

On *Sarcodes sanguinea*, Torr.

BY

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With Plates **XVII, XVIII, XIX, XX, XXI.**
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THE family of the Monotropeae presents many problems to the botanist, not only on account of the remarkable habit of growth and mode of nutrition of its members, but also in view of its curious distribution and affinities. Any addition to our knowledge of such a group will be, then, not without value, even if it serve only as a contribution to a biological and systematic monograph of the whole order by some future worker. Of the eight genera¹ of the order all, with the exception of *Monotropa* and *Cheilotheca*, are limited in their distribution to North America; *Monotropa* being spread widely throughout the whole north temperate zone, and *Cheilotheca* being found only in the Himalaya. With the exception of *Monotropa*, little is known of these forms beyond the bare descriptions, which are often imperfect. Nor, on account of their peculiar mode of growth, has it been possible, so far, to cultivate these plants successfully in our botanic gardens. In view of this general obscurity in which so many of the genera remain, it has long been desirable that an investigation should be made into the general morphology and mode of life of such of them as should be available.

¹ *Allotropa*, *Monotropa*, *Pterospora*, *Sarcodes*, *Schweinitzia*, *Newberrya*, *Pleuricospora*, and *Cheilotheca*.

When then, in the autumn of 1888, some very fine specimens of *Sarcodes sanguinea*, in excellent preservation, were presented to the Royal Gardens, Kew, by Messrs. F. D. Godman and Elwes, it was most willingly that I undertook, at Mr. Thiselton Dyer's kind suggestion, to work through the plant and have a portrait of it executed by a competent artist.

In the present paper I confine myself almost entirely to a description of *Sarcodes* without entering into any discussion as to the affinities of the order *Monotropeae*, or into any history of the various memoirs bearing on the morphology of the other genera. In the important contributions by Drude¹, and by Kamienski², sufficient references will be found.

Sarcodes sanguinea, Torr., the 'Snowplant' of California, was first described and figured by Torrey³ in the 'Plantae Frémontianae,' and later, indifferently, by Chatin⁴ in his 'Anatomie.' The only other representation that I know of it is a sketch by Miss Marianne North in her gallery of flower paintings in Kew Gardens. This shows the plant amid its natural surroundings of snow and pine-woods. The drawing which is reproduced here is by Mr. John Allen, and I would express my indebtedness to him for the trouble and care he has bestowed upon it. The drawing is the size of life; the specimen being about 35 c.m. in length excluding the tuft of roots.

Each complete specimen of *Sarcodes* consists of a flowering spike with fleshy scales and a considerable tuft of roots. The whole of the epigeal parts are coloured a brilliant crimson, due to the presence in the superficial cells of the plant of a soluble, red colouring-matter, allied probably to the tannin series. It is, like its allies, entirely destitute of chlorophyll.

¹ O. Drude, Die Biologie von *Monotropa Hypopitys*, L., und *Neottia Nidus avis*, L. Göttingen, 1873.

² Fr. Kamienski, Les organes végétatifs du *Monotropa Hypopitys*, L. Mém. Soc. Nat. d. Sc. Nat. et Math. d. Cherbourg, t. xxiv, 1882.

³ John Torrey, Plantae Frémontianae, p. 17 and Pl. x, Smithsonian Contributions to Knowledge.

⁴ G. A. Chatin, Anat. Comp. d. Végétaux (Plantes parasites), tab. lv.

The plant is vegetatively reproduced, I apprehend, by buds from the roots in the same manner as *Monotropa*; new flowering shoots arising in this way each spring. Besides this, the number of seeds formed is very great.

The following is Torrey's original description of the plant:—
'SARCODES, Torr. in *Plantae Frémontianae*, p. 17, tab. x.

'*Calyx* quinquesepalus; sepalis concavis, basi vix gibbosis. *Corolla* campanulata, persistens, quinquelobata; lobis ovatis, erectis. *Stamina* 10, hypogyna; filamenta subulato-filiformia; antherae oblongae, biloculares, didymae, fere ad basim introrsum affixae; loculis sacculaeformibus, apice oblique truncatis, foramine amplo hiantibus. *Ovarium* hemisphaericum, quinquelobatum, quinqueloculare; loculis multiovulatis. *Ovula* horizontalia, anatropa. *Stylus* elongato-columnaris; *stigma* capitatum, subquinquelobum. *Discus* nullus. *Capsula* depresso-globosa, subquinqueloba, quinquelocularis. *Semina* numerosissima, ovata, aptera; testa reticulata. *Embryo* in basi albuminis, minutissimus, indivisus.—Herba *Californica*, carnosa, rubra; caule simplici, squamis carnosis vestito, in spicam conferte bracteata desinens; floribus pedicellatis.

'*S. sanguinea*, Torr. l.c. (*sp. unica*). Hab. Sacramento Valley, California. Colonel Frémont.'

The specimens on which this paper is based were collected by Messrs. Godman and Elwes near San Bernardino in the San Bernardino range, some 250 miles south of the Sacramento Valley where the specimens described by Torrey were taken. This then considerably extends the range of the plant.

The structure of the vegetative and floral organs of *Sarcodes* will now be considered in detail.

THE VEGETATIVE ORGANS.

The vegetative organs of *Sarcodes* agree in general, both in external conformation as well as in histological differentiation, with those of a large number of other saprophytic phanerogams destitute of chlorophyll. The organs in general are fleshy; the leaves are reduced to scaly imbric-

cating structures; the much-branched roots are associated with an investing fungal mycelium. All the shoots which appear above the soil are flowering shoots; purely vegetative shoots do not occur. As in many other saprophytes, the vegetative organs are brightly coloured and the number of seeds produced is very great. The embryos also are very small, and the amount of food-material (endosperm) accompanying them meagre.

Histologically, the tissues are not so well differentiated as in plants with a normal metabolism.

The vascular bundles are accompanied by large quantities of parenchyma; the sieve-tubes are small and not very numerous; the vessels and tracheides of the wood narrow, and often only imperfectly lignified. Stomata are entirely wanting, and intercellular spaces infrequent. These points in histological differentiation are associated with an absence of carbonic acid assimilation and a reduced transpiration-current.

The whole of the succulent pith and cortex of the stem consists of very thin-walled parenchyma-cells, crowded with starch-granules during early stages of development; it serves as a store of food-material to be used in the production of flowers and ripening of seed.

The more detailed account of the various parts is treated in the following order:—(1) Roots, (2) Stem, (3) Leaves, (4) Morphology of Flower.

1. *The Roots.*—The structure of these is of great interest in view of the general habit of this plant and of its dependence on organic matter in the substratum for much of its nutriment. The roots are attached in great quantities to the bases of the flowering shoots and form large and intricately woven masses of 'coralline' appearance¹. The specimen of *Sarcodes* on which this account is based had lost all but a relatively small portion of its roots before it reached my hands. It will be noted that the tuft represented in the portrait (Fig. 1) is only a small portion of the total cluster of roots. These roots

¹ I understand that the mass of roots attached to each specimen is often so large as to equal in bulk the whole remaining epigeal part of the plant.

present very constant (if exceptional) characters which agree with those belonging to herbarium specimens collected at various periods. With a little care the different root-axes can be dissected away from one another. Fig. 41 shows a fairly young portion of one axis drawn under the simple microscope. It bears numerous short branches (rootlets) arranged in four or five longitudinal rows, thus differing from *Monotropa*, which bears its rootlets in two or three rows. These secondary roots, in time, elongate and bear, in the same way, numerous roots of the third degree. By this continued branching the characteristic, dense, interwoven mass is produced. The lateral roots (of whatever degree) are not produced at right-angles on the axis from which they arise, but always slope forwards; the axis of a lateral root making an angle of about 45° with the region of its mother root in front of its insertion. These lateral roots, while still very young and not exceeding three or four millimetres in length, are already beset with little tubercles. These tubercles represent the origin of young rootlets.

Everywhere the surface of the roots is of a deep brown colour, and under a strong lens it shows a certain roughness of texture not found on the roots of ordinary plants. The roughness in question is due to the fact that the roots of *Sarcodes* are everywhere invested in a close-fitting sheath of fungal mycelium. Further examination shows that the roots here, as in *Monotropa*, display in a marked degree the phenomenon of *Mycorrhiza*.

First as to the more intimate structure of these roots. They are usually relatively thick and fleshy. A transverse section reveals a central vascular cylinder surrounded by a broad parenchymatous cortex. If the diameter of any root be 2 mm., that of the vascular cylinder will not exceed .5 mm. The xylems, usually five in number, are arranged in a ring, alternating with softer regions, the phloems, in the manner characteristic of roots. In the younger regions there is a central pith, gradually however becoming lignified and binding the individual xylems into one mass. The xylem consists of

tracheides, for the most part with scalariform thickenings; there are a few, in the protoxylems, with spirals. The endodermis is difficult to define, and I doubt if such a layer can really be distinguished here. The succulent cortex is well stocked with starch, throughout, from bundle-cylinder to epidermis. The epidermis does not form a continuous mantle, with cells fitting everywhere closely edge to edge, but consists of a layer of tube-like cells—the long axis of each cell being at right-angles to the surface of the root (*e*, Fig. 44). Each epidermal cell is laterally not in contact with its neighbours, but is isolated by the ingrowth of hyphae from the investing mycelial sheath above mentioned. The epidermal cells at their first origin are in contact, but early in their history the hyphae penetrate between them, and closely invest each epidermal cell on every side except its base (cf. Figs. 44 and 45). In Fig. 44 the epidermal cells are seen in most cases in section; two only (*a* and *b*) show a side-wall lying in the plane of section with the hyphae creeping over them. The nuclei of the epidermal cells are rod-like, or even dumb-bell shaped, and lie in the basal third of each cell. They are placed for the most part at right-angles to the long axes of the epidermal cells (Fig. 44, *n*). Starch occurs in the epidermis very rarely, though in quantities in the subjacent cortex. Outside is the layer of fungal mycelium constituting the mycorrhiza. This layer is particularly well exhibited in *Sarcodes*, where it attains a thickness of .2–.25 mm. The inner part, abutting on and penetrating between the epidermal cells, forms a very compact pseudo-parenchyma. In the outer layers of this denser stratum are embedded layers of flattened, dead cells, coloured deep brown with tannin. These layers, as will be shown below, are the remains of the root-cap. In an ordinary plant, in the absence of an investing fungal layer, the outer layers of cells of the root-cap fall away and the cap is renewed from within by a generating layer. Here, however, from the manner in which the hyphae are interwoven around them, this does not happen. Indeed, on the oldest roots, this same sheath—the survival of the root-cap—remains still enclosed

in the hyphal zone. Proceeding outwards, the texture of the mycelium becomes looser, and it no longer forms such a dense pseudo-parenchyma. The individual, septate, tubules (hyphae) are distinguishable, and at the periphery their ends turn radially outwards, terminating blindly in a manner resembling root-hairs.

It will be well now to describe the relation of the parts at the root-apex before treating of the phenomenon of mycorrhiza in greater detail. Fig. 43 represents a longitudinal median section of a root-apex of *Sarcodes*. Right and left, low down, the columnar epidermal layer is seen (*ep*). It may be easily followed right up to the apex, where it is covered in by the several layers of the root-cap. Indeed the root-cap arises in common with the epidermis, being formed from it by repeated tangential divisions. The inmost, and youngest, layer of the cap (*rc'*) is shown as having arisen quite recently in this way. Each layer of the root-cap in turn has originated in this manner, as an examination of Fig. 43 will show. Each extends a little further down the root than the one inside it, the fifth or sixth layer forming the outermost functional layer of the root-cap. The older layers have separated some little way from these by the ingrowth of the mycelium, and are still held there as described. In Fig. 43 they are not represented. The dermato-calyptrogenic layer is quite distinct from the initial group of periblem and plerome cells. These latter arise in common, and it is only a little way backwards that the distinction between them becomes manifest—the cells of the plerome undergoing longitudinal division more frequently than those of the periblem. Such a grouping of the cells at the root-apex is likewise found in *Monotropa*. The cap, however, in this latter genus is exceedingly thin, being only one or two cell-layers thick¹.

The apex of the root is everywhere enveloped in the mycelium. In this point *Sarcodes* differs from *Monotropa*. In *Monotropa* the extreme tip is quite bare, and the fungus is

¹ Cf. Kamienski, l. c., Pl. I. Fig. 5: also p. 11.

entirely post-apical. This distribution, stated by various authors, I have been able to confirm. Embedded in the hyphae are found the old layers of the cap that have become detached (Fig. 42), and a little distance behind, where the epidermis is immediately presented to the mycelium (the outmost *adherent* layer of the cap ceasing here), the ingrowing tubules of the fungus may be seen penetrating between the epidermal cells in the manner shown in Fig. 44.

These filaments never *enter* the epidermal cells, nor do they penetrate to a lower level than the base of the epidermis. The same arrangement is found in *Monotropa*. As the apex grows forward the outer layers of the cap continually break away from the underlying ones, but the mycelial layer prevents their falling away from the organ, hence they remain as strata—or as a series of hollow shells—kept in place, to even a great distance from the apex, by the hyphal layer. The mycelium must also keep pace in its growth with the elongating tissues of the root-apex; otherwise a rupture would occur.

The mode of branching of the roots of *Sarcodes* is exceptional and of considerable interest. A glance at Fig. 41 shows lateral roots arising remarkably near the apex. When the matter is investigated more closely it appears that *all lateral roots in Sarcodes have an exogenous origin*. Fig. 42 shows an early stage in the development of a lateral root, as seen in longitudinal section. The first indication of this event is a slight bulging of the periblem, accompanied by a radial division of the overlying dermatogen. Tangential divisions then arise in the dermatogen and the first layer of the root-cap of a new lateral root is formed (*rc'*, Fig. 42). The lateral root arises so near the apex that it is enveloped in the root-cap of the mother-root. In the undifferentiated tissue a plerome is differentiated, becoming continuous with that of the primary root. This takes place before the young rootlet commences to grow, appreciably, in length (Fig. 42). I have examined the insertion of a great number of lateral roots of all ages, but in no case does any exception occur to the rule

that, in *Sarcodes*, all lateral roots are formed exogenously and not from any internal pericycle as happens in ordinary cases.

In *Monotropa*, on the other hand, the roots branch always normally, that is, endogenously. This was shown by Drude¹ and by Kamienski², and I have found it to be the case in all specimens examined. The only other genus of Monotropeae, the roots of which have been available for examination, is *Pterospora*. Here, not only is there a well-marked mycorrhiza, but the root-branching is *exogenous* and agrees with *Sarcodes*. That these root-like organs in *Sarcodes* and *Pterospora* are true roots is not, I think, to be questioned. They possess well-marked root-caps, their bundles are radially arranged, and there is a total absence on them of scale-leaves of any kind.

