# On the structure and relationships of Trigonocarpus shorensis, sp. nov. : a new seed from the Palaeozoic rocks.

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# T. SHORENSIS, sp. nov.

# On the Structure and Relationships of
# TRIGONOCARPUS
# SHORENSIS, sp. nov.,

## A new seed from the Palaeozoic Rocks.

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# I. INTRODUCTION

The bulk of the material which forms the basis of this communication was placed in the writer's hands for investigation by Prof. F. W. Oliver. And I gladly take this opportunity of expressing my deep indebtedness to him for much helpful advice and criticism and also for putting at my disposal for examination such slides of the University College Collection as I have had occasion to consult.

My thanks are also due to Dr. D. H. Scott and to Prof. F. E. Weiss for the loan of preparations of this seed. To Dr. Scott I am also indebted for permitting me to examine the more important sections in his unique collection of Trigonocarpus Parkinsoni, without which an adequate comparison between the two seeds would not have been possible.

A full description of the new seed is embodied in the following pages together with a consideration of its relationships and the theoretical questions to which its structure gives rise. In the former connection the organisation of Trigonocarpus Oliveri is reconsidered and good reasons are shewn for its exclusion from that genus.

The same methods have been employed in the reconstruction of the present seed as were used in the investigation of Conostoma oblongum and C. anglo-germanicum.[1] These have been recently described by the writer[2] and need not be recapitulated here.

In order to facilitate reference the same general plan of arrangement has been adopted as has been employed in other recent papers dealing with fossil seeds.

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[1] Oliver and Salisbury, On the Structure and Affinities of the Palaeozoic Seeds of the Conostoma group. Ann. Bot. 1911.

[2] Ann. Bot. Vol. XXVII. No.CVI. 1913.

## II. ENUMERATION OF SPECIMENS

The sections that furnish the data for the following account are all cut from seam nodules obtained from the well-known locality at Shore Littleborough, re-opened through the generosity of Mr. Sutcliff, and for that reason it has been thought appropriate to designate this seed by the specific name of <u>Shorensis</u>.

The following is an enumeration of the preparations giving the approximate plane at which the different series have been cut through the seed and the more notable features each exhibits. The directions of the individual sections are given in Text fig.1 plotted in relation to a median longitudinal section passing through a major and minor rib. In Text fig.2 the approximately longitudinal series U.C.Coll. S.32.a - S.32.h are also plotted in relation to a transverse section through the middle region.

<u>Text fig.1</u>. Plottings on an ideal median longitudinal section shewing the planes of all the preparations. D.H.S.= Dr. Scott's series. R.= Owen's College Manchester series. S = University College London Collection.

## University College Collection

### S.31.a - S.31.k    Shore

An obliquely transverse series of eleven sections from the upper part of a broken seed with beautifully preserved sarcotesta shewing vascular bundles and structure of the extreme periphery.

### S.32.a - S.32.h    Shore

A series of eight obliquely longitudinal sections through a seed from which most of the sarcotesta has gone. S.32.e shews the chalazal cushion and vascular strand and S.32.c passes through the well preserved pollen chamber. The other sections furnish information as to the course of the sclerotic and sarcotestal elements.

### S.33.a - S.33.e    Shore

Five nearly transverse sections with excellent internal preservation through the chalazal end of the seed. S.33.b shews the chalazal strand in almost perfect condition, whilst the succeeding sections furnish details as to the nucellar structure. The series is also of importance as shewing the extent of the minor ribs.

### Dr. D. H. Scott's Collection

A - K Shore

A series of eleven very oblique sections through a complete specimen, but exhibiting a rather poor type of preservation. Section I passes through the pollen chamber.

### Owen's College Manchester Collection

R.1161.a - R.1161.b Shore

A series of twelve rather oblique sections with good preservation and representing a complete seed. The sarcotesta is preserved almost to the exterior and in one section shews what is probably a vascular strand. The uppermost sections are of importance as to the structure of the micropyle and the question of an inner flesh.

Besides the specimens above enumerated two other preparations from the chalazal end of a seed, probably *T. Parkinsoni*, are also described as furnishing additional knowledge of the vascular organisation in that region.

## University College Collection

S.34.a - S.34.b

Two sections through the chalazal end of T.Parkinsoni shewing branching of the chalazal strand and the six sarcotestal bundles.

Text fig.2. Plottings of the longitudinal series S.32.a - h shewing their direction in relation to a transverse section through the region of maximum width.

## III. GENERAL FEATURES

The seed with which the present investigation deals was of large size, approximately elliptical in form, and as seen in transverse sections possessed a circular outline at all events in the median plane. The exact limits at either end cannot with certainty be determined, but the total length was over four centimeters and perhaps considerably more, whilst in breadth the seed attained a maximum diameter about half- way up of nearly two and a half centimeters.

Although we are without specimens shewing the actual attachment of the seed the chalazal end certainly tapered towards its point of insertion and, judging from the general direction of the surface curvature, followed a more gentle curve inwards to the apex.

The testa comprised three or perhaps four layers which will be described in detail later. The two outer of these constituted a broad sarcotesta remarkable for the presence of a number of scattered secretory sacs and representing nearly one third of the total width of the seed.

Within the sarcotesta was a hard sclerised shell bearing three salient ridges which extended from the base to the apex. These ridges were symmetrically placed around the body of the seed and from the chalazal end to about a third the height of the sclerotestal shell were present three more ribs much less pronounced than the former and occupying positions intermediate between them.

In the chalazal region there were thus six ribs of which three soon die out whilst the remaining three persist.

In general form the sclerotesta constituted an egg-shaped body, the pointed end corresponding to the chalazal region whilst the blunt end was surmounted by a triangular micropylar tube, the angles being continuations of the ribs lower down, into which they pass by a hollow curve.

Text fig.3. Diagrammatic restoration of an ideal median longitudinal section of Trigonocarpus Shorensis passing through a primary and secondary rib. The sclerotesta and limiting layers of the sarcotesta are shewn in black; the ribs are cross-hatched, and the inner flesh, the extent of which is hypothetical, is represented by diagonal shading. The branching of the chalazal bundle is based on analogy with T. Parkinsoni, and the direction of one of the sarcotestal strands is also shewn as a dotted line though not actually present in the plane of section. Nucellar tissue dotted, secretory sacs black.

Within the sclerotic tissue there was a fourth layer which may be regarded as representing the "inner flesh" of other seeds belonging to this affinity, but it was in all probability not very extensive, and most likely confined to the micropylar region. In any case the evidence is against its having extended into the body of the seed.

The megaspore cavity was much less pointed at the base than was the hard shell around, and through this divergence of the two surfaces a chalazal cushion of sclerotic tissue was formed from which arose a nucellus that stood up erect and free within the seed cavity, surmounted at its apex by a large pollen chamber.

The nucellus was bounded at the exterior by a well differentiated epidermis and within was a tracheal sheath forming the upward continuation of a single vascular strand which pierced the cone-shaped chalazal cushion.

The vascular organisation was essentially similar to that of other seeds of this group and consisted of two parts, viz.,

A sarcotestal system of bundles without, and

A nucellar system within.

None of our sections furnish any information as to the nature of the pollen and in no case is a prothallus preserved. This may indicate that all our specimens were abortive ovules, though the presence of numerous fungal spores within the megaspore cavity would seem to point to its former occupation by an organised tissue which served as nourishment to the saprophytic organisms.

In fig.3 is represented an ideal median longitudinal section through a restoration of this seed shewing the general features of its organisation and the appearance in transverse sections is represented as reconstructed from the different series in fig.4.

Text fig.4. Transverse restorations of Trigonocarpus Shorensis at the levels A, B, C, in fig.3. Tissues represented as in the previous diagram. The six sarcotestal strands are represented by large black dots and the secretory sacs by smaller.

## IV. THE TESTA.

### (1) The Sclerotesta.

As already stated the general outline of the sclerotic integument was obovoid, passing gradually at the blunt end into a short triangular beak and bearing six longitudinal ribs, of which three only, viz. the more prominent, persisted as far as the micropyle. The three minor ribs alternated with the three major (Pl. fig. 9) and only extended for about one third the length of the body of the seed. They were without commissures and reached their greatest radial extent some two millimeters from the base, where they measured about 0.4 mm. vertically from the outer surface. Above this level the minor ribs gradually decreased in size and finally died out some eight millimeters from the chalazal end. In Fig. 5. A. B. & C. are represented three consecutive sections of the Manchester series which pass obliquely through the basal part of the seed and thus cut a minor rib on their lower sides at successive levels nearly transverse to its direction. In the first of these the rib is cut through at its maximum extent, whilst in the uppermost its position is only marked by a slight protuberance of the surface, and in the section next above (not shewn in the figure) has completely disappeared.

Text fig. 5. Form of the sclerotesta in three successive sections of the Manchester series R.1161. b-c-d. shewing the gradual disappearance of the secondary ridges.

The major ribs are not equally developed in all the specimens, their radial extent from the outer surface in the middle region varying from .75 mm. in the series S.33.a-e to nearly 1.4 mm. in the specimen represented by the series S.31.a-S.31.k.

Unlike the minor ribs, the major were invariably commissured except at the base and remained of nearly the same dimensions from within some 6 mm. of the chalazal extremity to the base of the micropyle.

At the latter level the major ribs can be regarded as either having rapidly diminished till they became obsolete, or as having opened out and become suddenly much broader through widening of the commissural channel, resulting in the formation of a triangular micropylar beak in which the sclerotic tissue was thickest at the sides and thinnest at the angles.

At the chalazal end the sclerotesta ended in a solid inverted cone of stony tissue about 3.5 millimeters in height, perforated only by a narrow central canal through which the main vascular bundle passed to the base of the nucellus (Pl. fig. 7). As the ribs, both major and minor, approached the chalazal end, they became gradually smaller till at the extreme tip of this sclerotic cone all indication of ribbing had disappeared and sections passing through this region only present a ring of sclerotesta surrounding the chalazal canal. The cavity that the sclerotic shell enclosed was broadly ovoid and circular in transverse section, contracting gradually into the triangular micropyle. In the lower part the cavity tapered with a gentle curve, but owing to the chalazal cone (Pl. fig. 7.c.p.) was much blunter than the external form. Furthermore the sclerotic tissue in the central part forming the base of the inverted cone projected upwards into the cavity as a dome-shaped papilla about 1.5 mm. in diameter and .5 mm. in height, the margin of which served as the place of insertion for the nucellar epidermis.

From the apex of the papilla to the base of the micropyle the cavity measured some 19 mm., whilst the diameter in its broadest part was slightly over 14 mm., the whole surrounded by a shell of an average thickness of about .5 mm. Sections through the micropyle (Fig. 2. Pl. ) shew that the sclerised sides of the triangular canal about half way up formed of four layers of longitudinally directed fibres were from .13-.14 mm. in thickness and distinctly concave, the internal diameter of the canal measured from the apex of an angle to the middle of one of the sides being just over 2 mm. In the highest of our sections (Pl. fig. 5), viz. Man. Coll. R.1161. L., the outer edge of the sclerised layer has lost the regular outline and the limit between sclerotesta and sarcotesta become less well defined. The extreme internal diameter of the micropyle had at this level become reduced to 1.4 millimeters. On that side of this oblique section which is at the higher level, the sclerised layer is seen to be even less developed than on the lower side and the concavity of the flanks remarked on above has resolved itself into a slight double convexity, resulting from a more rapid thinning down of the sclerotesta in the median plane between the angles and a slight increase of thickness elsewhere (thickness between the angles .10 mm. and at the convexities .16 mm.) (Pl. fig. 8 m.c.)

Although this section is broken at the two higher angles, so that the facts relating thereto are open to some doubt, yet there is evidence that the sclerisation of the sides of the beak did not extend completely to the angles, but that the sclerotesta towards the apex segregated into three distinct portions separated at the angles by intervening soft tissue and each itself composed of two parts fused in the median plane.

Except for the slight local thickening, both here and in the preceding section, there is a thinning down of the sclerotic beak which if maintained at the same rate must have resulted in its complete elimination at a level not far above that at which our section was cut.

From these facts it would appear that the beak was comparatively short (probably not more than .8 mm. in length), although the extensive development of the sarcotesta at this level and the curve which successive sections shew its surface to have followed indicate a much further persistence of that tissue, so that in this respect our seed resembled most closely the condition that obtains in present day Cycads.

## Histology of the Sclerotesta.

The sclerotesta was built up of successive layers of thickened fibrous elements, which between the ribs were normally about 14 or 15 in number and attained an average thickness of about .5 mm. Of these the inner, comprising from 6-9 layers, though this is subject to considerable variation, run parallel to the surface of the seed and the ribs also were mainly composed of such longitudinally directed fibres. The innermost layer surrounding the megaspore cavity was composed of fibres with considerable flattening in the radial plane, and the internal surface thus formed does not in the best state of preservation present any irregularity which might be construed as indicative of a more interior and softer tissue. The majority of the fibres forming these inner layers appear rounded or polygonal in transverse section, with dark carbonaceous contents and separated from one another by a thin dark membrane (? middle lamella), on either side of which and surrounding the dark contents is a yellow translucent zone about 3.5μ in width, perhaps representing the cell wall. The average dimensions varied from about 28-42μ in width and their longitudinal extent can be traced in some cases for over 1.5 mm. without a transverse wall, though this is probably not the extreme limit, and the whole fibre was composed of several such superposed. The remaining more exterior layers, some 5-9 in number, were built up of the same kind of fibrous elements, but these except to a very slight extent in the ribs, owing to their changes in direction render the structure here highly complex.

<u>Text fig. 6</u>. A portion of the sclerotesta as seen in transverse section, shewing the vertically directed fibres at the interior and the almost horizontal direction at the periphery; a single secretory sac is also present.

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The sclerotic fibres forming the outer layers do not all traverse the same direction, but behave as aggregates or bands consisting usually of from one to two elements in the radial direction and of a very variable number in the tangential (Text fig.6). For a time each band follows the longitude of the seed and then almost abruptly all the fibres constituting the band bend some to the right and others to the left or all of them in the same direction, so that their course is at a very narrow angle with the horizontal plane, and in transverse sections they appear cut obliquely or almost longitudinally for some distance. Where the members of a band are in one layer they appear to all bend in a similar manner, but there is some evidence that where the band is more than one element in thickness those of each layer bend in opposing directions.

Owing to the great variability in the width of the bands and the distance which they traverse before assuming the nearly horizontal position, it has not been found possible to ascertain for certain whether or not they subsequently take up the longitudinal direction again, but their appearance in transverse sections would certainly seem to favour the affirmative view.

The extreme irregularity of the course of the fibres is shewn by the inconstant numerical relation that obtains in successive sections between those cut in the oblique and transverse directions. To still further complicate the structure the bands do not always remain in the same vertical plane, but when becoming bent may pass in front or behind those running longitudinally, though probably they more frequently maintain their course.

Owing to this complex interlacing of the outer elements of the sclerotesta it presents a plait-like appearance when cut by sections tangential to the surface, as is seen in fig.3 Pl.

Eventually the thickened elements of the sclerotesta pass obliquely outwards into the sarcotesta by a well marked transition the exact nature of which will be more profitably considered in relation to the latter tissue.

In the outer part of the sclerotesta and there only elongate secretory elements partially or entirely immersed in the sclerotic tissue are present, which follow a more or less sinuous course, passing out into the sarcotesta at one point, and occasionally into the sclerotesta again at another (Pl. fig.6, M. s.). In all respects these secretory elements resemble others found in the sarcotesta of which a detailed account will be given later.

For convenience of description we have treated the sclerotesta as consisting of two portions, an outer and more complex, an inner and more simple. But we have seen that the plane at which the more elaborate structure is assumed is subject to considerable variation. There seems in fact to be little doubt that the outer zone in reality represents the terminations of a large portion, and perhaps even all of the longitudinally directed and more interior fibres. We can in any case assert with certainty that no definite line of demarcation can be drawn and that the sclerotesta cannot be regarded as the region of fusion of two morphological surfaces as has been suggested for the stony layer of the Cycadean ovule.1)

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1) Stopes: The Double Nature of the Cycadean integument. Ann. Bot. Vol.XIX. 1905.

## (2) The Sarcotesta

### (a) General Structure

The sarcotesta was undoubtedly the most pronounced feature of this seed and in the living state must have attained a considerable thickness, for even in the petrified condition, with obvious signs of collapse at the exterior, this soft tissue shews a thickness in some sections of over 4 mm.

The sclerotesta was completely invested by the sarcotesta, of which the surface broadly followed the lines of the former. In the middle region of the seed an approximately even thickness of about 4 mm. was maintained; towards the base, however, there was, in all probability, a gradual thinning off, so that the surface of the sarcotesta, near the point of insertion of the seed, must have been considerably less than 2 mm. from that of the sclerotesta. From the almost sudden curve inwards of the sclerotesta, between the ridges at the micropyle, the sarcotesta, which followed a gentle curve inwards, is there found with a maximum thickness of about 6 millimeters. None of the sections passing through the extreme apex shew the exact boundaries of this tissue, but enough of it is preserved to indicate that, so far as the limits of our series go, no flattening took place, but that the sarcotesta around the micropylar tube gradually tapered on all sides towards the apex. This is in conformity with the impressions of seeds attached to Neuropteris Heterophylla and Neuropteris Obliqua described by Kidston (On the fructification of N. Heterophylla, Proc. Roy. Soc. London, 197, 1, 1904) and Kidston and Jongmans (Archives Néerlandaises d. Sci. Exactes et Naturelles, S.III.B.T.1.p.25, 1911).

The bulk of the sarcotesta was formed of parenchymatous thin-walled cells extending from the limiting layers, to be described later, to the sclerotesta within. At the point of junction with this latter tissue there is superficially a somewhat sudden change from the sclerised to the unsclerised portion; but the innermost cells of the sarcotesta can be recognised as direct continuations of the rows of sclerotestal elements. Viewed in longitudinal sections the inner sarcotestal cells were elongated and tubular in form, measuring some .15 mm. to .25 mm. in length and .033 mm. to .049 mm. in width. Of these most are directed longitudinally or obliquely outwards and upwards, forming an angle with the surface of the sclerotesta; it is therefore only in tangential or longitudinal sections that the transitional character of the structure in this region is adequately appreciated (Pl. fig. ). Transverse sections through the body of the seed exhibit an apparently much more sudden transition than those through the apex or the base, as owing to the curvature of the seed's surface these latter traverse the elements more obliquely, thus approaching more nearly to the plane in which the transition is most conspicuous. This may possibly be true also of the similar observations of Scott and Maslen (Ann. Bot. Vol.XXI, No.LXXXI, 1907) for <u>T. Parkinsoni</u> A study of the longitudinal sections shews that here at all events the transition was of the same gradation throughout.

Very frequently in transverse sections cells comprising the innermost layer of the sarcotesta are seen in close proximity to the sclerotesta cut in the longitudinal direction, shewing that their course was horizontal in relation to the axis of the seed. In tangential sections, e.g. S.32.g. (fig.5, Pl. St.C.) the inner sarcotestal cells are seen to alter their direction in the same sinuous manner, though to a slightly less extent, as do those of the outer layers of the sclerotesta. Here and there are present indications of slight thickening of the cell walls in this region and the intercellular spaces are either very minute or completely absent. It is clear then that apart from the actual sclerisation, and even that, as we have seen, is in places transitional, the structure of the cells and architecture of the innermost tissue of the sarcotesta were essentially the same as in the outer layers of the sclerotesta, - a continuity of structure which can only be reconciled with an homogeneous origin. As we pass further outwards the intercellular spaces become more and more pronounced, and the constituent cells which at the internal periphery were tubular very quickly become more rounded; and pari passu as we pass to the exterior develop irregularities in the form of projections which connect on to those of adjacent cells.

Near its external limit the sarcotestal tissue had become so lacunar and these projections so pronounced as to give an almost stellate appearance to the component elements (Text fig.7). Owing to the rounded character of the middle sarcotestal cells the intercellular spaces between them were of more or less equal dimensions in every direction. At a very little distance out, however, the cells evinced a slight flattening in the horizontal plane and a tendency to form short vertical series separated from one another by elongated lacunae. The latter feature reached a maximum at the periphery, where the sarcotestal cells had assumed the irregularly lobed outline, and in tangential sections vertical series of variable extent formed of slightly flattened cells can be seen separating lenticular intercellular spaces. Sections in this plane also shew that the arms or projections of successive cells were often superposed so that not only is each large lacuna frequently without trabeculae, but where the projections are cut through transversely they themselves often appear as narrow vertical series partially or completely separating adjacent intercellular spaces (fig.10, Pl. ). Although the above fundamentally expresses the arrangement of the cells in this region there was the greatest irregularity, but having nevertheless this general plan for its basis.

In the living condition this tissue must therefore have been remarkably light and spongy in character and if these seeds were shed into water would render them of great buoyancy. Several seeds of this affinity, e.g. *Trigonocarpus Parkinsoni* (Scott and Maslen, loc. cit. p. 101), *Pachytesta* (Renault, Bassin Houiller et Permien d'Autun et d'Epinac, Vol.IV. p.390 and Pl.LXXXIII.fig.10) and *Aethiotesta elliptica* (Renault, Mém. Soc. d. Sci. Nat. d. Saône-et-Loire, p.1, 1887) exhibit a lacunar sarcotesta and the suggestion put forward by Renault for *Aethiotesta* that this served as a mechanism for dispersal by water may well have been true also in the present instance, all the more that the method of occurrence of fossilised vegetable remains favours the view that they were in part components of water--borne drift.

*Text fig.7*. A small portion of the outer sarcotesta shewing the large intercellular spaces.

## *(b) The Peripheral Zone*

At the exterior the sarcotesta was bounded by a narrow epidermis of thin-walled cells of which usually only the external and radial walls are preserved even in the few places where this region still remains. The tangential dimensions of these epidermal cells were from 1.5μ- 3μ, whilst their radial extent was probably about 2μ. Beneath this epidermis there were numerous sclerised fibres between which a soft-walled parenchymatous tissue was most likely present originally, though all except a few remnants of walls have become disintegrated.

The total width of this peripheral zone where there is no evidence of crushing or contraction is about .3 mm. In most cases the sclerised elements appear irregularly scattered, but this is probably due to post-mortem changes, as in several places where this zone has almost retained what was probably its original width they are seen to be grouped together to form somewhat irregular radial plates (Pl. fig.19). Each plate was formed of from 2-6 elements in the radial plane, the higher number probably being the more usual, whilst tangentially the groups generally form either a single or a double row.

There seem, however, to have been not infrequently considerable local aggregations of these elements tangential to the surface, forming broad bands which may well have arisen through the lateral fusion of a number of the sclerotic plates. In outline each of these broad bands formed a continuous hypodermal layer of sclerotic elements with occasional projections inwards. Owing to the crushing and contraction which has taken place many of the sclerotic bands have come to occupy an oblique or even tangential direction and in some cases the resulting superposition of the originally radial plates gives rise to the greatest irregularity and confusion.

The individual sclerotic fibres were roughly rectangular in form with a slight flattening in the radial direction. They were somewhat variable in size, as seen when cut transversely, but the average element was about 2.5μ (radially) by 4.5μ. The wall was much thickened with a uniform width of about .8μ and formed of an outer transparent yellowish layer and an inner and slightly thicker brown layer, both of which in the thinnest sections shew clearly defined lamellation.

The longitudinal sections do not shew the outer region of the sarcotesta preserved,so that the form of the elements in this direction can only be inferred from their appearance where cut obliquely, either in consequence of the plane of section or through post-mortem displacement. The maximum longitudinal dimensions which these shew is a quarter of a millimeter, and no doubt the real length of each element was much longer.

The width of the intervals between successive plates is usually fairly regular, but rarely they are seen in very close proximity even where there is no evidence of displacement, and these are perhaps,like the larger aggregations, to be interpreted as indications of anastomoses.

Interspersed amongst the sclerotic cells are numerous secretory sacs some 7.5μ in diameter which were no doubt situated in the soft parenchyma that formed the ground tissue between the sclerotic plates.

These secretory elements are also numerous just beneath this zone, but so far as can be interpreted from the available material their distribution seems to have been somewhat irregular.

Here and there the secretory sacs occur two or three together arranged radially, and it is possible that these too formed rows alternating with those of the sclerised elements, a possibility that gains weight from their occurrence in this manner in the nucellus of the seed.

Where cut obliquely the secretory cells shew fine longitudinal striation of the external surface of their walls; in one section which is especially well preserved this wall is seen cut transversely and presents at the exterior a series of dark beads separated by clear spaces of about equal width, which obviously precludes the possibility of the appearance being due to a matrix effect. Surrounding the carbonised contents is a clear space which probably represents a thick sclerotic wall: the elements in fact were probably almost identical in appearance with the thick-walled mucilage sacs found in the sporophylls and testa of present--day Cycads.

In favourable cases four or five connections at more or less regular intervals can be seen between the dark central mass and the thin external wall. They probably represent radial pittings of the cell wall as found in their modern representatives. These must not be confused with the numerous and much finer and fainter radial striations which are often present here and doubtless result from the structure of the matrix.

In general, as we have already indicated, the secretory sacs are found at the exterior between the sclerotic plates, but occasionally they were situated at one or other end of these or even in the middle, replacing the sclerotic elements themselves (cf. Petiole of Medullosa, Scott's Studies in Fossil Botany, fig.176).

The presence of the numerous hard plates in the peripheral zone of the sarcotesta must have given to that region considerable rigidity, and the dark layer often seen between it and the soft underlying tissue is no doubt to be interpreted as originating through the compression of the outer cells of this latter.

## (c) The Secretory System

The sarcotesta is however not only distinguished from that of other seeds by its extreme development but also by the numerous secretory sacs which permeate it throughout (Pl. fig.2 M.S.) In all respects the secretory elements of the interior appear to agree with those of the periphery. As we have previously remarked these sacs were most likely thick-walled, but there is the bare possibility that the apparent pittings may be the radial walls of a secretory epithelium or even cracks in the matrix. Occasionally the dark carbonised contents is seen to one side of a large space formed by contraction of the surrounding sarcotesta and there does not seem to be any indication of a thick wall, the dark mass abutting directly upon the parenchymatous cells around. On the whole, however, the impression gathered from a careful examination of hundreds of these sacs in various parts of the seed and in diverse conditions of preservation is that their walls were thickened, though this appearance may possibly be due to post-mortem swelling of the inner layers of the wall, as has been suggested for Lepidodendron. However, the presence of almost identical structures in modern cycads adds weight to the view that the walls were really thickened in life. At the periphery of the seed these elements have frequently become isolated and in this condition the thickened wall stands out quite distinctly from the transparent matrix which surrounds it, as can be seen in fig.     Pl.

Each secretory sac is sheathed by a continuous layer of parenchymatous cells which separates it off from the surrounding lacunar tissue. Component cells of this sheath are seen in tangential sections to have been vertically elongated and to have reached a length of some five times their width.

<u>Text fig.8</u>. Plottings of the secretory sacs in three successive sections. In order to make the corresponding sacs more clear they have been connected up by means of dotted lines.

By carefully mapping the distribution of the secretory sacs in successive sections of a series one can recognise, from the relative positions which they occupy to one another, that the same sacs often extend for a considerable distance (Text fig.8). The only series which show any extent of the sarcotesta well preserved are the Manchester series, R.1161.a-k and S.31.a-k from the

University College Collection. Both of these series are oblique, so that in order to institute comparisons as to the numerical relations at different levels, only the secretory sacs between one pair of adjacent ribs will be considered: also since the peripheral zone containing the sclerotic plates is only partially preserved in the University College series and almost entirely absent in the Manchester series, the sacs in this region have been altogether ignored. By mapping the sacs in S.31.b-1 it was found that in this region, which is that between the middle of the seed and about half way up the micropyle, the number of sacs varied from 64 to 93, the latter figure being attained at the level of the shoulder with a slight falling off in number both above and below.

In the subjoined table an analysis of the results obtained from S.31.b-1 is given; the vertical series shew the number of sacs in each section which can be traced back as far as that of which the designating letter heads the column. In Section F the sarcotesta is much broken, so that one cannot determine which sacs arise there first, hence the figure for G is probably double its real value. If we assume this to be the case then the number of additional sacs appearing at any given level is a fairly constant one, being an average of about 31, or 63 for the entire circumference. The whole interval included between S.31.b and S.31.i is about fourteen millimeters and out of the total of 195 separate secretory elements encountered, not more than 8 persist throughout. A few are only present in one section, whilst the greater number extend into the next (an interval between sections of about 2 mm.) with a falling off in each successive section.

| S.31. | B | C | D | E | F | G | H | I | Total |
|---|---|---|---|---|---|---|---|---|---|
| Section S.31.C | 46 | 23 | | | | | | | 69 |
| " D | 45 | 16 | 26 | | | | | | 86 |
| " E | 35 | 12 | 24 | 22 | | | | | 93 |
| " F | ? | ? | ? | ? | 10 + | | | | ? |
| " G | 23 | 6 | 2 | 8 | 10 | 37 | | | 86 |
| " H | 20 | 5 | 2 | 7 | 6 | 32 | 11 | | 83 |
| " I | 8 | 4 | 2 | 6 | 6 | 13 | 5 | 20 | 64 |

In the Manchester series the obliquity is in the opposite direction to that of the University College series and the sarcotesta between the two ribs on the lower side has been used for the purpose of calculation. The level of K in this series is the base of the micropyle and of C that at which the nucellus is attached to the chalazal cushion. In the accompanying table the number of secretory sacs in each case is given and represents approximately $\frac{1}{3}$ of the total at that level.

| | | | |
|---|---|---|---|
| Man. Coll. C | 34 | Man. Coll. H | 101 |
| Man. Coll. D | 46 | Man. Coll. I. | 92 |
| Man. Coll. E | 65 | Man. Coll. J | 93 |
| Man. Coll. F | 82 | Man. Coll. K | 109 |
| Man. Coll. G | 98 | | |

Although there is a certain amount of irregularity in their number there is a decided decrease of secretory sacs towards the base of the seed and in the U.C.L. series in which the sarcotesta is preserved to a higher level a similar decrease is observed near the apex. From a comparison of the same sacs cut at different levels they are seen to have tapered gradually both above and below, so that where cut across near their terminations they are of very small size and, where the surrounding wall is disclosed, very closely resemble developmental stages in the formation of secretory canals, the surrounding sheath simulating an epithelium, which may perhaps be the explanation of the similar appearances described by Prof. Seward in the medullosean petiole Rachiopteris Williamsoni (Ann. Bot. Vol. VIII. No.XXX, p. 1894).

