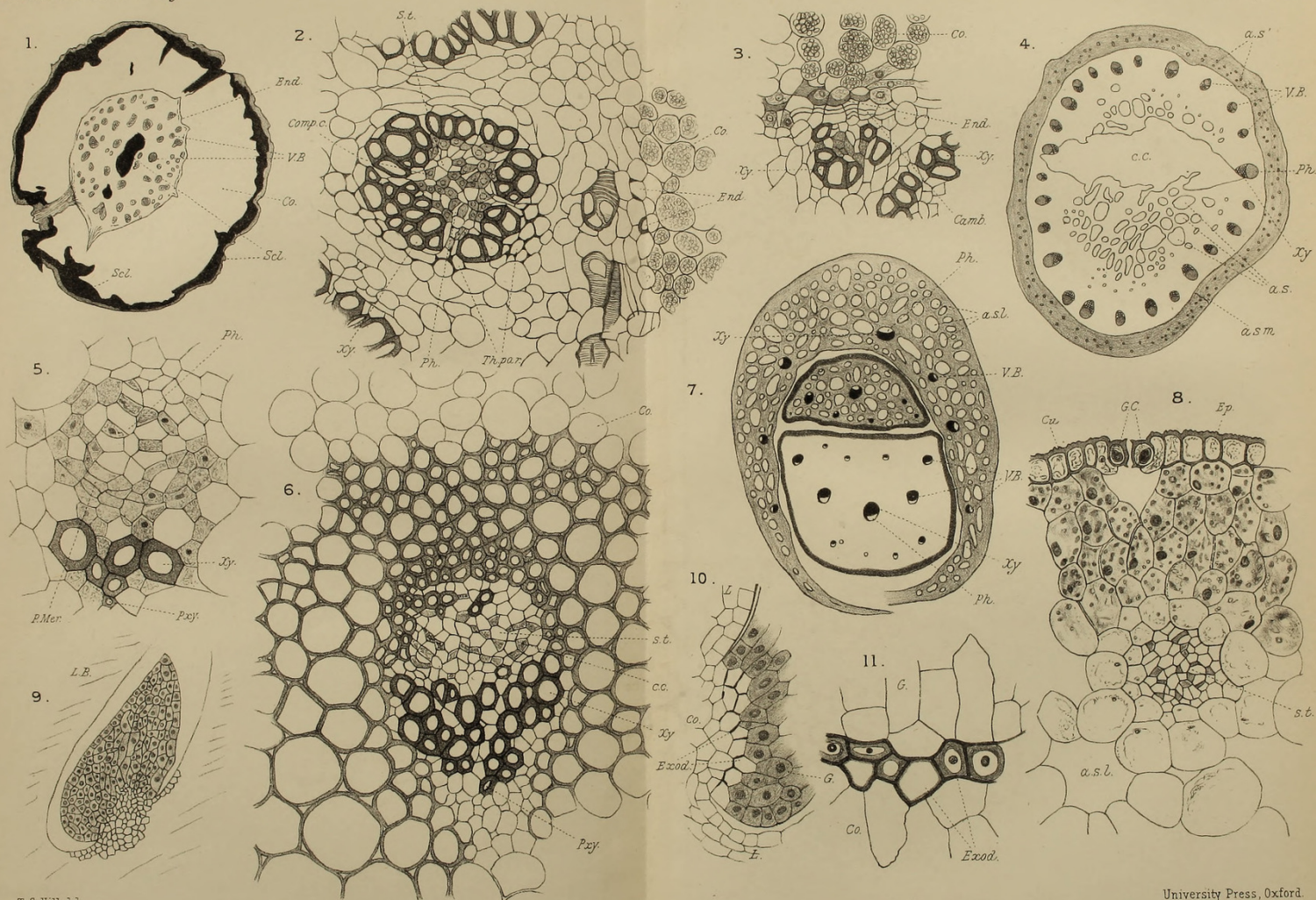
Fig. 20. An older flower with all the perianth-lobes complete.

- Fig. 21. A flower with the outer staminal whorl complete, and showing the first signs of the inner whorl at the base of p^1 .
- Fig. 22. A flower with the staminal whorl complete.
- Fig. 23. Part of a flower, showing the horse-shoe-shaped primordium of a carpel.
- Fig. 24. A longitudinal section of a young carpel, showing the basilar nature of the ovule.
- Fig. 25. A somewhat older carpel seen from above.
- Fig. 26. Longitudinal section of a slightly older carpel, showing the bending over of the outer wall and the development of the stigmatic surface.
- Fig. 27. A complete flower but immature.
- Fig. 28. Longitudinal section of an ovule, showing numerous antipodal cells. $\times 680$.