The exogenous branching of the roots, occurring in *Sarcodes* and *Pterospora*, may be regarded as a special adaptation, in these plants, that has been perpetuated as being a useful variation. By an exogenous method of root-branching the formation of a wound, which must always occur in endogenous branching, is avoided, and the inner tissues of the plant will not be so liable to the entry of the fungus forming the mycorrhiza. In the case of endogenous branching the wounds formed in the cortex, by the penetration of the lateral roots, must be points of weakness should there be any tendency on the part of the fungus to make an entrance. It must be admitted that in *Monotropa*, where lateral roots arise endogenously, no such behaviour of the fungal hyphae has been observed. However, before discarding the view above put forward it must be remembered that at present really very little is known of the nature of these mycorrhiza-fungi, and whether the conditions that obtain in one case hold good for another. An alternative, and perhaps simpler, explanation of the phenomenon may be suggested by the general reduction of the vegetative organs, as a whole, in these saprophytic plants. The organs of plants which obtain most of their food in the form of complex organic substances show less histo-

¹ Drude, l. c., p. 43, and Pl. III. Fig. 15.

² Kamienski, l. c., p. 18, and Pl. I. Fig. 8.

logical differentiation than where a normal metabolism exists; and processes of a complex nature—as for instance the endogenous development of lateral roots—may gradually, in the general degradation, give place to simpler methods. My own view, however, is that here the exogenous root-branching is an advantageous variation that has been perpetuated.

As regards the relation of the roots of *Sarcodes* to the substratum:—from notes kindly communicated by Mr. Elwes no direct connection would appear to exist between them and the pine-roots among which *Sarcodes* grows. The plant vegetates amongst decaying portions of the pines, leaves and the like, and possesses nothing of the nature of haustoria or parasitic attachments. No doubt *Sarcodes* resembles *Monotropa* in this respect, and, as in this case, although the roots of the saprophyte come into very intimate relation with the roots of other plants, still they are never organically united¹. I have been at some pains to ascertain whether *Monotropa* roots ever form haustoria, and for this purpose have examined many specimens of *M. glabra* from beech- and of *M. hirsuta* from pine-woods, without meeting with a single case to support the view of parasitism. Not infrequently I found the

¹ In view of the prominent position now held among botanists by the Mycorrhiza question, it may not be without interest to call attention here to the observations of certain British naturalists of a past generation, more especially as they have been quite lost sight of in the recent discussion of the matter. In the years 1841-2 a lively discussion was running in the pages of the now defunct 'Phytologist.' Ed. Lees (p. 97) speaks of 'a hirsuture that appears like a byssoid fungus' on the roots of *Monotropa*. This 'hirsuture' he considered to be a portion of the *Monotropa* plant, which he regarded as a parasite. Wm. Wilson (l. c., p. 148) failed to discover any parasitic attachments, and considered the 'byssoid growth' as certainly no part of the plant. A little later (l. c., p. 297) we find Ed. Newman speaking of the 'byssoid growth' as an essential part of the plant, thus agreeing with Lees in that point. He differs from Lees, however, in denying its parasitic habit. Finally, T. G. Rylands, in a detailed paper (l. c., p. 341), ends the discussion. His paper is illustrated with a number of woodcuts. The 'byssoid substance,' he says, 'is really fungoid, and performs no essential function in the economy of the *Monotropa*.' He detected three types of Fungi—*Sepedonium*, *Epiphagos*, and *Zygodesmos*, the last characterised by buckle (geniculated) hyphae. Hence it appears that although the anatomical relations of the *Monotropa* roots were long ago familiar to naturalists, the view as to the symbiotic nature of mycorrhiza is essentially modern.

beech-roots (generally dead) wrapped round with a weft of the same mycelium that formed the mycorrhiza on the *Monotropa*, but never any haustoria. Drude¹, who though he had found such connections, and figured them, has not been confirmed by Kamienski². My own examination confirms Kamienski on this point. *Sarcodes* may safely I think be regarded, like *Monotropa*, as a saprophyte or humus-plant³.

2. *The Stem*.—This is everywhere hidden from view; below by the imbricating scale-leaves, above by the bracts and flowers and by the flower-buds. It is very thick and succulent; its diameter at different heights in the specimen drawn in Fig. 1 was 2.5 cm. at the base; 4.5 cm. at a distance of 10 cm. from the base; then gradually tapering off towards the apex. The thickest portion corresponds to the thickest part of the 'bulb.' The bulk of the stem is built up of a succulent parenchyma in which is disposed a ring of vascular bundles, which is somewhat nearer to the periphery than to the centre of the stem. In this specimen, in which the seed was not yet ripe, the parenchyma was everywhere well-stocked with starch grains. In their chemical and physical properties these grains are indistinguishable from those in the tissues of ordinary green plants. This I mention as Drude⁴ finds the 'starch grains' of *Monotropa* differing in certain respects from normal starch, and gives to the substance of which they are composed the name of Monotropin. The bulk of the starch in the stem of *Sarcodes* is employed in the ripening of the seeds. With the ripening of the seed the shoot dies down, new shoots being formed each year by direct budding from the roots.

Any transverse section through the stem in the lower

¹ Drude, l. c., p. 45, and Pl. IV. Fig. 16. Drude only found them exceptionally.

² Kamienski, l. c., p. 30.

³ An interesting observation is communicated by Mr. Wolley Dod to the *Gardeners' Chronicle* (August 17th, 1889, p. 195). He found that *Monotropa* which flourishes amongst the roots of Willows in the neighbourhood of Southport was often growing in rings, after the manner of a 'fairy ring.' He suggests that this phenomenon is perhaps due to the same cause.

⁴ loc. cit., p. 49.

'bulbous' portion of the plant shows an irregular outline, due to the bases of the closely imbricating scales (Fig. 46). The shield-like sections of these latter are not quite symmetrical (Fig. 46, *lb*), owing to the rather oblique insertion of these scales.

As regards the distribution of the vascular bundles in the stem: the bundles form an undulating ring around the succulent pith. Between this ring and the periphery of the stem are seen the bundles which pass off to supply the leaves and, where they occur, to the flowers. Fig. 46 is a transverse section through the lower portion of the stem. The bundles to the leaves pass out in groups of two, these again spreading in a tangential direction when they reach the leaf. Higher up, in the region of the inflorescence (Fig. 47), there is, on the inside of each pair of bundles passing to the leaves, a small group which supplies the axillary flower-stalk. The distinction between these two groups of bundles is well shown in Fig. 48 (*fb* and *lb*). The orientation of the bundles is that characteristic of Dicotyledons, an inner xylem and outer phloem arranged collaterally (Fig. 48). The bundles undergo no secondary increase in thickness. The xylem is small in quantity in comparison with the total bulk of the plant; a reduction doubtless correlated with the small transpiration-current. The ring of bundles is traversed by relatively broad medullary rays at frequent intervals. The elements of the xylem are scalariform vessels and (in the protoxylems) narrow spiral vessels.

Corresponding to each xylem-group is a phloem-group (Fig. 49). The phloem is built up entirely of soft elements. These consist of narrow sieve-tubes with slightly oblique sieve-plates, companion-cells, and a large amount of small-celled phloem-parenchyma. Thin callus-plates are present on the plates of some of the more peripheral sieve-tubes. Neither the sieve-tubes nor their companion-cells show any special peculiarity.

3. *The Leaves* show a gradual transition in form, from the small scales at the base, to the thick, fleshy ones covering the

greater part of the vegetative portion of the shoot. These again pass over into the linear bracts. This is illustrated in Fig. 50, *a-e*, each drawing being of the natural size. The leaves and bracts are fringed with stalked glands. The whole outer face, especially in the case of the bracts, is pubescent. Fig. 51 shows the margin of a bract, under the simple microscope, with the glands; whilst in Fig. 52 a longitudinal section of a single gland is given. The structure of the scales calls for no special comment. They consist of a number of layers of thin-walled parenchymatous cells traversed in the median plane by a number of reduced, collateral, vascular bundles. The limiting epidermis is cuticularised except at the glands. No stomata are present, and the intercellular system is not well-marked.

4. *Morphology of the Flower*.—Each individual shoot, as in *Monotropa*, terminates in an inflorescence, here crowded and bearing a large number of flowers. The inflorescence is built on the indefinite type (racemose), and *Sarcodes* would appear to be unique amongst Monotropeae in this respect. *Monotropa* and the others have the leading flower of the inflorescence terminating the axis. The proportion borne by the inflorescence to the rest of the plant is sufficiently shown in the portrait of the plant (Fig. 1). The closely imbricating scales of the 'bulbous' portion pass over gradually into others, less fleshy, more loosely arranged, and somewhat narrower and longer (cf. Fig. 50, *a, b, c, d*, and *e*). These may be spoken of as the *bracts*; each subtends a single flower. The lower flowers have fairly long pedicels, exceeding the length of the flower several times; those above are gradually shorter. At the time when the shoot is elongating, and the spike of flowers being pressed through, and elevated above, the surface of the ground, each flower-bud is ensheathed and protected by its subtending bract. The bracts themselves are hollowed out in a boat-like manner, as shown in Fig. 4. Later, when the flowers are about to expand, the bracts curve backwards and the flowers are exposed. The bracts persist until the ripening of the fruit. Like the scaly,

fleshy leaves, they are fringed with a series of short processes of a glandular nature, and the whole outer face is covered with small glands. The head-cells of these glands possess a very granular protoplasm, but with the nature of the secretion I am unacquainted. It is not improbable that they serve to ward off the visits of 'unbidden guests,' creeping insects abounding in the humous mould in which *Sarcodes* grows.

Throughout, I have found the flowers to possess 5-merous symmetry with superior ovary, and all floral members entirely hypogynous. There are no bracteoles, and the sepals form a very definite whorl. The individual sepals are entirely free from one another down to the base. They are bright crimson in colour, and are covered externally with small glands resembling those of the bracts. The sepals are inserted on the two-fifths arrangement, and, like the petals, are persistent.

The corolla, unlike the calyx, is entirely smooth, almost waxy in appearance. It is sympetalous, its members being united to about half-way up. It equals the calyx in length, but its lobes are slightly curved outwards at the tip and project between the tips of the sepals (Fig. 3). The aestivation of the corolla in the bud is always contorted, as shown in the floral diagram (Fig. 23).

Passing on to the stamens. These are ten in number, and stand, in the mature flower, and in the youngest flower-buds available, in apparently one whorl. They are little more than half the length of the corolla, and the anthers are held vertically in a ring, just below the stigma. The filaments are subulate and, at the base, slightly expanded, becoming connate. These relations are shown in Fig. 3. The lower thirds of the filaments are pressed closely against the ovary, and between them project the ten lobes of the ovary, the stamens lying in the grooves between these lobes. The anthers are basifixed, and the two halves are parallel. Each anther-half possesses, in the usual manner, two loculi. Dehiscence takes place by two oval pores at the top, and towards the *outside*, of

the anther: dehiscence is thus extrorse. The method of dehiscence is of some interest. The two oval pores situate on the dorsal (outer) side of the anther are shown in Fig. 5. The pores lead, *immediately* only, into the two loculi which are directed *away from* the ovary (Fig. 6, A). During development (after the maturing of the pollen) the walls separating the anterior and posterior loculi of each anther-half break down, so that pollen formed in the loculi *towards* the ovary can likewise escape by these pores. Fig. 6, A, B, and C, represent transverse sections of the anther taken at heights corresponding to A, B, and C in Fig. 5. A alone traverses the region of dehiscence and shows the openings leading into the dorsal cavities. The wall that breaks down in development is indicated by dotted lines.

Dehiscence is not effected by any 'fibrous layer,' but the epidermis in the region where rupture occurs is strongly developed and columnar; dehiscence is caused by the separation of these cells along a certain line as they dry. This is shown in Fig. 7, which represents as it were the left-hand bottom corner of such a section as Fig. 6, A. The dorsal loculus (*dl*) very small, then the broken down partition (*p*), and the much larger ventral loculus (*vl*). Noteworthy is the occurrence of a strand of fibrous and lignified cells (*f* in Fig. 7) immediately below the epidermis. This strand runs down the outer lip of the pore. A dotted line around the left pore (Fig. 5) marks the course of the strand in question. I attribute a strengthening function to this hardened tissue; perhaps it prevents rupture of the wall of the anther directly into the ventral loculus (as at such a point as *x*). Fig. 8 is a transverse section across a young anther, just after the partitions have broken down, but before any opening to the outside has been made.

The pollen is powdery and simple, and not massed together, as in many Monotropeae. The grains are spherical, with outer and inner walls (Figs. 13, 14, and 15). The two nuclei of each grain are very easily seen on staining. One is spherical (the vegetative nucleus), the other spindle-shaped (the generative nucleus) and curved in a crescentic manner (Figs. 13 and

14). At an earlier stage, at the time when the tapetal layer is breaking down, and immediately after the division of the pollen-mother-cells, the division into two cells in each pollen-grain is very clearly shown (Figs. 10, 11, and 12). These cells are unequal; the larger one contains a larger nucleus, often with two nucleoli at this time; the other, small and bi-convex, a much smaller nucleus. It is the larger nucleus that is afterwards spindle-shaped and constitutes the generative nucleus of the pollen-grain. There is an absolute separation of the protoplasmic bodies of the two cells within the pollen-grain; later however they fuse. Occasionally the division is found to be into equal parts (Fig. 15). The division of the mother-cells into pollen-grains takes place in the ordinary, dicotyledonous manner, the pollen-grains lying, as tetrads, in the mother-cells (Fig. 9).

A great number of pollen-grains is present on mature stigmas, and the pollen-tubes may be very readily dissected out from the style and ovary. In these tubes very large plugs are developed cutting off the lumen of the younger portion from the lumen of the older. These plugs arise first as annular cushions on the inside of the wall whereby the lumen is constricted. This goes on until the cavity at that point is obliterated (Fig. 16, *a* and *b*). Deposition of substance often continues till the pollen-tube is plugged for a length of .25 mm. Often the thickening is very irregular and recalls the callus-depositions in the trumpet-hyphae of certain *Laminarieae* (cf. Fig. 16, *c*, *d*, and *e*). No layers of stratification are demonstrable even with the highest powers of the microscope, nor after using re-agents.