The position occupied by a single secretory element as seen in one section in several instances exhibits two in intimate contact in the succeeding section (Pl fig. 12), an appearance that may be due either to branching of the original sac or to the origin of a second in contact with it, but the fact that both are usually of nearly the same cross sectional area favours the former alternative.

The normal course followed by the secretory elements was approximately parallel to the direction of the surface with a slight outward tendency exhibited by the more interiorly situated. Occasional departures from the general direction occur and give a slightly sinuous character to the sacs affected. The distribution was an irregularly scattered one with a marked increase in number, especially of those with a narrow lumen, towards the periphery. The largest secretory elements are found in the region midway between the sclerotesta and the external surface, and attain a diameter which averages about .124 mm. but may be as much as .166 mm.

## (3) The Inner Flesh

All those sections which pass through the body of the seed, even where the preservation of soft tissues such as the sarcotesta or nucellus is excellent, shew no indications of an inner flesh. It is certainly true that in most of the preparations the internal surface of the sclerotesta exhibits an irregularity of outline that might seem to indicate its former presence, but in the transverse series S.33.a - S.33.d, in which the internal preservation is, apart from contraction, almost perfect, the inner margin of the sclerotesta is in some places bordered by the radially flattened fibres already referred to, forming a perfectly even surface. This latter affords positive evidence of far more value than the negative evidence of a ragged surface, and still more so since we find in the badly preserved material that the sclerotesta does shew signs of superficial disintegration.

In dealing with the nucellus we shall find that it was possessed of a highly differentiated and probably strongly cuticularised epidermis and there is evidence that it was in close contact with the sclerotic tissue.

Having due regard to all these facts one is forced to the conclusion that in this species of <u>Trigonocarpus</u>

an inner flesh was not present in the middle part of the seed cavity.

When we come to the consideration of the upper or apical region the facts are, however, different, for at about the level of the insertion of the micropylar beak the zone of sclerisation begins as it were to shift slightly outwards and we thus find within the sclerotic micropyle several layers of cells which, though possessing thick walls, have not the dark brown contents of the sclerotestal fibres themselves, and moreover become thinner-walled as we pass inwards. This tissue reached its maximum thickness, of some four layers, midway between the angles and on its inner margin exhibits a broken surface that here might well indicate a greater extent of probably more parenchymatous elements (Pl. fig.8.i.f.).

Even then if we regard this micropylar lining as homologous with the inner flesh of other Trigonocarpeae our seed is as extreme a member of the variational series in this respect, on the one hand, as <u>Pachytesta</u> on the other, whilst most of the remaining members of the group probably occupy a more or less intermediate position.

# V. THE VASCULAR ORGANISATION

## (a) The Chalazal bundle and Nucellar system.

The lowest of our transverse sections, viz., S.33.a, is ill preserved and yields us no information as to the vascular structure, but from S.33.b Man., R.1161.b, and the longitudinal section S.32.e, we find that a single vascular bundle entered the chalazal end of the seed. This passed up to the base of the nucellus, at which level it is cut by the section S.33.b (Pl.    fig.16). The bundle is there seen to have been a solid mass of xylem very slightly triangular in outline, the angles corresponding in position with the three main ribs of the seed. It was formed of from sixty to seventy elements and attained a diameter of about .18 mm. The larger tracheae are situated mostly at the periphery (Text fig.9) and in their radial dimension, which varies from about 30-40μ, considerably exceed their width, which may be as much as .025 mm. or as little as 75μ (average about .015 mm.). The central elements are polygonal in form and from .015 mm. - .03 mm. in diameter. The bundle therefore has the appearance in transverse section of a central core surrounded by a single layer of radially flattened elements.

Text fig.9. Transverse section of Chalazal bundle from section S.33.b, shewing the six protoxylem groups (pt.xy.) and the radially extended tracheids at the periphery surrounded by a parenchymatous sheath.

The smallest tracheae, measuring some .8µ in diameter, lie just within this outer layer and appear to form six not very clearly defined groups, two corresponding to each of the three angles. That these are the protoxylem elements is rendered the more probable by an examination of the single longitudinal section passing through the chalazal bundle (S.32.e). From this we find that the majority of the elements were scalariform or densely spiral (fig.18, Pl. ), whilst separated by one such element from the periphery of the bundle there appear to be one or two narrow elements with distant spiral thickenings.

The xylem is completely surrounded by a ring of parenchymatous tissue (Pl. fig.16, p.s.) composed of three to five layers of thin-walled elements which together attain a width of about .05 mm. In the obliquely transverse section through this region and in the longitudinal section this tissue is seen to consist of narrow vertically elongated components which may have represented a sort of undifferentiated phloem. The whole bundle, including this delicate sheath, was surrounded by larger-celled and thin-walled nucellar tissue amongst the cells, of which numerous secretory ducts were present. One element to be observed here exhibits parallel markings and may be a transfusion tracheid comparable perhaps to those found by Scott and Maslen between the bundles of the sarcotesta of <u>T. Parkinsoni</u> (p.114 and Pl.XIV. fig.25 st.).

The single bundle passed through the base of the nucellus where it expanded in a cup-like manner and formed a tracheal investment to the megaspore cavity. This is well seen in section D of Dr. Scott's series, which passes obliquely through the base of the megaspore cavity and shews the continuous and several-layered tracheal cup around its base. Also in section S.33.c, which passes almost transversely through the seed at about five millimeters from the chalazal end, the tracheal elements appear as a continuous layer situated at the inner limit of the nucellus. The sheath of tracheids is not of uniform thickness, but the number of elements in the radial direction varies from one to four.

As seen in transverse section the tracheal mantle appears to be built up of broad laterally fused bands traversing the longitudinal direction, which are thickest in the middle and gradually diminish towards the sides. As can be seen from the plottings (Fig.1) the section S.33.c is slightly oblique to the axis of the seed and it is on the higher side of the section that this grouping of the tracheids into bands can be observed; the lower side exhibits a much more uniform thickness of the xylem sheath, though even at this level, which is nearly one millimeter below the upper edge, a slight thinning at places is to be recognised.

Presumably then the vascular tissue between the level of this section and the base of the megaspore cavity consisted of a uniform zone of tracheids which on the upper side became incompletely segregated into bands. The number of these latter cannot be ascertained with certainty, owing to the oblique direction of our most nearly transverse sections, but if we assume the slight indications of thinning on the lower side to mark the lateral limits of vascular aggregations, then there were probably twelve such bands, the width of the more clearly delimited varying between 1 mm. and 1.3 mm.

The internal diameter of the megaspore cavity as seen in section S.33.c, from which the above data were obtained, is 4. 4 mm., which represents a periphery of approximately 13.8 mm. If we assume each band to have been of equal width this gives us 1.15 mm. as the measurement of each if their number were twelve. This figure is sufficiently close to the actual measurements to support the belief that this was the actual total of the bands. Unfortunately none of our other preparations furnish any corroborative data, so that whether this number is a constant one must remain an open question, but it is worthy of note that the repeated hexamerous character of the seed structure again recurs in this figure.

In the next section of the series (S.33.d) the vascular tissue is in many places badly preserved, but it is clear that at this level the tracheids were completely segregated into strands that were lenticular in transverse section and much narrower (0.25 mm.- 0.5 mm.) and also much more numerous than at the preceding level (probably over twenty, but on one side the tracheal zone is badly preserved).

In one case where a vascular strand has been cut across transversely this shews four to five elements in the median radial plane with a diminution both in number and size on either side. The smallest elements are to be found in the middle of the strand, so that these bundles were in all probability mesarch in structure. There is some evidence afforded that anastomoses may have taken place between the attenuated margins of the distal ends of adjacent bands, but in general, except for some 7 mm. at the base where they form the continuous sheath, these appear to have been distinct from one another and to have passed longitudinally up the internal periphery of the nucellus separated by narrow intervals.

In some of the transverse sections tracheids can be seen at the edge of the xylem bands which pass horizontally as is the case in *Trigonocarpus Parkinsoni* (Scott and Maslen, loc. cit. Pl.XIV. fig.13) but it has not been found possible to establish that these formed actual connections from one band to the next.

Sections passing through the nucellus tangentially shew that whilst the general direction of the bands was vertical the individual tracheids were often oblique or curved, and the appearance of horizontally directed elements, in the slightly oblique transverse sections, might easily be accounted for in this way.

No indication of phloem has been observed in relation to the nucellar strands, though in most places the preservation is sufficiently good to warrant the expectation that remains of such a tissue would be present had it existed.

The final section of the transverse series adds little information as to the vascular structure. It contributes, however, confirmatory evidence that the bands of xylem were disconnected and also that their smallest elements were centrally placed.

For the further course of the bundles only such data as can be gleaned from longitudinal and oblique series is available. From these the bands of scalariform tracheids can be traced to what must have been a level close to the floor of the Pollen chamber. Only two sections, viz. S.32.c and Section I of Dr. Scott's series, actually pass through this structure; neither of these shews any tracheids within the Pollen chamber, but the internal preservation of the latter section is very poor, whilst that of the former, though in some respects leaving little to be desired, has a broken and ill preserved pollen chamber floor.

The vascular elements which go to form the nucellar system appear to be very uniform in structure with an average width of from .023 - .03 mm. and exhibit scalariform thickenings which occasionally shew anastomoses between adjacent horizontal bars. (Width of interval between bars .0015 - .003 mm.).

From the above description it will be seen that the internal vascular system is almost if not quite identical in its essentials with that described by Scott and Maslen for Trigonocarpus Parkinsoni (Loc. cit. p.120-121) and it may be of some significance that in neither species has the nucellar system been traced beyond the plane of insertion of the Pollen chamber.

## (b) The Sarcotestal system.

In several sections of the University College series S.31.a - S.31.k, and perhaps in section R.1161.h of the Manchester series, bundles in various conditions of preservation are to be found occupying positions at the extreme periphery of the sarcotesta proper, upon the line of separation between the outermost lacunar tissue and the limiting layers containing the radial sclerotic plates. The only parallel amongst nearly allied seeds to so external a position is to be found in *Pachytesta* (Renault, loc. cit.) where, however, if we regard the exotesta as representing sarcotesta and sclerotesta combined (Oliver, On Gymnospermous Seeds, New. Phytologist, Vol.I, No.7, p.148, 1902) the bundles are only far out if considered in relation to the testa of the seed as a whole, and not as to the sarcotesta in particular.

Owing to the extreme peripheral position which these bundles occupy in *Trigonocarpus Shorensis* and the incompleteness of the preservation of this region, it is hardly surprising that in no slide do we find more than three sarcotestal bundles present at one and the same time. In several of the University College series S.31.a - S.31.k two bundles are cut in successive sections and both of these are fortunately situated between the same pair of major ribs, and also occupy the same positions relative to them. Altogether four distinct bundles can be distinguished in this series and two possible bundles are also recognisable in one of the Manchester sections (R.1161.h). In every case these sarcotestal vascular strands are situated in the radial plane midway between a major and a minor rib and though the bundles are not present, in any one of our specimens, on all three faces yet the occurrence of two, and two only, in several successive sections between the one pair of major ribs seems, in view of the preservation in this part of the periphery, to point conclusively to the total number as being six symmetrically disposed around the circumference of the seed.

The sarcotestal system was then at all events in the upper part of the seed identical as to the number of its components, and almost so as to their arrangement, with that which has been described for <u>Trigonocarpus Parkinsoni</u> and <u>Polylophospermum</u> (Oliver, Ann. Bot. Vol.XXI. No.LXXXII. pp.303-304, 1907), only differing in the latter respect with regard to the proximity of the bundles to the sclerotic shell.

The structure of the individual strands is beautifully shewn in S.31.1. (Fig.17, Pl. ), where, owing to the curvature of the surface, the section which is oblique to the axis of the seed passes transversely through a sarcotestal bundle exhibiting extraordinarily perfect preservation. As can be seen from the figure the bundle is slightly more extended in the tangential than in the radial direction (.29 mm. × .17 mm.) and consists of some seventy xylem elements of which the smallest occupy the central region (Pl. fig.17, pt.x). The latter, which probably represent the protoxylem, comprise some four tracheids (.0075 mm. by from .0075 mm.-.015 mm.) with thicker walls than those around. From the mesarch protoxylem there extends in the centrifugal direction an irregular fan-shaped group of tracheids (fig.17. Cf.x), the elements of which, though larger than those of the protoxylem, are distinctly smaller than both those which lie on their flanks and those on the inner side of the bundle.

The centripetal xylem (Pl. fig.17, cp.x) exhibits a further distinction in that though the section is transverse to the bundle as a whole the elements here are mostly cut more or less obliquely, so that the scalariform or reticulate sculpturing of their walls can be seen. It should, however, be said that a single layer of xylem elements on the centripetal side of the bundle immediately next the protoxylem do not shew this character, although they exhibit the increased dimension.

The bulk of the centripetal wood evidently then consisted of short tracheids such as are frequently present in centripetal xylem that is becoming obsolete, as is exemplified in Lepidodendron vasculare (Hovelacque, M. Recherches sur le Lepidodendron selaginoides, Sternb. Mém. Soc. Linn. Normandie, Vol. XVII) or Osmundites Kolbei (Kidston and Gwynne-Vaughan, On the Fossil Osmundaceae, Pt. IV. Trans. Roy. Soc. Edinburgh

### (c) Additional facts as to the vascular system of Trigonocarpus Parkinsoni

The course of the sarcotestal bundles at the base of the seed of Trigonocarpus Shorensis cannot be traced, as the peripheral portion is lacking in the sections which pass through that region.

Two sections probably belonging to Trigonocarpus Parkinsoni, viz. S.34.a and S.34.b of the University College collection have, however, recently come to hand, which Prof. Oliver has also placed at my disposal for description and which, owing to their excellent preservation add considerably to our knowledge of the vascular structure in this region. These two preparations will now be fully described, as the absence of similar data regarding our own seed and the essential similarity between the vascular systems of the two species is sufficient justification for inclusion here.

The first section, viz. S.34.a, just passes through the lower limit of the sclerotesta and the second, parallel to the first, obliquely through the base of the seed, but without traversing the megaspore cavity. In this latter section eight ribs can be distinguished, of which three are doubtless the primary ribs, and from the distribution of the remaining five it seems likely that the seed was twelve-angled, the missing ribs having become obliterated either by the obliquity of the section or in consequence of the lower level at which the seed is cut on the side on which these ribs are absent. A further point of importance is that this seed was evidently blunt at the base and not tapering, as shewn by the great difference in the area of sclerotesta sectioned at the two successive levels. These facts, taken together with the position of the sarcotestal bundles, which are relatively close in near the sclerotesta, seem to justify the assumption that the seed was *Trigonocarpus Parkinsoni*.

In both of the sections a few secretory sacs can be seen. Dr. Scott has permitted me to examine his best preparations of *T. Parkinsoni* with the sarcotesta preserved, and particularly Wild's Section s.1952, figured by Scott and Maslen (loc. cit. Pl.XII. fig.11), in which there are present some dark bodies surrounded by a clear space .045 mm.-.053 mm. in diameter. Neither for these nor for similar bodies in other preparations can one definitely assign a secretory nature, but a comparison with ill-preserved secretory sacs of *T. Shorensis* discloses a striking similarity between them. Probably then secretory sacs were present in T. Parkinsoni both at the base and apex of the sarcotesta, but in very much smaller numbers than in T. Shorensis.

The central region of the lowest of the two sections is beautifully preserved and cuts the single main chalazal bundle at the level where the sclerotesta begins to be differentiated. The direction is doubly oblique, so that regarding the structure of the bundle itself there is difficulty of interpretation; but as shewing the course of the sarcotestal strands this obliquity is of supreme importance.

The general outline of the vascular bundle was very slightly triangular, with a diameter of about .3 mm., the angles corresponding in position to the secondary ribs. From each of the two upper of these angles (Pl.  fig. 14 v.b.) a strand is seen in process of being given off into the sarcotesta.

The main bundle is surrounded by a thin-walled parenchymatous tissue (par.) consisting of vertically elongated elements. In the centre is a solid mass of xylem, throughout which are scattered short tracheids horizontally directed, so that the scalariform or pitted thickenings of their walls can be seen. The section is sufficiently oblique to shew that the thickenings of the longitudinally directed tracheids were scalariform.

In the centre of the xylem a single secretory cell can be detected (Pl. fig.14 M.S.).

The periphery of the bundle is formed of a band of short tracheids 1-2 elements in width which, for the most part, are separated from the central xylem mass by what appears to have been parenchymatous tissue similar to that surrounding the bundle as a whole. But this tissue is interrupted at several points by junctions between the outer and inner tracheids. The smallest xylem elements lie mostly at the periphery of the central core, but others are situated more interiorly.

From an examination of the angle which is cut at the highest level it can be seen that from this peripheral zone pass out the xylem elements of the sarcotestal bundles. In this particular case the portion has partially separated off from the central mass and the corresponding bundle, owing to the double obliquity of the section, is again cut further out in the sarcotesta. What was doubtless the second half of this strand is seen at the edge of the bundle cavity, and clearly shews that the course of the two halves was divergent.

In the next section, viz. S.34.b, which is nearly parallel to the former, five sarcotestal bundles can be distinctly recognised, whilst the position of a sixth is marked by a lacuna.

Where the bundles are cut on the lower side of this section the level is only about one third of a millimeter above that at which the central bundle is cut in the previous slide, so that the distance is scarcely sufficient for other bundles to have been given off.

It would appear then from these two preparations that three bands of xylem in continuity with the peripheral part of the chalazal strand were given off simultaneously, each of which then almost immediately underwent bifurcation into two halves that diverged from one another, the six strands thus formed constituting the sarcotestal vascular system.

The soft parenchymatous tissue which surrounded the bundle consisted of cells which, when cut transversely, appear more or less polygonal and isodiametric, where cut longitudinally they measure about .12 mm.× .032 mm. and are separated by slightly oblique transverse walls. This tissue may perhaps have served the purpose of phloem, though apparently quite undifferentiated; that it had some definite function is supported by its sharp delimitation from the surrounding tissue even where this too was parenchymatous in nature. Whatever its character a similar sheath accompanied each of the 6 sarcotestal strands in this, the basal region of the seed, though perhaps not throughout their extent.

As seen in S.34.b (Pl.     fig.15) the central part of each bundle was occupied by a strand of elongated scalariform tracheids and around this was a complete ring of much shorter and stouter spiral or slightly reticulate elements. Separating the outer zone from the central core was a narrow space from which the bulk of the tissue has perished, but here and there can be seen patches of elongate parenchymatous elements similar to those forming the bundle sheath and no doubt they originally constituted a complete ring.

Each sarcotestal bundle was then essentially similar to that supplying the chalaza. An examination of the bundles of Dr. Scott's section 626 of a T. Parkinsoni through the same region as S.34.b, though exhibiting far less perfect preservation, seems to agree with the description here given.

Before leaving these sections it should be said that though the type of preservation is the same as that of the bulk of the specimens of _T. Shorensis_, in none of the secretory elements present was I able to find the longitudinal striation characteristic of the wall in that species, though this feature is exhibited by well preserved ducts in the stems of _Medullosa anglica_.

# VI. THE NUCELLUS

The nucellus was attached to the dome-shaped projection of the sclerotesta at the chalazal end of the seed and stood up free within the seed cavity. The total length from the point of junction with the testa to the base of the pollen chamber was about 18 mm. and its diameter in the middle or widest region about 11 mm. As the cavity in this part was some 15 mm. in width there is thus left a space of 2 mm. all round for which to account. The question of an inner flesh has already been discussed but in any case these dimensions for the nucellus are probably much too small, owing to post mortem contraction.

The general outline of the nucellus conformed closely to that of the cavity within which it stood, following the same lines until near the base of the micropyle, where the nucellar tissue curved sharply inwards to the insertion of the pollen chamber.

Disregarding this latter structure the conformation was that of a sharply pointed egg with its narrower end directed downwards and attached to the sclerotesta, whilst the blunt free end was surmounted by the pollen chamber.

The nucellar tissue is in most cases either lacking altogether or ill preserved, but fortunately in the transverse series S.33.a to S.33.d the structure is beautifully shewn, though as a whole there is evidence of considerable contraction having taken place. In the uppermost of the series the nucellus is seen occupying a one-sided position which is in part due to the slight obliquity of the plane of section, but no doubt in the main to displacement caused by asymmetrical shrinkage.

In the second of this series the nucellar tissue is seen surrounding the chalazal bundle. As already described this consists of parenchymatous tissue of which the cells are thin-walled and vary in size from about .01 - .050 mm. interspersed with secretory ducts the largest of which are at the periphery and measure about .07 mm. in diameter. This ring of tissue is only .2 mm. in width but from its ragged edge was evidently much more extensive in life.

The following sections of this series shew the whole of the nucellar tissue, in general, beautifully preserved from the tracheal mantle bordering the megaspore cavity within to the epidermis which constituted its limit without. Owing to the shrinkage of the soft underlying tissue the much less contractable epidermis is thrown into numerous folds, but the projections thus formed do not, as in Trigonocarpus Parkinsoni, correspond to underlying vascular strands (Maslen and Scott, loc. cit. p.119), but to radial files of secretory elements (Pl. fig.20 M.S. and N.T.). Taking the distance from the edge of the megaspore cavity to the summit of these ridges as the basis of our estimate the thickness of the nucellar tissue must have been, near the chalazal end of the seed, at least a third of a millimeter, though above this level it diminished slightly and then remained of constant width until the base of the pollen chamber was reached. At the outside, as already stated, there was a very strongly defined epidermis, as seen in S.33.c. Fig.20, Pl. where the cells stand out all the more clearly since their contents are preserved as dark carbonaceous masses that have contracted away from the cell walls. The epidermis had a radial extent of some .05 mm., its component cells were about .03 mm. in width (tangential) and in one or two places where, owing to the contortions of the surface their longitudinal dimension can be estimated it is about three times as great as their width (.09). As seen in this view the cells are more or less oblong in shape, whilst cut transversely they appear distinctly convex on the external face, which latter feature seems to point to the absence of any very close contact with an inner flesh.

Under the best conditions of preservation the epidermal cells resemble very closely the secretory sacs already described and, like them, have the appearance of possessing a somewhat thickened wall. In several places the outer layer of the exterior walls, together with part of the middle lamellae from between each pair of the component cells, has split away, so that as seen in transverse sections the appearance presented is that of a thin membrane with radially directed pegs projecting inwards. Evidently this outer layer was of a durable character as it can occasionally be recognised even where the interior tissue has decayed away, suggesting that it may probably have been a cuticularised layer such as we find with similar pegs amongst modern plants. A further point to be noted is that the epidermis as a whole is much less affected by contraction than the tissue below, as indicated by the wide separation between them which is seen in the less well preserved material.

Whether then the epidermis were actually cuticularised or not, it was undoubtedly of a very specialised character, such as we should hardly expect to find in a completely enclosed structure like the nucellus if it were in close contact with a soft inner flesh, a point to which we shall have occasion to revert in dealing with the relatively primitive characters that this seed exhibits.

Between the epidermis and the tracheal sheath there intervened a zone of tissue consisting of soft parenchymatous elements in which numerous secretory cells were present. The ground tissue was without intercellular spaces and formed of polygonal cells with very thin walls, and where preserving their original form vary from about .03 mm. to .08 mm. in diameter. As seen in transverse section they appear roughly isodiametric but longitudinally they traversed a distance of about .15 mm. Occasionally they themselves appear filled with a honey-comb-like tissue of thin-walled cells .01 mm. in diameter. The secretory cells were embedded in this ground tissue and where they did not occur singly formed radial plates of varying extent and usually consisting of a single row of secretory elements, though more rarely at the base of the seed of two such rows. The greatest number of secretory cells which were present in any one radial plane appears to have been five. The proximity of the radial plates and the number of elements in each decreased as the apex of the seed was approached so that some two-thirds from the base of the pollen chamber the plates were about a third of a millimetre apart and reduced to one, two, or at the most three elements. The secretory sacs themselves exhibit much the same structure as those of the sarcotesta; in width they vary from about .06 to .09 mm. and where favourably preserved exhibit the same delicate striation of the wall. This latter is, however, not so thick as in those of the sarcotesta. In the longitudinal direction the carbonised contents shew segmentation into short lengths but the septation thus produced probably bore no relation to transverse walls, as no evidence of their presence can be traced.

In two of the seeds, viz. S.31.U.C.Coll and Man.R. 1161, besides the longitudinal ridges already referred to, others more pronounced are present, occupying positions opposite to the commissural ribs, and bear no relation to contained radial files of secretory elements. In the series S.33.U.C.C. with its excellently preserved nucellus no such ridges are, however, to be seen, which may be correlated with the fact that this seed was probably in an immature condition, judging from its relatively small size, the thinness of the testa, and the slight development of the ribs. In S.31.g such ridges, corresponding to both the major ribs preserved, can be distinguished, and one of them is even more pronounced lower down, though the other has somewhat lost its original form and is represented by a blunt protuberance of nucellar tissue. Such commissural ridges,[1] of which an example is figured in Pl. fig.13, n.f.) from section S.31.e furnish the strongest evidence that the nucellar surface was in close contact with the sclerotic testa, at all events in the mature condition, and the well developed cuticle further emphasises the improbability of a soft intervening tissue which would give an intimate contact such as could not obtain between an hard sclerotic surface and a cuticularised epidermis.

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[1] Cf. Renault, Flore Fossile d'Autun et d'Epinac, pt.2, p.398. Angling of nucellus in Trigonocarpus pusillus.

# VII. THE POLLEN CHAMBER

Our information respecting the structure of the pollen chamber is extremely meagre, as only three of the sections pass through this region, and of these two alone furnish data of any importance. S.32.c, however, of the nearly vertical series, is excellently preserved except for the pollen chamber floor, which in part is missing. The general form of the pollen chamber as seen in this section is rectangular, with longer sides forming the roof and floor, the dimensions being 3 mm. in width by 1.26 mm. in height. As will be seen from the diagram shewing the directions of the sections the plane is slightly oblique and passes tangentially through the pollen chamber in a plane slightly oblique to that of a minor rib.

The central part of the roof in this section shews a triangular, blunt-ended upward projection of the epidermis which may be the base of the micropylar tube obliquely sectioned close to the point of its insertion, though if this be the correct interpretation the projection would have been expected to present a more ellipsoidal apex.

The epidermis of the pollen chamber is continuous with that of the nucellus and the component cells up to about half its height are of the same form in both. Beyond this point they become much larger (.066 radial by .04 to .08 vertical), with thinner walls, and do not possess the black carbonaceous contents present in the lower part. The increased size is especially noticeable where the sides curve inwards to form the roof, these shoulders project somewhat laterally, partly owing to the larger size of the epidermal cells and partly to the slightly greater internal diameter (Pl. fig.11). The blunt apex of the angular projection is formed of cells which are much narrower in the tangential direction .005. Interiorly the sides of the pollen chamber were occupied by a soft parenchymatous tissue consisting of elongated cells with tapering ends. This is most pronounced in the shoulders and the appearance presented very closely resembles that described and figured for other seeds of this affinity, as for example T. Parkinsoni (Scott and Maslen, loc. cit. p.121), T. Pusillus (Oliver, New. Phyt. Vol.III. 1904, Plate II, fig.3), Aethiotesta (Renault, Mém. Soc. d. Sci. Nat. de Sâone et Loire, 1887, Pl.XVI. fig.3), and Stephanospermum (Oliver, Trans. Roy. Soc. Lon.

p.370, Plate XLII. figs.11 and 18).

In S.32.h the pollen chamber is incomplete and cut through in an obliquely transverse direction, the only point of interest it furnishes being the presence of a pronounced projection or fold of the wall corresponding in position to one of the major ribs; this bears no relation to the secretory ducts like the folds in the lower part of the nucellus, so that possibly the pollen chamber may have been three-angled, though its mutilated character in this section precludes confirmatory evidence from its other two faces. If the pollen chamber really were ribbed then the angular projection of the wall seen in S.32.c may have been such an one, corresponding to a minor rib cut through transversely, since the plane of section is fully consonant with such an interpretation, though it is not borne out by other sections. Section I in Dr. Scott's series, which passes obliquely across the axis of the pollen chamber, is of importance in this connection. In the upper part of this organ are seen the shoulders occupied by the parenchymatous tissue already described, but these, in place of being curved, present a double angle, and the roof of the pollen chamber through which the section passes is quite flat. This flat surface corresponds to the interval between two major ribs and the upper of the four angles constituting the double-angled shoulders correspond to the radial planes of the ribs themselves. The lower pair of angles are doubtless the true shoulders, so that from this preparation and the evidence already adduced it seems probable that the wall of the pollen chamber was three-angled, with flattened sides corresponding to the three internal faces of the triangular micropyle.

Before leaving this section we may mention that a single short and broad parenchymatous element occupying a position just within the epidermis of the pollen chamber and close to its insertion on the nucellus exhibits faint transverse markings, giving a somewhat tracheid-like appearance to this element, but the preservation is not sufficiently good in the absence of confirmation from other sections to lay any stress on this fact. In all the sections rounded bodies are present in considerable numbers in the pollen chamber or megaspore cavity; they are probably all to be referred to the spores of some fungus the hyphae of which can here and there be detected.