- Fig. 29. The next section, showing more antipodal cells. $\times 680$.
- Fig. 30. The micropylar end of the same embryo-sac, showing two cells of the egg-apparatus. $\times 360$.
- Fig. 31. The next section, showing three more cells of the egg-apparatus. $\times 360$.
- Fig. 32. Embryo-sac in longitudinal section, showing the fusion of the polar nuclei.
- Fig. 33. Longitudinal section of an embryo-sac, showing the first division of the embryo-sac nucleus. The synergidae are disintegrating. $\times 360$.
- Fig. 34. Longitudinal section of an embryo-sac, showing the two daughter-nuclei of the embryo-sac nucleus dividing, and also a two-celled embryo. $\times 360$.
- Fig. 35. Longitudinal section of a three-celled embryo, the basal cell slightly collapsed. $\times 650$.
- Fig. 36. Similar section of a four-celled embryo. $\times 650$.
- Fig. 37. Similar section of a five-celled embryo. $\times 650$.
- Fig. 38. Similar section of a seven-celled embryo, the cell beneath the terminal cell undergoing division. $\times 650$.
- Fig. 39. Diagram of a longitudinal section of a young embryo.
A. The first section, showing two terminal cells.
B. The next section, showing one terminal cell.
C. Plan of the topmost tier of cells.
C¹. Plan of the second tier of cells.
- Fig. 40. A. Longitudinal section of a nine-celled embryo. $\times 650$.
B. Plan of terminal cells.
C. Plan of tier immediately below.
- Fig. 41. Longitudinal section of a young embryo. Cell-contents not indicated. $\times 650$.
- Fig. 42. A similar section of an older embryo. The stem-apex is just arising; suspensor-cells also shown. Somewhat diagrammatic. $\times 160$.