The Ovary has a very broad attachment to the receptacle. Its horizontal diameter exceeds by more than one-third its vertical. It is produced upwards into an erect style, bearing a 5-lobed stigma. The whole height of the gynaeceum is about two-thirds that of the corolla. Externally the ovary is prominently 10-lobed, each lobe projecting between two stamens (Fig. 3). Each lobe is continued down into a nectar-secreting region (*n*, Figs. 3 and 17), and in longitudinal section

it is seen that the wall of the ovary is thickened at points corresponding to the nectariferous areas. The arrangement of the nectaries in the different genera of Monotropeae is a matter of much interest. Thus, in *Monotropa glabra* (Fig. 22), each lobe of the ovary is produced downwards into a small appendix, the nectary *n*. These appendices curve in pairs, embracing the antipetalous stamens, and drop their nectar into the gibbosities of the petals. This is shown in Fig. 22, the petalline stamens (*p s*) in each case being thus embraced. The petal (*p*) shown in the figure receives the nectar from glands surrounding the stamen *p s*². The other petals have been removed, but their scars do not show since their insertion is so close up under the stamens: *s s* are the basal portions of the sepals which stand in a very loose spiral. Other genera, likewise, afford most interesting details, but a special account of these structures in other members of the order is deferred to a future paper.

The ovary itself is 5-carpellary, each carpel being bilobed (cf. Fig. 21, *H*, a transverse section taken midway between the base of the ovary and the insertion of the style). The figure shows the five septa and the enormously developed axis, with a bilobed placenta projecting into each 'cell' of the ovary. The lobing of the ovary wall corresponds entirely to the lobing of the placentas. In this type the transition, from parietal to axile placentation, is well shown, and is illustrated in the series of transverse sections, Fig. 21, *A-H*. *A* is through the stigma, and the inwardly projecting lobes appear lower down as the ovarian dissepiments; *B* is across the style, and shows the 'style-canal'; *C* is through the insertion of the style on the top of the ovary, and shows the enlarging lobes. In 21 *D* the region where ovules are borne has been reached. In *E* the placentas are much enlarged and the central cavity correspondingly diminished; in *F* this is carried till finally in *G* there is absolute fusion of the placentas, and, in the greater part of the ovary, the lines of fusion are indicated by the median groove in each of the five placentas (Fig. 21, *H*). This series of sections shows sufficiently clearly that in the

same ovary the placentation is parietal above, axile below. Further remarks on the nature of the placentation and on its possible origin are deferred till further investigations on the floral morphology of the *Monotropeae* are completed. It is exceedingly difficult to argue from one particular case whether axile is derivable from parietal placentation, or whether the reverse is the case.

That the style-canal gives access to each ovarian chamber is easily to be inferred from the series of transverse sections described. In Fig. 17 is drawn a dissection of an ovary showing more exactly this communication. On the left the section has passed exactly in the median plane of a loculus, and the continuity of the ovarian chamber and the style-canal is seen to be direct. On the right, the section has passed through *one side* of the loculus, and the direct continuity does not appear. However, the dark shading *ch'* indicates the chink leading into the loculus, and a bristle can be easily passed through it and out into the ovarian cavity. In the same way the chink *ch²* leads into that chamber of the ovary immediately behind. The lighter regions, between the chinks (Fig. 17), indicate ridges running longitudinally down the style (the same as are figured in Fig. 21, *b* and *c*). The ovules are small and exceedingly numerous, as in Orchids.

The calyx and corolla are persistent till the ripening of the fruit. The wall of the ovary becomes hard and brittle, but dehiscence is not effected by a separation of the ovary into valves, as happens in *Monotropa*, and in some other genera of the order; it is *circumscissile*. Dehiscence is effected by the formation of a circular split, around the base of the style, at a little distance ($1-1\frac{1}{2}$ mm.) from it. It is by this that the seeds escape, since the wall of the fruit does not separate into valves. The circular chink is shown in the drawing of the dissected fruit (Fig. 20, *d*). The bi-lobed placentas in two of the chambers of the ovary are exposed in the dissection.

The method of dehiscence here obtaining illustrates how, by a special adaptation, advantage is taken by a plant of a structure common to it and its allies, but which has not been

made use of by the allied genera. At the time of flowering, there is around the base of the style a ring-like depression, or invagination, of the epidermis. This is seen in the longitudinal sections of the ovary represented in Figs. 17 and 18; also in the transverse section, Fig. 21, C, taken at the insertion of the style. In a more highly magnified longitudinal section (Fig. 19) the nature of the depression is seen. It penetrates three quarters of the way through the ovary wall, and only a narrow zone of tissue separates it from the cavity of the ovary. It is the small cells (*x*, Fig. 19) of this region that, breaking down as the fruit ripens, bring about the peculiar dehiscence (circum-scissile) described above. In *Monotropa* a circular depression occurs in the same position, but its depth is only one-third of that in *Sarcodes*, and it does not lend itself to this method of dehiscence. Similarly, in some other genera of Monotropeae.

In old specimens of *Sarcodes*, when many of the fruits are already in seed, small flowers appear in the axils of the fleshy leaves, below the general inflorescence. These, in ordinary flowering specimens as that figured, are still minute buds, 1 mm. in length, embedded in the fleshy bases of the scale.

Development of the Ovules. — The ovules are very numerous, and their development can be easily followed. Each arises on the young placenta as a small upgrowth of tissue, by the formation of tangential divisions in the layer immediately below the epidermis. At an early period the terminal cell of the hypodermal tissue of the young ovule is marked out by its relatively large size (Figs. 24 and 25, *a*), and as the terminal portion of the ovule (nucellus) begins to curve over, it becomes very prominent. At the same time, the commencement of the single coat of the ovule arises (Fig. 25, *int*). The large terminal cell is the *archesporium*, and it undergoes a number of divisions, prior to the formation of the embryo-sac. These are shown in Figs. 26–30. There is, cut off from the apical end of the archesporium, first one and then a second ‘cap-cell’ (*cc* in Figs.); this number is not exceeded. The large, third cell of the row, so formed, is the embryo-sac. In succeeding stages the cap-cells gradually dwindle as the

embryo-sac elongates. The nucleus of the embryo-sac divides (Fig. 30), and the daughter-nuclei travel to the two ends; a large vacuole arising in the protoplasm between them (Figs. 31 and 32). Each nucleus divides a second time (Fig. 33), and then once again. Two of the four nuclei, at the micropylar end, become the nuclei of the two synergidae, a third that of the egg-cell (oosphere), whilst the fourth moves downwards and fuses with a similar, ascending one from the lower group, constituting the 'definitive nucleus of the embryo-sac' (Figs. 34 and 35). The three nuclei, remaining at the basal (chalazal) end of the embryo-sac, are the nuclei of the antipodal cells. They become invested with cell-membranes, and play no further part (Figs. 34, 35, and 38). The embryo-sac, as represented in Fig. 34, is ready for fertilization. The definitive nucleus is suspended by delicate filaments of protoplasm. After fertilization, the synergidae disappear and divisions arise in the egg-cell. Soon, a rudimentary embryo is formed, consisting of a short suspensor of three cells and an enlarged embryonic cell, in which the formation of one or two anticlinal walls may be traced (Figs. 36, 37, 38, and 39). Simultaneously with the segmentation of the egg-cell, the definitive nucleus divides. Each nuclear division is accompanied by the formation of a delicate transverse wall (Figs. 36, 37, and 39). The cells so arising constitute the endosperm. Even in the ripe seed the endosperm is relatively scanty. The seeds formed are extremely numerous, small and light, a condition not infrequently met with among plants with saprophytic or parasitic habit. They are destitute of any wing. I was unable to study the later stages in the development of the seed, owing to lack of material sufficiently advanced, but very few more divisions arise either in the embryo or in the endosperm. The history of this development agrees closely with that given by Strasburger¹ and Koch², for the allied *Monotropa*.

In this paper I have confined myself to the description of

¹ E. Strasburger, Ueb. Befruchtung und Zelltheilung. 1878.

² Koch, Entwickl. d. S. in Pringsheim's Jahrb. f. wiss. Bot. xiii.

the more salient points presented by *Sarcodes*, and do not propose to enter here into any discussion as to its position in the order Monotropeae and affinities. This can be done with more profit in a paper dealing with the morphology of all the members of the group, as to which at present our knowledge is imperfect. That the group as a whole will repay investigation I have little doubt. Amongst other matters of interest would be the determination of how far the points of distinction of its several members are adaptive. That many of them are so is, I think, probable.

JODRELL LABORATORY, KEW.

EXPLANATION OF FIGURES IN PLATES XVII,
XVIII, XIX, XX, XXI.

Illustrating Mr. F. W. Oliver's paper on *Sarcodes sanguinea*.

Fig. 1. Life-size portrait of the plant at the time of flowering in natural colours. Only a portion of the roots of the plant is shown. Drawn by Mr. John Allen.

Fig. 2. A single flower with two sepals removed. *k*, calyx; *c*, corolla. Natural size.

Fig. 3. View of the interior of a flower after removal of part of corolla, showing the stamens and anthers with porous dehiscence, the nectaries, ovary and stigma. *k*, calyx; *c*, corolla; *st*, stamen; *n*, nectary. (2/1.)

Fig. 4. A single flower-bud with its subtending bract attached. To show the curving of the bract round the bud. *br*, bract. Natural size.

Fig. 5. View of an anther seen from the dorsal (outer) side. Right and left are the two halves of the anther adnate to the filament. The letters A, B, C, indicate the heights at which the corresponding sections in Fig. 6 were made. *cn*, connective; *f*, shows position of sclerized layer at margin of pore; *fl*, filament; *p*, pore. (12/1.)

Fig. 6, A, B, C. Transverse sections of anther cut at heights indicated in Fig. 5. The dotted lines indicate the partitions which break down in development. *v*, ventral side; *d*, dorsal side. (12/1.)

Fig. 7. Transverse section of part of an anther more highly magnified to show the sclerized strand running in the wall just to the outside of the dorsal pollen-sac. *cn*, connective; *d l*, dorsal pollen-sac; *f*, sclerized strand; *p*, remains of broken-down partition; *v l*, ventral pollen-sac. (120/1.)

Fig. 8. Transverse section of a younger anther, showing first rupture of partition between dorsal and ventral pollen-sacs. *d*, dorsal; *v*, ventral side. (18/1.)

Fig. 9. A pollen mother-cell containing a tetrad of pollen-grains, each as yet with a single nucleus. The fourth grain not shown.

Figs. 10, 11, and 12. Single pollen-grains after division of contents into a larger and a smaller cell.

Figs. 13 and 14. Somewhat later stage in development of pollen. The cell-protoplasm no longer shows division into two masses. The two nuclei show characteristic differentiation, one being spindle-shaped, the other globular.

Fig. 15. Showing division of contents of pollen-grain into equal portions. Not frequently met with.

Fig. 16, *a, b, c, d, e*. Callus-like thickenings in the pollen-tubes. (400/1.)

Fig. 17. Longitudinal section through the ovary, showing the fleshy axile placenta, the ovules and the style-canal, and the method of communication between it and the various chambers of the ovary. *c*, corolla; *ch*, chinks leading from style-canal into ovarian chambers; *k*, calyx; *n*, nectary; *p*, placenta with ovules; *r*, annular invagination surrounding base of style, by the agency of which circumscissile dehiscence is afterwards effected; *sc*, style-canal; *st*, insertion of stamen. (Enlarged several times.)

Fig. 18. Longitudinal section of the upper part of the ovary, showing the ring-like depression around the base of the style. *ov*, ovarian cavity; *r*, annular depression; *sc*, style-canal. (8/1.)

Fig. 19. Much enlarged view, showing the annular depression in a longitudinal section similar to that represented in Fig. 18, and its relation to the cavity of the ovary. *bs*, base of style; *r*, annular depression; *ov*, cavity of ovary; *ow*, wall of ovary; *x*, cells which in dehiscence break down. (60/1.)

Fig. 20. A ripe fruit laid open so as to show the bi-lobed placentas covered with very numerous minute seeds, the circumscissile method of dehiscence, and the rupture of the dissepiments; *d*, region of dehiscence.

Fig. 21, *A, B, C, D, E, F, G*, and *H*. A series of diagrams representing the placentas and their relation to one another as shown in a number of transverse sections of the stigma, style and ovary. *A* is through the stigma; *B* through the style, with central cavity the style-canal; *C* is through the insertion of the style on the ovary, and so on to *H*, which is cut about half-way down the ovary. It is seen that in the upper part of the ovary the placentas, which are directly continuous with the ridges projecting into the cavity of the style, are free from one another; that fusion occurs lower down (*G*), and that in the whole of the lower part of the ovary they are completely consolidated (*H*). (Enlarged.)

Fig. 22. Flower of *Monotropa glabra* dissected so as to show the nectaries at the base of the ovary. *p*, a petal remaining *in situ*; *ss*, insertion of sepals; *nn*, nectaries, each occurring as an appendix at the base of a carpellary lobe; *ps*, petaline stamens. (Enlarged.)

Fig. 23. Floral diagram of *Sarcodes sanguinea*.

Figs. 24-40. Series of drawings illustrating the development of the ovule and of the embryo-sac up to the time of formation of the embryo. *a*, archesporium; *aes*, accessory embryo-sac; *ant*, antipodal cells; *cc*, cap-cells; *dn*, definitive nucleus of embryo-sac; *emb*, embryo; *end*, cells of endosperm; *es*, embryo-sac; *int*, developing integument; *o*, egg-cell; *s*, suspensor; *syn*, synergidae. (Enlarged.)

Fig. 41. A small portion of a root, showing its habit of branching as seen under a low magnifying power. (5/1.)

Fig. 42. A somewhat diagrammatic sketch of a longitudinal section of the apex of a rootlet, showing the fungal investment, the various layers of the root-cap, and the exogenous origin of a new lateral root. *c*, cortex; *ep*, epidermis; *f*, the investing fungal hyphae in which are embedded the outer dead layers of the root-cap (dark); *pl*, plerome of root; *pl'*, plerome of lateral exogenous root; *rc*, root-cap (with calyptrogen); *rc'*, root-cap of exogenous root. (100/1.)

Fig. 43. Longitudinal median section of a root-apex, showing origin of layers of root-cap from dermatogen. *c*, cortex; *dc*, dermato-calyptrogenic layer; *ep*, epidermis; *pl*, plerome; *rc*, root-cap; *rc'*, youngest layer of root-cap. (130/1.)

Fig. 44. Radial longitudinal section through the outer part of the cortex, epidermis, and investing fungal hyphae of a root. *a* and *b*, side walls of epidermal cells with hyphae on surface; *c*, cortical cells (some containing starch-granules); *e*, epidermis; *h*, investing fungal hyphae; *n*, rod-shaped nuclei of epidermal cells; *rc*, old layers of the root-cap retained in position by the investing hyphae. (300/1.)

Fig. 45. Tangential longitudinal section through the epidermis of a root, showing *e*, the epidermal cells; *h*, the mycelium investing each cell. (300/1.)