# VIII. COMPARISON WITH OTHER TYPES

## (1) Trigonocarpus Parkinsoni, Brongniart.

It is hardly necessary to recapitulate in detail the many points of general resemblance which Trigonocarpus Parkinsoni and Trigonocarpus Shorensis have in common. The main structural plan in both seeds is essentially the same, but this only serves to throw into greater prominence the many differences of their more minute structure.

In respect of the sclerotesta, whilst the arrangement of the primary and secondary ribs is the same in both, we note the entire absence in Trigonocarpus Shorensis of tertiary ribs subtending the vascular bundles. The behaviour of the primary sutured ribs is alike in each, though the beak into which these pass is short in T. Shorensis and long in T. Parkinsoni.

The secondary ribs of the latter seed are subject to considerable variation, sometimes being almost absent, but usually they persist to near the apex, where they die out before the micropylar beak is reached. This earlier disappearance of the secondary ridges is still more pronounced in T. Shorensis, where they only extended for about one-third of the body of the sclerotesta. Scott and Maslen give the thickness of the stony layer in T. Parkinsoni as from 1 - 1.5 mm. (loc.cit. p.106), which is two to three times the corresponding dimension for our seed. Probably this added thickness and the increased number of ribs is to be correlated with the small extent of the sarcotesta as compared with that of T. Shorensis necessitating greater mechanical strength in the layer beneath; or perhaps put more correctly, the broad sarcotesta in the latter species with its peripheral sclerotic system had not involved the necessity for development of such mechanical strength in the sclerotesta.

The most interesting comparison between these two seeds is afforded by the sarcotestal structure. This tissue was in T. Parkinsoni bordered at the exterior by a narrow epidermis, followed by a thickened palisade-like hypodermis (loc. cit. p.102). As we have seen, the limiting layers in the present seed were much more complex, and formed a, probably anastomosing, complex of radial plates, accompanied by numerous secretory elements present also further in, which, though represented, were extremely few in T. Parkinsoni. Now the occurrence of radial sclerotic plates at the periphery and of secretory elements both within these and interiorly are characteristic features of the vegetative organs of Medulloseae and especially of their petiolar structure (D.H. Scott on Medullosa anglica, Phil. Trans. B. Vol.191, p.101, and Pl.8. fig.18, 1899), so that T. Shorensis in this respect would appear to be far more primitive than its congener. The absence of the prolonged sclerotic beak and secondary ridges opposite the bundles also point to a less degree of specialisation.

A further striking difference is the tapering insertion of the seed of T. Shorensis as compared with its abrupt insertion in T. Parkinsoni; the former is probably a relatively older type than the latter, just as the horizontal departure of the leaf trace characterises the modern plant in contradistinction to their oblique insertion as found in the more ancient.

Analogy with Physostoma elegans (Oliver, Ann. Bot. Vol.XXIII, p.73) would seem to suggest that the presence of a secretory system in the nucellar tissue is a more primitive feature than its absence. If this has any significance and the close relationship between the Trigonocarpeae and Lagenostomales supports such an assumption, then in this respect T. Shorensis stands in the same relation to T. Parkinsoni as does Physostoma to the other known members of the latter group.

We have shewn good reason for believing that *T. Shorensis* was without a definite inner flesh, except in so far as we can apply that term to the lining of the micropylar canal. Such a tissue would, however, appear to have been present in *T. Parkinsoni*. Perhaps at first sight this might seem to be a pronounced distinction between the two, but the extreme peripheral situation of the sclerised layer in *Pachytesta* surrounding an extensive inner flesh coupled with the undoubtedly close relationship of the two genera, indicate that the position taken up by the region of sclerisation was subject to considerable fluctuation in the group as a whole, and therefore of no great significance when exhibited in a smaller degree by members of the same genus.

The well defined nucellar epidermis, even more pronounced than that of *T. Parkinsoni*, indicates a stage less far removed from the condition in which the nucellus was a naked sporangium unprotected by a surrounding integument; and probably the production of an inner flesh is likewise correlated with a phylogenetically more prolonged contact between the two surfaces.

As we have previously indicated, the vascular organisation of the two seeds was essentially similar, perhaps the most outstanding distinction between them being the much more peripheral position occupied by the sarcotestal strands in Trigonocarpus Shorensis. On the whole the internal vascular system of our seed probably shews a somewhat more pronounced tracheal investment at the base of the nucellus, whilst the separate strands into which this passed were broader, though this may well be an outcome of the larger nucellus they supplied. If, as may have been the case, the Trigonocarpeae were derived from fern--like plants having sporangia with a complete internal tracheal investment, then it would appear from Scott and Maslen's description that in this respect Trigonocarpus Parkinsoni were more primitive than T. Shorensis, for in the latter anastomoses, if they existed, were probably of infrequent occurrence.

## (2) T. Oliveri

This seed was described and figured by Scott and Maslen in 1907 (The Structure of the Palaeozoic seeds Trigonocarpus Parkinsoni and Trigonocarpus Oliveri, Ann. Bot. Vol.XXI, LXXXI, 1907) from a series of four sections through a single seed, and the diagnosis there given is as follows:

"Length nearly 2 cm., diameter about .9 cm., characteristically coffin-shaped in vertical sections. Base flattened. Sclerotesta produced around the base of the seed in the form of a circular ridge enclosing the stalk of the seed. Longitudinal ridges of the sclerotesta acute-angled, not rounded as in Trigonocarpus Parkinsoni."

The number of longitudinal ridges which the seed bore is not explicitly stated, but was presumably from the description given assumed to have been six.

The writer has carefully examined the preparations and employed for their interpretation the methods recently described (Salisbury, Methods of Palaeobotanical reconstruction, Annals of Botany, April 1913). The conclusions arrived at differ essentially from those of Scott and Maslen, who evidently did not fully recognise the marked effects of obliquity in this seed, which are so clearly brought out by the modelling method employed.

As can be seen, the first section (S.28.d) is tangential to the surface of the seed and passes at unequal depths through two ribs the divergent axes of which, towards the upper part, indicate that the plane was below the middle region, sloping away from the chalaza. The next section (S.28.c) shews the more deeply cut of these ribs sectioned nearer the axis and consequently represented by two angular projections, one at the apex and the other at the base. This section cuts the seed so far in that two lateral ribs, one on either side, are also encountered; where these are cut near the apex they appear as angular projections, whilst near the base they exhibit a curious truncated outline, but are unequal in size, owing to the obliquity which was also manifested in the previous section. It is these two lateral ridges at the base which have been interpreted as a circular ridge, though the true character where sectioned near the apex was recognised. In order to explain the peculiar form of the lower projections the assumption was made that they were incomplete. The objections against such an interpretation furnished by this section alone are, that if a chalazal ring were present it is highly improbable that the central rib would extend below it and the lateral ribs be in no way represented; whilst this difficulty cannot be overcome, since the interpretation of the median ridge as a part of the stalk is inadmissible, owing to the plane of section.

On the interpretation here put forward no difficulties are involved, since converging ribs cut in a plane at a narrow angle with that which they themselves follow would necessarily acquire in section the square-ended form which they actually present.

In the section just described one notes that the region of attachment of the nucellus is cut through, so that since in the next preparation the nucellus shews as a complete oval membrane it is clear that this section passes right across the axis of the seed, cutting through a rib on either side almost vertically, and it is the slight angling of the cavity corresponding to these which, as in similar sections of Conostoma oblongum, results in the coffin-shaped appearance.

At the apex of S.28.b we see the three ribs represented in S.28.c and at the lower end three other ribs sectioned almost transverse to their direction, so that the triangular form is preserved. If on the other hand they were really a chalazal ring, a section in this plane should render them convergent, not divergent, and furthermore their size on that view is incompatible with the projections in the previous section, especially if the latter are to be regarded as incomplete.

*T. Oliveri* was then an eight-angled seed, and until further specimens are obtained with better preserved internal tissues, its systematic position, except for inclusion in the vague group of the Radiospermeae must for the present remain uncertain. The removal of this seed from the genus *Trigonocarpus* makes it therefore unnecessary to institute any comparison between it and *Trigonocarpus Shorensis*.

### (3) Fructifications of Neuropteris heterophylla and Neuropteris obliqua.

Attention has already been called to the two types of insertion, viz., the tapering and the abrupt, found within the genus Trigonocarpus, and these are represented in the fructifications which have been found attached to Neuropteridian foliage. Three specimens of Neuropteris heterophylla have been described by Dr. Kidston with attached seeds (Proc. Roy. Soc. London, 197.I.1904) in which the abrupt insertion of the Parkinsoni type is clearly exhibited. More recently Kidston and Jongmans (Archives Néerlandaises d. Sci. Exactes et Nat. S.III.B.T.I.p.25, 1911) have described fructifications attached to the fronds of Neuropteris obliqua, in which the seed tapers towards its insertion on a bifurcated axis, thus conforming to the second type as represented by T. Shorensis. Owing to the incomplete preservation of the latter at the apex its longitudinal extent cannot be exactly estimated but nevertheless the comparison of the approximate dimensions of the two types of impressions and petrifactions given below shews that broadly the resemblances of insertion are accompanied by an approximately similar ratio in size.

| Species | Length | Breadth |
|---|---|---|
| T. Parkinsoni | 4-5 cms. | 2 cms. |
| N. heterophylla | 3 cms. | 1.1 - 1.4 cms. |
| T. Shorensis | Over 4 cms. | 2.4 cms. |
| N. obliqua | About 6 cms. | 2.25 cms. |

A further feature that the fructification of N. obliqua and T. Shorensis have in common is found in the marked striation exhibited by the surface of the former and attributed by the authors cited above to the presence of a large number of sclerenchymatous strands of tissue near the surface of the seed. These are no doubt identical with the numerous radial sclerotic plates which we have described as a prominent feature in the peripheral layers of the sarcotesta in T. Shorensis.

In view of the occurrence of the seeds of N.obliqua in pairs on a bifurcated axis it may be of some significance that in one of our series a portion of a second seed is present having approximately the same orientation as the more complete specimen close to which it lies.

These considerations render it likely that our seed was itself borne on a plant possessing foliage of the Neuropteris type and almost certainly belonged to the same subsection of the genus as Kidston and Jongman's specimens.

## (4) *T. corrugatus*.

Amongst the casts of Trigonocarpean seeds none approach so closely to *Trigonocarpus Shorensis* as that described by Renault under the name *Trigonocarpus corrugatus*. The following is the diagnosis given by that author:

"Graines trigones, dilatées un peu au-dessus du milieu de leur hauteur longues de 22 millimètres et larges dans la partie renflée de 12 millimètres,marquées de trois côtes saillantes qui vont jusqu'au sommet de la graine sans produire de point. Entre ces trois côtes on remarque trois plissements en relief qui s'étendent à peu près jusqu'à mi hauteur." (B. Renault, Bassin Houiller et Permien d'Autun et d'Epinac, p.399).

From the above we see that the dimensions of the seed, though smaller than those of our own species, bear very nearly the same ratio for the corresponding parts of the sclerotesta.

| Species | Width (max.) | Length | Ratio $\frac{\text{Length}}{\text{Width}}$ |
|---|---|---|---|
| *T. corrugatus* | 12 mm. | 22 mm. | 1.83 |
| *T. Shorensis* | 15 mm. | 28 mm. | 1.86 |

The presence of the three secondary ribs extending for only a part of the total length of the hard shell though persisting for a greater distance than in T. Shorensis, also the absence of a beak (a description that might easily in this type of preservation be consistent with the presence of a very short structure of such a character) still further strengthen the resemblance between the two seeds. Both species possess the characteristic tapering base, so that though they may well have been distinct they were at all events extremely close in their affinity.

## (5) Comparison with Cycads

Recent work on the Cycadean ovule (Kershaw, Structure and development of the ovule of *Bowenia spectabilis*, Ann. Bot. Vol.XXVI. No.CIII. 1912) and the additional facts regarding the structure of *Trigonocarpus* here brought forward serve to emphasise the unmistakable relationship between the two groups. In the organisation of the integument differentiated into three layers the agreement is extremely close, even as regards the broad structure of the stony layer which in Cycads as well as in *Trigonocarpus* is formed of longitudinally directed fibres on the inside which at the outside become interwoven with horizontally directed elements. (Stopes, On the double nature of the Cycadean Integument, Ann. Bot. Vol. XIX. p. 564, 1905; Chamberlain, The Ovule and female gametophyte of Dioon, Bot. Gaz. 42, 1906, p.332). Also in the vascular organisation and the structure of the pollen chamber (Kershaw, loc. cit. p.643) the resemblances are particularly evident.

The chief interest of the present work in this connection results from the recognition of the short Cycadean type of sclerotic beak within the genus *Trigonocarpus* and the presence of secretory elements situated in the sarcotesta of the latter and resembling very closely the mucilage sacs of the modern group.

The tendency for the non-vascular ribs to die out of which an early stage is shewn by T. Shorensis reaches its culmination in the Cycadean family, where, too, the development of ribs in relation to the sarcotestal bundles as found in T. Parkinsoni likewise constitutes a prominent feature of certain genera.

We have stated that the absence of a nucellar system in the Lagenostomales is probably correlated with the fusion between testa and nucellus. How then are we to account for the retention of this same system under similar conditions in the Cycadean ovule? The explanation seems to be found in the isolation of the nucellar and integumental systems from one another by the intervening sclerotesta, which thus prevents the latter from performing the functions of both.

The suggestion advanced by Worsdell (New. Phytologist, Vol.IV. 1905, p.58: Fasciation, its meaning and origin) that the fused integument and nucellus was brought about by a congenital fusion rather than that it arose as an intercalated zone of growth as suggested by F. W.

Oliver (The Ovules of the Older Gymnosperms, Ann. Bot. Vol. XVII. 1903), seems the more probable both on the grounds there adduced and in view of the absence of any evidence in Cycads, comparable to that found in the Lagenostomales, of such having taken place.

## IX. GENERAL DISCUSSION OF THE TESTA

### (1) The Multiple Origin of the Integument in the Trigonocarpeae

The general facts supporting the theory of a multiple origin for the integument of the Lagenostomales are well known (Oliver and Salisbury, Palaeozoic seeds of Conostoma, Ann. Bot. Vol.XXV, p.41, 1911) and form a sufficiently well connected chain of evidence to warrant the expectation that a parallel phenomenon would be exhibited by closely related groups.

In the Trigonocarpean series the integument is also composed of several equivalent units and in order to fully appreciate the problem we shall briefly review the chief testal features which the members of this group exhibit.

Text fig.10. Transverse sections of the seeds of various *Trigonocarpeae*. Corresponding ribs are in each case marked $R^1$-$R^2$, etc.

In the genus Trigonocarpus itself *T. Parkinsoni* had twelve ribs, three primary, which were fissured, three secondary and non-fissured, and six tertiary opposite which the sarcotestal bundles were situated.

In _T. corrugatus_ (Renault, loc.cit.) six ribs only were present, of which three died out about half-way up the seed and, as we have seen, _T. Shorensis_ differed from that species, as regards the sclerotestal characters, in the more rapid disappearance of the secondary ribs, which in neither case were commissured.

In _Trigonocarpus pusillus_ (F. W. Oliver, New. Phyt. Vol.III. pp.96-104, 1904) the ribs had almost become obsolete and the sclerotesta was nearly circular in outline, with three commissured ribs only projecting slightly from the general surface.

_Polylophospermum_ (F. W. Oliver, Ann. Bot. Vol.XXI, pp. 303-4, 1907) possessed twelve ribs, of which six were fissured, whilst the alternating and non-fissured ribs corresponded to the radial planes of the six sarcotestal bundles.

_Ptychotesta_ and _Hexapterospermum_ (Brongniart, Comptes rendus, t.LXXVIII, pp. 15a, 16, 1874) were both six-angled seeds with very prominent ribs, all of which in the case of the former were fissured (perhaps also in the latter) and enlarged at the ends, owing to the separation of the two parts in that region.

Polypterospermum (Brongniart, loc. cit. p.16). An hexagonal seed with six acute ribs corresponding to the angles of the testa and alternating with them six others which were short and blunt.

Pachytesta (F. W. Oliver, New. Phyt. Vol.I. No.7, 1902). A circular seed, but exhibiting, like T.pusillus, three commissures. The bundles had undergone considerable branching, so that not only are they numerous tangentially but also form two concentric series, a complexity of vascular organisation that goes hand in hand with an elaborate internal structure, based, however, on the Trigonocarpean plan.

Stephanospermum (Oliver, Trans. Linn. Soc. Vol.VI. 1904). The two species belonging to this genus were circular in transverse section and all vestiges of ribbing have disappeared. The sarcotesta is usually only represented by the tissue occupying the apical cup, so that its vascular structure is unknown.

First of all, considering the species of Trigonocarpus, we see that they form a consecutive series involving the gradual elimination of the secondary ribs.

The production of ribs in relation to bundles does not call for any special explanation, as it is a phenomenon of widespread occurrence, being met with elsewhere in the seeds of Dicotyledons, Gnetales, and Cycadales, as well as in the vegetative organs of many plants. They are probably an expression of mechanical utility and in any case have little or no morphological significance. Except from the taxonomic standpoint the absence of such ribs from the seeds of T. Shorensis and T. corrugatus is a point of little importance, but on the other hand the identity of plan in the arrangement of the non-vascular ribs and bundles is probably of supreme phylogenetic significance.

Disregarding, then, for the time being the ribs which stand in relation to bundles, the general sclerotestal structure in Trigonocarpus Shorensis and T. Parkinsoni are identical. Scott and Maslen (loc. cit. p.107) remarked on the variability in development of the secondary ribs which always die out before the primary and in some cases are so slightly developed as to be practically absent. The two species T. corrugatus and T. Shorensis constitute further stages in the reduction series, for in the former they only extend for half the length of the seed, and in the latter are mere chalazal vestiges. In T. Noeggerathi only the primary ribs are present. And finally in species such as T. pusillus and T. elongatus all indication of the ribs is lost, and this applies almost equally to the primary as to the secondary. It is evident that the secondary ridges in the genus Trigonocarpus were in an obsolescent condition, which would fully account for the absence of commissures if such did, as the writer believes, originally exist.

Prof. Oliver has called attention to the remarkable resemblance between the plans of T. Parkinsoni and Polylophospermum (Ann. Bot. Vol. XXI, pp.303-4, 1907), one which is rendered complete if we assume that the secondary ribs of the former were the representatives of originally commissured structures. The conclusion then seems warranted that the six ribs of T. Shorensis and the non-vascular ribs of T. Parkinsoni are homologous with the six commissured ribs of Polylophospermum. (In other respects, of course, this seed is specialised.) It is moreover probable that the sutures themselves represent the planes of lateral fusion between six originally free members - a view which is further supported by the recognition of six component units in the micropylar region of T. Shorensis.

Newberry (Rep. Geol. Survey of Ohio, Vol.I. Pt.II. p.336 and Pl.42, fig.5, 1873) has figured a cast of considerable importance in this connection, showing the apex of a Trigonocarpus with its sarcotesta preserved, and in which the micropylar canal is seen as a star-shaped opening surrounded by six small but free sarcotestal lobes.

We have already noted how in species of the genus Trigonocarpus ribs have become completely eliminated and each pair of units fused laterally, so that three sutures only remain; a similar condition obtains in the genus Pachytesta and a further reduction might well result in the production of a non-commissured seed, as in Stephanospermum, though until we know details of the sarcotestal structure the degree of relationship of this genus to the Trigonocarpeae is naturally uncertain.

The remaining genera cited above are either six or twelve-ribbed seeds and in the latter case the additional members may well correspond to the six vascular ribs of Polylophospermum.

Other genera there are belonging to the Radiospermeae which nevertheless possess ribs that in number are some multiple of two, e.g. Eriotesta, Codonospermum. Our review has, however, shewn that there existed a group of seeds agreeing in their internal structure and consistent with our hypothesis in their sclerotestal plan, moreover including all those forms in which an undoubtedly Trigonocarpean organisation has been established.

The possible origin of dimerous from trimerous forms is considered in the sequel, but the Radiospermeae is doubtless an artificial aggregate of which the Trigonocarpeae is one of the included natural groups; a statement that is borne out by the constant association with these seeds of the Neuropteridian type of foliage. (See Grand' Eury, Comptes rendus, CXXXIX, p.3, 1904).

We see, then, that none of these genera militate against the theory that the integument had its origin in a whorl of six free members, each with a single vascular bundle, which subsequently became laterally fused. Such an interpretation necessitates the recognition of the sarcotesta and sclerotesta as constituting a phylogenetically homogenous structure and in the next section will be given data that amply warrant that conclusion.

A striking feature of the Trigonocarpeae is not only the occurrence throughout of the hexamerous type, but also the absence of variation in the individual species. This stereotyped character suggests the analogy with present-day monocotyledons and is a marked contrast to the variability in this respect evinced by the Lagenostomales, not only as between different genera and species but also as between individuals. For example, in *Physostoma* (Oliver, Ann. Bot. 1909) nearly 50 per cent. of the seeds had 10 ribs, but the remainder exhibited from 9 to 12. In *Conostoma* the number was 6 or 8 according to the species, with one recorded variant of *Conostoma oblongum* possessing 7 (Oliver and Salisbury, Ann. Bot. XXV 1911 ). In *Lagenostoma Lomaxi* the normal number was nine (Oliver and Scott, Phil. Trans. Roy. Soc. V. 197, 1903) and for *L. ovoides* eight with variation from 6-9 (Prankerd, T.L. Jour. Linn. Soc. Bot. Vol.XL. No.278, p.463). Finally in *Gnetopsis elliptica* the number of ribs was four, with perhaps two others vestigial. In this series we see that there is almost every variation from four up to twelve, and whilst a multiple of three is by no means infrequent, a reminiscence perhaps of the relationship to the Trigonocarpeae, the more normal feature is some multiple of two.

Our knowledge of the structure of *Conostoma* and *Gnetopsis* has shewn how narrow is the dividing line between radiospermy and platyspermy (Oliver and Salisbury, loc. cit.). Also the recent discoveries of *Aneimites fertilis* (Dr. David White, The seeds of Aneimites, Smithsonian Misc. Coll. Vol. XLVII, pt.3) and *Pecopteris Plukeneti* (M. Grand' Eury, Comptes Rendus, Vol.CXL, p.920), together with the obvious relationships between Pteridosperms and the Cordaiteae render it necessary to consider the possibility of deriving bilateral forms from a trigonous group. The fact that the fructification Pecopteris Plukeneti was borne on a Medullosean type of foliage certainly indicates such a change, so that the analogy afforded by examples from the carpellary structures of the present-day Flora may not be without value. To instance only two groups, one from the Dicotyledons and one from the Monocotyledons. The Carices are represented in the British Flora by about fifty species, of which over thirty possess three stigmas associated with a triangular nutlet; the remaining species mostly have two stigmas and the nut is either bilaterally symmetrical or plano-convex. In a few species with two stigmas the nut is slightly trigonous and in Carex paludosa Good. the stigmas vary from three to two, accompanying which the nut is either trigonous or lenticular.

As an example from the Dicotyledonous series the Polygonaceae furnish us with a group in which triangular fruits are the rule. In part of the genus Polygonum and in the genus Rumex a triangular nut is associated with three stigmas. In the section Persicaria of the genus

Polygonum and in Oxyria the fruit is lenticular and composed of only two carpels, as evinced by the pair of stigmas.

To come much nearer the group under consideration the normal bilaterally symmetrical fructification of Ginko biloba has been found with three ribs in place of two, a variation that may even be a reversion to the ancestral condition.

These examples are sufficient to shew that the assumption of an originally hexamerous integument (later becoming trimerous in some of the forms) for the Trigonocarpeae does not preclude the origin of closely allied genera possessing bilaterally symmetrical structures. (The position of the tetramerous Radiosperms awaits details of their internal structure.)

In view of the frequent association in the monocotyledonous series of trimerous flowers with a triangular stem structure, an expression probably of similar mechanical relations, it is of interest to note that the general outline of the stems both of Medullosa anglica and Sutcliffia insignis was broadly triangular (Scott, Phil. Trans. Roy. Soc. B. Vol.191, 1899, and De Fraine, Ann. Bot. Vol.XXVI, No.104, p.1035, 1912), though the character does not of course hold for other species of the former genus.

Before leaving this subject it is of interest to note that Drs. Fuji and Stopes regarded Yezostrobus Oliveri as more nearly approaching to Trigonocarpus than any other known fossil or recent group (Phil. Trans. Roy. Soc. Ser. B. Vol. 201 1909 ) and therefore on the foregoing hypothesis the triangular outline which this seed exhibits in transverse section (loc. cit. fig. 14 ) may have a phylogenetic significance.

### (2) The question of an homogenous or dual phylogeny

The question at once arises in relation to the integument: Was this structure of uniform origin or was it dual, as suggested by Stopes for Cycads? (Ann. Bot.1905 ). The close agreement of the two groups makes the assumption of a double nature for the one almost necessitate its acceptance for the other. The main grounds on which this theory is based are, put briefly the presence of two series of bundles, both supposed to be integumental, and the resemblances that exist between the female fructification of Lyginodendron with its cupule on the one hand and the Cycadean ovule with its sarcotesta on the other. The recent work of Miss Kershaw (Ann.Bot. Vol.XXVI, No.CIII, p.636, 1912) on Bowenia spectabilis has shewn that in this species at least the inner vascular system is nucellar. On the other hand Dr. Stopes traced some members of the inner vascular system of Cycads into the integument beyond the free part of the nucellus, and unless future work should shew that it is only the accessory branches from the integumental system that behave in this manner, the evidence as to the nature of the inner bundles must remain in its present contradictory state. But in any case in view of the diverse data at present available, we are not warranted in attaching any great importance to the occurrence of two systems even should they prove to be both integumental in certain cases. The branched and double system of integumental strands in *Pachytesta* ~~evinces~~ exemplifies a tendency that might well have subsequently developed and its origin in consequence have gradually become obscured.

With regard to the second argument in relation to *Lagenostoma* recent work has shewn that, in spite of the free nucellus exhibited by the Trigonocarpeae, they agree, both in the structure of their fructifications and stem anatomy, much more closely with the modern group than do the Lagenostomales (Kershaw, loc. cit. and de Fraine, On *Sutcliffia insignis*, Ann. Bot. 1912).

When we turn to the consideration of *Trigonocarpus Shorensis* we find that the evidence for an homogenous origin for the whole integument is abundantly clear. Such inner flesh as is present, is but the unsclerised internal lining of the hard shell, and this latter, though broadly composed of an outer and inner part, is, as already explained, formed from one and the same tissue by the different course which its elements pursue.

The sarcotesta on its inner periphery shews a complete transition from the outer sclerotestal cells, so there is no zone to which we can point as possibly representing the fusion plane of two morphological units. And if further evidence were necessary it is furnished by the course of the secretory elements which pass from sclerotesta to sarcotesta irrespective of the differences of texture which in the mature fruit they present.

# X. THE ORIGIN OF THE INTEGUMENT IN THE TRIGONOCARPEAE AND THE LAGENOSTOMALES

The addition of yet another Trigonocarpean seed, shewing a well defined nucellar epidermis, adds to the certainty that the group was characterised by the possession of an extensive free region of the nucellus, to which part the megaspore cavity was almost entirely confined. This would seem to be a fundamental difference separating them off from the other members of the Pteridospermeae.

The considerable resemblances which the Trigonocarpeae bear to the Lagenostomales, both as regards the general organisation of their seeds and the broad features of anatomy, in the few stems which have been allocated to fructifications, seem to indicate that the two must have had a closely allied ancestry either in some semi-Pteridospermic group which possessed a generalised type of fructification, giving rise to the characters of both, or in two parallel developments arising independently from the Pteridophytic stock.

The theory of intercalated growth was put forward by F. W. Oliver in a similar connection (The Ovules of the Older Gymnosperms, Annals of Botany, Vol.XVII, 1903) to homologise modern with fossil forms, and the same idea applied in the manner indicated below seems to offer the best explanation of both the resemblances and differences which these two groups exhibit.

If we consider the most archaic type of the Lagenostomales, viz. *Physostoma*, we find that the megaspore cavity projects into the free portion of the nucellus, the plinth or free part of the latter below the lagenostome being only slightly developed.

In the more advanced member~~s~~ of the group, *Lagenostoma*, the plinth exhibits intercalary growth, so that there is a greater extent of free nucellus in the older than in the younger phase, whilst in *Conostoma* the plinth reaches its greatest extent.

These facts seem to indicate that the free apical portion of the nucellus was in this series a phylogenetically late development resulting from a zone of intercalated growth.

On various grounds *Physostoma* is regarded as the most primitive seed yet known (Oliver, loc. cit.) therefore it is of great interest to note that it is the only member of the Lagenostomales exhibiting a free apex of the nucellus into which the megaspore cavity projects.

It does not therefore seem an unjustifiable assumption to suppose that the potentiality for the development of a free nucellus was possessed by the ancestors of Physostoma; a potentiality which was only evinced by the majority of the group in the intercalated growth of the region above the contained megaspore resulting in the elaboration of the plinth.

One may suppose that the common ancestors which gave rise to the Lagenostomales on the one hand and the Trigonocarpeae on the other possessed a nucellus unenclosed at the apex and around the base of which were fused a whorl of members with free apical portions affording protection to the sporangium in which the prothallus was now retained. With the inception of the seed habit came an increase in the size of the megaspore cavity accompanying enlargement of the nutritive prothallus. Here is where it may be supposed the divergence in the two lines of descent arose. In the one case there was an upward extension of the megaspore cavity and the surrounding free pro-integumental lobes, resulting in the production of a free nucellus which may either have had its origin in an already vascularised sporangium (Oliver, A vascular sporangium. The New Phytologist, Vol.I. p.60, 1902) or the nucellar system may have arisen in relation to the greater demands upon the water supply now created.