- Fig. 43. Similar section of a mature embryo, showing the stem-apex with a second leaf and also the primary root. $\times 45$.
- Fig. 44. Longitudinal section of a somewhat younger embryo, showing the stem-apex and the primary root.
- Fig. 45. A. Diagram of a transverse section of the sheathing-base of a leaf.
B. Similar diagram of the upper region of the same leaf.
- The corresponding numbers in each refer to the same bundles. The letters in diagram B refer to bundles which were not found in the sheathing-base of the leaf.



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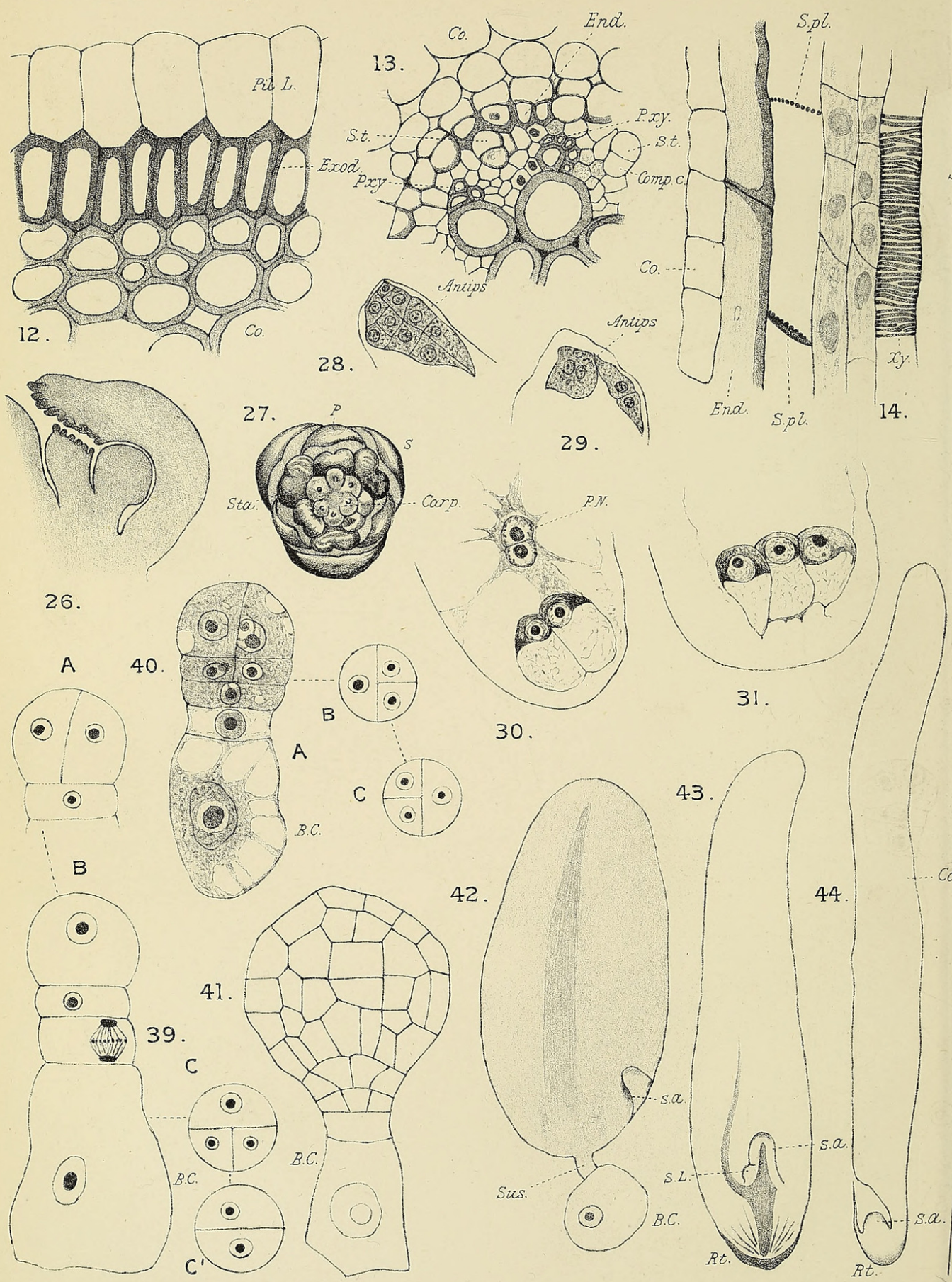




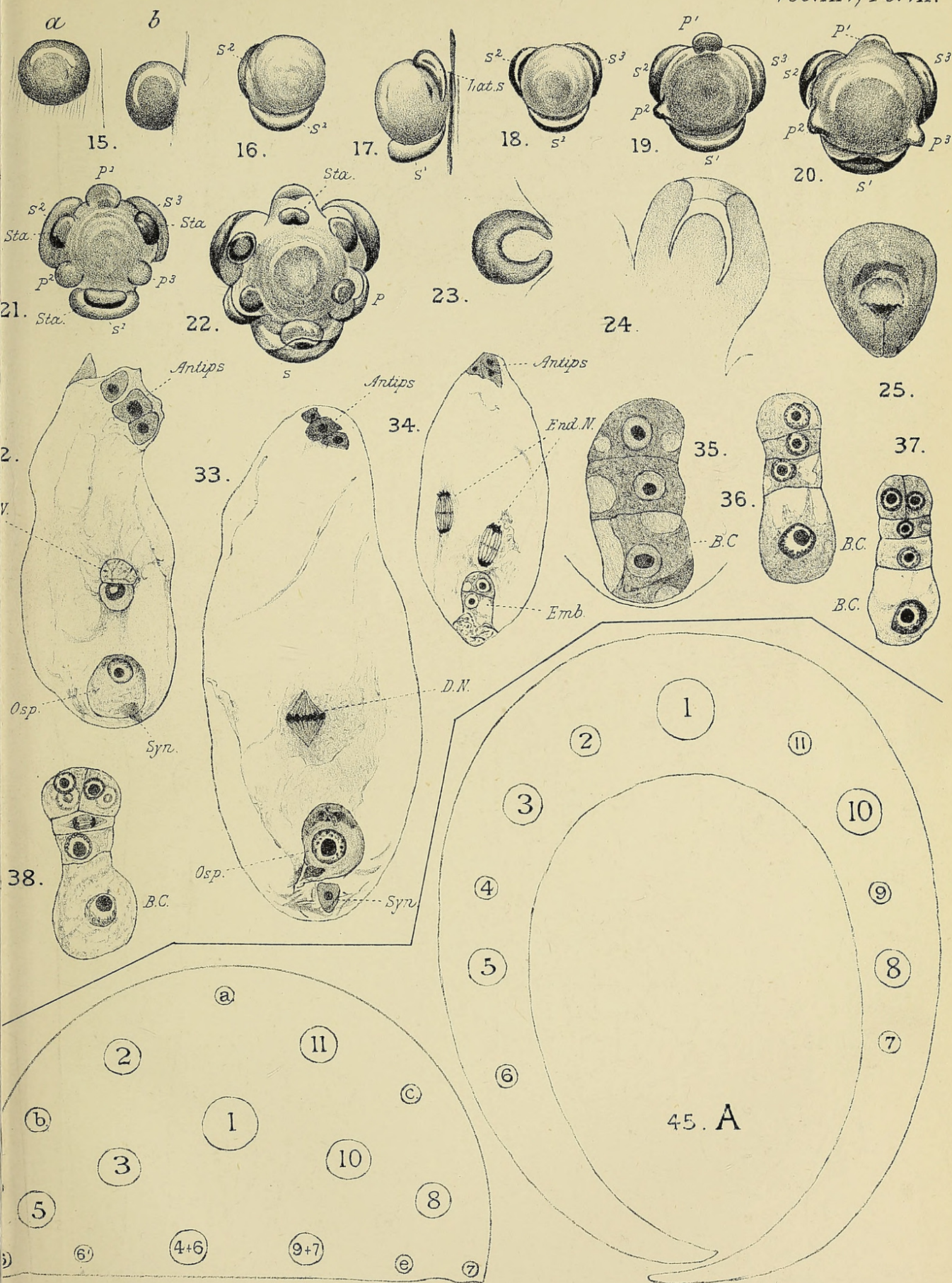
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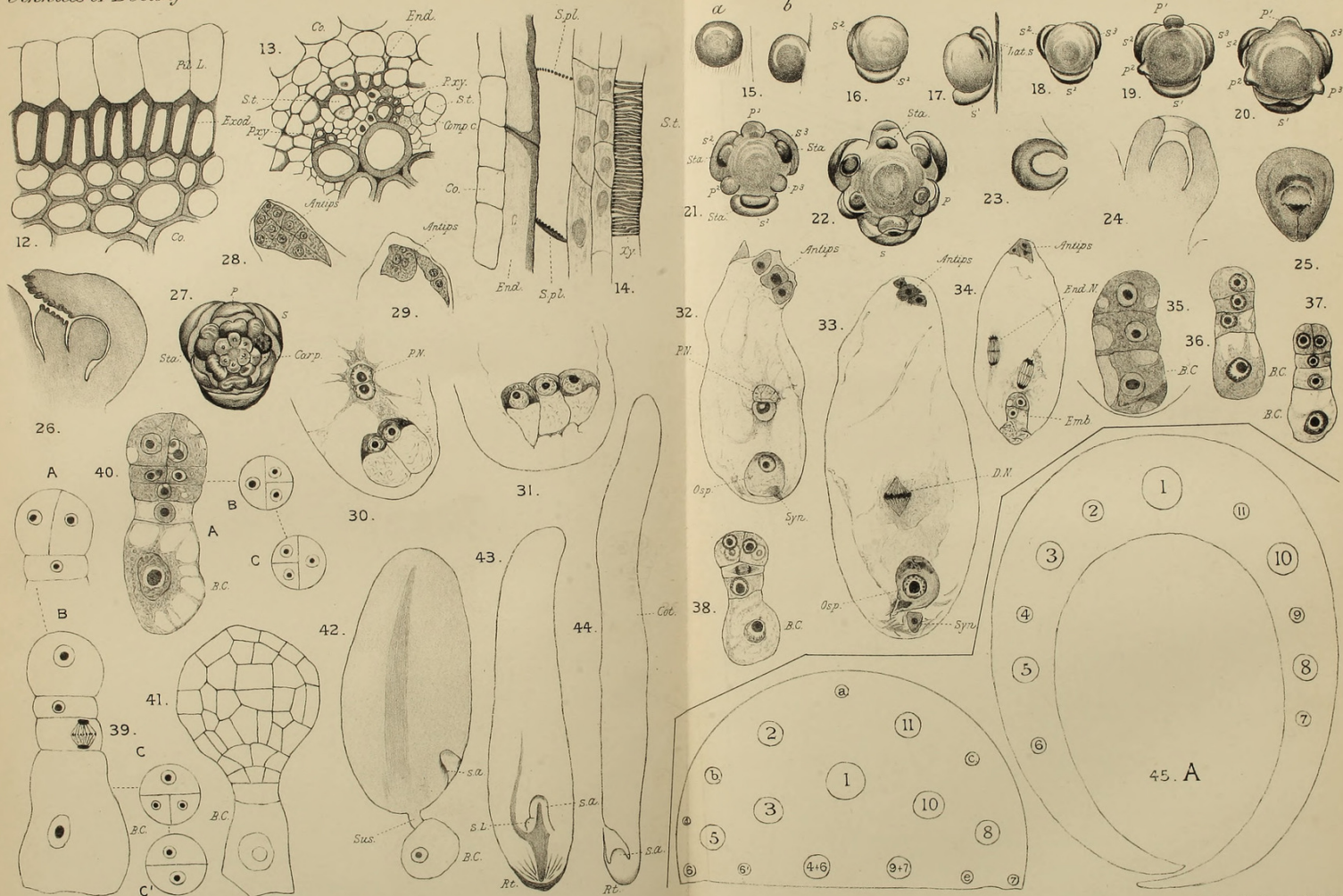
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