Figs. 46 and 47. Transverse sections of the stem taken respectively 6 cm. and 18½ cm. from the base. The distribution of the vascular bundles in a ring is shown, together with those passing out into the leaves (and in Fig. 47 into the axillary flower-stalks). The irregularity of the peripheral outline is due to the insertion of the closely imbricating leaves. *c*, cortex; *fb*, groups of bundles passing into the flower-stalks; *lb*, bundles passing into the leaves; *p*, pith; *vr*, ring of vascular bundles. (Fig. 46, natural size; 47, 2/1.)

Fig. 48. Enlarged view of a small portion of the ring of vascular bundles, and of the clusters of bundles passing out to the leaves (bracts) and flower-stalks. *c*, cortex; *fb*, bundles to flower-stalk; *lb*, bundles to leaf; *p*, pith; *ph*, phloem; *x*, xylem. (25/1.)

Fig. 49. A small portion of the vascular ring seen under a high power of the microscope. The arrow points towards the centre of the stem. *c*, cortex; *par*, parenchyma; *ph*, phloem; *px*, proto-xylem; *x*, xylem. (Enlarged.)

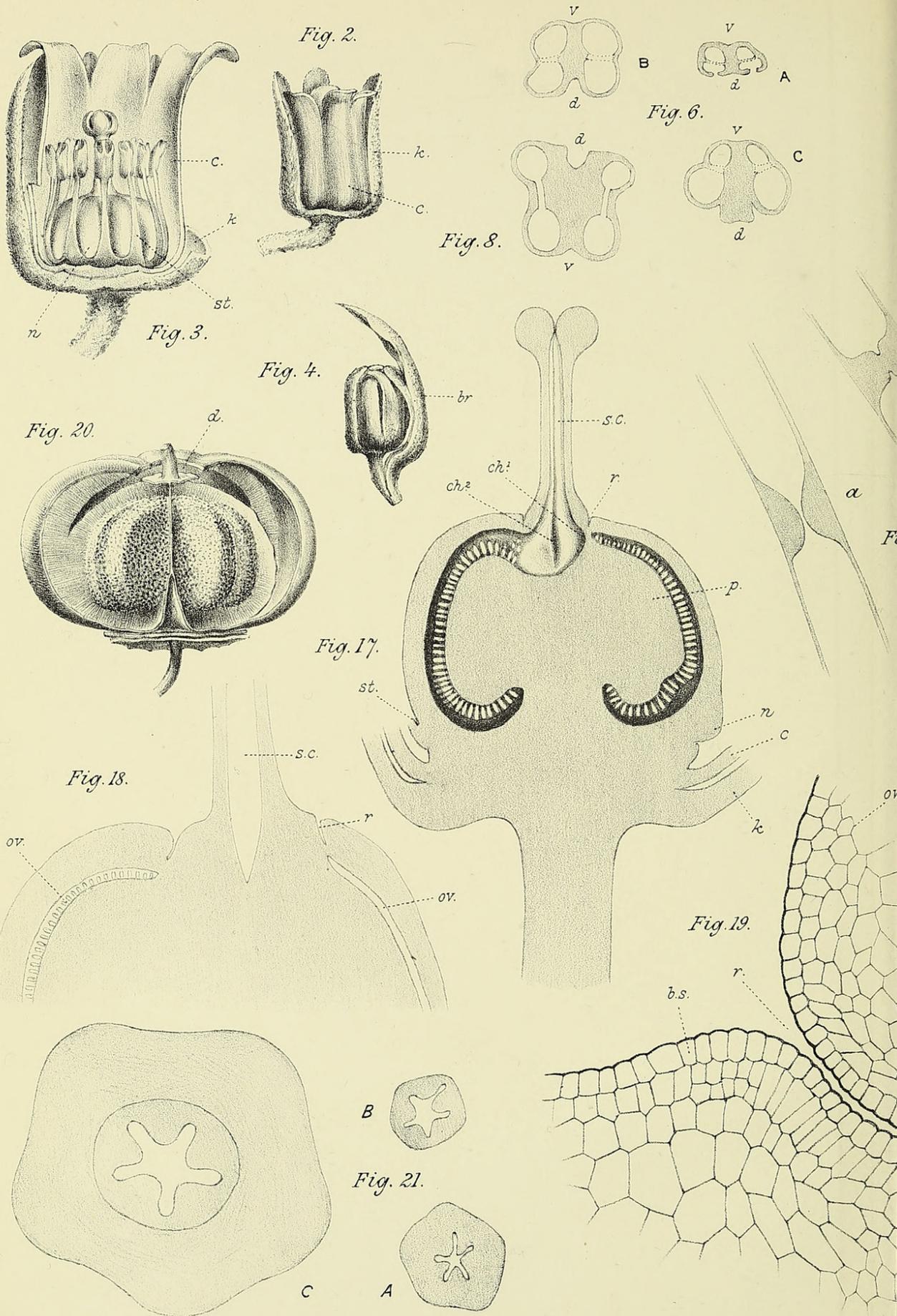
Fig. 50, *a*, *b*, *c*, *d*, and *e*. Series of leaves showing transition from one form to another as seen from the outer (under) face. *a*, from the base of the stem; *b* and *c*, from the thick bulb-like portion; *d*, bract subtending an expanded flower; *e*, bract subtending an unopened bud. (Natural size.)

Fig. 51. Margin of a bract, showing the glands as seen under a simple microscope.

Fig. 52. A single gland in median longitudinal section. *c*, cuticle of epidermis. (Much enlarged.)







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Fig. 7.

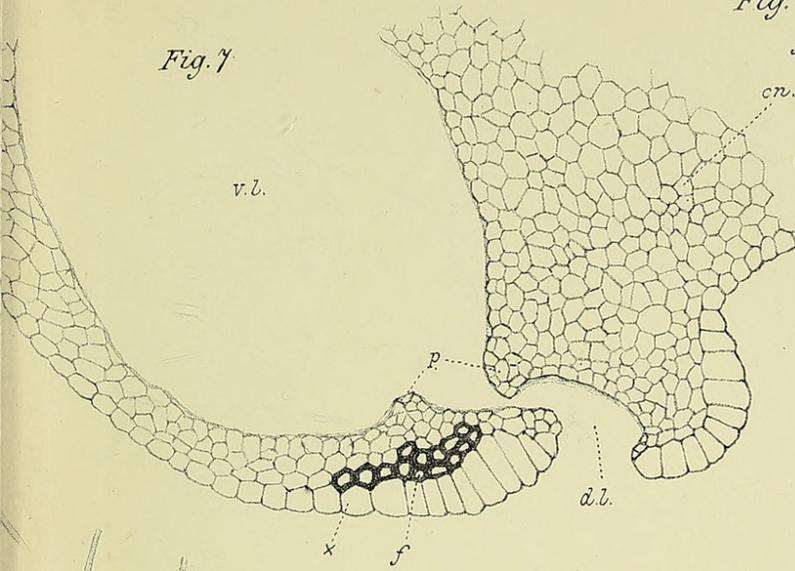


Fig. 5.

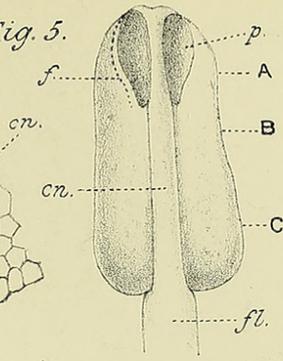


Fig. 9.

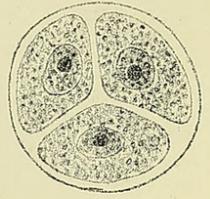


Fig. 11.

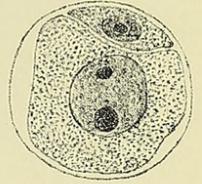


Fig. 10.

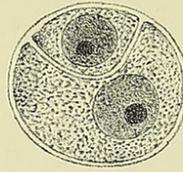


Fig. 12.

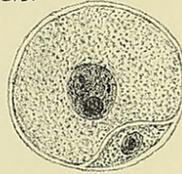


Fig. 13.

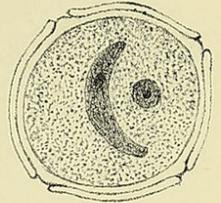


Fig. 14.

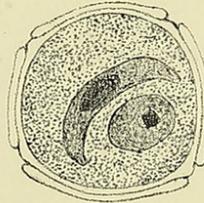


Fig. 15.

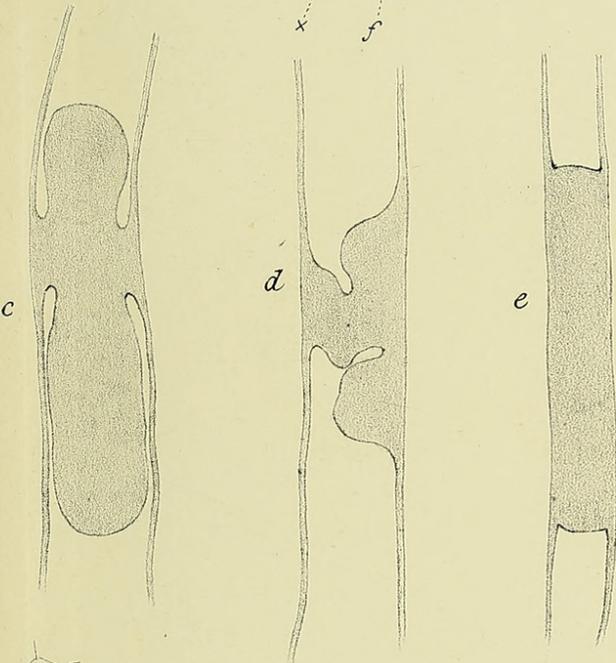
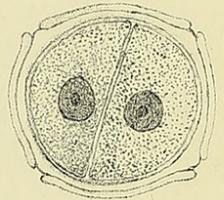
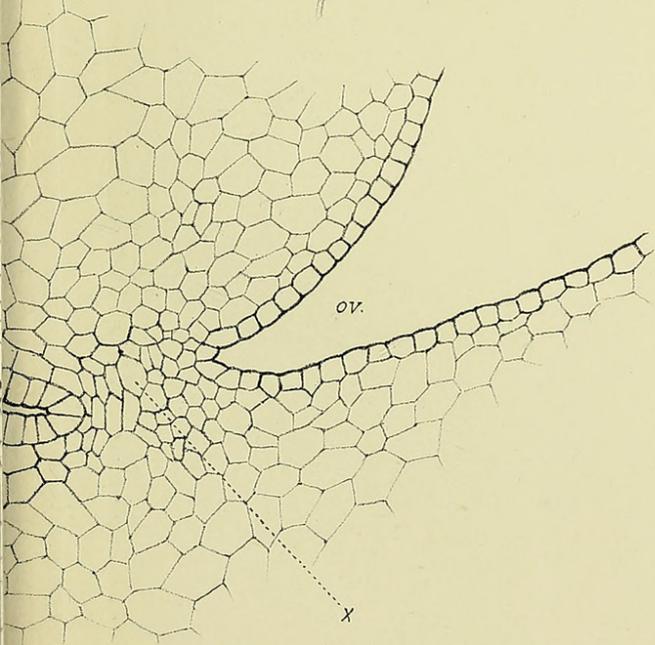
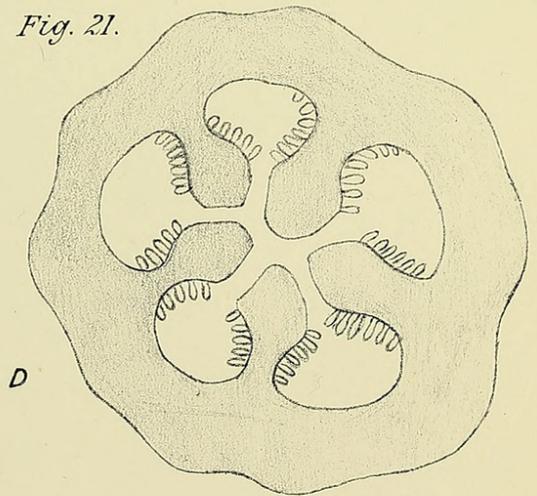
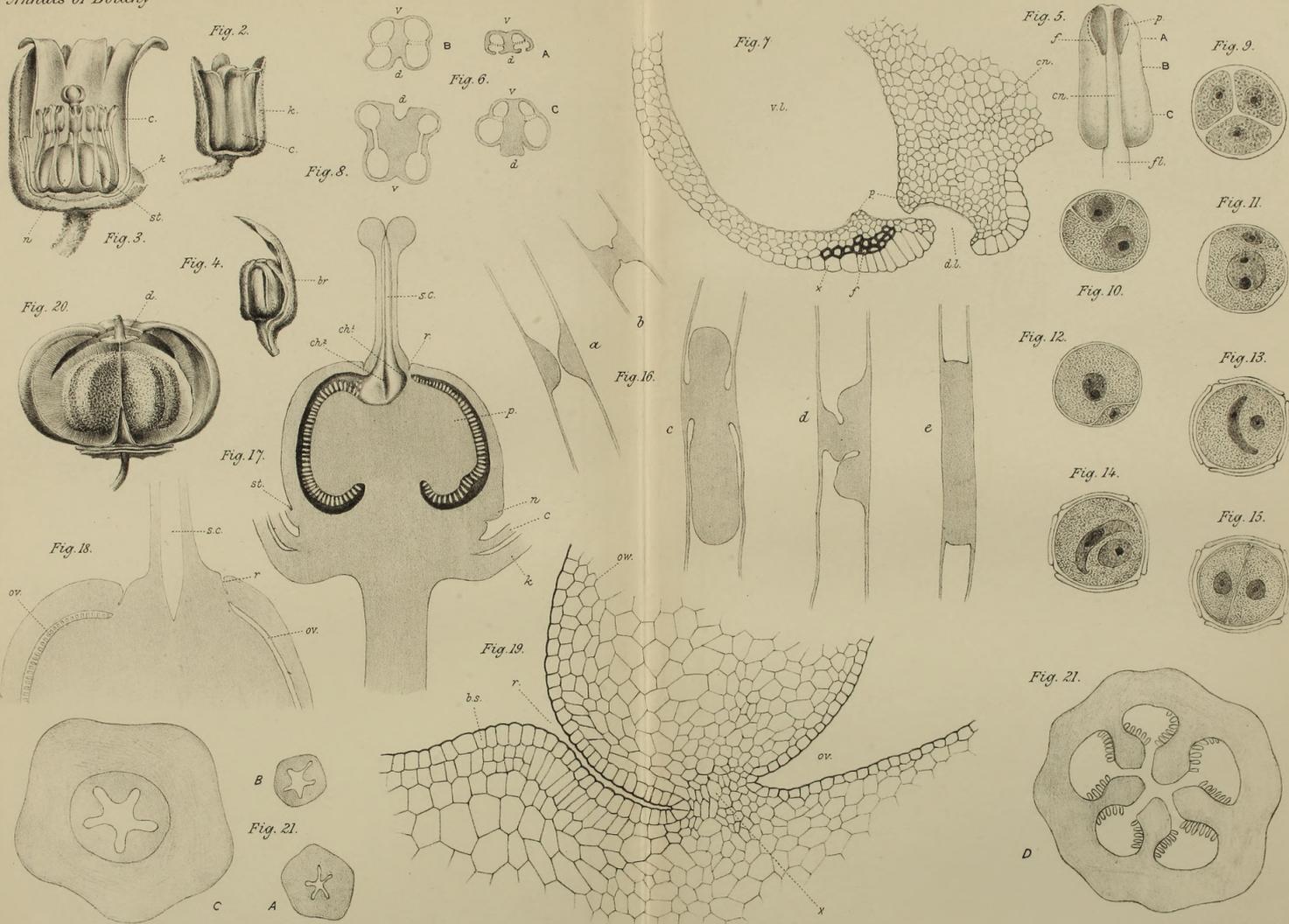


Fig. 21.