Along the line of the Lagenostomales the increased dimensions were brought about by a similar phylogenetic intercalation of growth which took place, however, in the lower part where the whorl of protective members constituting the pro-integument were laterally fused to form a ring around the base of the sporangium. The close proximity of the integumental bundles would account either for the suppression or non-development of a special nucellar system. Such a view would not only explain the intermediate characters exhibited by the archaic Physostoma, but it further accords with the broad features of the testa as seen in the two groups.

A marked characteristic throughout the known members of the Lagenostomales is that at the apex of the seed the multiple nature of the integument exhibits itself with almost sudden clearness after it becomes free from the nucellus. In the seeds of the Trigonocarpeae, on the other hand, the component units of the testa are in general evinced equally at the base as at the apex or even throughout their length. These two conditions seem only explicable on the hypothesis that in the one group lateral fusion was simultaneous throughout, representing in fact the elongation of the free parts, and in the other took place in the "canopy" and body of the seed at phylogenetically distinct periods which, as stated in another form, is the view put forward above.

Our investigation of the present seed has shewn us that the external periphery of the integument was circular in outline for its whole length, in other words the lobing is only shewn superficially at the internal periphery, where it extends from near the base to the apex, though in the body of the seed the six lobes manifest near the chalaza and reappearing at the micropyle had become reduced to three.

What is true of this species was, judging from impressions with sarcotesta preserved, true also for its congeners, and may well have been a group character. At all events we are certain that the Trigonocarpeae were characterised by an internal lobing almost to the base of the seed, whereas in the Lagénostomales such internal lobing is only to be found in the apical region, so that superficially as well as internally the major part of the integument in the one is to be homologised with the distal extremity in the other.

We have assumed that the primitive structure from which the type of fructification in the two groups was derived possessed a whorl of surrounding members fused at the base between themselves. In both Trigonocarpus Shorensis and Trigonocarpus Parkinsoni the sutures of the primary ribs disappear a little before the floor of the seed cavity is reached.

The structural facts therefore justify the assumption that in both groups there was a phylogenetically earlier lateral fusion of the pro-integumental members at the base, followed later by their fusion at the apex.

The congenital fusion of the integument with the contained nucellus was but a matter of time, naturally evinced first in the basal region or zone of earlier lateral fusion. This latter in the Trigonocarpeae is well nigh vestigial, so that a free nucellus resulted, whilst in the Lagenostomales it represents the greater part of the seed body.

Later on in the history of the Trigonocarpeae and their descendants congenital fusion followed in the upper part, giving us the condition in modern Cycads, though here as in the more recent Lagenostomales the apical region has remained permanently free in relation to its specialised structure and functions.

# XI. RELATION TO VEGETATIVE ORGANS

In two of our series of sections there occur, associated with the seed structures, Medullosean petioles of which portions of as many as three are present in one and the same preparation. This fact would, in the light of present knowledge (Scott, Progressus Rei Botanicae, I.p. 206), appear of itself significant, and added to this numerous secretory elements are present in these petioles which agree in structure with those found in the sarcotestal tissue of <u>Trigonocarpus Shorensis</u>. Each is enclosed by a sheath-like layer of somewhat flattened cells and the wall surrounding the dark carbonaceous mass in the centre exhibits externally the characteristic longitudinal striations. Both of these features are also exhibited in the stems and petioles of <u>Medullosa anglica</u>.

The individual bundles are collateral in structure, the position of the phloem being represented by an empty space upon which the smallest protoxylem elements abut. The xylem is surrounded externally by a band of sclerotic fibres which lie in close contact with the tracheids. The xylem exhibits no admixture of parenchymatous elements, so that in all respects the bundles are distinct from those of *Rachiopteris Williamsoni* (Seward, Ann. Bot. Vol. VIII. No.XXX, p.208, 1894), but agree very closely with those of *Myeloxylon* (Seward, Ann. Bot. Vol.VII, p.1, 1893). If then the petioles above described really belonged to the plant which bore our seed, the petrifaction known as *myeloxylon* probably represents an aggregate of petiolar structures corresponding to at least two species of Trigonocarpan fruits and possibly in both cases having as their stem a structure of the *Medullosa anglica* type. In any case the evidence at present available is against any suggestion that *Trigonocarpus Shorensis* was the fructification of *Sutcliffia insignis*, though of course the above association may be an accidental one and entirely without significance.

The presence of numerous secretory ducts is a feature shared by both the known British Medullosean stems, and in the structure of the chalazal bundle, whilst the protoxylems of *Trigonocarpus Shorensis* appear to be grouped in pairs (a feature of *Sutcliffia insignis*), in the presence of internal parenchyma and a secretory duct within the xylem our sections of *Trigonocarpus Parkinsoni* shew a closer agreement with that stem.

## XII. DIAGNOSIS.

### Trigonocarpus Shorensis. sp. nov.

LOCALITY: Shore Littleborough.

HORIZON: Lower Coal Measures.

A radially symmetrical obovoid seed tapering to its insertion and circular in transverse section. Length over 4 cms., width 2·4 cms.

Testa differentiated into two parts:-

(a) SCLEROTESTA (Length 2·8 cms., Width 1·5 cms.) produced at the apex into a short triangular beak and bearing six ribs, viz: three principal and commissured extending throughout and three minor and non-sutured reaching to some 8 mm. from the base. (b) SARCOTESTA about 4 mm. in thickness, lacunar in structure with numerous secretory sacs and six peripherally situated vascular bundles alternating in position with the ribs. Limiting layers containing sclerotic strands. NUCELLUS free containing vertically directed secretory sacs and limited within by vascular tissue forming a continuous lining at the base but above passing into separate bundles.

# XIII. SUMMARY.

In the foregoing pages a detailed description is given of the Palaeozoic Seed Trigonocarpus Shorensis of which the chief diagnostic features are summarised in the preceding section.

The Sclerotesta differed principally from that of the well-known species in its obovoid form and tapering insertion, the absence of ridges in relation to the vascular bundles, and in the relatively short beak. In the early disappearance of the secondary ribs it resembled closely the external cast Trigonocarpus corrugatus.

Both Sarcotesta and Sclerotesta showed considerable complexity, with nevertheless a well-marked transition such as can only be reconciled with differentiation of the same organic unit. The Sclerotesta was built up of fibrous elements longitudinally directed within and without intertwined in a complex manner. The Sarcotesta was unusually broad, lacunar in structure, and contained numerous secretory sacs comparable to those of Cycads.

The limiting layers were formed of a ground tissue of parenchyma containing a system of probably anastomosing tangentially flattened strands of fibres, and secretory sacs like those of the interior. The whole structure in this region approached much more nearly to that of the peripheral layers of a Medullosean petiole than in Trigonocarpus Parkinsoni.

The Sarcotesta exhibited no flattening but was circular in form throughout and an inner flesh was probably only present as an inconspicuous layer within the micropyle.

The vascular system comprised two parts, viz: a sarcotestal and a nucellar.

The most notable feature of the former is the extreme peripheral position occupied by the six mesarch vascular bundles.

The single chalazal bundle had the protoxylem groups just within the periphery and expanded into a tracheal cup at the base of the nucellus which was probably formed of twelve laterally fused bands that gradually increased in number to form numerous mesarch lenticular bundles lining the inner limit of the nucellus.

The nucellus was attached at the base to a sclerotic papilla but was otherwise free from the testa and its outstanding features were, a well developed and thick-walled epidermal layer, the occurrence of three longitudinal flanges, corresponding with the commissures, and the presence of numerous secretory sacs in the ground tissue arranged in radial files.

Two sections of Trigonocarpus Parkinsoni are described which indicate that the chalazal bundle gave off three branches simultaneously which almost immediately bifurcated to form the six sarcotestal strands.

A comparison with Cycads and allied types leads to the conclusion that Trigonocarpus Shorensis is in several respects a relatively more primitive type than its congeners. In this connection Trigonocarpus Oliveri is shown to have been an eight-angled seed and is therefore probably to be excluded from the Trigonocarpeae.

In the general discussion on the testa the evidence for its homogenous origin is set forth, and the theory is advanced that it had its inception in the lateral fusion of a whorl of six originally free members. The testal structure of the various genera are discussed in the light of this theory.

The resemblances and differences between the Trigonocarpeae and Lagenostomales are shown to be explicable on the hypothesis of intercalated growth followed by subsequent congenital fusion between the nucellus and integument.

Medullosean Petioles associated in the coal-balls with Trigonocarpus Shorensis are briefly described and resemble Myeloxylon.

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those of Rachiopteris Williamsoni (Seward, Ann. Bot. Vol. VIII. No.XXX, p.208, 1894), but agree very closely with those of Myeloxylon (Seward, Ann. Bot. Vol.VII, p.1, 1893). If then the petioles above described really belonged to the plant which bore our seed, the petrifaction known as myeloxylon probably represents an aggregate of petiolar structures corresponding to at least two species of Trigonocarpan fruits and possibly in both cases having as their stem a structure of the Medullosa anglica type. In any case the evidence at present available is against any suggestion that Trigonocarpus Shorensis was the fructification of Sutcliffia insignis, though of course the above association may be an accidental one and entirely without significance.

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## XV. EXPLANATION OF PLATES

Illustrating Mr. Salisbury's paper on *Trigonocarpus Shorensis*

R = Owen's College Manchester Collection.

S = University College Collection

D.H.S. = Dr. Scott's Collection.

### PLATE

Figs. 1-10, photo-micrographs.

Fig.1.

Nearly transverse section through the middle of the seed shewing the three commissural ridges ($R^1$, $R^2$, $R^3$) and the extensive sarcotesta St. The nucellus is seen in part on the right with a ridge near the commissure slightly displaced (n.f.). The black dots in the sarcotesta are the carbonaceous contents of the mucilage sacs. R.1161.h.× about 4.

Fig.2.

Slightly oblique section through the micropyle shewing the extensive sarcotesta with numerous secretory sacs (M.S.). Within the triangular sclerotesta the inner flesh can be faintly seen. R.1161.k.× 2.5.

Fig.3.

Tangential section through the outer sclerotesta. The band-like aggregates of fibrous cells are seed overlapping in a plait-like manner (f.b.) and passing in different directions. S.32.g.× 60.

Fig.4.

Slightly oblique transverse section near the base of the seed on one side a small projection is seen representing the termination of a minor rib (r'). Within is the contracted nucellus (nu) with numerous secretory sacs in radial files over which the contracted epidermis has formed ridges. S.33.c.× 2.

Fig.5.

A tangential section through the zone of transition between the sclerotesta (Scl.) and the sarcotesta (St.c). The slightly thickened walls, the elongated form and the sinuous course of the sarcotestal cells is here seen. S.32.g.× 90.

Fig.6.

An oblique section through the base of the micropyle shewing the extensive unflattened sarcotesta with the limiting layers at 1.1. and the secretory sacs in the outer sclerotesta (M.S.) S.31.1.× 5.

Fig.7.

Obliquely longitudinal section through the chalazal end of the seed shewing the vascular bundle (v.b.), the chalazal papilla (c.p.) and the tapering outline of the base of the seed. S.32.e.× 2½.

Fig.8.

Section through the extreme apex of the sclerotic beak. The sclerotesta is seen to be thinning out rapidly and at the higher level on the right is only some three elements in width. The sides shew a median constriction (m.c.) resulting in a six-lobed structure (m.l.) The inner flesh (i.f.) shews a gradual transition from the sclerotic tissue. R.1161.e.× 28.

Fig.9.

Oblique section through the base of the seed passing through all six ribs ($R^1$, $R^2$, $R^3$ and $r^1$, $r^2$, $r^3$). At c.p. the chalazal papilla is seen perforated by the single vascular bundle (v.b.). R.1161.b.× 4.

Fig.10.

Tangential section through the periphery of the sarcotesta shewing the lacunae (lac.) separated in places by the superposed peg-like projections of the stellate cells (p.) and elsewhere by the cells proper. S.32.h.×

## PLATE

Figs. 11-20, photo-micrographs.

Fig.11.

Vertical section through the pollen chamber wall (P.W.) from which the cuticle has become separated (cu). The shoulder is occupied by thin-walled parenchymatous tissue (sh.). The oval bodies are fungal spores (sp.). S.32.c.× 50.

Fig.12.

Transverse section through the sarcotesta with two secretory elements, probably derived by branching, in close contact (m.s.) S.31.× 60.

Fig.13.

A portion of a transverse section to shew the nucellar flange consisting of parenchymatous tissue (n.f.) and corresponding in position to a commissural rib (com.). A lenticular nucellar strand is seen on the left (v.b.) S.31.e.× 30.

### <u>Trigonocarpus Parkinsoni</u>.

Fig.14.

Transverse section through the chalazal bundle of <u>Trigonocarpus Parkinsoni</u> at the level at which the sarcotestal strands (v.b.) are given off. At the top one of these has branched into two. The central xylem mass (c.xy.) is surrounded by a discontinuous sheath of parenchyma (par.), exterior to which more tracheids (tr.) are seen. A single secretory element (m.s.) occupies a position within the xylem mass. In the space between the bundle and the sclerotesta several more secretory elements are seen and remains of parenchymatous tissue. S.34.a.× 90.

Fig.15.

A single sarcotestal bundle from near the base of <u>Trigonocarpus Parkinsoni</u>, shewing the dual nature of the xylem. The centre of the strand is occupied by narrow tracheids (n.tr.) surrounded by a parenchyma sheath (par.) and this again is followed by a zone of short broad tracheids (s.tr.) S.34.b.× 90.

Fig.16. <u>Trigonocarpus Shorensis</u>

Transverse section through the chalazal bundle of <u>T. Shorensis</u>. The parenchyma sheath (p.s.) around the bundle and the radially extended tracheids of the outer zone are clearly seen. The protoxylems are seen occupying a position just within these latter. M.s. mucilage sacs. S.33.b.× 100.

Fig.17.

Transverse section through a sarcotestal bundle shewing the thick-walled protoxylem elements (pt.x), the small elements of the centrifugal xylem ( cf.x. ) and the large short tracheids comprising the centripetal (cp.x. ). Touching the bundle on the right is a sclerotic strand of the limiting layers. M.s. mucilage sac. S.31.1.× 100.

Fig.18.

Oblique section through the chalazal bundle from the same preparation as fig.7, shewing the scalariform thickenings of the tracheids (tr. ). scl. sclerotesta. S.32.e.× 80.

Fig.19.

Transverse section through the limiting layers of the sarcotesta occupied by several radially extended sclerotic strands (scl.p. ) partially displaced by contraction. The sclerotic plate on the extreme left is interrupted by a medianly placed mucilage sac and both here and in the other here present (m.s. ) the thickened wall stands out clearly as a transparent zone around the dark contents. S.31.1. × 100.

# POLYMORPHISM IN THE FLOWER OF *SILENE MARITIMA.*

By E. J. Salisbury.

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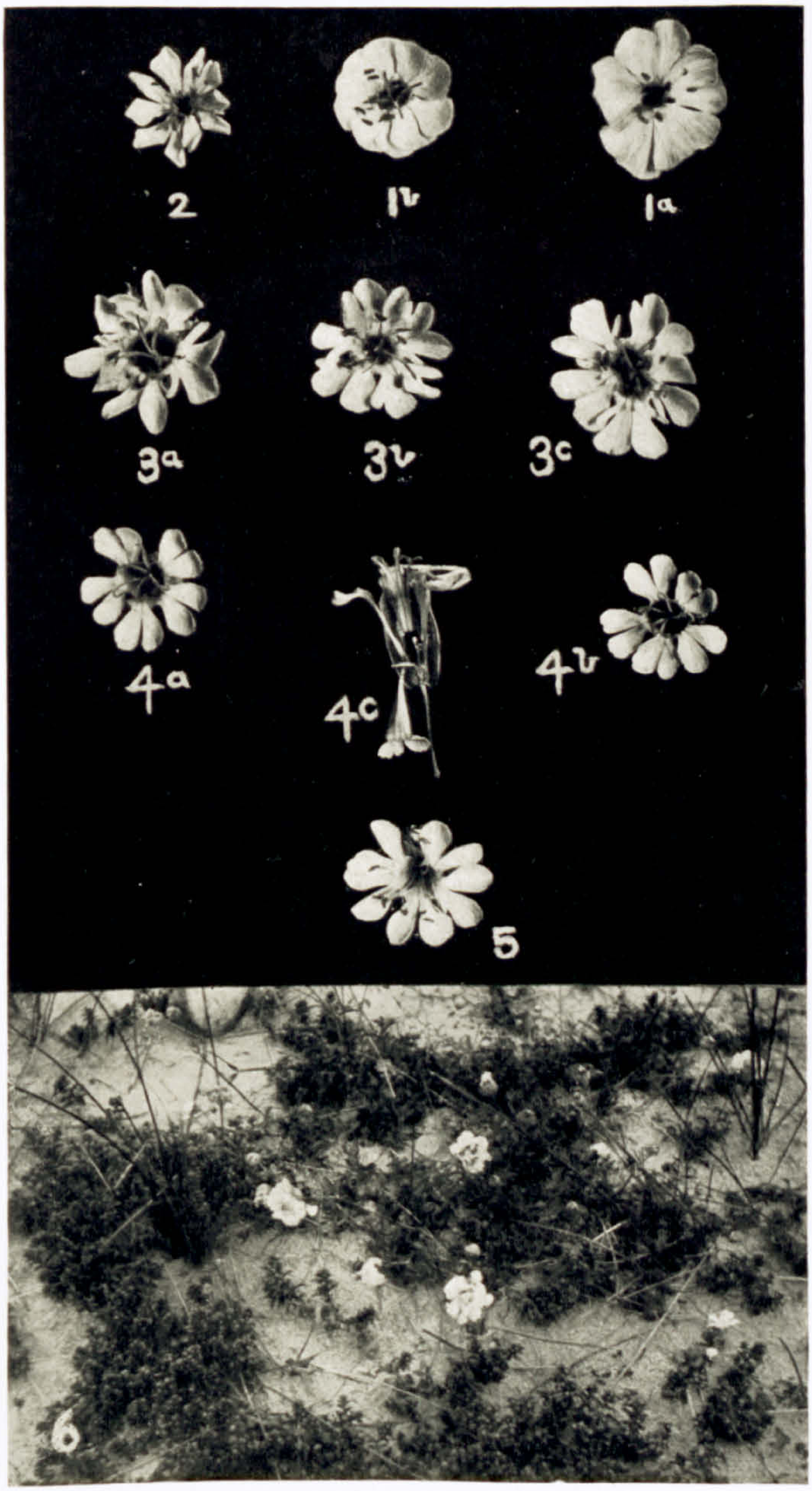
[*Reprinted from* The New Phytologist, *Vol. XI, No. 1, January, 1912*].



*E.J.S. phot.*

SALISBURY—*SILENE MARITIMA.*

# POLYMORPHISM IN THE FLOWER OF *SILENE MARITIMA.*

# POLYMORPHISM IN THE FLOWER OF *SILENE MARITIMA*.

By E. J. Salisbury, B.Sc., F.L.S.

*(Quain Student in Botany, University College, London).*

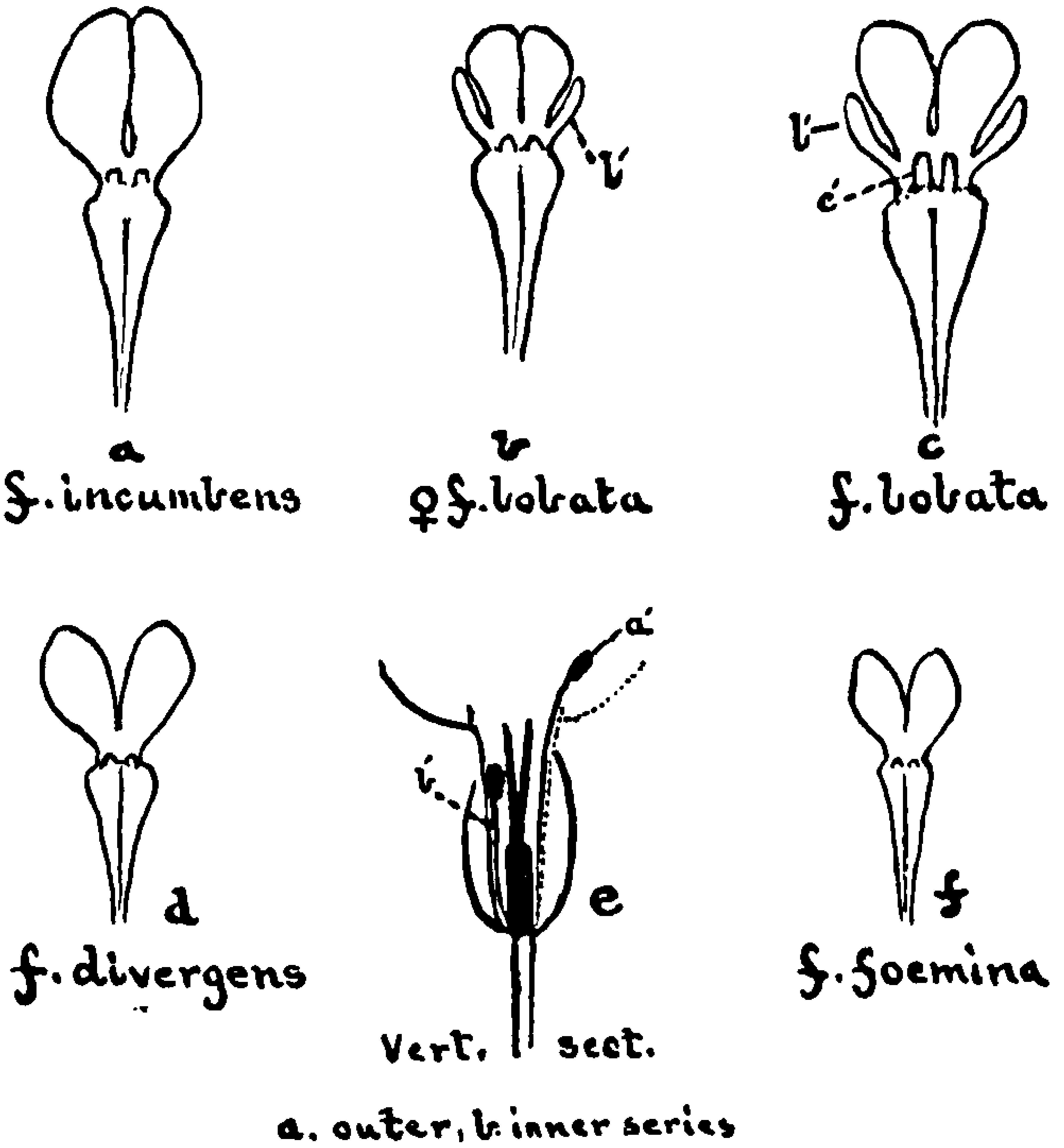
[With Plate I and a Text-Figure].

[*Reprinted from* The New Phytologist, *Vol. X, No 1, January, 1912*].

THE material used in the present paper was obtained in the summers of 1910 and 1911 whilst engaged as a member of Professor Oliver's ecological party in a study of the shingle beach flora at Blakeney Point in Norfolk. Here, as on nearly all pebble beaches, the Sea Campion (*Silene maritima*) is one of the most striking features of the vegetation, and it would probably be difficult to find a locality better suited to the study of this particular plant. At its distal extremity the main beach is, to a large extent, covered by sand dunes; and where the depth of sand is not great the Sea Campion is perhaps even more prevalent on this than on the shingle itself. The incursion of the typical sand dune plants soon, however, drive it out from the association.

Constantly coming before one's notice, the marked difference which the flowers exhibit is perhaps the most vivid impression that the plant presents. But here, and probably in many cases where there appears to be great structural range, further analysis shows that the centre of variation is not single but multiple; even those forms which we do, after careful consideration, group together as continuous variations may, after all, be but an aggregate of strains, the differences between which are so small as to give the series an appearance of continuity. Recent research seems to point more and more to the external and visible differences as criteria of change established, relegating to the internal and invisible the steps which lead up to these mutations.

In the case under consideration there appear to be several well defined types around which variations of a lesser degree may be grouped. But in the absence of cultural experiments the conclusions can only be tentative: such evidence as is available, however, regarding their occurrence points strongly to the distinctness of the forms to be described.



Text-figs. a to d and f, show spetals of some of the forms of *Silene maritima* represented as flattened into one plane. e, diagrammatic longitudinal section of an hermaphrodite flower in the phase when the outer series of stamens (a') are ripe and the inner series (b') are still in the corolla tube. c', coronal scale; l', lobelet.

In all cases observed the different types of flower occurred on different plants, often widely separated and frequently found as isolated specimens amongst other forms. All but three of the flower types were also met with on the famous Chesil Bank in Dorset, thus indicating a wide distribution. In some of the forms to be described the sexual organs are incomplete, but in the four cases, where both stamens and stigmas are present, there is marked protandry. The sequence of development is as follows:—there are ten stamens in two whorls of five members each and of these the outer series elongate first and shed their pollen; at this stage the second series may be seen with their anthers about half-way up the corolla tube (Text-fig., e). When this inner series has developed and dehisced the anthers of the outer series have usually either shrivelled, or fallen off the filaments. By the time all the anthers have shed their pollen the styles will have elongated beyond the corolla tube and their stigmatic surfaces diverged and curved backwards.

It may perhaps be well to mention that the unisexuality of some of the forms referred to above in which there are no functional stamens, have not been brought into this condition by the action of *Ustilago antherarum*; this fungus is of very rare occurrence at Blakeney, so far having only been observed in one instance.

## Description of Forms.

The commonest of all the forms has flowers from 20 to 25 mm. in diameter, and each of the five petals is divided into two lobes which either touch or slightly overlap in the median line (Text-fig. a). The contiguous petals also overlap and thus the flower at a short distance has the appearance of possessing a sympetalous corolla. Where the main portion of the petal joins on to the claw there is an abrupt waist-like narrowing and at this point two scale-like structures (the coronal scales) may be present, but are usually either small or entirely absent.

In Plate I, Fig. 1a, this form is shewn at the stage when the outer five stamens have dehisced and the inner series have appeared at the mouth of the corolla. Fig. 1b shews the same in a later stage; the filaments of the outer series can be seen, but the anthers have dropped, the inner series have dehisced, and the stigmas are spread out for the reception of pollen from a flower in a younger stage of development. The points of variation are: the extent to which the petals are cleft; the development of the coronal scales; and the number of stigmas, which may vary from three to five.

Whilst fully recognising that the various types may themselves be aggregates of more closely allied forms it will be convenient both for description and reference, if we designate each by a name. The form just described with its characteristic overlapping petals may thus be appropriately termed f. *incumbens.*

A second form which we shall call f. *divergens* approaches most closely to f. *incumbens*, and is nearly as frequent in its occurrence; also it has flowers of about the same size. The petals here are deeply divided and the two somewhat narrow lobes diverge from one another (Text-fig., d), whilst the outer margins of adjacent petals are either separate or only just overlap at the apex. Coronal scales are usually present, and the essential organs are normal. In the specimen figured (Plate I, fig. 5) one of the petals is slightly displaced so as to overlap the one adjacent.

Approaching rather closely to the last is another form, in which the lobes and petals diverge somewhat, but differing in the involution of both edges of each lobe, this extends from about half-way from the base to the apex. Owing to this character the lobes appear acute at the tip instead of rounded as is seen in Plate I., fig. 2. This form, which we will term f. *involuta*, is not of very frequent occurrence, its flowers are hermaphrodite and range in diameter from about 20 to 25 mm.

The last of the hermaphrodite forms is not very commonly found, but, of them all, it is perhaps the most beautiful. The flowers are not infrequently as much as 30 mm. in diameter, so that this form is the largest of any of the Sea Campions with the exception of a double form to be described later. Each petal is deeply divided, the two lobes diverging in the upper part; the petals as a whole also diverge very markedly from one another. The feature, however, which completely separates this from all but one of the other forms, is the presence of narrow lobelets arising symmetrically near the base of each lobe of the petal from its outer edge (Text-fig. b, c, $l^1$). These lobelets are narrow finger-like processes standing away from the major lobe and curving slightly towards the apex. They may attain a length of more than 5 mm. and usually curve slightly upwards from the general plane of the petal. The name f. *lobata* therefore seems to be most appropriate for this type.

Three flowers of this form are illustrated in figures 3a, 3b and 3c, where besides the characters already described the long coronal scales at the base of the petals are readily seen (especially in fig. 3c). The prominent development of these structures is a marked feature of this form which together with the upstanding lobelets give an almost double appearance to the flowers as seen in nature. There are the normal number of stamens present and the stigmas vary, as is usual, from three to five.

A single plant was found at Cley with lateral lobelets as in f. *lobata*, but with somewhat smaller flowers (Text-fig. b): the stamens were all reduced to staminodes and the coronal scales were small. Whether this plant is more nearly related to f. *lobata* or to the next form is uncertain, but in the absence of corroborative specimens bearing this type of flower, a form name would be premature.

The next type, which will be best designated by the name f. *foemina* is very distinct both superficially and in detail. The flowers are much smaller than in any of the other forms, varying in diameter from about 10 to 15 mm., and are usually slightly purplish in colour. The petals are widely separated from one another and deeply cleft into divergent lobes which may bear at their base coronal scales (Text-fig. f); these are either very small or almost absent.

The most important feature of this plant is the unisexual character of its flowers which, as in the sub-form of f. *lobata*, possess no functional stamens, these organs having been reduced to staminodes. They are short, of about 5 to 6 mm. in length and bear very small abortive anthers at their apex. Plate I, figs. 4a, 4b, and 4c, illustrate three flowers: one of these (4c) has had part of the calyx and corolla removed to shew the staminodes which scarcely reach to the apex of the ovary.

The last type to be described has only been found at Blakeney Point, where three specimens now grow; of these the first was found by Mr. R. J. Pinchin some years ago and two others in 1911.