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OLIVER.—ON SARCODES SANGUINEA, Torr.

University Press, Oxford.

Fig. 21, E.

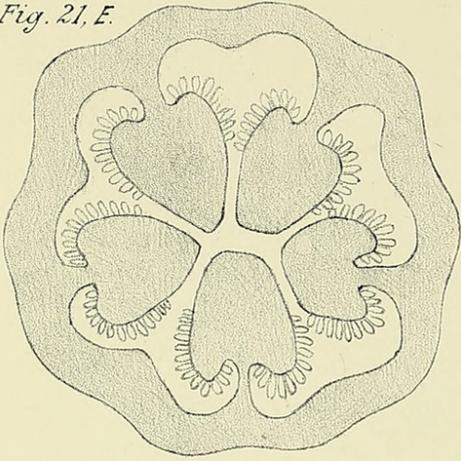


Fig. 21, F.

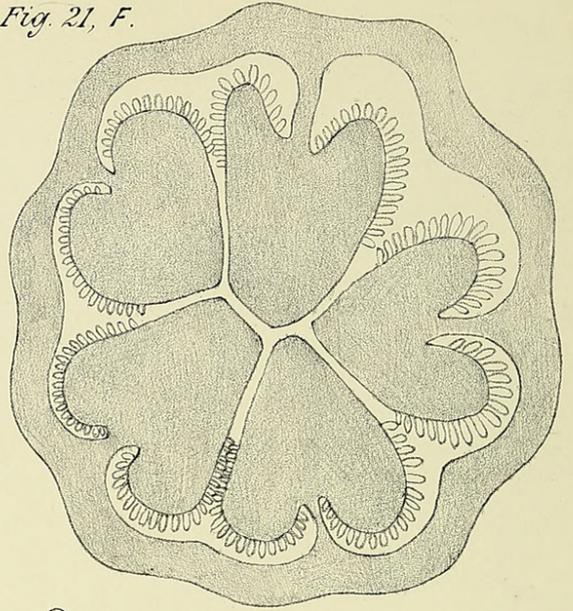


Fig.

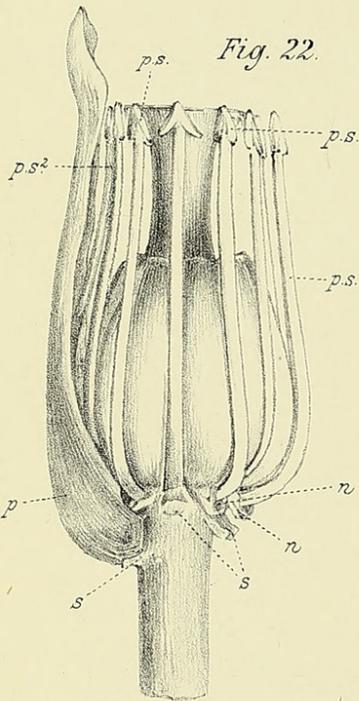


Fig. 22.

Fig. 23.

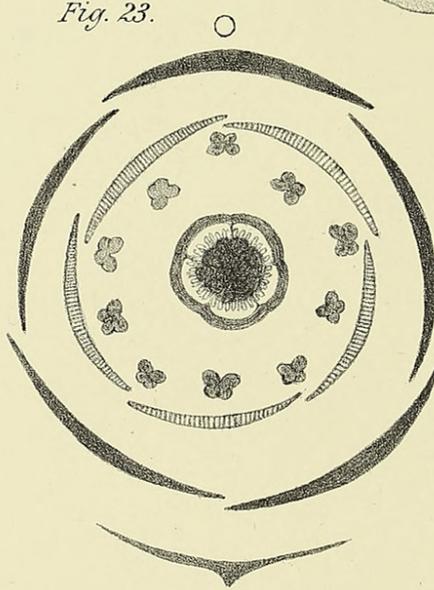


Fig. 24.

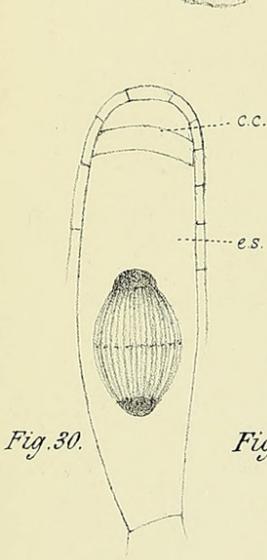
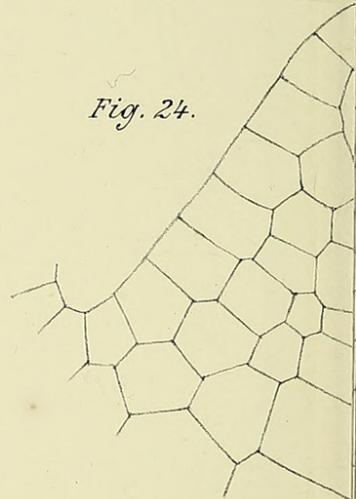


Fig. 30.

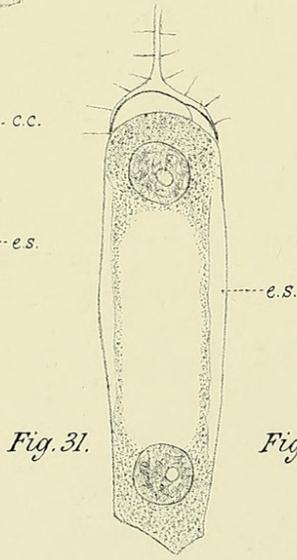


Fig. 31.

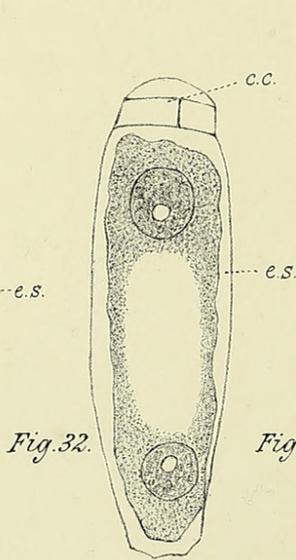


Fig. 32.

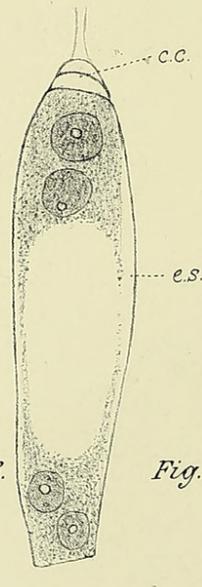


Fig. 33.

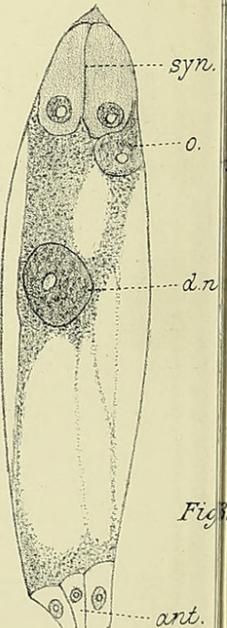


Fig. 34.

Fig.

F.W.O. del.

G.

Fig. 21, H.

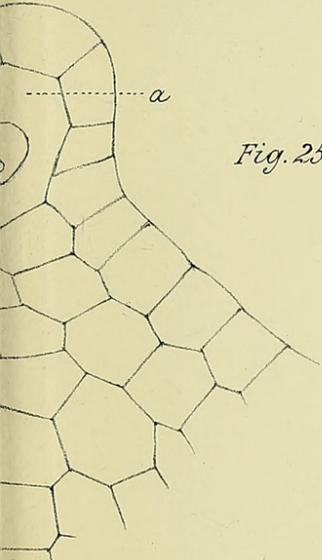
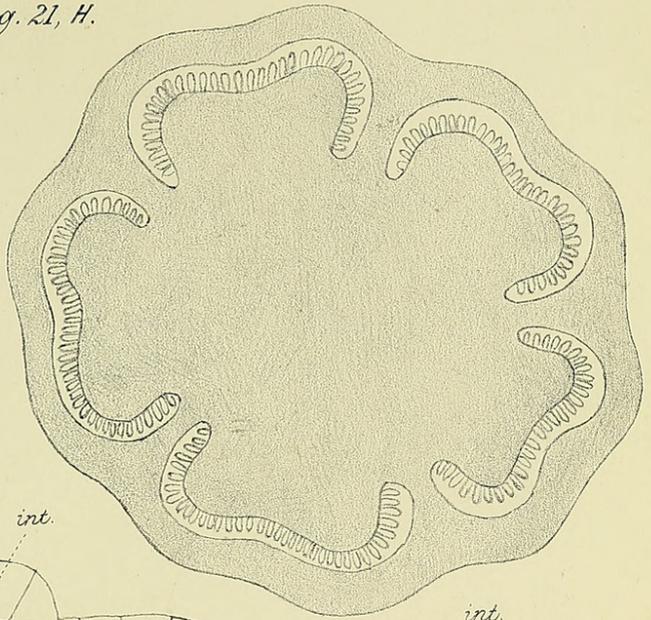
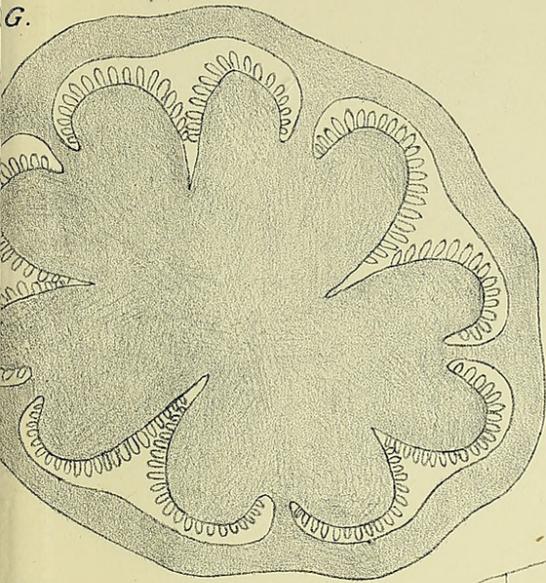


Fig. 25.

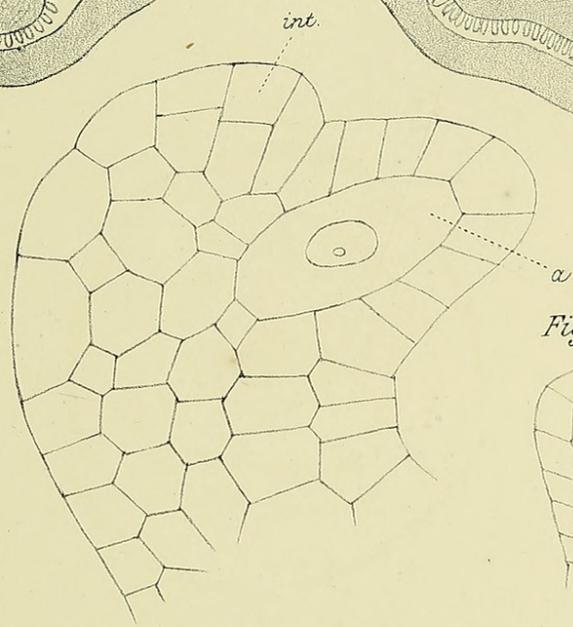


Fig. 26.

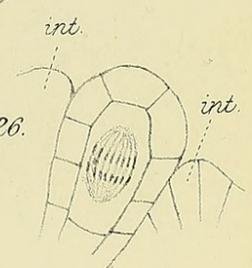


Fig. 27.

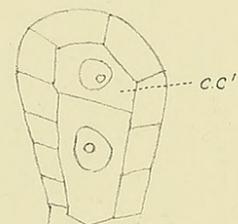


Fig. 29.

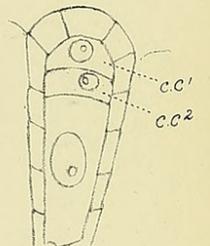


Fig. 28.

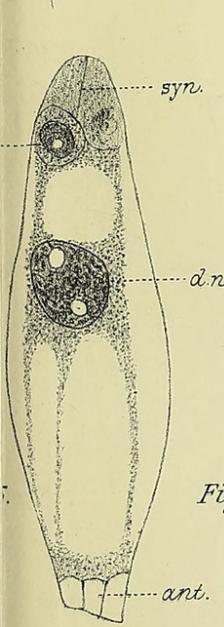


Fig. 36.

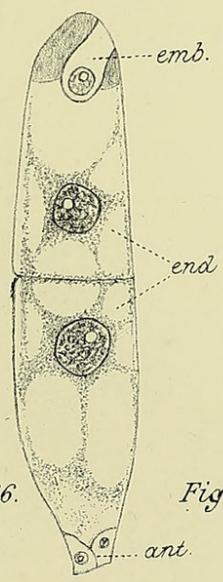


Fig. 37.

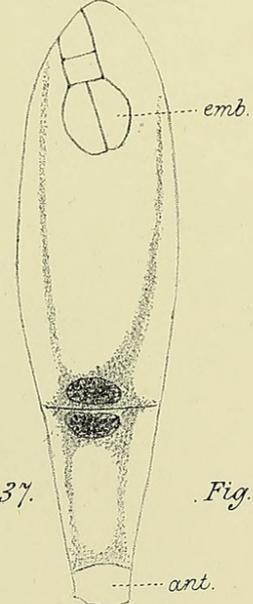
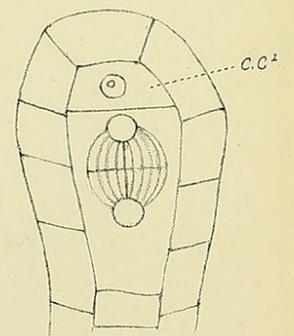
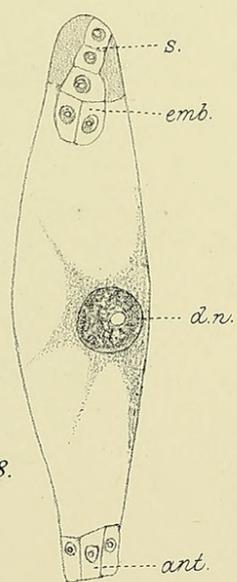
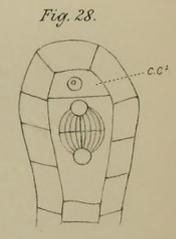
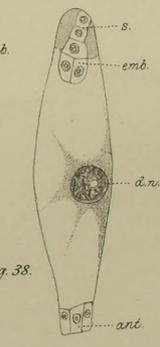
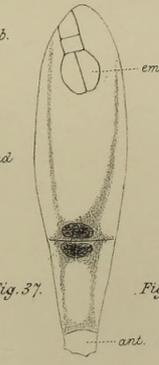
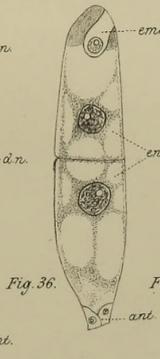
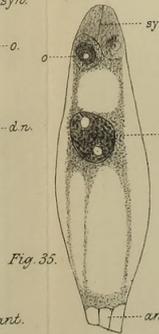
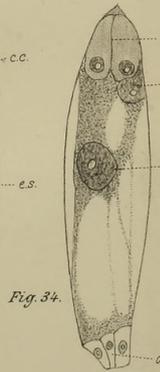
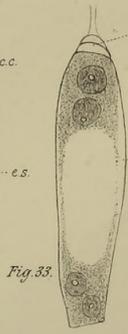
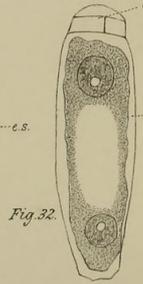
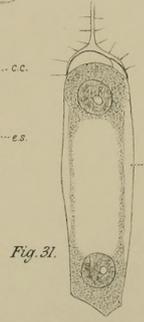
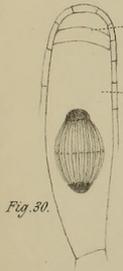
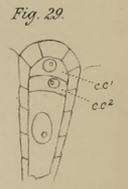
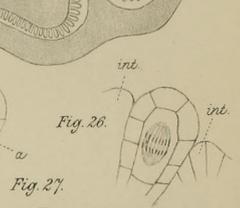
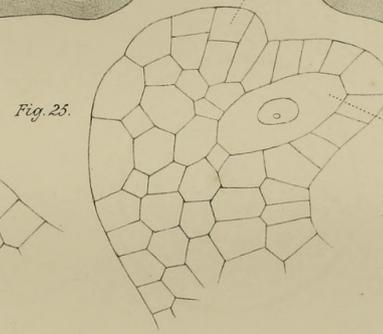
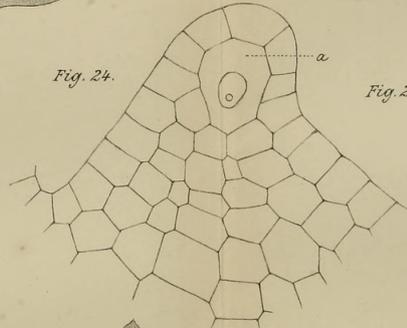
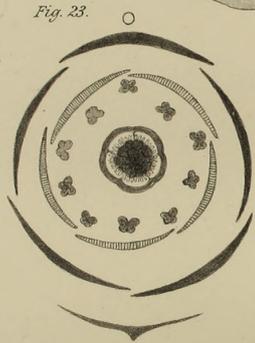
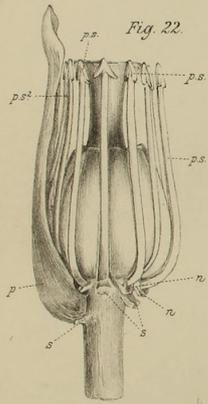
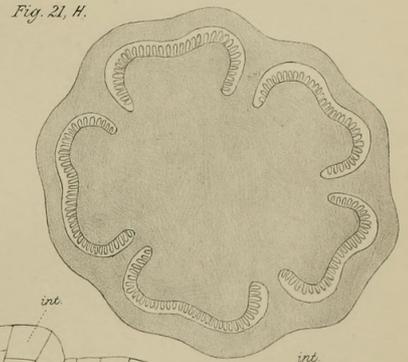
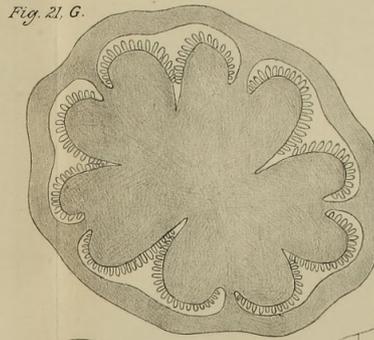
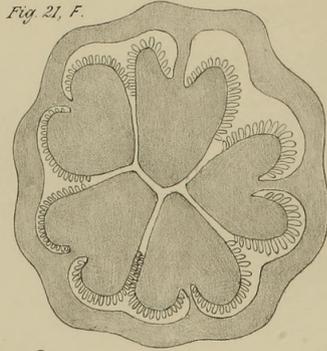
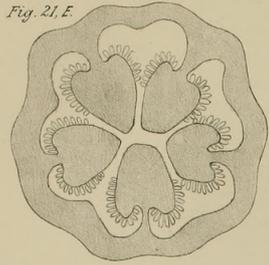


Fig. 38.





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Fig. 39.

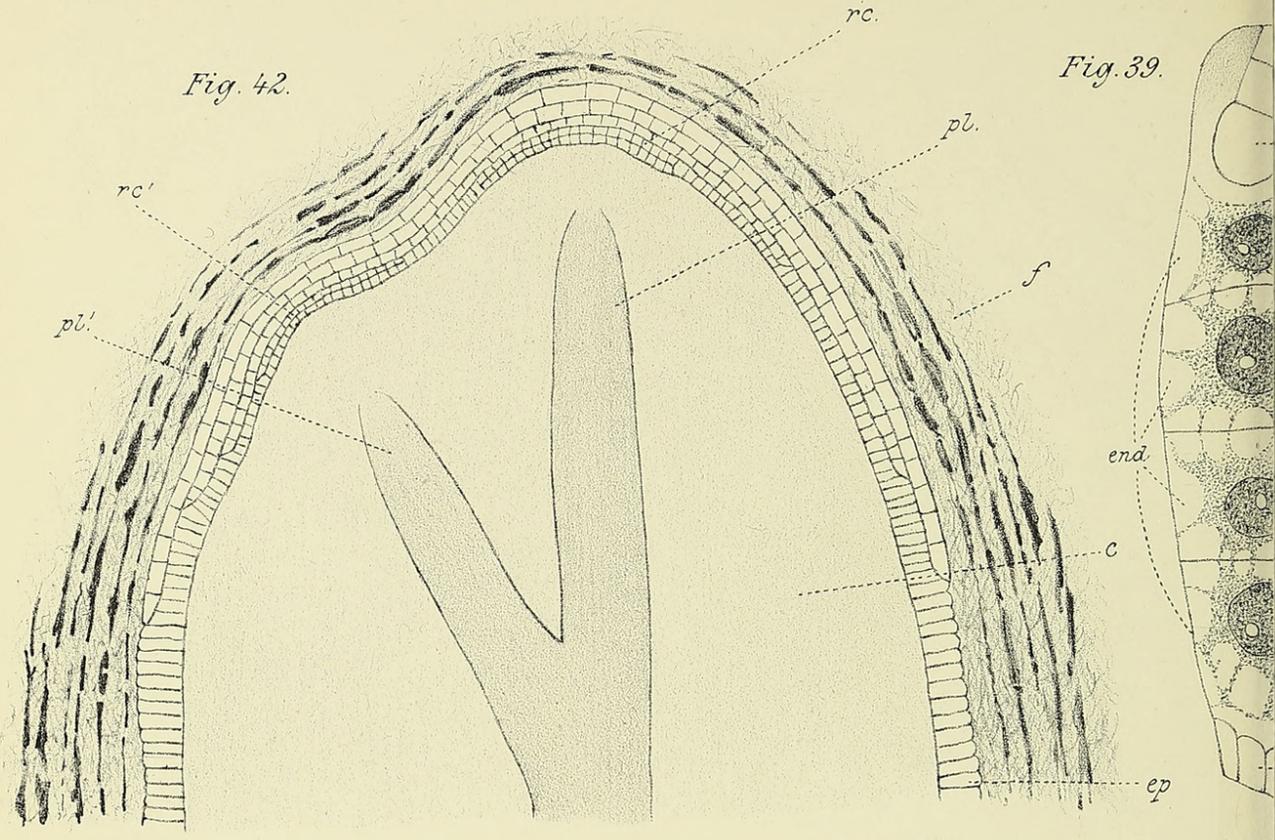


Fig. 42.

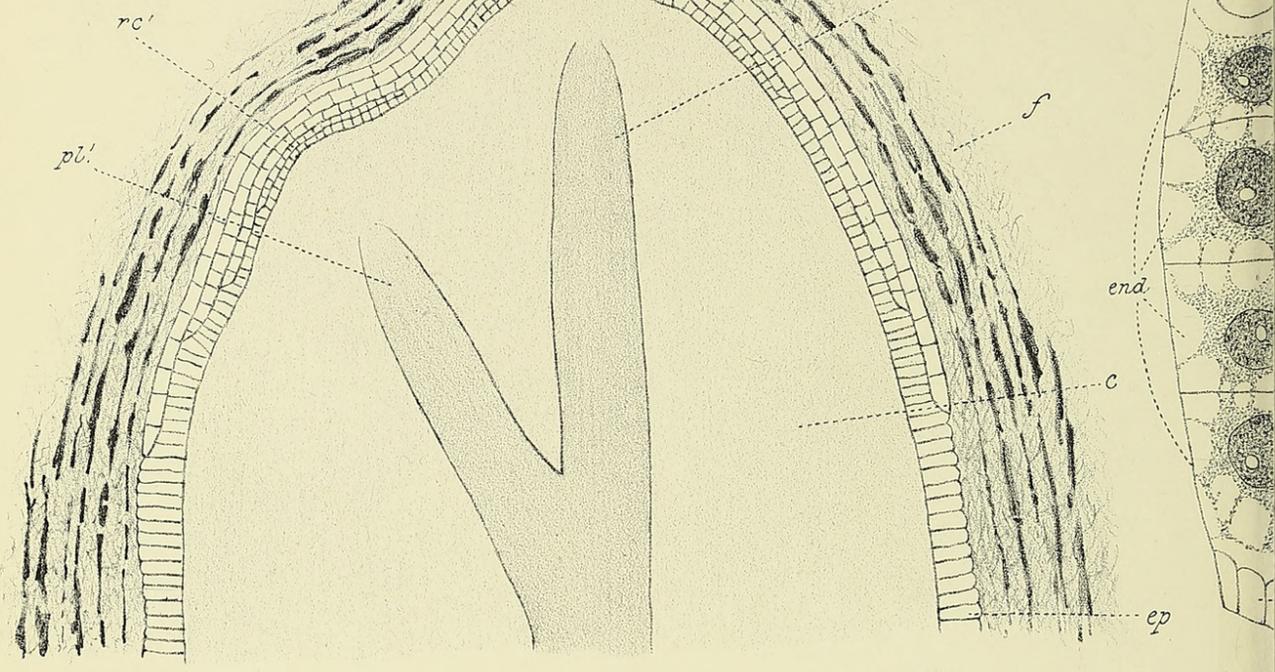
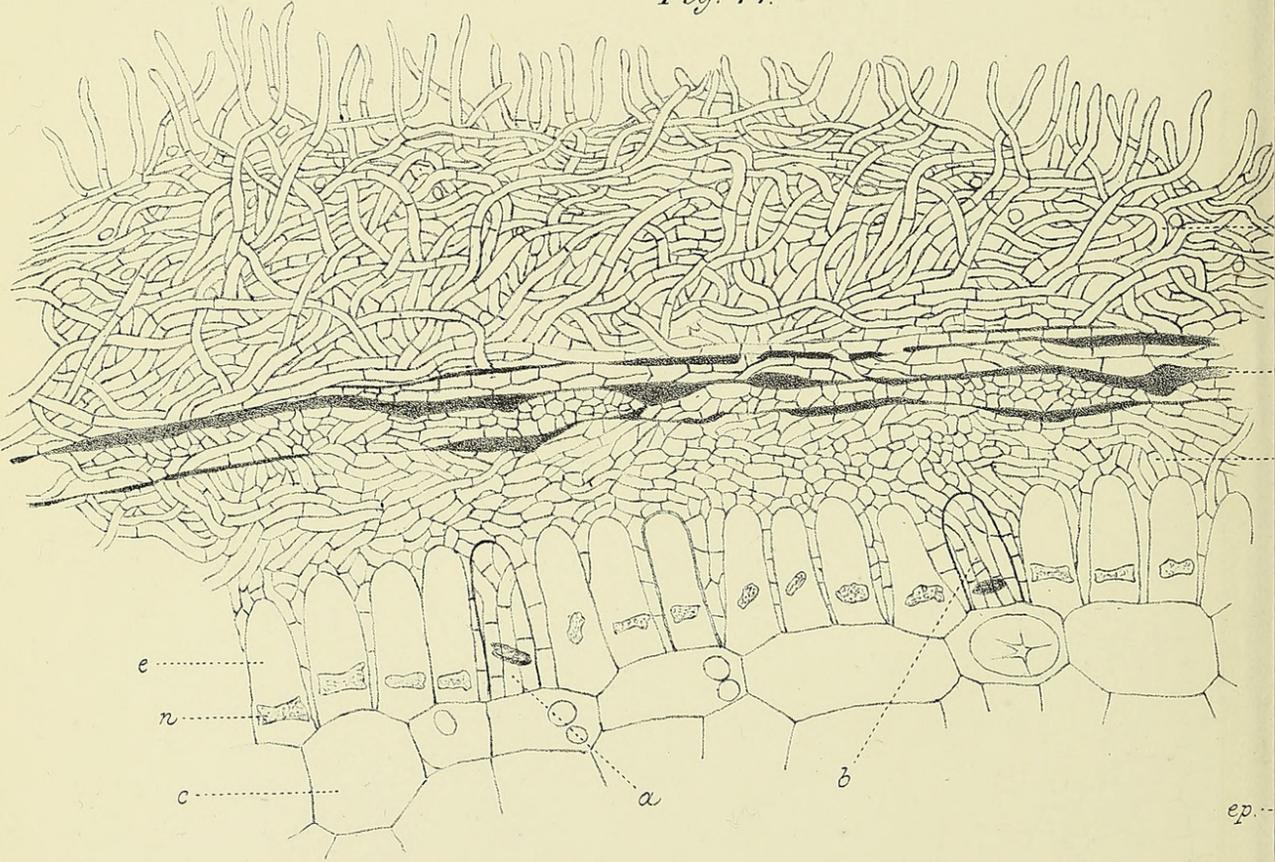


Fig. 44.