All the essential organs have in this form become converted into petals and a considerable amount of "dédoublement" has taken place often resulting in a splitting of the calyx—a common feature in garden pinks which these flowers greatly resemble. In size the blooms vary from 30 to 40 mm. in diameter and are, if anything, slightly more cream-coloured than the single flowered forms. A plant growing in its natural habitat is shewn in Plate 1, fig. 6 with *Arenaria peploides* in the foreground.

The unisexuality met with in two of the types described may be regarded as a further advance upon the lines indicated by the marked protandry of the hermaphrodite forms. For whilst this mechanism ensures fertilisation by a different flower it does not of course preclude fertilisation by the pollen of a bloom on the same plant, as does the total suppression of functional male organs found in f. *foemina*.

Correlated with the differences in the flower there do not appear to be any constant corresponding differences in the vegetative organs.

The periods of flowering for the different forms have not been determined as this would require continual observation of the same area during some three to four months in the year. That they are of considerable duration may be gathered from the fact that all the seven forms were in flower at Blakeney during the first fortnight in July and four of these, viz., f. *incumbens* ; f. *divergens* : f. *lobata* and f. *foemina*, were found at the Chesil Bank still bearing a few blooms as late as September 23rd. This much, however, can be said that from such observations as could be made some forms appear to differ in their period of maximum bloom ; f. *foemina* for instance seems to come into full flower slightly later than most of the other forms, whilst f. *incumbens*, and f. *divergens*, tend to flower early.

The following is a tabulation of these forms, together with their salient floral characters : –

| FORM. | SEX. | CHARACTERS. |
|---|---|---|
| f. *incumbens* ... ... | ☿ . | Petals overlapping. |
| f. *divergens* .. | ☿ | Petals divergent. |
| f. *involuta* ... .. | ☿ | Petals divergent and involute. |
| f. *lobata* .. .. ... | ☿ .. | Petals with lateral lobelets. |
| f. *lobata*, female . | ♀ . | Petals with lobelets. Andrœcium represented by staminodes. |
| f. *foemina* ... ... | ♀ | Petals without lobelets, Andrœcium staminodal, fls., small. |
| f. *flore pleno* ... ... | O ... | Flowers double |

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## EXPLANATION OF PLATE I.

Figs. 1a and 1b, f. *incumbens*. 1a, first series of anthers dehisced. 1b, second series of anthers dehisced, stigmas ripe. 2, f. *involuta*, stigmas not yet emerged. 3a–3c, f. *lobata*, shewing the lobelets and coronal scales. 4a–4c, f. *foemina*, shewing the diverging lobes and petals. 4c, calyx partially removed to shew the staminodes. 5, f. *divergens*. 6, plant of f. *divergens* in its natural habitat. *Arenaria peploides* in the foreground and f. *foemina* on the right.

# THE NEW PHYTOLOGIST.

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OLIVER AND SALISBURY

# PALAEOZOIC SEEDS OF CONOSTOMA

[Annals of Botany, Vol. XXV, No. XCVII, January, 1911.]

# On the Structure and Affinities of the Palaeozoic Seeds of the Conostoma Group.

BY

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AND

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*Quain Student of Botany in University College, London.*

**With Plates I-III and thirteen Figures in the Text.**

## CONTENTS.

## INDEX TO TEXT-FIGURES.

[Annals of Botany, Vol. XXV. No. XCVII. January, 1911.]

## I. INTRODUCTION.

THE object of the following paper is a twofold one. In the first place, to present a detailed account of a small and homogeneous group of palaeozoic seeds, the hitherto practically unknown Conostoma group; in the second place, closely to compare these newly-described seeds with forms already familiar, viz. with the Pteridospermic seeds, *Lagenostoma* and *Physostoma*, and with *Gnetopsis.* Thanks to the kindness of Professor C. E. Bertrand and the extreme courtesy of Professor H. Lecomte of the Musée d'Histoire Naturelle at Paris, we have had at our disposal for comparison the superb and unique series of type specimens of *Gnetopsis elliptica* from the Renault collection. We are thus in a position to state our conclusions after consulting at first hand the whole of the preparations which bear on the subject.

The little-known genus *Conostoma* was founded by Williamson in 1877[1] for the reception of three of the smaller palaeozoic seeds, viz. *C. oblongum*, from the Gannister beds of the Lancashire coalfields, and *C. ovale* and *intermedium* from the Calciferous Sandstone Series of Burntisland. With the Burntisland seeds we have no concern here, as they are under reinvestigation at the hands of Miss Benson. We understand, however, that the two species are not really distinct and are being reduced to one, for the reception of which, in view of its structural peculiarities, Miss Benson is founding a new genus to be named *Sphaerostoma.*

*Conostoma oblongum* is one of the very rarest of Coal Measure seeds, and apart from a passing notice by one of us,[2] has not, so far as we know, found mention in the literature of Palaeobotany since the publication of Williamson's brief description in 1877. At intervals during the last nine years, however, specimens from Mr. James Lomax have been added to the University College Collection; these, together with one from Mr. W. Hemingway and two kindly lent us for description by Mr. D. M. S. Watson, form the whole of the new material at our disposal. One of Williamson's two type specimens is available for reference in the Williamson Collection;[3] his other type, the more valuable of the two, we have been unable to consult. It is probably in the Butterworth Collection, but we have not been successful in tracing the section.

During the course of our reinvestigation of *Conostoma oblongum* occasional sections of what appears to be a closely allied but undescribed species came into our hands. The first sections (received in 1904) were from Shore and Dulesgate; more recently a series of four transverse sections of a single

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[1] W. C. Williamson: On the Organization, &c., pt. viii, Ferns, Gymnospermous stems and seeds. Phil. Trans., 1877, p. 243.

[2] F. W. Oliver: On *Physostoma elegans.* Ann. of Bot., vol. xxiii, pp. 99, 105, and 110.

[3] Nos. 1443 and 1444.

specimen were cut from a small block obtained many years ago by Dr. Kidston at Langendreer in Westphalia, and again this year another specimen has been found at Shore.

These specimens by themselves would have been inadequate for satisfactory description had they not been supplemented by Dr. J. W. Jongmans of Leiden, who, hearing that we were at work upon *Conostoma,* placed at our disposal with the greatest liberality both the sections from Duisburg, in Rheinpreussen, that were already in his collection, and uncut blocks from the same locality which have yielded us additional specimens of this undescribed seed. Thus it comes about that whilst the earliest and latest specimens are from Shore, Littleborough, the majority, and certainly the most valuable preparations, are derived from the nodules of Langendreer and Rheinpreussen. In view of this double source of type specimens we propose to name our new seed *Conostoma anglo-germanicum.*

The two members of the Conostoma group with which we deal fully in this paper are *C. oblongum* and *C. anglo-germanicum.*

Before proceeding to the detailed descriptions, it will be convenient briefly to outline the methods on which we have placed reliance in the reconstruction of these two seeds.

With objects preserved as petrifications in coal-balls accurate knowledge of form mainly depends on the interpretation of sections cut at different heights and at varying angles. When the object under investigation is of convenient size it is usually possible to procure series of sections cut parallel to one another at regular intervals. Such series are readily drawn or photographed, and models in wax or other plastic material constructed, so that the object can be faithfully reproduced on any desired scale. In the case of small objects only a few millimetres in length and of complex structure, like our seeds, this direct method is not available. For in virtue of its smallness such an object is apt to evade detection in the matrix until a chance section reveals its presence. Moreover, for the same reason, even when detected before cutting, its very smallness places a limit to the number of sections which can be cut through it. In other words, the ordinary methods of the palaeobotanist break down when applied to the investigation of minute objects.

Our experience with *C. oblongum* affords a good example of what must be a common predicament. In all, sixteen sections were available, cut at varying angles through sixteen distinct specimens. Of these sixteen sections fourteen were oblique longitudinal sections through the body of the seed, one a transverse oblique, and one transverse across the stalk.

In one respect our task was sensibly lightened at the outset, for, owing to the histological peculiarities of the testa, no serious doubt was ever entertained as to whether a given section belonged to our seed or not.

Our object was to reconstruct our seed in the form of an enlarged model upon which the planes of the various sections could be plotted, and then, by cutting along the appropriate plane, any given section could be reproduced. We began by plotting a sketch of a provisional median longitudinal section, using for the purpose such data, not exaggerated by obliquity of plane, as could be derived from the most favourable preparations available. As each successive section was handled the sketch of course underwent gradual modification.

Thus, every section contributed something; and in the end, after repeated correction, a sketch was obtained upon which all our sections could be approximately plotted. This 'ideal' section could at best be no more than an approximation, because the sections upon which it was founded had been cut from a large number of specimens which from the nature of the case would show some variability of dimensions, even if the extreme assumption were made that they all belonged to the same developmental phase.

With the 'ideal' longitudinal section as basis, a model of the halved seed on a scale of 40:1 was constructed in papier mâché, together with a number of identical plasticine models of the complete seed on the same scale from which to reproduce our original sections. The papier mâché model, which gave internal details as well as surface relief, was of course of great utility in orientating the planes to be followed in sectioning the plasticine models. For accuracy in cutting the sections of the models a simple guillotine or microtome was devised. It consisted essentially of an oblong frame hinged at its narrower end on to a board which formed the support on which the model was placed for sectioning. The plasticine model projected through this frame (which could be adjusted at any required angle), and the section was cut by sliding a taut copper wire along the smooth upper surface of the frame. By the use of this contrivance we have found it possible to reproduce in essentials any given section of our series. Repeated trials have often been necessary, for the slightest differences in either the plane of cutting or in the relation of the point of entrance of the stretched wire to the surface bring about very marked differences in the contours of the sections produced. In other words, form, as expressed in a section, is an extremely sensitive thing, subject to very striking fluctuations from apparently trivial causes. What is true of the form of an object like a seed holds also in the case of minute histological detail.

When reliance has to be placed on the study of oblique sections (an everyday occurrence in palaeobotanical work) we have found wrong inferences, as to the three-dimensional figure of the elements cut, to be almost inevitable without checking by means of models.

In the case of the seeds described in this paper, the plotting of almost every section has been verified by following the method outlined above, and as a result we are able to publish our results and reconstructions with much more confidence than would otherwise have been the case.

We now pass on to the detailed description of *Conostoma oblongum* and *anglo-germanicum.* This is followed by comparisons with allied seeds and by a series of diagnoses, including those of the genus and species; the paper concludes with a general discussion on points arising out of the work.

## II. CONOSTOMA OBLONGUM.

### 1. *Enumeration of specimens.*

Our account of this seed is based on the following preparations, all from the seam nodules of the Lower Coal Measures of Lancashire and Yorkshire.

*University College Collection.*

| | | When received, |
|---|---|---|
| R. 110 | Dulesgate . . . . . | Feb., 1905 |
| R. 111 | Shore . . . . . . | May, 1906 |
| R. 112 | Shore . . . . . . | 1906 |
| R. 113 | Halifax . . . . . . | Dec., 1907 |
| R. 114 | Halifax . . . . . . | Dec., 1902 |
| R. 115 | Shore (contains two specimens) | 1906 |
| R. 116 | Shore . . . . . . | Dec., 1905 |
| R. 117 | Shore . . . . . . | Oct., 1904 |
| R. 118 | Shore . . . . . . | 1906 |
| R. 119 | Shore (contains two specimens) | 1908 |
| R. 120 | Shore . . . . . . | Feb., 1906 |
| R. 121 | Shore . . . . . . | Apr., 1907 |
| R. 122 | Shore . . . . . . | May, 1909 |
| R. 123 | Deighton, Yorks. . . . . | 1910 |

*Mr. D. M. S. Watson's Collection.*

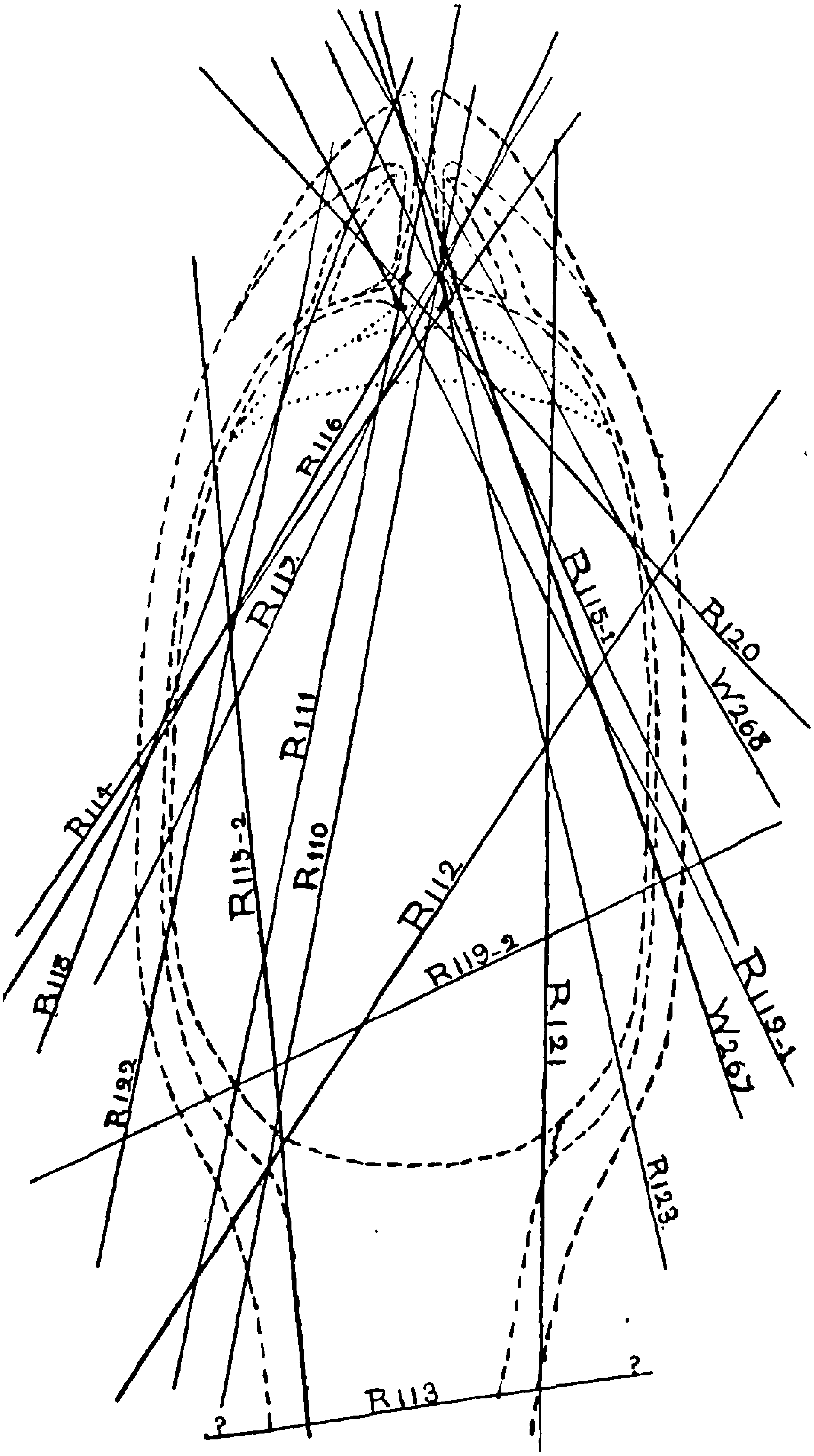
| | | |
|---|---|---|
| W. 267 | Shore . . . . . . | 1908 |
| W. 268 | Shore . . . . . . | 1908 |

*Williamson Collection.*

Nos. 1443 and 1444 Oldham.

The only other specimen that we know of is that figured by Williamson in his 8th Memoir (1877), Pl. XII, Fig. 86. It was lent him by the late John Butterworth, and has not been seen by us.

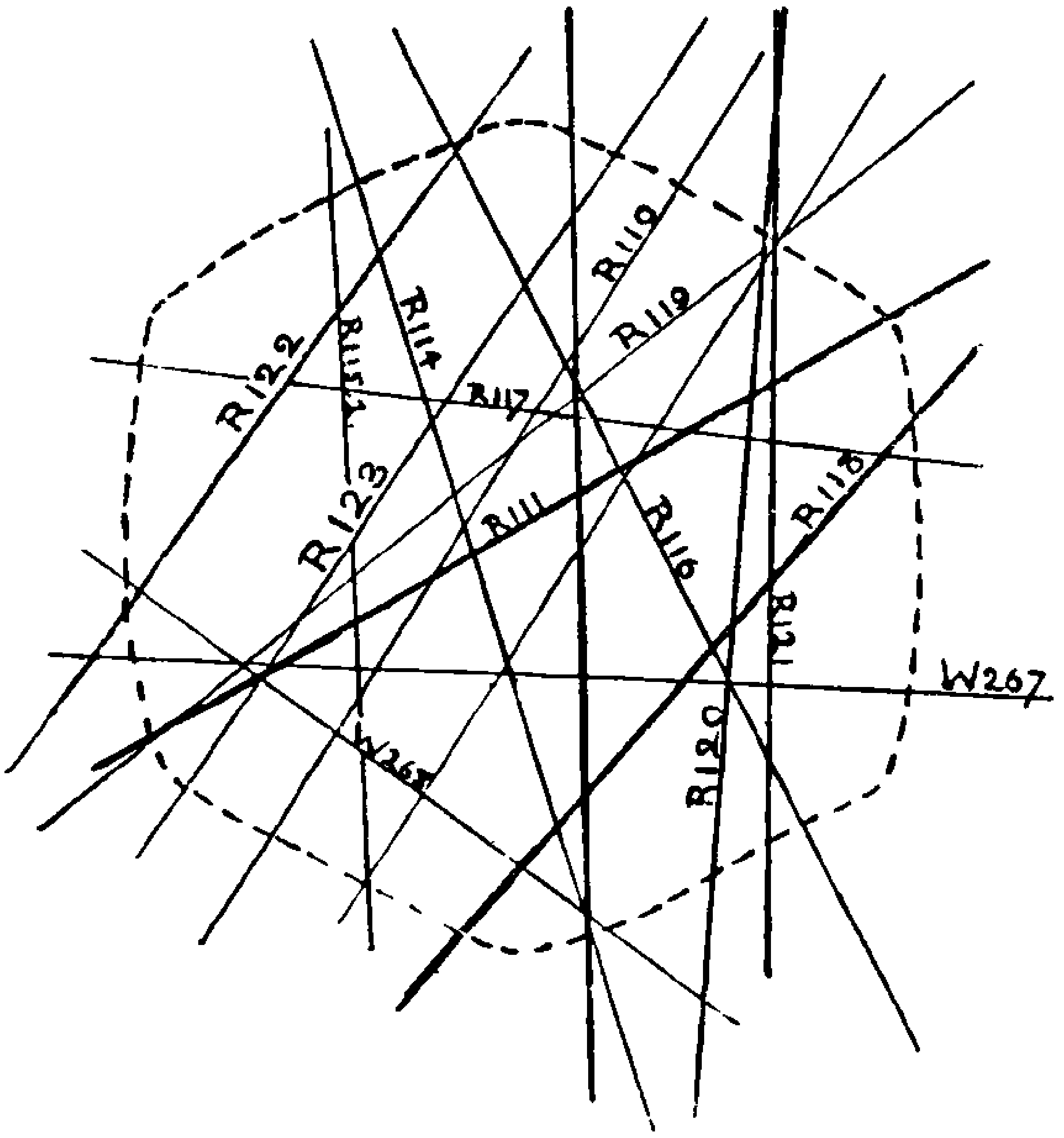
The positions of these sections, other than those in the Williamson Collection, are plotted in relation to the median longitudinal section of the seed in Text-fig. 1, and in relation to the transverse section just below the level of the tapetal septum in Text-fig. 2.



TEXT-FIG. 1. Diagrammatic sketch of a median longitudinal section of *Conostoma oblongum* upon which are plotted the approximate positions of the planes of section of all preparations used in this paper. The reference letters and numbers given with each section on the figure are the designations under which the preparations are cited in the explanation to the plates. R = University College Collection; W = Mr. D. M. S. Watson's Collection.

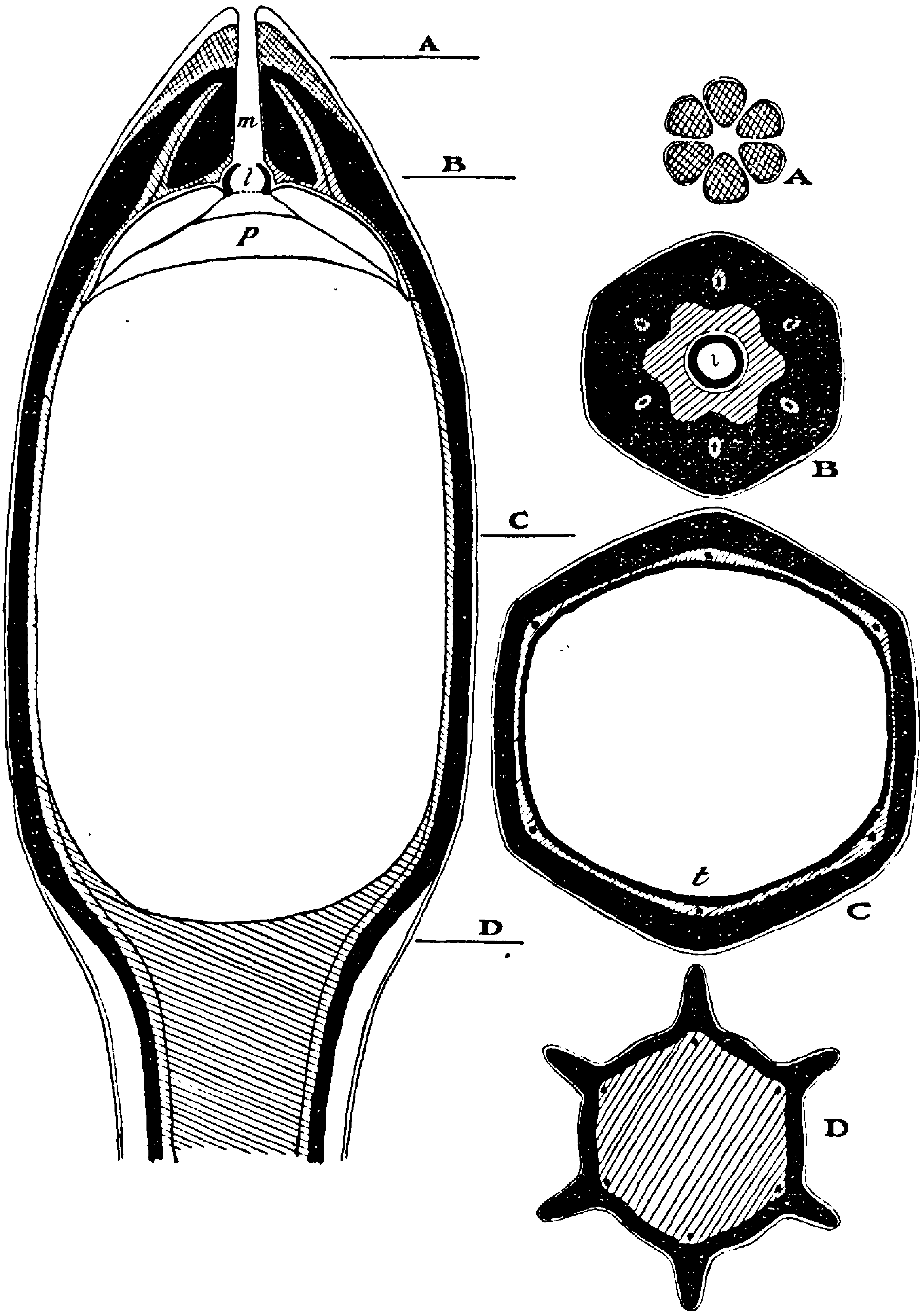
## 2. *General Features.*

*Conostoma oblongum* is a straight, cylindrical, or obscurely prism-shaped seed, tapering gently to a blunt point above, where it is perforated by the micropyle, whilst below, in the chalazal region, it narrowed more abruptly to its insertion on a fairly thick stalk (Text-fig. 3 and Pl. I, Fig. 1). The average length was 5 mm. and the maximum diameter 2·3 mm. The seed-base bore six salient ridges, which, running up from the peduncle, died out almost at once, reappearing, however, at the apex to form a crown around the micropyle. On the main body of the seed these ridges are represented by a slight angling of the surface, hardly prominent enough to be called ribbing. Perhaps the most interesting feature in the form of this seed is the existence of a slight bilateral symmetry, only trifling in amount, but sufficient to rank it technically with the 'platysperms' (Text-fig. 3, C).



TEXT-FIG. 2. *Conostoma oblongum.* Diagrammatic transverse section of seed cut about 1 mm. below the lagenostome, with plottings of the sections used. References as in Text-fig. 1.

The internal organization of the seed resembles that of a *Lagenostoma* in so far as the more general relations of integument, nucellus, and pollen-chamber are concerned, though it differs from that genus in many important particulars. As in *Lagenostoma*, the single integument or testa is coalescent with the nucellus from the seed-base to within about 1·3 mm. of the apex. It formed a hard shell to the seed about 0·1 mm. in thickness, and exhibited a very characteristic histological structure. At the summit it undergoes marked thickening to form a conical 'canopy' surrounding the micropyle.



Text-fig. 3. *Conostoma oblongum.* Restorations. The longitudinal section passes through two opposing ribs; in the middle region the vascular bundles and nucellar wall are represented by a single line except in the transverse sections of the latter; A and D are in part hypothetical. The hard testa is in black, parenchymatous tissue shaded, and the soft apical tissue cross-hatched. The ribs and 'blow-off' layer are in white and the lagenostome in black. *m*, micropyle; *l*, lagenostome; *p*, plinth; *t*, tapetum (omitted from longitudinal section). × about 25.

The canopy shows conspicuous lobing, each of the six lobes corresponding to a ridge. The six vascular strands which enter the seed at the chalaza traverse the soft lining of the hard shell of the testa below the ridges and angles, and, continuing to the apex, enter the lobes of the canopy. The surface layer of the seed appears to have undergone mucilaginous degeneration, thus recalling the condition of *Lagenostoma.* Curiously enough, the actual tip of the seed was succulent, thus contrasting in a striking way with the otherwise sclerotic texture of the integument. This unique feature may well have been correlated with secretory activity at the moment of pollen reception.

The nucellus, which, as usual, stood erect in the axis of the seed, had a length of 3·7 mm. over all. Its lower 3·1 mm., coalescent throughout with the testa, were occupied by the megaspore cavity, which possessed a well-marked tapetal lining or jacket. The free summit of the nucellus, which was closely ensheathed by the lining layer of the integument, was dome-shaped, the dome resting on the tapetal septum which stretched across the nucellus at this level. Above, in the centre of the convex extremity, was a low depression or dimple on which rested the smallest pollen-chamber we have seen in an English seed. This pollen-chamber —or lagenostome, as we prefer to call it—was a tiny, truncated, globular body, open above, and possessed a one-layered wall of characteristically sculptured cells. Its mouth lay immediately below the micropylar tube of the integument, which was clamped to the rim of the lagenostome by a ring-like flange (Text-fig. 5, *u f.*, p. 17). In this way the efficient transport of pollen would be amply secured. Pollen-grains when present in the seed have never been found in the lagenostome, which would appear to have served in this case merely as a vestibule to a more spacious lower chamber occupying the interior of the plinth. Into this lower chamber the unusually large pollen-grains were conveyed through the collapse of the floor of the lagenostome. The details of this curious mechanism, so far as we apprehend them, will be fully set forth in the sequel.

The main points in the structure of this interesting seed which merit full description are (1) the testa with its wings, succulent tip, and highly specialized micropyle; (2) the free part of the nucellus closely invested by the lining of the integument and consisting of a two-storied appliance for the reception and maturation of the pollen.

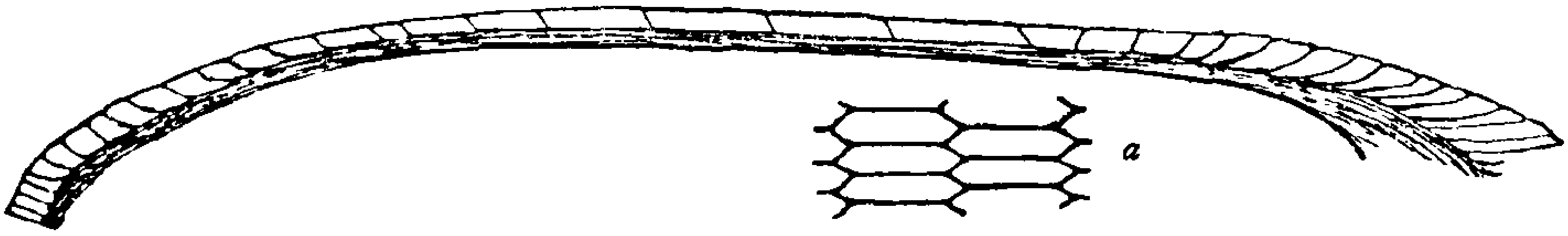
We embody in the accompanying Text-fig. 3 an attempt to reconstruct the median longitudinal section of this seed, together with transverse reconstructions at the several heights indicated.

### 3. *The Testa.*

The hard part of the testa which gave form to the seed was of a rounded, hexagonal shape, tapering with a steep curve towards the micropyle, and passing into the stalk below more abruptly. Thus, disregarding the peduncle, the seed, as seen in longitudinal section, was approximately boat-shaped—the apex representing the prow and the base the stern (R. 111, Pl. I, Fig. 1).

There is only a single transverse section, somewhat distorted in form, owing to its obliquity both to the axis of the seed and to the two ridges first cut; but if reliance can be placed on this solitary section, the seed was flattened, to a very slight extent, in a plane passing symmetrically between the angles, two of which were thus rendered more obtuse (Text-fig. 3, C). At these angles the sclerotesta was thickest, whilst it was thinnest at the other four (R. 119, 2, Pl. I, Fig. 5, *ma., mi.*). At the apex the angling of the middle region passes into definite ridges which end around the micropyle in six not very prominent lobes (Text-fig. 3, A).