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Fig. 41.

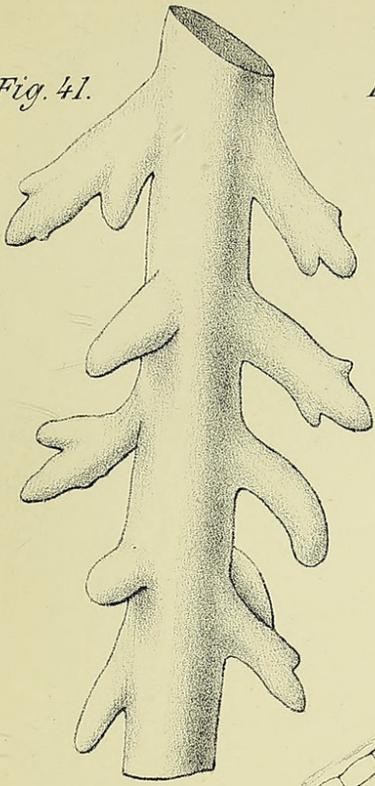


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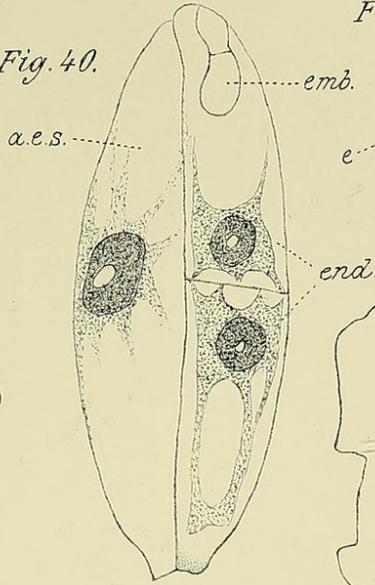


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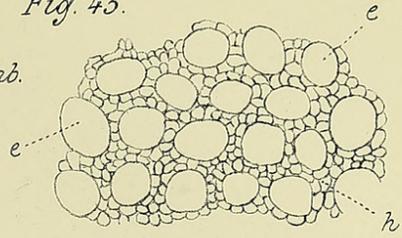


Fig. 46.

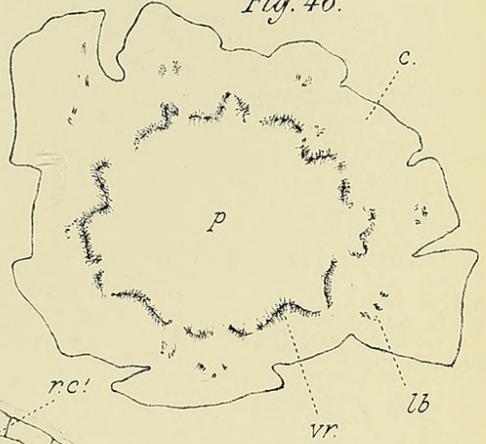
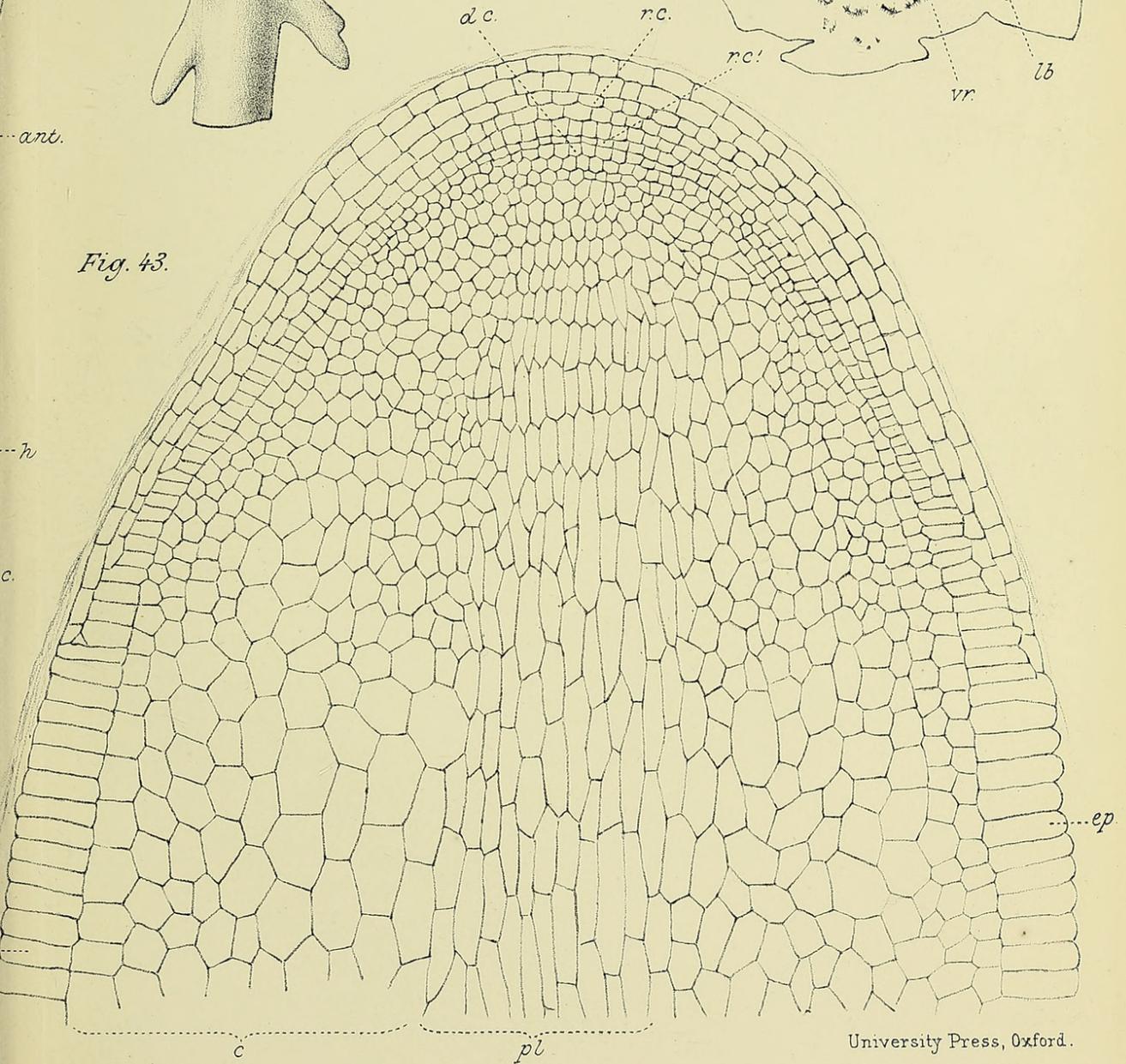


Fig. 43.



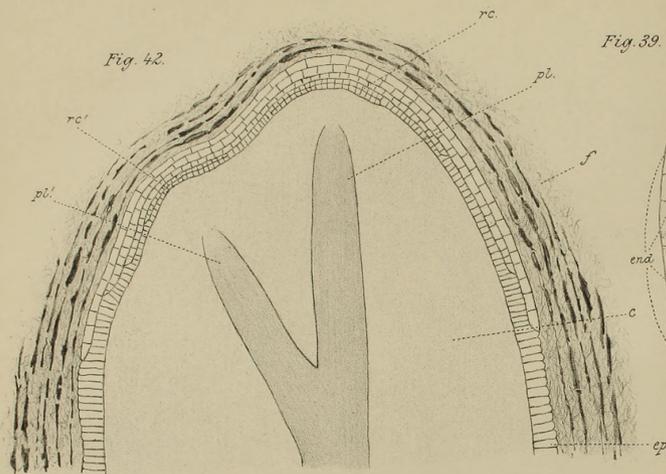


Fig. 42.

Fig. 39.

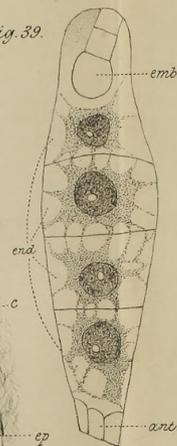


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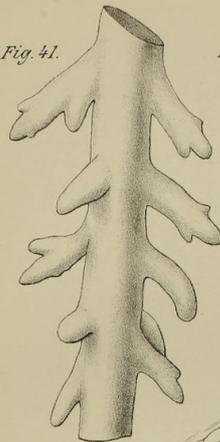


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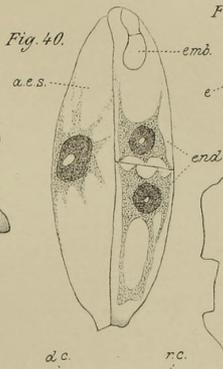


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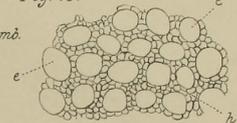


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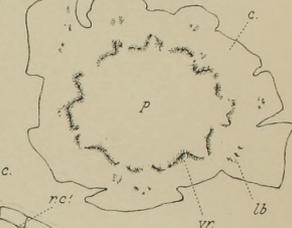


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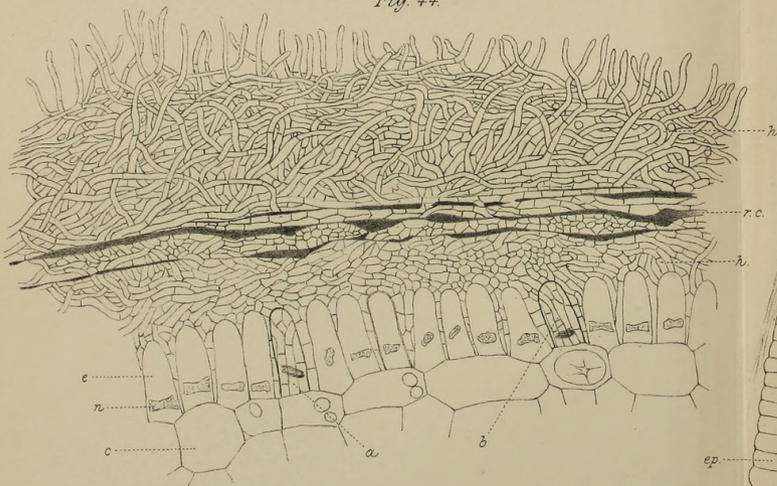
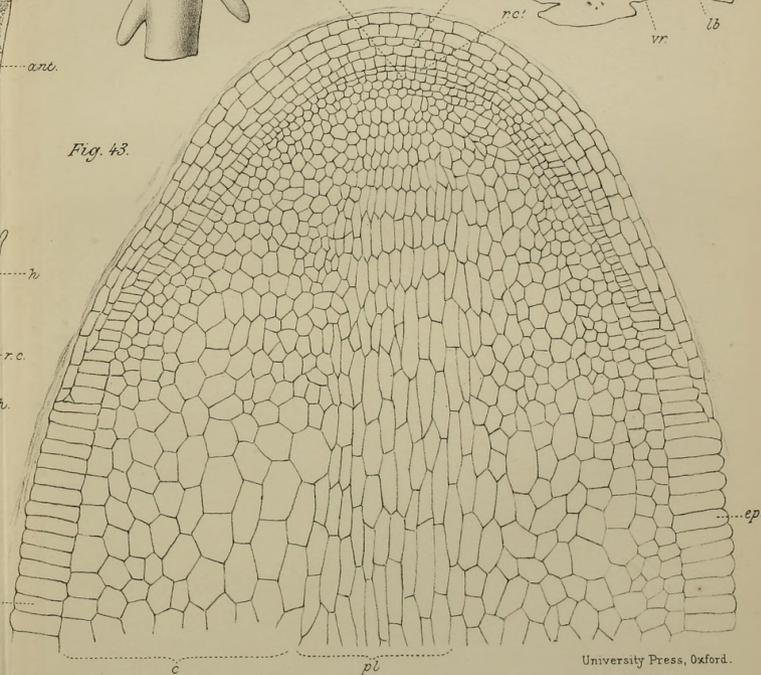


Fig. 43.



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Fig. 49.

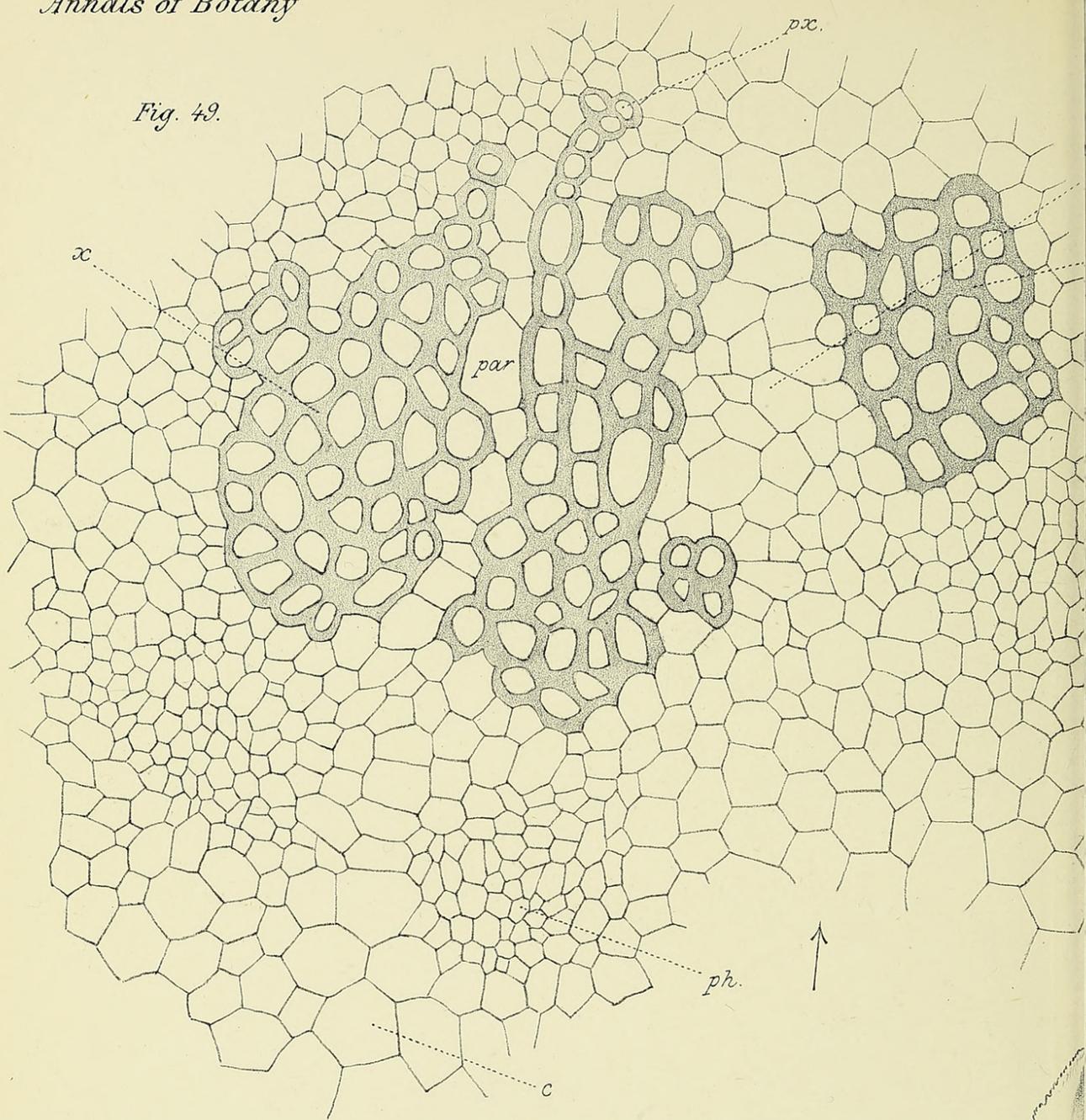
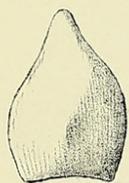
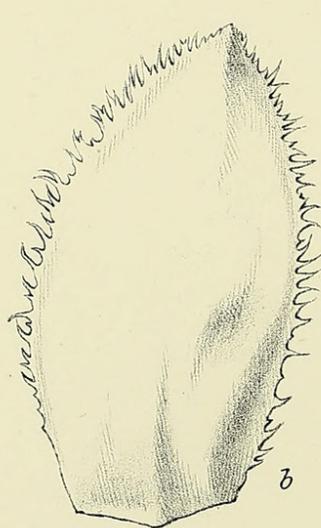


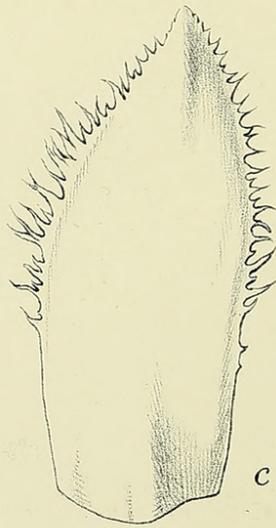
Fig. 50.



a



b



c

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Fig. 48.

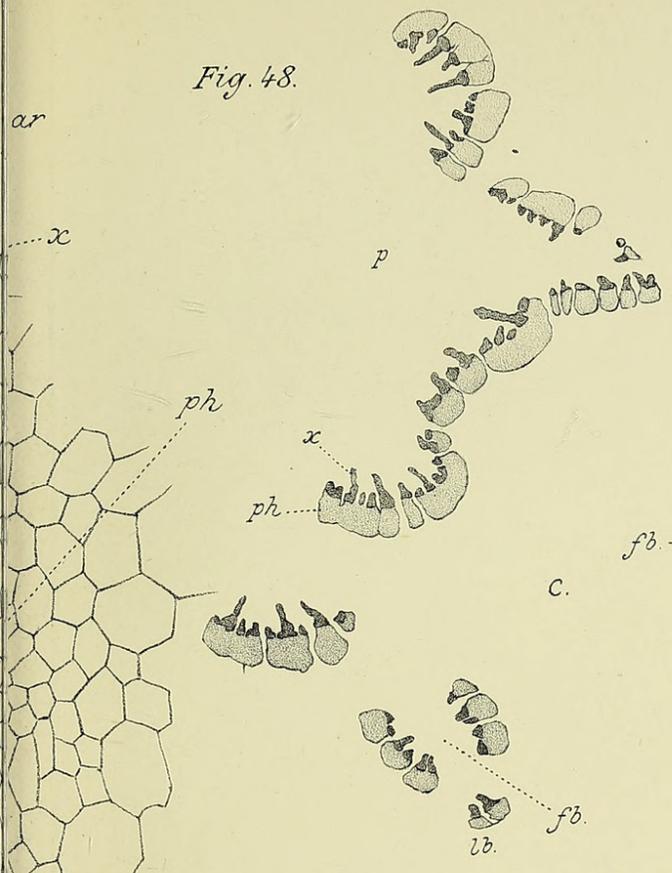


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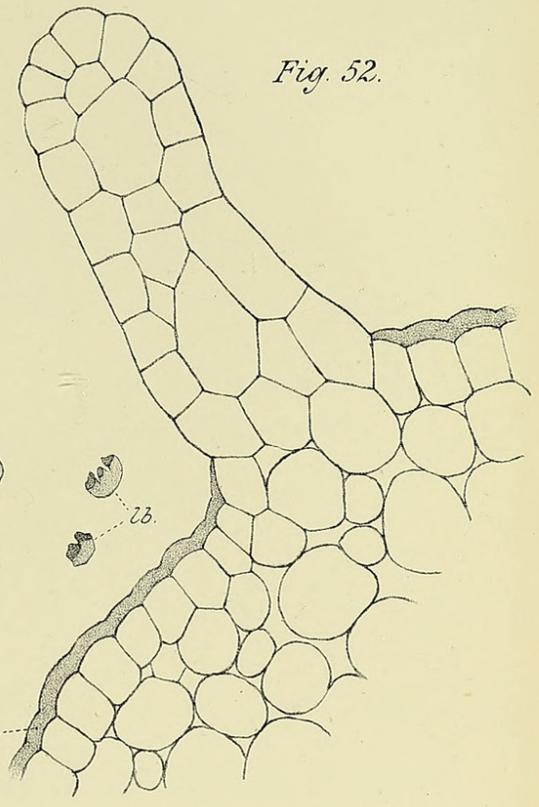


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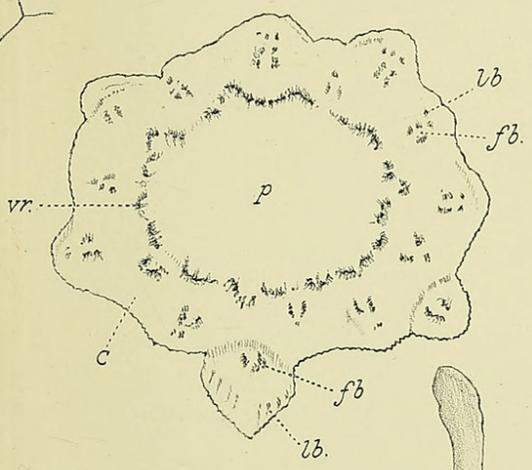


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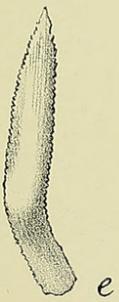
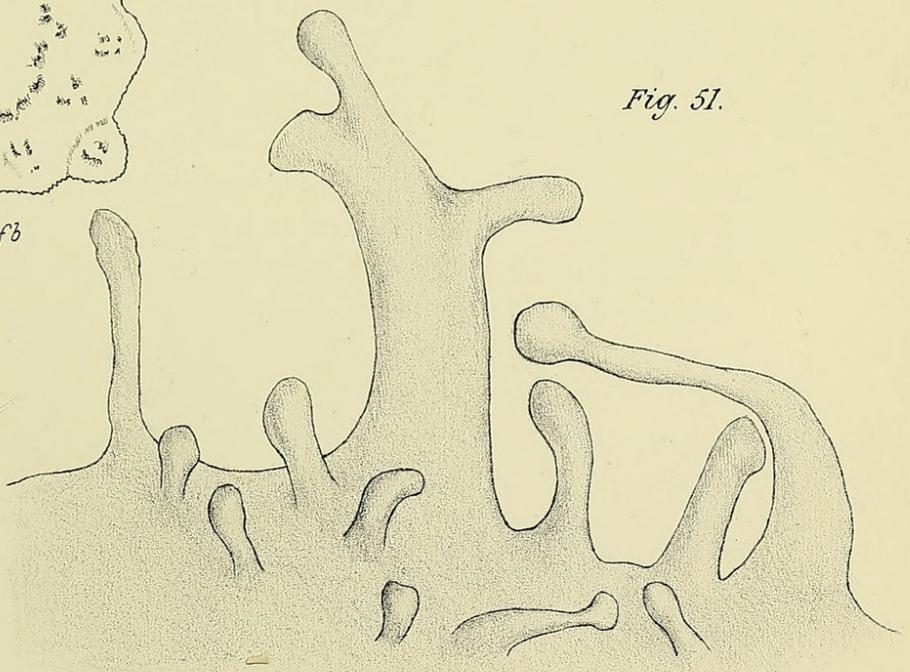


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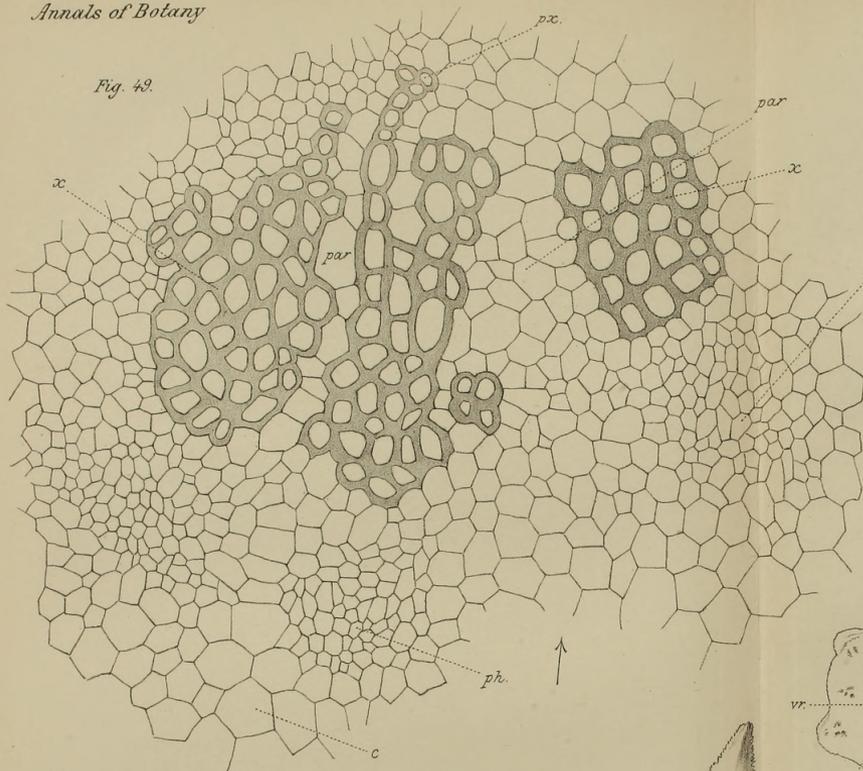


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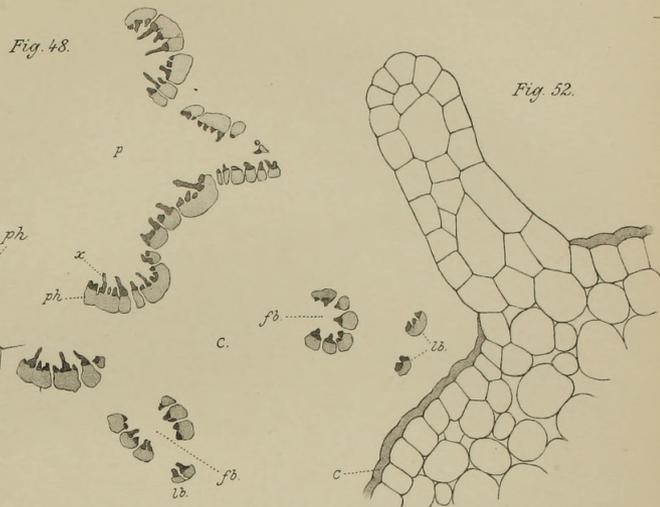


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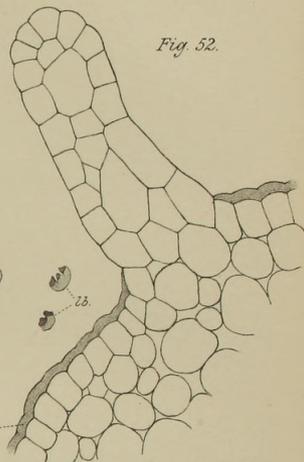


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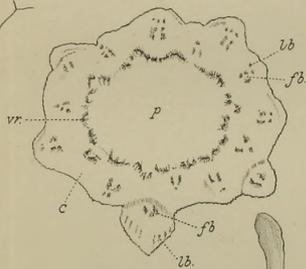


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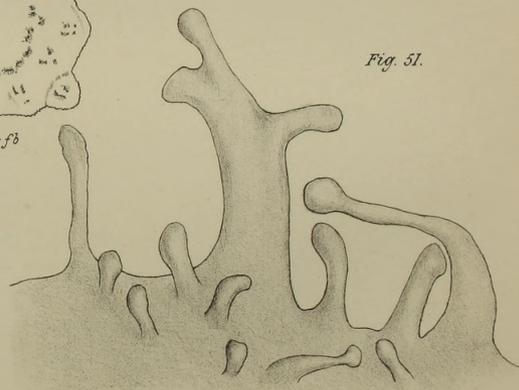
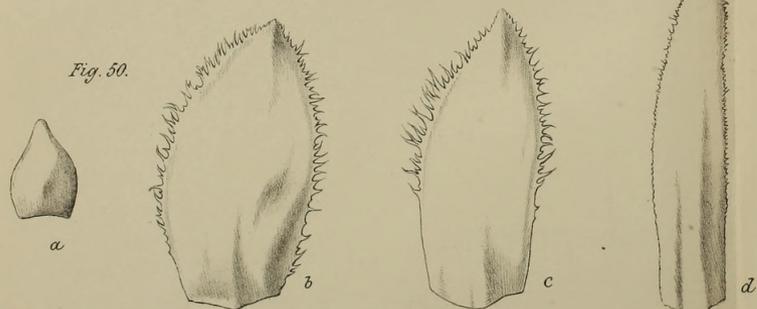


Fig. 50.



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