In the basipetal direction the angles develop as prominent ridges (R. 110, Pl. I, Fig. 4) and must have extended downwards, giving a winged character to the seed stalk. (In the instance referred to they are exaggerated by reason of the obliquity of the plane of section.) Although six ridges appear to have been the general rule, variations, which are so marked a feature of the ribbing in *Physostoma*, no doubt occurred, if only in the direction of increase. The instance is shown in R. 110, Pl. I, Fig. 10, $r^7$, where a seventh rib is seen on the left. In one other case, although the number of ribs remains constant, two of them were abnormally close together.



TEXT-FIG. 4. Cells of palisade layer of the testa cut obliquely, showing the forward slope at the apex and the backward slope at the base (left of fig.). R. 122. *a*, cells of testa in surface view.

The internal form of the testa was, in the main body of the seed, similar to that of the exterior. The absence of transverse sections at the base leaves the lower limits of the interior doubtful; at the apex the cavity was dome-shaped, passing into the funnel-like lower end of the micropyle. The dome-shaped apex of the cavity and the acute apex of the exterior thus rendered the testa around the micropyle of considerable thickness (0·57 mm.) as compared with that of the general body of the seed (0·13 mm.).

In detail, the testa, like that of *Lagenostoma Lomaxii*, consisted of two kinds of elements, viz. an outer palisade layer and an inner hypoderm. Seen in transverse section the palisade layer presents the form of a continuous investment of radially elongated elements about $70\mu$ in width, whilst near the apex it attains a much greater radial thickness (114 μ).

The vertical measurement appears to vary considerably, reaching a maximum of about 323 μ in the body of the seed, though adjacent elements cut in the same sense may scarcely reach a quarter of that length. Where the plane of section passes through the curved surfaces of the apex and base, the cells of this layer appear to curve respectively forwards and backwards (Text-fig. 4). Since tangential sections of this layer are wanting, no direct evidence is available as to their external form; but the appearances described can be satisfactorily explained if we assume the exterior wall to have been a hexagon, in which the sides *parallel* to the main axis of the seed were longest, and that these cells were arranged in vertical rows (Text-fig. 4, *a*). Models based on these assumptions, when cut, reproduced with striking fidelity the appearances in the various sections. The invariable obliquity of our preparations will account for the variations of the palisade cells with regard to their vertical dimensions; the maximum will correspond to cells cut in the direction of the long axis of the hexagon, and the minimum to cells cut across the corners.

If a cylinder with longitudinal ribs be cut obliquely it will be found that the ribs appear in the sections to slope forwards at the apex and backwards near the base; this is exactly what we find to be the case with the palisade cells; though here the effect is exaggerated both by their tapering ends and the fact that their outer surfaces are slightly more extensive than their inner. Similarly in the oblique transverse section where the palisade cells are cut through their tapering ends, these show varied trapezial forms, in some places even appearing two-layered.

The carbonized contents of these cells are usually of a uniform dense brown with much lighter or almost colourless walls. In some specimens the cells near the apex show a dark body occupying a nearly central position and surrounded by a lighter portion resembling a vacuole. In general, they resemble the structures seen in the cells of the testa of *Stephanospermum*, only far less well defined (R. 114, Pl. I, Fig. 2, *t*).

Abutting internally upon the palisade cells were three to four layers of fibrous elements constituting the hypoderm; these were ellipsoidal in transverse section, the flattening being in the radial direction. So far as can be judged from oblique sections, their length varied considerably. In the body of the seed this layer reached a thickness of from 57–76 μ, and if the single transverse section is to be relied upon, was thickest at the two major angles and thinnest opposite the four minor. It is chiefly due to increase of this tissue that the hard testa attains its greater thickness around the micropyle. In contents and nature of the cell-wall the elements of this layer resemble those of the palisade. The sections all show the testa cut obliquely, the most nearly vertical being R. 111, Pl. I, Fig. 1. The others fall into two categories with regard to their direction, viz. :—

1. Sections in which the plane of symmetry *passes through* a rib or angle (e. g. R. 110, Pl. I, Fig. 10) will taper above and below—the two ends appearing longer and more pointed as the plane of section approaches the vertical, shorter and more rounded as it approaches the transverse.

2. Those in which the plane of symmetry *falls between* two ribs, the sections appearing boat to coffin shaped according as they pass through the apex or not.

Asymmetrical variations of these two types are the rule, due to the median plane of the section falling between the planes of symmetry (the median plane being that radial plane of the seed which is cut at right angles), or more strictly—regarded as variations of these two groups—due to obliquity of the plane of section to one of these planes of symmetry.

Section R. 119, 1 (Pl. I, Fig. 11) is a good example of such a variation of the second type. The outline is roughly that of a coffin with sloping ends, the upper half foreshortened owing to the tapering of the apex ; as will be seen from the plotting on the transverse diagram (Text-fig. 2) the plane of section stands asymmetrically with regard to the two ribs first cut ($r^1$ and $r^2$). For convenience of description, such sections may be termed *doubly oblique.* In the case of a perfectly cylindrical seed doubly oblique sections are not possible, since the plane of any section is always at right angles to a plane of symmetry. In a ribbed seed, the number of planes of symmetry being only twice that of the ribs, where these, as in the present instance, are few, it is only rarely that a section presents a regular outline.

It appears highly probable that sclerization of the hard testa took place in an acropetal direction. This is suggested by two of the seeds which on general grounds we regard as immature. In the first of these (R. 122, Pl. I, Fig. 3) the soft-celled tissue (*s.t.*) which constituted the apical cap is not sharply delimited from the hard tissue below (*t.*), as is the case in the mature condition, where the demarcation was sufficiently abrupt to have fissured, in some cases, along this line (W. 267, Pl. I, Fig. 8, *s.t.*). This seed (R. 122) would furthermore appear to be young, since the 'blow-off' layer is mostly *in situ*, and also the plinth, which having regard to the plane of section should have been cut across, is not present—a fact which seems to indicate the later development of this structure.

The second example of a young seed (R. 114) also shows less sclerization of the testa cells—their contents, usually so obscure, being here comparatively well defined (Pl. I, Fig. 2). The presence of the pad of tissue beneath the lagenostome with well-preserved cells (*ls.*), the exhibition of cellular structure by the integumental lining, and a plinth only half the height of those in the mature seeds, all seem to point in the same direction.

### 4. *The Vascular System.*

Corresponding in position to the six ribs of the testa were six bundles which occupied the internal angles. These passed up just outside the nucellus till they reached a level slightly above the base of the lagenostome, where they turned upwards and entered the sclerotesta, accompanied by a strand of soft-celled parenchymatous tissue (R. 117, Pl. II, Fig. 16, *loc.*); thence they again curved inwards, probably ending at the limit of the hard testa close to the micropyle; here the accompanying parenchyma, which gradually narrows towards the apex, dies out (Text-fig. 3, between B and A).

Around the micropyle the hard testa was slightly lobed, the lobes corresponding in number and position to the vascular strands within; to this lobing is due the internal asymmetry of the apex seen in some of the sections where they pass through a ridge on one side of the micropyle and through a 'furrow' on the other (R. 110, Pl. II, Fig. 14; R. 123, Pl. II, Fig. 19, *i.r.*).

The apex of the hard testa in *Conostoma* was therefore very like the canopy of *Lagenostoma Lomaxii*, where likewise the lobes corresponded in number and position to the vascular bundles which passed into them. They did not, however, agree in position with the external ridging of the apex, which, as has been pointed out before,[1] was associated with the radial septa. The chief point of difference in *Conostoma* lies in the reduction of the soft tissue which occupied the loculi of the canopy to mere strands accompanying the bundles. The vascular bundles themselves consisted of four to five elements (each about 10 $\mu$ across) with delicate scalariform thickenings which occasionally exhibited fusion between adjacent bars.

### 5. *The Soft Integument.*

Surmounting the apex of the hard testa was a cap of soft-celled tissue (R. 122, Pl. I, Fig. 3, *s.t.*) which was thickest around the micropyle, where it formed six free lobes (Mr. Watson's specimen 268, Pl. II, Fig. 12, *l.*) corresponding to the obscure lobing of the hard tissue below, and thinned out in the basipetal direction, ending just above the shoulder of the seed (Text-fig. 3). The only evidence that the vascular supply extended into this region is a very doubtful vascular bundle in one of the preparations. This soft tissue may have been of a secretory nature, supplying in part the necessary fluid for the process of pollination, by furnishing a drop mechanism as in *Taxus*. The specialized epidermis around the micropyle, to be described later, somewhat resembles the protective epidermis

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[1] Oliver: On *Physostoma*. Ann. of Bot., vol. xxiii, p. 105.

('lip') surrounding the glands of *Polygonum*, &c., and may even have served a similar purpose.[1]

Lining the micropyle and continuous with this soft tissue was a single layer of cells, of which only the membrane forming the micropylar tube is preserved (R. 111, Pl. I, Fig. 7, *m.m.*). This latter consists of several tiers of longitudinally elongated elements, which here and there show faint spiral markings; the cells of each tier are of approximately equal length, and, in the middle region, stand directly above those of the tier below. In width they were nearly the same throughout (17 $\mu$), the increased circumference of the micropyle at the base entailing a corresponding increase in their number. At the level of the lagenostome this lining layer of cells suddenly thickened to form a triangular flange, which rested on the upper edge of that organ. A similar flange occupied the shallow sinus where the lagenostome rested upon the plinth. In section the flanges appear as angular projections into the micropyle (R. 117, Pl. II, Fig. 18, *u.f.* and *l.f.*). Below the lagenostome the membrane closely ensheathed the dome-shaped plinth, at the base of which the nucellus and integument become fused. In two of the sections the sinus between this membrane and the plinth is seen cut across at the base (R. 110, Pl. II, Fig. 14, *s.*, and R. 117, Pl. II, Fig. 16, *s.*). Below this point the nucellus and testa were connected by soft-celled tissue, through which the vascular bundles passed. In section R. 114 (Pl. I, Fig. 2, *pl.j.*) the single layer of cells forming the lining membrane of the micropyle is seen cut across between the flanges. From this we see that the lagenostome and plinth, although free, were closely ensheathed by the integumental membrane, which by means of the flanges held the lagenostome in a tightly fitting socket, thus ensuring perfect continuity between the passage of the micropyle and the cavity of the lagenostome; to such an extent was this the case that the contraction of the nucellus previous to fossilization, which usually takes place, has not only caused the lagenostome to descend, but has in some cases brought down the micropylar tube with it, causing rupture near the apex (R. 111, Pl. I, Fig. 7). So long as these were the only sections available, the tube appeared to belong to the lagenostome, but the sections which have more recently come to hand show clearly that its true nature is integumental (Watson's 268, Pl. II, Fig. 12, *m.m.*, and R. 123, Pl. II, Fig. 19, *m.f.*), as the continuity with the soft tissue at the apex is completely shown.

### 6. *The 'Blow-off' Layer.*

Investing the whole external surface of the seed was a differentiated epidermis, which we shall term the 'blow-off' layer. This, together with

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[1] E. J. Salisbury: On the Extrafloral Nectaries of the Genus *Polygonum*. Ann. of Bot., vol. xxiii, 1909, p. 239.

the soft-celled tissue of the apex, formed a kind of sarcotesta around the seed. The 'blow-off' layer consisted of longitudinally elongated cells with an almost uniform radial dimension of about 20 $\mu$. Near the apex, however, they reached a maximum of about 80 $\mu$. These cells, as preserved, stand in marked contrast with the palisade cells upon which they rest. Their interior is almost colourless and their walls are dark and slightly thicker towards the exterior. Just below the apex of the seed the cells of this layer reached a maximum radial extension (Watson's specimen 268, Pl. II, Fig. 12, *bl.*), bevelling off suddenly towards the micropyle, so that the extreme end of the seed was covered by an undifferentiated epidermis.

The chief point of interest is the exfoliation which the 'blow-off' exhibits: in only one other section besides W. 268 has it remained *in situ* (R. 122, Pl. I, Fig. 3, *bl.*). Elsewhere, the layer stands away from the hard testa as if forced off, and in most cases only the basal portions of the radial walls remain to indicate its former presence. These latter appear as projecting pegs from the margin of the testa, to which they give a crenated appearance (R. 110, Pl. I, Fig. 4, *bl.w.*)

The method by which this exfoliation took place is shown in R. 111 (Pl. II, Fig. 13, *pe.*) near the apex, where the cuticle-like layer, formed by the outer walls, is raised up by cones of mucilage which bear a remarkable resemblance to those already described for *Lagenostoma Lomaxii.*[1] But whereas the cell-walls in *Lagenostoma* were raised up as separate entities, in *Conostoma* they formed a continuous layer, which was removed as a whole, although it underwent fission, due to its rigidity and lack of elasticity, points well shown in one section (R. 116, Pl. I, Fig. 6, *bl.*) where the exfoliated 'blow-off' at the apex still retains the lobing of the tissue beneath, but, owing to the increased circumference, has fissured along the grooves.

A section which is perhaps correctly allocated to this seed, viz. R. 113 (Pl. I, Fig. 9), is presumably an oblique transverse section passing through the stalk. It was winged with a central cavity (*c.s.*), probably lysigenetic, and a narrow, angled band of hard tissue following the outline of the exterior (*scl.*). Its attribution rests upon the general appearance of its tissues, bounded at the exterior by an epidermis which closely resembles the 'blow-off' layer as seen in certain of the sections. Its prominent wings, to the number of seven, corresponding to seven vascular bundles (*v.b.*), might well have been the base of such a seed as R. 110, which, as we have already pointed out, varied in this respect from the normal number of ribs, the hard tissue being perhaps the basal limit of the testa. The chief difficulties in the way of its acceptance are (*a*) the rapidity with which the bundles are passing out, and (*b*) the presence in the wings of secretory passages (*s.p.*), one in each. In any case it seems possible that the bundles of *Conostoma* remained distinct for some distance below the seed-base,

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[1] Oliver and Scott: On *Lagenostoma Lomaxii.* Phil. Trans., B, vol. 197, p. 206.

perhaps to converge suddenly later to a single strand. Another section (R. 115–2) which gives food for speculation passes tangentially through the stalk. This shows what may have been a cupule containing a vascular strand. A peculiar feature of this preparation is that the plane of section should theoretically (if the seed be borne vertically on a straight stalk) pass through the axis of the stalk, but actually it cuts the stalk or cupule, as the case may be, tangentially and passes out on the same side; therefore either the stalk in this instance was bent or else the seeds in this species were borne in a cupule in a similar manner to the closely allied seed *Gnetopsis elliptica*, where the insertion of the seeds and cupule is oblique to the main axis.[1] The continuity is not convincing, but the fact that the possible cupule contains secretory canals suggests that the section R. 113 may have been cut through the stalk at the base of the cupule, which would account for both the difficulties of its acceptance. In any case we ourselves regard the present evidence as quite inadequate for a definite decision.

### 7. *The Nucellus.*

This, the central body of the seed, requires detailed description in view of the unusual and possibly significant elaboration of structure shown by its distal portion which was concerned in the reception and storage of the pollen.

The nucellus falls into three regions:—

(1) The *lagenostome*, a structure evidently corresponding with the pollen-chamber of such a seed as *Lagenostoma Lomaxii*. It lies in a saucer-like depression at the summit of (2) the *plinth*, which forms the truncated continuation of (3) the main body of the nucellus or megaspore chamber.

The lagenostome and plinth, though closely invested by the integumental lining ('micropylar funnel' and 'plinth jacket'), were free from the integument; the megaspore chamber, which extends from the chalaza to the level at which the apical tapering of the seed begins, shows on the other hand complete coalescence with the testa.

The horizontal septum separating the plinth cavity from the megaspore chamber is formed by the tapetum, and may for convenience of reference be termed the tapetal septum (cf. Text-fig. 3).

### 8. *The Lagenostome and Plinth.*

These two organs were so intimately related that it will be convenient to deal with them in the same section. The *plinth* is the tapering free end of the nucellus, on the flattened end of which the small urceolate *lagenostome* was inserted in a shallow, saucer-like depression. Apart from the remains of its internal filling tissue, to which reference will shortly be made, the plinth is as a rule in our specimens represented by its epidermis—

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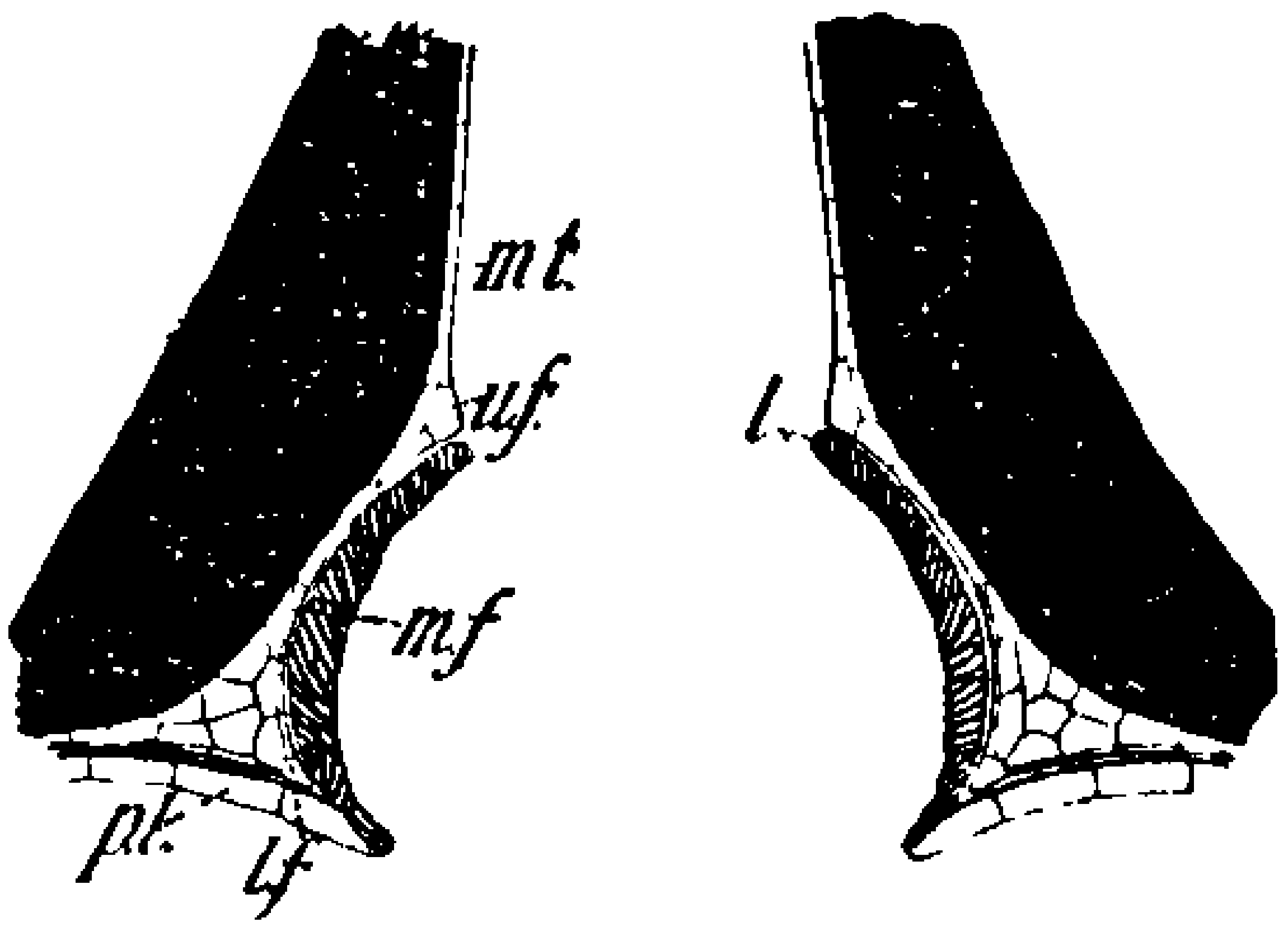
[1] Renault: Cours de Bot. foss., vol. iv, Pl. XX, Fig. 1.

a mere shell—usually completely carbonized and appearing as a continuous black, structureless crust (cf. specimen R. 123, Pl. II, Fig. 19). Occasionally, the individual cells of which this shell was composed are preserved (specimen R. 114, Pl. I, Fig. 2, *pl.*), showing it to have consisted of a single layer of flattened epidermal cells destitute of special sculpturing.

Tracing this layer down the steep slope of the plinth to the level at which the tissues of nucellus and integument became confluent (R. 110, Pl. II, Fig. 14), it is found to curve sharply outwards and upwards (below *s.*), returning on its course as the lining layer of the integument which fitted the plinth like a jacket (cf. p. 14).

Followed in the other direction the epidermis of the plinth dips slightly at the summit to form the depression in which the lagenostome was lodged. It does not, however, reach the central part of this recess, which, as sections across this region clearly prove, was perforated (specimen R. 117, Pl. II, Fig. 16). The epidermis of the plinth at the insertion of the lagenostome curves abruptly upwards and outwards, and at the same time, changing completely its histological character, becomes evaginated to form the sculptured wall of the lagenostome (Pl. II, Fig. 18). Thus we see that the epidermal layer of the interior of the seed is in complete continuity throughout and that the various regions termed the micropylar tube, micropylar funnel, plinth jacket, plinth and lagenostome walls, are merely different specialized portions of one and the same layer.



TEXT-FIG. 5. *Conostoma oblongum.* Diagram of median vertical section of lagenostome to show how it was enclosed by the micropylar tube and funnel. *m.t.*, micropylar tube; *m.f.*, micropylar funnel; *p.l.*, wall of plinth; *u.f.* and *l.f.*, upper and lower flanges holding lagenostome (*l*) in place.

The lagenostome was a tiny goblet-shaped body, the cavity of which communicated with the plinth cavity. In shape it was slightly pyriform, its greatest horizontal diameter being about one-third up from its insertion. The mouth, which is rarely if ever shown in the sections, communicated directly with the micropylar tube, with which it closely engaged by a bevelled flange from the latter (Text-fig. 5, and Pl. II, Fig. 18). Unlike *Physostoma* and *Lagenostoma*, the mouth was unprovided with any tube or beak. In the former the mouth was placed on a low papilla (Text-fig. 12, p. 39), whilst in the latter the tapering tube of the pollen-chamber reached the surface of the seed (Text-fig. 12).

The principal dimensions of the lagenostome of *Conostoma oblongum* were as follows:—greatest horizontal diameter, 0·23 mm.; diameter at mouth, 0·12 mm.; height, 0·15 mm.

In *Physostoma* the lagenostome or pollen-chamber was 1 mm. high

× 1·2 mm. wide; in *Lagenostoma Lomaxii* the corresponding dimensions were 0·75 mm. × 0·7 mm.

The cells which formed the wall of the lagenostome were in lateral continuity by about a third of the depth of their radial walls, thus leaving their major exterior portions free. It is due to this peculiarity, together with the obliquity of the sections, that the misleading appearance of a two-layered wall is due. This feature, strikingly shown by the preparations R. 110 (Pl. II, Fig. 14, *lg.*) and R. 117 (Fig. 18, *lg.*), might readily give rise to the view that the lagenostome was a two-layered structure. The radial dimension of these cells ranges from 26 μ to 30 μ; the tangential horizontal is approximately 26 μ, and the tangential vertical 39 μ.

In form, the cells are roughly hexagonal as seen in tangential view. They were arranged in successive tiers with their shorter sides directed upwards and downwards. The wall seems to have been continued right up to the mouth without marked change in character, unless perhaps the appearance of thinning shown by preparation R. 117 (Pl. II, Fig. 18) at the top of the lagenostome be not merely the result of post-mortem shrinkage.

TEXT-FIG. 6. Sketch slightly diagrammatic, showing the sculpturing on the cells of the lagenostome.

A great feature of the cells of this layer was the elaborate, tracheid-like sculpturing of their walls—well shown in specimen R. 115, 1 (Pl. II, Fig. 20, *lg.*), and, on a much enlarged scale, in the adjacent text-figure (Text-fig. 6). These sculpturings, which were of the scalariform or slightly reticulated type, reach a maximum development on the tangential wall, i. e. the wall in contact with the integument. Other characteristic sections of the lagenostome are shown by specimens R. 111, R. 114, and R. 116 (Pl. I, Figs. 7, 2, and 6). These figures also illustrate the marked tendency of this cell layer to undergo degeneration prior to fossilization. Thus in preparation R. 111 (Pl. I, Fig. 7, *lg.*) the outer walls of one layer and the inner walls of the adjacent layer have perished, whilst in R. 116 (Fig. 6, *lg.*) solution has proceeded still further, so that little remains beyond the common radial walls of the obliquely cut cells.

Though these tracheid-like elements of the lagenostome were of delicate construction, they must, in virtue of their sculptured walls, have had a marked capacity to resist crushing forces. Occasionally the lagenostome is slightly retracted from the micropyle in consequence no doubt of post-mortem shrinkage (e. g. Fig. 7), but in all cases that have come under observation the form of the lagenostome is perfectly preserved.

The floor of the lagenostome did not consist of differentiated, sculptured cells, but was occupied by a pad of soft tissue which readily underwent displacement, leaving a clear orifice—well shown in preparations R. 117

and R. 116 (Pl. II, Fig. 18, and Pl. I, Fig. 6). The plug which formed the floor is only slightly displaced in R. 116 (Fig. 6, *ls.*), whilst in R. 110 (Pl. II, Fig. 14, *ls.*) the cushion of soft tissue which hangs suspended from the lower rim of the lagenostome appears to be still in position.

The central cone of soft tissue that projected into the cavity of the pollen-chamber of *Lagenostoma Lomaxii* (Text-fig. 12, p. 39) does not appear to be represented in any of our specimens of *Conostoma*, though from analogy with that seed we regard it as certain to have been present in early developmental stages. Its absence from our specimens is best to be explained as a consequence either of very early deliquescence in development or imperfect preservation.

Before turning to the plinth cavity and its contents it will be convenient to mention a general character of this organ.

In occasional specimens of *Conostoma* we find that the plinth had not reached its full height, and as a rule lack of extension in this region seems to be correlated with other features which support the view that such specimens belonged to a younger stage of development than that usually found. Thus, in R. 114 (Fig. 2), where, having regard to plane of section, the plinth is only half the usual height, the testa is immature and shows progressive sclerization. Again, in R. 122 (Fig. 3), a very immature specimen as judged by the testa, no trace of the plinth is visible, though were the specimen a normal one this region should fall within the plane of section. In view of these data and of the well-ascertained fact that the plinth is undeveloped in the small-sized seeds of *Lagenostoma Lomaxii*,[1] there is good reason for supposing the plinth to have arisen as an intercalation at a relatively late stage in development. This extension of the nucellus just below the lagenostome must of course have been accompanied by a corresponding elongation of the free part of the testa, for, as we have seen, the relations between plinth and integumental lining were of the closest.

The cavity of the plinth now claims attention. It was a hemispherical chamber of variable height, as we have seen, extending from the tapetal septum, which formed its floor, up to the lagenostome. Its maximum height all over was 0·5 mm.; centre of floor to base of lagenostome, 0·3 mm. Its contents, which only partly filled it, included (1) remnants of the soft interior tissues of the plinth, (2) pollen-grains. So far as information is afforded by our preparations, pollen when present in the seed was invariably contained in the plinth cavity, not in the lagenostome.

The soft interior tissue of the plinth is mainly preserved in the form of a horizontal, circular cushion which in section has the form of a concavo-convex lens, the convex side being uppermost. This cushion or lens, which

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[1] Oliver and Scott: On *Lagenostoma Lomaxii*. Phil. Trans., B, vol. cxcvii, p. 212, Pl. IV, Figs. 1 and 2.

was preserved in the form of a delicate tissue, is not as a rule high enough to fill the space between the tapetal septum below and the base of the lagenostome above.

As regards the position occupied by the lens we find two extreme states. (*a*) In some cases the lens is found attached by its convex upper surface to the under side of the saucer in which the lagenostome rested (specimen R. 110, Pl. II, Fig. 14, *ls.*), whilst its periphery hangs down into the plinth cavity—its edge being continued as a mere membrane which, often interrupted, can be traced obliquely downwards in the direction of the angle between the floor and sides of the plinth cavity, where it loses itself in the other tissues of the nucellus. Sometimes this membrane runs into the plinth wall just above the angle, sometimes it descends more steeply and strikes the floor just within the edge.

In addition to the lens, traces of plinth tissue are also found resting on the centre of the floor vertically below the lagenostome in the form of a hemispherical pad (R. 110, Pl. II, Fig. 14, *pd.*, and R. 111, Pl. I, Fig. 10, *pd.*), the constituent cells of which usually show very poor preservation. The relation of this pad to the lens above suggests that it has been derived and separated from the middle concave part of the lens as a result of an increase in the height of the plinth cavity, with which extension the tissue which doubtless originally filled it has not kept pace (Text-fig. 7, C).

(*b*) An example of the other extreme state is afforded by specimen R. 117 (Pl. II, Fig. 16), in which the whole of the plinth tissue (*pl.t.*) is found resting on the level floor of the plinth cavity. In this preparation what appear to be the same two portions of tissue are recognizable, viz. the lens tissue (*pl.t.*, Fig. 15) with good preservation of its cells, and the central projecting boss or pad (*pd.*) around which the former has collapsed.

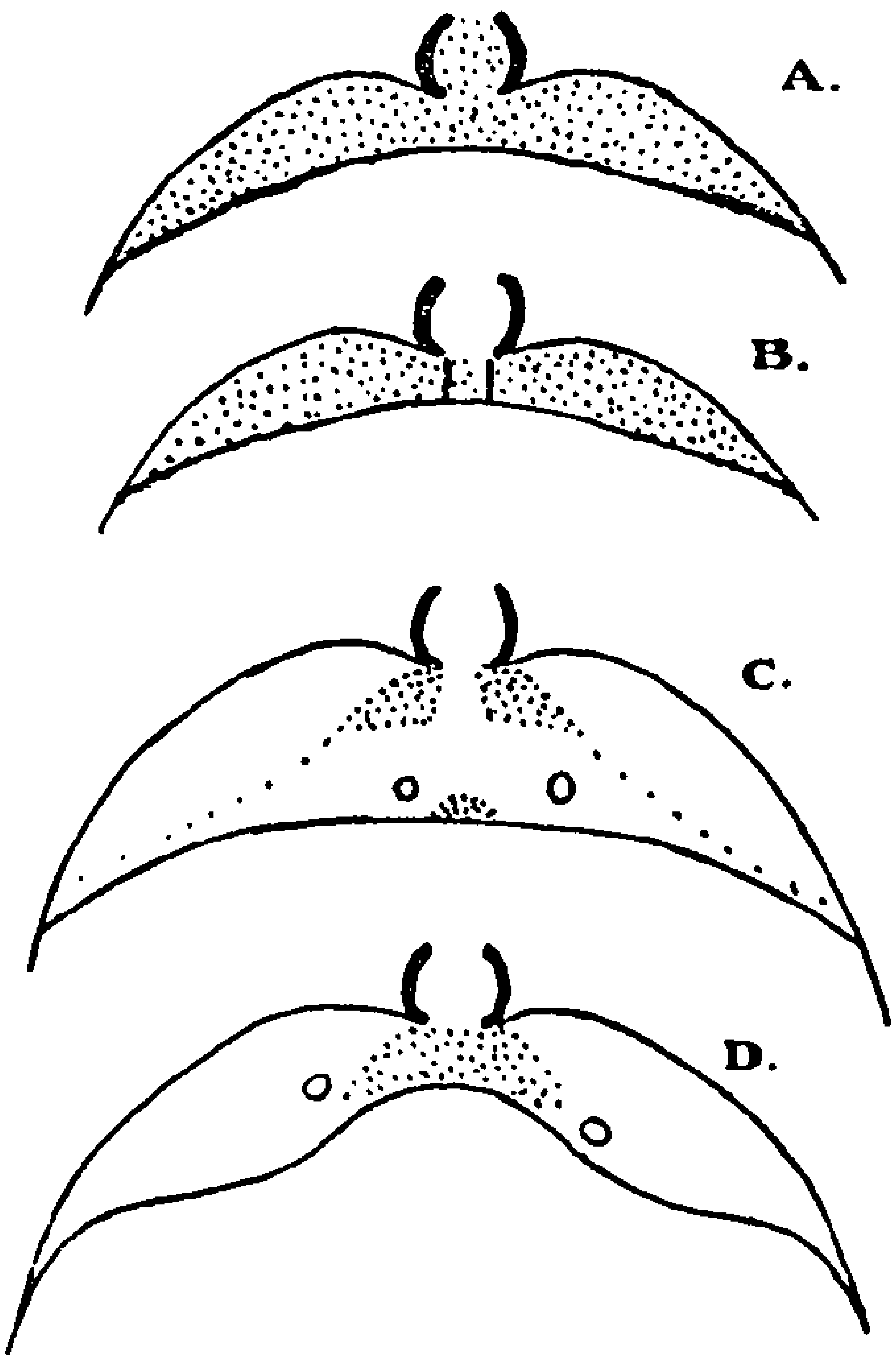
These two states are connected by intermediate conditions. Whilst in state (*a*) the convex summit of the lens is in position and still adheres to the base of the lagenostome, specimen R. 111 (Pl. I, Fig. 7, *ls.*) shows some slight separation which is a good deal more evident in specimen R. 116 (Pl. I, Fig. 6, *ls.*).

In addition to these cases, which include the majority of specimens, there are still others in which the parts seem to approximate to their original positions (R. 119 and 123, Pl. I, Fig. 11, and Pl. II, Fig. 19). It should be mentioned perhaps that in these two specimens evident traces of a prothallus are present in the megaspore chamber (Figs. 11 and 19, *pr.*), so that it may be conjectured that the stages in question are relatively old ones, whilst the presence of a pollen-grain in the closed plinth cavity of R. 123 (Fig. 19, *p.g.*) is a remarkable fact which requires explanation.

With a view to elucidating the significance of the various states of tissue distribution in the plinth cavity we shall now consider whether and how far it is possible to reconcile them with the probable course of events in the history of ovular maturation.

At an earlier stage of development than any represented by our preparations, the tip of the nucellus must have been occupied by a soft internal tissue which filled both lagenostome and plinth, the tissue in question being continuous from the one to the other through the narrow orifice by which these structures communicated (Text-fig. 7, A). As the time of pollination drew near the tissue of the lagenostome doubtless underwent solution through the agency of appropriate enzymes spontaneously secreted. At this time the floor or septum which lay between the plinth and the megaspore cavity must have been arched right up so that it was separated from the base of the lagenostome by the thickness of the lens-shaped cushion of tissue which we find surviving in later stages. Peripherally this tissue must have extended considerably further than does its surviving remnant in any of our specimens, and in particular it must have occupied the curving sides or 'shoulders' of the plinth. Text-fig. 7, A, may perhaps serve as a reconstruction of this early stage.

As the solution of the core of the lagenostome advanced the enzyme-action would traverse the base and involve the tissues of the plinth (Text-fig. 7, B).



Text-fig. 7. Diagrams of series of developmental stages (in part hypothetical) of plinth and lagenostome in a *Conostoma*, showing arrangements for entry of pollen into the plinth chamber. The dotted areas represent soft filling tissue. A, young stage; B, cavity of lagenostome cleared of tissue and central patch of plinth tissue ready to separate as the plinth elongates (C); in D the prothallus has encroached on the plinth by means of a 'tent-pole' extension. Pollen present in C and D.

To account for the next stage one of two assumptions has to be made: either the tapetal membrane (floor of plinth) tended to contract, or else—and we think this the more probable—the summit of the nucellus (including the lagenostome) continued to rise in consequence of a late extension localized in the plinth, whilst the tapetal septum remained stationary or at any rate lagged behind in its growth. Only in one of these two ways does it seem possible to explain the separation of the small central pad which rests on the tapetal septum from the lens suspended above (Text-fig. 7, C).

The state of tension in the plinth tissue, depicted above, would become effective as the enzyme-action, which had already dissolved the core of the lagenostome, advanced basipetally and involved the tissues of the plinth. For the effect of the enzyme would be to soften the central tissue of the cushion or lens (Text-fig. 7 B), thus removing serious resistance to the vertical extension of the plinth cavity. In this way a central pad, adhering to the floor, would be likely to separate from the cushion, which in its turn would remain hanging to the base of the lagenostome. The separation of the flanks of the cushion from the shoulders of the plinth may well have been effected at the same time, whilst in occasional examples (like R. 117, Pl. II, Fig. 16) the whole of the tissue of the cushion may have been liberated from the top of the plinth.

It is of course possible that only the peripheral layers of the core of the lagenostome were softened (and not the whole dissolved), so that when the enzyme-action had reached the base the whole of the central mass of tissue became separated from the lagenostome to form the pad on the floor. This would perhaps account for the unusually large dimensions of the pad in R. 117 (Fig. 15, *pd.*). For a decision on this point, which is not very material, the needful data are wanting. As to this, however, we are satisfied: that a hole was drilled which established communication between the cavities of the lagenostome and plinth, and that the pollen descended through this orifice into the plinth chamber.

The second stage in the development of the mechanism is reconstructed in Text-fig. 7, C.

Our third stage is represented by specimens R. 119 and R. 123 (Figs. 11 and 19), in both of which—unlike any of the others—a prothallus is present. In both we find the lens in contact with the lagenostome above, whilst its lower surface rests on the arched floor. Moreover, in R. 123 a pollen-grain is present in the plinth cavity, whilst one of the bodies in a similar position in R. 119 may possibly be of the same nature, though the preservation is not good enough to say definitely. The problem we are trying to solve is the presence of the grain in this position with the other parts apparently blocking the way (Fig. 19).

Our conclusion as to the course of the pollen has already been stated; it made its way through a temporary orifice.

As the seed continued its development the prothallus made its appearance and a 'tent-pole' prothallial apex pressed on the septum from below, restoring the relations as we see them in specimen R. 123 (Fig. 19). The presence of a 'tent-pole' is indicated in both specimens—especially striking is it in R. 119 (Fig. 11, *t.p.*), where the somewhat oblique plane of section has cut the prothallus twice, once at the projecting shoulder and again at the tip. Williamson's figure[1] appears to represent a seed in the same phase as

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[1] Williamson: loc. cit., Pl. XII, Fig. 86.

these two specimens, but we cannot speak critically as the preparation has not passed through our hands.

It still remains to be shown that warrant exists for the assumption that the wall of the plinth underwent a long-continued or intercalary extension which would provide the necessary machinery for 'uncorking' the basal orifice of the lagenostome, and thus letting the pollen through. We have already had occasion to comment on the structure of specimen R. 114 (p. 12), which has all the appearance of being a young seed. It was shown that in this case the plinth had only reached one-half the normal height, so that evidently the main extension of this organ must have been effected at a late period in development.

Again, in the related seed *Lagenostoma Lomaxii*, the plinth was the last part of the seed to develop, as we know from the fact that it had not yet appeared in the small-sized seeds, although the pollen-chamber was already of full size and properly developed (cf. Text-fig. 12, p. 39).[1]

The pollen is not sufficiently well preserved to justify detailed description; suffice it to say that it was multicellular, ellipsoidal in form, and measured $75\,\mu \times 65\,\mu$.

## III. CONOSTOMA ANGLO-GERMANICUM, sp. nov.

### 1. *Enumeration of Specimens.*

In the spring of 1904 an isolated section passing obliquely through an eight-ribbed seed was obtained from the Shore locality. This specimen remained of doubtful affinity until 1909, when Dr. Kidston put at our disposal a series of four transverse sections from a coal-ball obtained many years before at Langendreer in Westphalia. These emphasized the previous suspicions that the seed was nearly allied to *Conostoma oblongum*. The close relationship was put beyond doubt when, owing to the generosity of Dr. Jongmans, who placed his slides and uncut coal-balls at our disposal, details of the internal structure were obtained.

Owing to the general character of its external form and the almost identical internal structure, we have no hesitation in provisionally referring this seed to the genus *Conostoma*;[2] altogether some twenty sections of this fructification are now available, of which the greater number are from the German material of Dr. Jongmans. Having regard to this double source of origin of our sections we propose the specific name of *anglo-germanicum*. Up to the present time four sections of this seed have occurred from English material, of which one is the oblique section already referred to and the other three are more or less imperfect transverse sections, though of value as supplying our only information as to the histological structure of the testa.

In the following list the sections are enumerated, with their source of

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[1] Oliver and Scott: loc. cit., p. 212, and Pl. IV, Fig. 1.

[2] See footnote, p. 38.

origin and approximate plane. Those marked with an asterisk are figured in the plates.

| | | |
|---|---|---|
| U.C.L., R. 140 a*, b*, c, d* | Series of four transverse sections | Langendreer, Westphalia |
| J. 3* | Oblique through pollen-chamber | Rheinpreussen (nr. Duisburg) |
| J. 4 | Tangential | ,, ,, |
| J. 5 | Oblique transverse | ,, ,, |
| J. 6* | Oblique longitudinal | ,, ,, |
| J. 9* | Oblique through pollen-chamber | ,, ,, |
| J. 10 | Tangential | ,, ,, |
| J. 11 | Oblique through middle | ,, ,, |
| J. 12* | Longitudinal, passing through micropyle | ,, ,, |
| J. 13 | Oblique transverse | ,, ,, |
| J. 14 | Tangential | ,, ,, |
| J. 15 | Oblique transverse | ,, ,, |
| J. 16 | Oblique transverse | ,, ,, |
| U.C.L., Q. 18* | Oblique transverse near base | Shore, Littleborough, 1904 |
| U.C.L., R. 141 | Very imperfect transverse | Dulesgate |
| U.C.L., R. 142 a and b | Imperfect transverse | Shore, Littleborough, 1910 |

The specimens marked 'J.' are in the collection of Dr. J. W. Jongmans of Leiden. (The numbers of these specimens are provisional.)

The approximate plane of all the more important sections has been plotted on the longitudinal and transverse diagrams in Text-fig. 8.

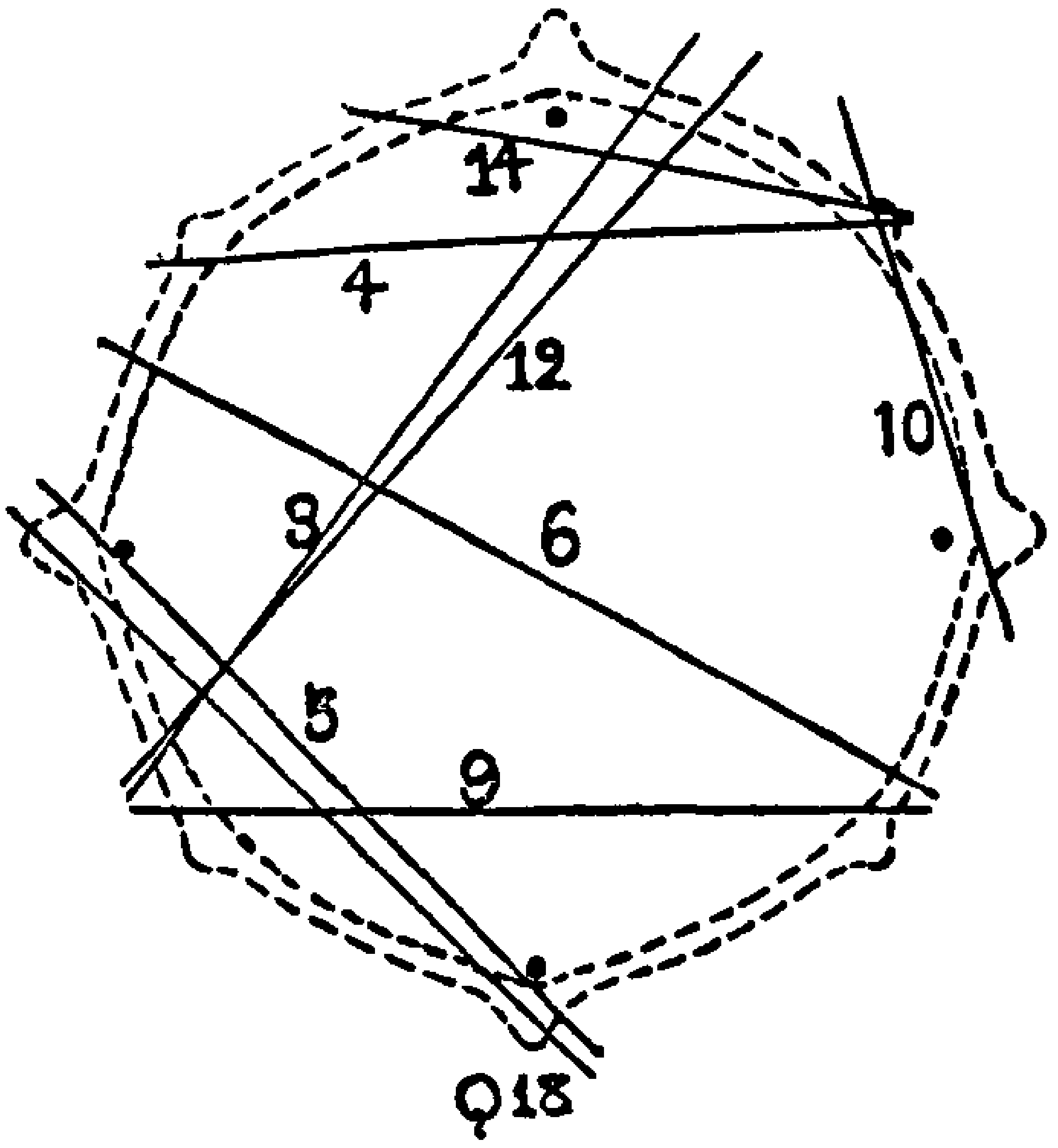
### 2. *General Features.*

In the fundamental characters both of external form and internal organization the present species agrees closely with *Conostoma oblongum*. Like that species it was a straight, angled seed, roughly bullet-shaped, with a tapering apex and gradual insertion.

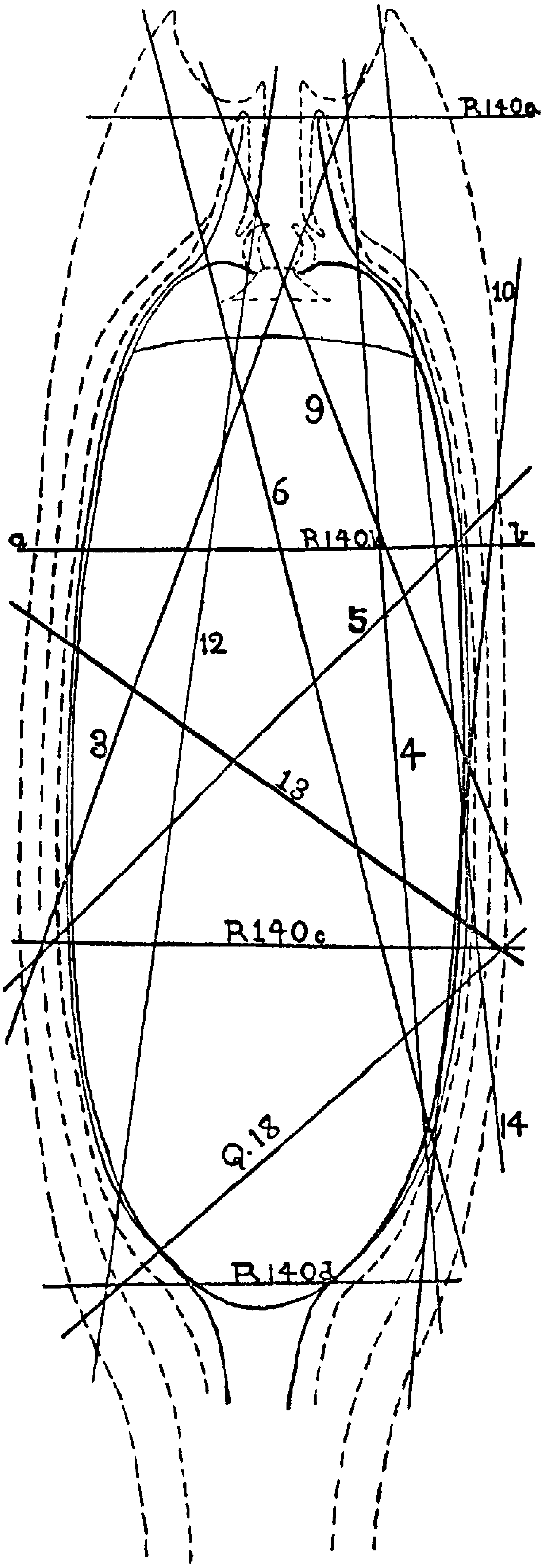
Internally there was an extensive plinth which had a comparatively small globular lagenostome at its apex. But whilst in essentials it was an undoubted *Conostoma* it possessed a very characteristic individuality of its own.

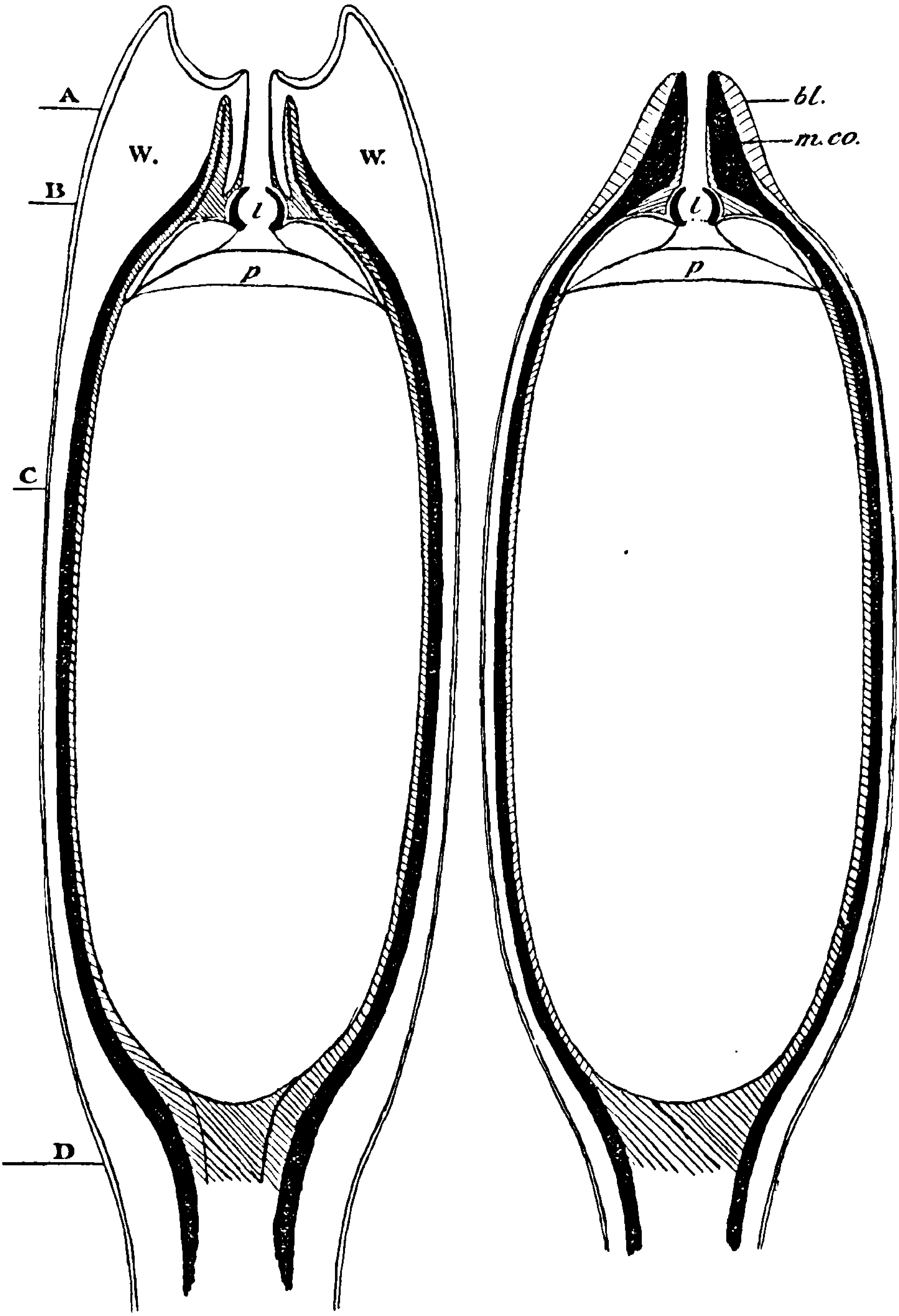
Superficially, the most striking feature was its extreme length as compared with its width; this latter was the same as in the other species, but it attained a maximum length of 7 mm. The main body of the seed was eight-angled, the angles bearing externally ribs which were alternately large and small; the former in the middle region being twice as prominent as the latter (0·11 mm. and 0·05 mm.).

The base of the seed tapered gradually to a thick stalk bearing eight wings, the lower extensions of the ribs. At the summit the surface curved inwards almost abruptly, terminating in a short conical apex pierced by the micropyle (Text-fig. 9). At the base of this tube the smaller ribs die out, but the four larger persist as wing-like expansions around the micropylar region, beyond the orifice of which outer margins are produced as free points. At the apex of the seed was an almost hemispherical depression about 0·4 mm. deep, bounded by the internal edges of the wings (Text-



TEXT-FIG. 8. *Conostoma anglo-germanicum.* Plottings of the plane of section of all the more important preparations in respect to the vertical and horizontal planes. R and Q. = Univ. Coll. Collection. J. = Dr. Jongmans' Collection. The horizontal plane is at the height *a-b* on the right-hand figure.

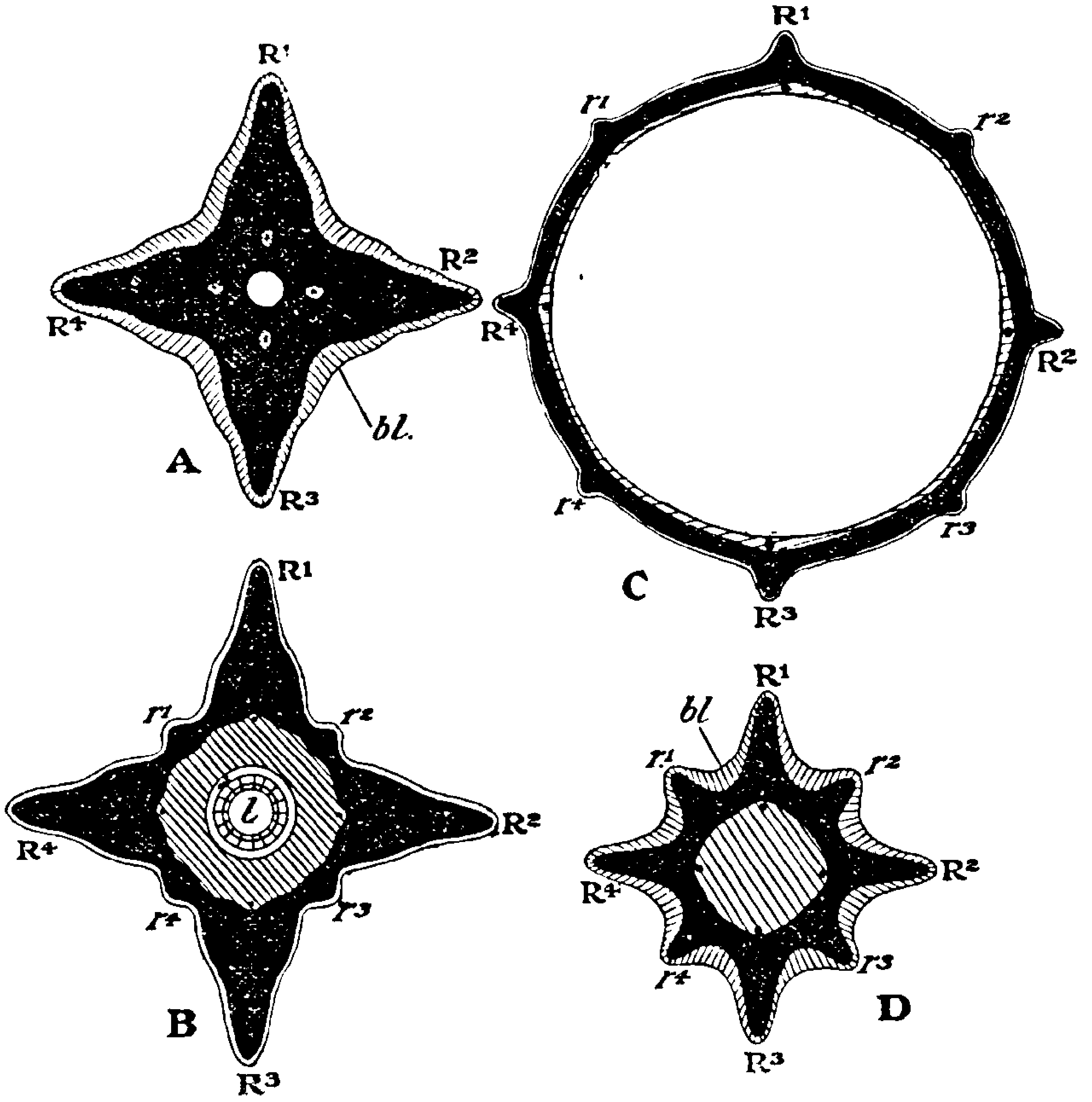




TEXT-FIG. 9. Restorations of *Conostoma anglo-germanicum* passing longitudinally through an opposing pair of major and minor ribs, respectively. The vascular bundle and nucellar wall are represented by a single line. The hard testa and lagenostome are in black, ribs and 'blow-off' white, and parenchymatous tissue shaded. *bl.*, 'blow-off'; *m.co.*, micropylar cone; *l.*, lagenostome; *p.*, plinth; W, W., wings formed by major ribs. × about 25.

fig. 9, W.), and into this depression the summit of the micropylar cone slightly projected (0·01 mm.). The main cavity of the seed was nearly cylindrical, rounded at either end, and passing by a funnel-shaped portion into the tubular micropyle above.

The megaspore cavity was about 4·6 mm. long and 2 mm. wide, surmounted, as in *C. oblongum*, by a dome-shaped plinth which bore the characteristic lagenostome in a slight depression at its apex. Compared with the internal structure of *C. oblongum*, the nucellus was narrower and much longer, whilst the plinth cavity remained of about the same depth, though slightly less extensive in width. The plinth contents appear to have been as in *Conostoma oblongum*.



TEXT-FIG. 10. *Conostoma anglo-germanicum.* Series of transverse sections at the levels marked A, B, C, and D in the vertical reconstructions (Text-fig. 9). The 'blow-off' layer is left white except in A and D. The testa is black and the parenchymatous tissue shaded. $R^1$, $R^2$, $R^3$, $R^4$, major ribs; $r^1$, $r^2$, $r^3$, $r^4$, minor ribs; *bl.*, 'blow-off'; *l.*, lagenostome. × about 25.

The lagenostome was slightly higher and broader than in the other species, perhaps referable to the larger size of the pollen-grains in *Conostoma anglo-germanicum*. From the base of the plinth downwards, the nucellus and integument were joined, and between these two ran the four vascular strands which corresponded in position to the larger ribs.

The lobes of the canopy internally have almost entirely disappeared, and only four tapering loculi remain, no doubt filled with soft tissue into which the vascular strands passed. The general appearance of the seed may be gathered from Text-figs. 9 and 10, which give restorations in longitudinal and transverse section respectively.

### 3. *The Testa.*

Although *Conostoma anglo-germanicum* resembled *C. oblongum* in the general features of its testa, yet the angling of the body of the seed, in the latter species obscure, was in the former marked by prominent external ribs, to the number of eight, symmetrically placed around the seed, which interiorly in this region formed a much rounded octagon (Pl. III, Fig. 22). In the middle region, for about half the total length, the sides were nearly parallel, tapering gently below to a thick stalk; whilst above, the surface curved rapidly inwards till the diameter diminished to about a third its maximum, and thence tapered abruptly upwards so as to form a conical tube 0·65 mm. high around the micropyle (Pl. III, Fig. 26, *m. co.*, and Text-fig. 9). The eight ribs traversed the whole body of the seed and formed prominent winged expansions to the stalk (Pl. III, Fig. 21, *R* and *r*, and Text-fig. 10, $R^1 R^2 \ldots, r^1 r^2 \ldots$). The ribs exhibit an interesting differentiation of the alternating members; four were large, and projected in the middle region about 125 μ from the surface, and may be termed the major ribs (Pl. III, Fig. 22, *R.*); the alternating members, which were only about half as prominent, we may term the minor ribs (Pl. III, Fig. 22, $r^1$, &c.). The relative thinness of the testa between the ribs, which only attains a thickness of 0·11 mm., coupled with the very marked prominence of the ribs, suggests that this latter feature may be of the nature of a mechanical adaptation. The differentiation becomes most marked at the apex; here the minor ribs, which remain of nearly uniform width, follow the outline of the seed, but die out suddenly where the curvature of the surface alters as it passes into the micropylar cone (Text-fig. 9, *m. co.*); the four major ribs continue their former gentle curvature above the shoulders of the seed, so that around the micropylar cone they become extensive wing-like expansions. A section cut at this level has the form of a four-rayed star, with the centre occupied by the micropyle (Pl. III, Fig. 23). Beyond the orifice of the latter the free pointed ends of the ribs projected, and their internal margins bounded the cup-like hollow in which the micropyle stood (Pl. III, Fig. 24, $R^1$. *e.* and $R^3$. *e*).

A median longitudinal section passing through two opposed major ribs appears concavely mucronate (Pl. III, Fig. 26), and somewhat resembles a similar section through the apex of *Stephanospermum*, where perhaps the cup-like expansion might be regarded as a lateral fusion of a number of such major ribs, of which, however, the individuality has been completely lost.[1]

In detail the hard testa was, as in *C. oblongum*, composed of two kinds of elements, viz. an external palisade and an internal fibrous layer; these together attained a width in the middle region of about 0·11 mm. (palisade 75 $\mu$ and fibrous 38 $\mu$).

The inner soft portion of the integument is, as in the other species, only represented by a micropylar membrane continuous with the plinth jacket, and was fused with the nucellus from the base of the plinth downwards; the sinus between the plinth and integument is very clearly seen in J. 3 (Pl. III, Fig. 29, *s.*), which forms a close parallel to R. 110 (Pl. II, Fig. 14).

### 4. *The Vascular System.*

The vascular supply further emphasized the differentiation which existed between the major and the minor ribs. There were four vascular strands, and these occupied the internal angles corresponding to the major ribs (Pl. III, Fig. 27, *v.b.*)—were embedded in the soft tissue between the hard testa and the nucellus. The lowest transverse section (Pl. III, Fig. 21, *v.b.*), which passes through the base of the megaspore cavity, still shows four vascular bundles cut across nearly transversely; so that if they united it was presumably some way down into the stalk. Above, the bundles entered the testa at the base of the micropylar cone and passed into the tapering loculi of the canopy, which reached to just below the apex (Pl. III, Fig. 29, *loc.*); these were no doubt filled, as in the other species, with parenchymatous tissue. We see then that the testa here has reached a much more advanced stage than in *C. oblongum*; the progressive fusion of the unit portions of the canopy has gone further, and, corresponding to the disappearance of the alternate bundles, their loculi have become completely obliterated (Pl. III, Fig. 23, also Text-fig. 10).

This differentiation of alternate members in a whorl, of which *Conostoma anglo-germanicum* is so striking an example, finds a close parallel amongst modern plants in the ribbed seeds of certain Umbelliferae, where, too, we find primary and secondary ridges with vascular bundles situated below alternate members.

There is no evidence for the existence of any soft apical tissue in this seed, but the 'blow-off' layer which extended over the whole seed attained very considerable dimensions between the major ribs at the apex (Pl. III, Figs. 23 and 29, *bl.*); and radial sections through the minor ribs show the cells of this layer with a dimension of as much as 0·19 mm.; it attained, however, its greatest development between the wings at the base (Pl. III, Fig. 21, *bl.*), thus contrasting with the other species in which this layer found its minimal development in this region.

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[1] F. W. Oliver: On *Stephanospermum*. Trans. Linn. Soc., 2nd ser., Botany, vol. vi, Pl. XLIV.

The fact that the 'blow-off', in all the sections where preserved, is still *in situ*, seems to point to its either having functioned differently or to the specimens in each case being immature; the presence of pollen in at least one of these preparations seems to render the former alternative the more probable.

Owing to the greater complexity of its outline, especially at the apex, this seed presents very varied appearances when cut in different planes of obliquity; this point is sufficiently well illustrated by specimen J. 6 (Pl. III, Fig. 31), which cuts the seed obliquely, entering near the apex of a major rib and passing out at the base above the insertion of the stalk. The major rib on the left ($R^1$) and the minor rib on the right at the apex ($r^2$) are both exaggerated by the obliquity; but owing to the curvature of the proximal end of the seed this does not apply to the corresponding ribs at the base, which are cut nearly transversely. The upper lateral ribs ($r^1$, $R^2$) are followed for some way, and consequently appear as obtuse angled appendages of the testa, whilst the lower lateral ribs ($r^3$, $r^4$) are rendered cuspidate. The major ribs are respectively $R^1$, $R^2$, $R^3$, $R^4$, and the minor ribs $r^1$, $r^2$, $r^3$, $r^4$.

## 5. *The Nucellus.*

The structure of the nucellus of *Conostoma anglo-germanicum* closely resembled that of *Conostoma oblongum* in all essential points. The dimensions of the various parts differed as between the two seeds, the most notable divergence being in the height of the nucellus, which reached to 5 mm., as compared with 3·7 mm. in *Conostoma oblongum*. As in that seed, the lagenostome rests in a depression of the plinth (specimens J. 3 and 9, Pl. III, Figs. 28 and 30, *lg.*), whilst the plinth itself is characterized by the same peculiar features that have been so fully described in the case of *Conostoma oblongum*. As we find the preservation of *Conostoma anglo-germanicum* to be generally inferior to that of *Conostoma oblongum*, we shall restrict our detailed account of the former to the material points.

## 6. *The Lagenostome.*

The lagenostome resembled that of *Conostoma oblongum* in form, though its dimensions are slightly larger. Its height is 0·19 mm., and the breadth 0·26 mm., as compared with 0·15 mm. x 0·23 mm. in the allied seed. The cells of the wall appear somewhat more robust than in *C. oblongum* and, as in that seed, the cavity of the lagenostome is destitute of contents. Here also the appearance of a two-layered wall is suggested locally as in specimen J. 9, on the right-hand side low down (Pl. III, Fig. 25, *lg.*); the explanation is doubtless the same as in *C. oblongum* (see p. 18) and depends upon the sectioning of a curved surface combined with post-mortem change. The state of preservation is as a rule inadequate to show the nature of the cell-walls; however, as at least one cell of the lagenostome bears distinct traces of sculpturing, it may be regarded as probable that in this respect also our seed was in agreement with *Conostoma oblongum*.

### 7. *The Plinth.*

The wall of the plinth survived as a carbonized crust, much as we find it in the poorer specimens of *Conostoma oblongum*. At its summit a similar depression was present, corresponding with the insertion of the lagenostome (Figs. 25, 29, and 30). The close relations already noted in the case of *Conostoma oblongum* between the plinth and lagenostome on the one hand, and the plinth jacket and micropylar funnel on the other, repeat themselves here in all essentials, even including the well-marked sinus just above the region at which nucellus and integument were confluent (cf. Pl. II, Fig. 14, and Pl. III, Fig. 29, *s.*).

The contents of the plinth are represented by the same structures as in *Conostoma oblongum*. From the base of the lagenostome the 'lens' hung suspended (Pl. III, Fig. 29, *ls.*), and below it in the same figure is found the pad of tissue which adhered to the tapetal septum (*pd.*). In specimen J. 9 the 'lens' is slightly displaced, but its primitive position is still indicated by a connecting shred of membrane (Fig. 25, *ls.*). Pollen-grains are present in the plinth cavity of specimens J. 9 and J. 12 (Figs. 25 and 24, *p.g.*). Their average dimensions are $85\,\mu \times 75\,\mu$—somewhat in excess of those for the companion species.

Very distinct traces of a tapetum enclosing the megaspore chamber are present (Fig. 31), but the character of the preservation hardly warrants detailed description. At the micropylar end the tapetum stretches across the nucellus as a septum, delimiting the base of the plinth (Fig. 30).

## IV. COMPARISON WITH RELATED TYPES.

### *Comparison with Gnetopsis elliptica.*

This famous seed was described and illustrated with some fullness by Renault in 1884 from specimens discovered in one of the Grand'Croix nodules.[1] Apart from the supposed relations with the Gnetales, *Gnetopsis* remained for many years a very isolated type until the reinvestigation of *Lagenostoma* revealed the existence of certain features which these two seeds appeared to have possessed in common.[2]

With *Conostoma oblongum* the points of agreement are numerous and striking, and demand some notice here.

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[1] Renault: Cours de Bot. fossile, vol. iv, p. 180, Pl. XX, XXI, XXII.

[2] Oliver and Scott: On *Lagenostoma Lomaxii*. Phil. Trans. B., vol. cxcvii, p. 233.

The lagenostome of *Gnetopsis* has essentially the same form and insertion as in *Conostoma*. It is a small goblet-shaped body resting in a depression of the plinth with which its cavity became continuous.[1] The cells of its wall constitute only a single layer, so far as we can judge from the specimens, but they show evident traces of sculpturing like that of *Conostoma*, though less well preserved.

Our examination of Renault's original type specimens shows that the presence of papillae around the mouth of the pollen-chamber in the preparations B. 230, C. 2 and 11 ('languettes disposées en couronne') is to be interpreted as the result of partial resolution of the wall cells of the lagenostome by means of fissures corresponding in position with some of the vertical lines which, as in *Conostoma*, separated the adjacent rows of sculptured cells. The resulting lobes or finger-like packets, which included as a rule two or three vertical series of these cells, remained attached below to the summit of the plinth.[2]

The dimensions of the lagenostome in the three seeds are as follows:—

| | *Gnetopsis.* | *C. oblongum.* | *C. anglo-germanicum.* |
|---|---|---|---|
| Maximum width | 210 μ | 230 μ | 260 μ |
| Width of basal orifice | 115 μ | 180 μ | 190 μ |
| Height | 145 μ | 150 μ | 190 μ |

The agreement with *Conostoma* is complete when the nature of the lobing in *Gnetopsis* is apprehended.

*The Plinth.* The broad low cavity between the prothallial chamber and the lagenostome corresponds with the plinth of *Conostoma*. It was naturally termed the 'pollen-chamber' by Renault as it is here that the pollen is usually found.[3] The central portion of its cavity is occupied by a plug of tissue which rests on the floor, much as in our *C. oblongum*, specimen R. 117 (Pl. II, Fig. 16). Occasionally in *Gnetopsis* (B. 230, C. 12) this somewhat robust lump of tissue is produced towards the lagenostome into an upwardly directed, more delicate continuation. It is hardly possible to say whether the latter alone represents the displaced central core of the lagenostome whilst the lump below is the residual tissue of the plinth, or whether both may not have been derived from the lagenostome—a difficulty also found in the interpretation of our R. 117 (cf. p. 22).

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[1] Renault: loc. cit., Pl. XXII, Fig. 4.

[2] In Renault's preparations the lagenostome occurs under two types of preservation, i. e. the fingered or papillose type (which we interpret as macerated) represented in Cours de Bot. foss., vol. iv, Pl. XX, Fig. 3, and Pl. XXI, Fig. 3, *e*, and the intact type represented on his Pl. XXII, Fig. 4, *l*¹. The information, for which we are indebted to Prof. Bertrand, that the intact type (which differs slightly in other respects) was probably derived from a source other than Grand'Croix (which provided the main series of specimens) explains the differences referred to.

[3] In all the specimens of seeds of the *Conostoma* group that have passed through our hands we have only detected a single pollen-grain in the lagenostome, viz. in *Gnetopsis*, the specimen being the one figured by Renault on his Pl. XXI, Fig. 4.

The pollen-grains found in the plinth have 80 μ × 65 μ as average dimensions, as compared with 75 μ × 65 μ in *C. oblongum,* and 85 μ × 75 μ in *C. anglo-germanicum.*

*The Integument.* The micropylar tube, funnel, and plinth jacket present in specimens B. 230, C. 2 and 6,[1] were doubtless integumental in origin. The tube reached a considerable length and was named the 'entonnoir' by Renault; in specimen B. 230, C. 6,[2] it contained grains of pollen fossilized *en route* to the lagenostome and plinth cavity.

A conspicuous feature of the integument, especially towards the apex of the seed, was the presence of 'un tissu lacuneux formé de grandes cellules disposées en lames parallèles'.[3] This tissue, conjectured by Renault to function as a float giving buoyancy to the seeds in water, resembles in the closest way the 'blow-off' tissue found in *Conostoma,* and we see no reason to doubt their essential identity.[4]

A great peculiarity of the seeds of *Gnetopsis* was the tuft of apical plumes inserted around the micropyle. Of these structures no trace is shown by *Conostoma,* so that unless they were caducous in the latter, their absence must be regarded as an important point of distinction between the two seeds. In view of the slight flattening detected in the body of *Conostoma oblongum* it is of interest to note that in *Gnetopsis* the symmetry was likewise modified in the direction of platyspermy;[5] whilst in *C. oblongum,* however, the whole of the six vascular bundles are accounted for, in *Gnetopsis* there are only four, those corresponding with the positions we suppose to represent the two major angles being absent. *Gnetopsis* thus appears to combine in itself the peculiarities of both our seeds, in showing the flattening of *C. oblongum,* with the disappearance of some of the bundles as in *C. anglo-germanicum.*

Another point in which *Gnetopsis* perhaps differed from our seeds was in the relatively slight development of a 'tent-pole'. As practically every specimen of *Gnetopsis* contained a prothallus these seeds should be of the right age, as judged by *Conostoma,* to show the 'tent-pole' had it reached any degree of prominence.

Turning to the cupule which formed the common enclosure of from two to four seeds in *Gnetopsis,* we have, as yet, no parallel in *Conostoma,* where the seeds are only known as detached objects.[6]

Having regard then to the various points cited, viz. the lagenostome, plinth, micropyle and plinth jacket, 'blow-off,' symmetry and distribution of vascular strands, we think the case for the close association of *Gnetopsis* with, or even its inclusion in, the Conostoma group a very strong one.

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[1] Renault: loc. cit., Pl. XX, Figs. 2, 3, 4.

[2] Renault: loc. cit., Pl. XXI, Fig. 3, *o.*

[3] Renault: loc. cit., Pl. XX, Figs. 2 and 3, *l.*

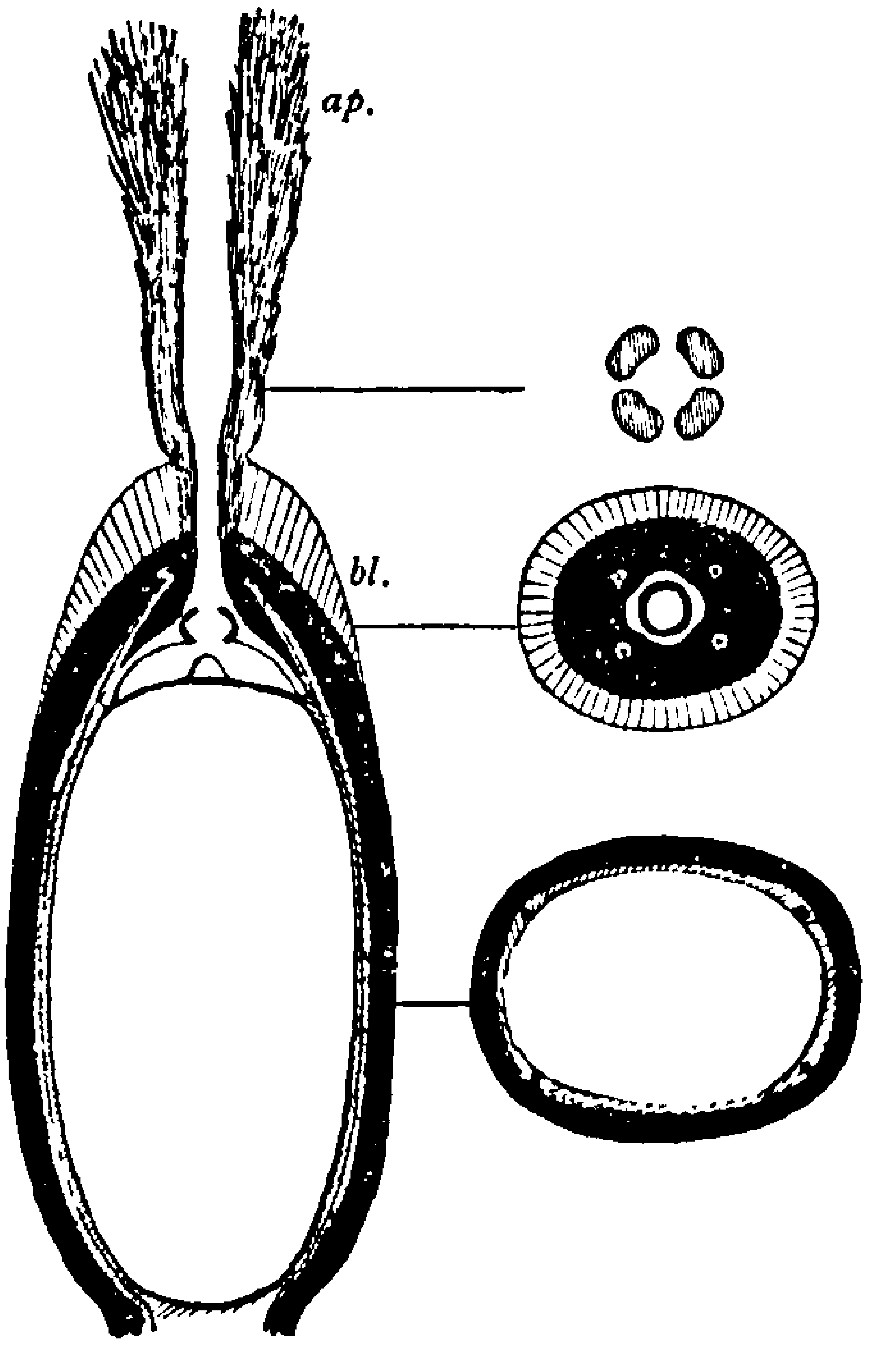
[4] Cf. our Pl. III, Fig. 29, and Renault, loc. cit., Pl. XXI, Fig. 3.

[5] Cf. our Text-fig. 11, p. 34, and Renault, loc. cit., Pl. XXI, Fig. 6.

[6] See however pp. 15 and 16.

The only important point in which *Gnetopsis* differs from our seeds is in the presence of plumes at the apex, for which there exists no evidence in *Conostoma*; a minor point is the very slight development of a 'tent-pole'. It is of course possible that even these points of difference may disappear as the seeds of the group become more fully understood.

Having regard to the occurrence of *Gnetopsis*, which reaches from the Middle Coal Measures up to the Stephanian at the top of the Carboniferous Formation, it is a matter of no little interest to find plants with the Conostoma type of seed mechanism persisting from the Lower Coal Measures right on to the close of the Carboniferous.



TEXT-FIG. 11. Longitudinal and transverse restorations of *Gnetopsis elliptica*, largely hypothetical. *ap.*, apical appendage. *bl.*, 'blow-off'.

This long persistence points to the fact that the small lagenostome and large pollen-grain formed a combination at least as perfect as any other of the contemporary seminal arrangements of which we have any knowledge.

Before leaving the subject of *Gnetopsis* it seems worthy of remark that the cupule of that seed presents an interesting point of agreement with that of *Lagenostoma Lomaxii*. After comparing the specimens, we are much struck with the close resemblance in structure between the long tubular hairs with which the cupular lining of *Gnetopsis* was so abundantly provided and those met with in considerable quantity on the cupule of an ovular stage of *Lagenostoma*, and more sparingly on the old effete cupules.[1]

The occurrence of similar hairs in analogous positions on the cupules of the two seeds, though in itself a trivial point, gains in importance when taken in connexion with the other features of organization which these seeds had in common.

Until a detailed knowledge of the structure of the apical region of the testa in *Gnetopsis* is forthcoming, any close comparison between this region and the multilocular canopies of the other seeds is out of the question. The

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[1] Oliver and Scott: On *Lagenostoma Lomaxii*. Phil. Trans., B., vol. cxcvii, Pl. X, Fig. 34, *h*, and Pl. VIII, Fig. 8.

presence, however, of a series of apical tufts at the micropyle is at least consistent with a lobed antecedent, and this equally whether these tufts consist of hairy prolongations of the actual ribs of the seed or whether, on the other hand, they are merely the expression of localized proliferations of the trichomes which may, however, have corresponded in position. In order to give precision to the remarks on *Gnetopsis* and to facilitate comparison with the other types, we have embodied our view of the structure of this seed in the convenient form of a text-figure (p. 34). The necessity for a detailed reconstruction happily does not arise, as we understand there is some prospect of *Gnetopsis* undergoing re-investigation at the hands of our friend Professor C. E. Bertrand, to whose good offices we are deeply beholden for the opportunity of consulting the specimens on the present occasion.

### 2. *Comparison with Physostoma.*

This seed belongs to an interesting generalized type in view of the prominence of the ribbing and the lobing of the testa. Moreover, the presence over the surface of the seed of large hairs probably containing mucilage affords a further variant of the mechanism which is illustrated by the 'blow-off' of *Conostoma* and the mucilage pegs of *Lagenostoma.*

The lagenostome of *Physostoma* with its all but sessile mouth forms a connecting link between those of *Lagenostoma* and *Conostoma* ; the former with its tubular prolongation reaching to the surface of the seed, the latter with a true micropylar tube, integumental in origin, which fitted to the rim of the cup-like lagenostome with marvellous nicety.

Within the seed the 'tent-pole' prolongation of the megaspore chamber projected into the floor of the lagenostome, thus outstripping all other known cases. On the other hand the plinth is practically undeveloped. These facts of structure taken in connexion with the large number of ribs and lobes appear to be consistent with the view that *Physostoma* preserves several of the more archaic traits of the unknown precursors from which the various types may be supposed to have sprung. Among the features which on this view would belong to these precursors must be included the lobed, unfused micropyle, the many ribs, the mucilage epidermis, the terminal, indurated, capacious lagenostome, and the 'tent-pole'. The extension of the plinth, on the other hand, is to be regarded as a later intercalation.

### 3. *Comparison with Lagenostoma.*

The features which unite *Lagenostoma* and *Physostoma* are too well known to need recapitulation here.[1] As compared with *Conostoma* the loculi of the canopy in *Lagenostoma* had a more extensive filling tissue and relatively thinner peripheral and radial layers of sclerized elements, the

[1] Oliver: On *Physostoma.* Ann. of Bot., vol. xxiii, p. 108.

filling tissue in the former being reduced to a mere parenchyma sheath accompanying the vascular strands into the loculi.

A peculiarity of *Conostoma oblongum* was the soft tissue at the apex of the integument, of which no indications have been detected in *Lagenostoma*.

In both genera the integumental units show a high degree of coalescence in the micropylar region, the degree of fusion being considerably greater however in *Lagenostoma* than *Conostoma*, which appears somewhat to approach the condition of *Lagenostoma* (*Physostoma*) *Kidstonii*, Arber.[1] This coalescence of integumental units may be regarded as yet another example of a generally diffused tendency, no doubt correlated with a simplifying of the mechanism of development, viz. the replacement of separate parts borne at the same height by a continuous structure.

The lagenostome of *Lagenostoma* reaches the exterior of the seed by a tubular prolongation, thus contrasting markedly with the etubular condition of *Conostoma*, where a functional micropyle is provided on the lines of most existing Gymnosperms. In view of this difference, it is not possible to regard the two types of seed as very closely related.

Other contrasting features include the nature of the wall sculpturings of the lagenostome—which are not reticulate in *Lagenostoma*; its relatively large size and the persistence of a central core of tissue—not yet detected in *Conostoma*.

The plinth, which was present in full-sized seeds of *Lagenostoma* but not in the small ones (Text-fig. 12), sloped up at a very gentle angle as compared with the corresponding part of *Conostoma*; its presence being correlated rather with a transverse than with a material longitudinal expansion of the nucellus. A 'tent-pole' does not appear to have been produced.

Thus it is plain that whilst both *Conostoma* and *Lagenostoma* have proceeded along similar lines in the coalescence of the integumental units, they show considerable divergence in the details of lagenostome structure, in the plinth, and in the arrangements for the reception of the pollen.

## V. CLASSIFICATION AND DIAGNOSES.

In the light of the previous discussion it is convenient to separate the various seeds that have been enumerated into three series or types, all of which possessed in common:—

(1) A nucellus and integument confluent up to the level of the plinth; (2) a free part of the integument consisting either of separate lobes, or of a more or less completely fused series of lobes forming what has been termed a 'canopy'; (3) a vascular system of strands running in the deeper parts of the integument and passing into the lobes or their representatives at the apex; (4) an epidermis to the testa which was mucilaginous, at any rate

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[1] E. A. N. Arber: On some New Species of *Lagenostoma*. Proc. Roy. Soc., B., vol. lxxvi.

locally; (5) a terminal, specialized, more or less pear-shaped receptacle for the pollen known as the lagenostome.

These three series of types, with provisional diagnoses, are as follows:—

### i. The Physostomeae.

Free parts of the ribbed integument consisting of separate segments surrounding and overlapping the large, globose lagenostome which opened by a small orifice inserted on the apex of a low papilla. Plinth rudimentary. The apex of the megaspore cavity projected into the floor of the lagenostome. Ribbing at base obsolete.

*Physostoma elegans*, Will.
*Physostoma Kidstonii*, Arber.

### ii. The Conostomeae.

Seeds ribbed or angled, tapering at apex: free part of integument consisting of more or less fused lobes. The lining of the integument formed the passage for the large pollen-grains and was thus a true functional micropyle leading down to the very small, included lagenostome, the wall of which consisted of cells with reticulated or scalariform sculpturings; base of lagenostome communicating with the extensive plinth cavity into which the pollen-grains penetrated. Integument with a mucilaginous epidermis extensively developed at the apex.

*Conostoma*, Williamson.

Cylindrical or slightly flattened seeds with tapering insertion. Ribbed throughout, or at base with angles passing into ribs. Lobing at apex variable; vascular bundles equalling or fewer than the ribs or angles; loculi of canopy nearly obliterated and equalling the vascular bundles in number; epidermis mucilaginous.

Lagenostome very small, included; cells of wall sculptured.

Plinth conspicuous, dome shaped, with internal tissue; well-marked 'tent-pole' and tapetum present.

1. *Conostoma oblongum*, Will.

Organization of the Fossil Plants of the Coal Measures, Pt. viii. Phil Trans., 1877, p. 243, Figs. 80, 80* (Pl. XI), 80* (Pl. XII), 81 and 86.

*Localities.* Oldham; Dulesgate; Shore, Littleborough; Halifax; Deighton, Yorks.

*Horizon.* Lower Coal Measures.

Seed six-angled, winged at base only; six vascular strands; apex ending in six soft, free lobes.

Dimensions: length 6 mm., broadest diameter 2·3 mm.

### 2. *Conostoma anglo-germanicum*, sp. nov.[1]

*Localities.* Shore, Littleborough; Dulesgate; Langendreer, Westphalia; Colliery Rheinpreussen, near Duisburg—Seam Finefrau, Nebenbank.

*Horizon.* Lower Coal Measures.

Seed eight-ribbed, the four major vascular more prominent than the four minor non-vascular, which fall short of apex.

Dimensions: length 7 mm., broadest diameter 2·3 mm.

*Gnetopsis elliptica*, Ren. and Zeill.

### iii. Lagenostomeae.

Free part of integument consisting of more or less completely united segments; very obscurely angled. Lagenostome with tube reaching surface of seed and persistent central cone of tissue; low plinth with gentle gradient; no 'tent-pole'.

*Lagenostoma ovoides*, Will.
*Lagenostoma Lomaxii*, Will. MS.
*Lagenostoma Sinclairii*, Arber, perhaps came here.

An outer envelope or lobed cupule has been described for *L. Lomaxii* and *L. Sinclairii.*

It is probable that Miss Benson's *Sphaerostoma ovale* (Will.) will have to be added as a fourth type to the three enumerated above. Its inclusion here would be premature as the seed is undergoing re-description.

With the exception of *Lagenostoma Lomaxii*, which has been definitely referred to *Lyginodendron Oldhamium*, the parentage of none of the seeds has been determined. In view, however, of the broad agreement in type which they all show, an ultimate reference of these seeds to plants of *Lyginodendron* affinity seems not improbable.

As a convenient collective name for the whole of the seed types or series just enumerated we would suggest, at any rate for provisional use, the name Lagenostomales.

## VI. THE POLLINATION MECHANISMS OF THE LAGENOSTOMALES.

The detailed study of the various seeds grouped under the Lagenostomales has led to the recognition of three distinct types of mechanism

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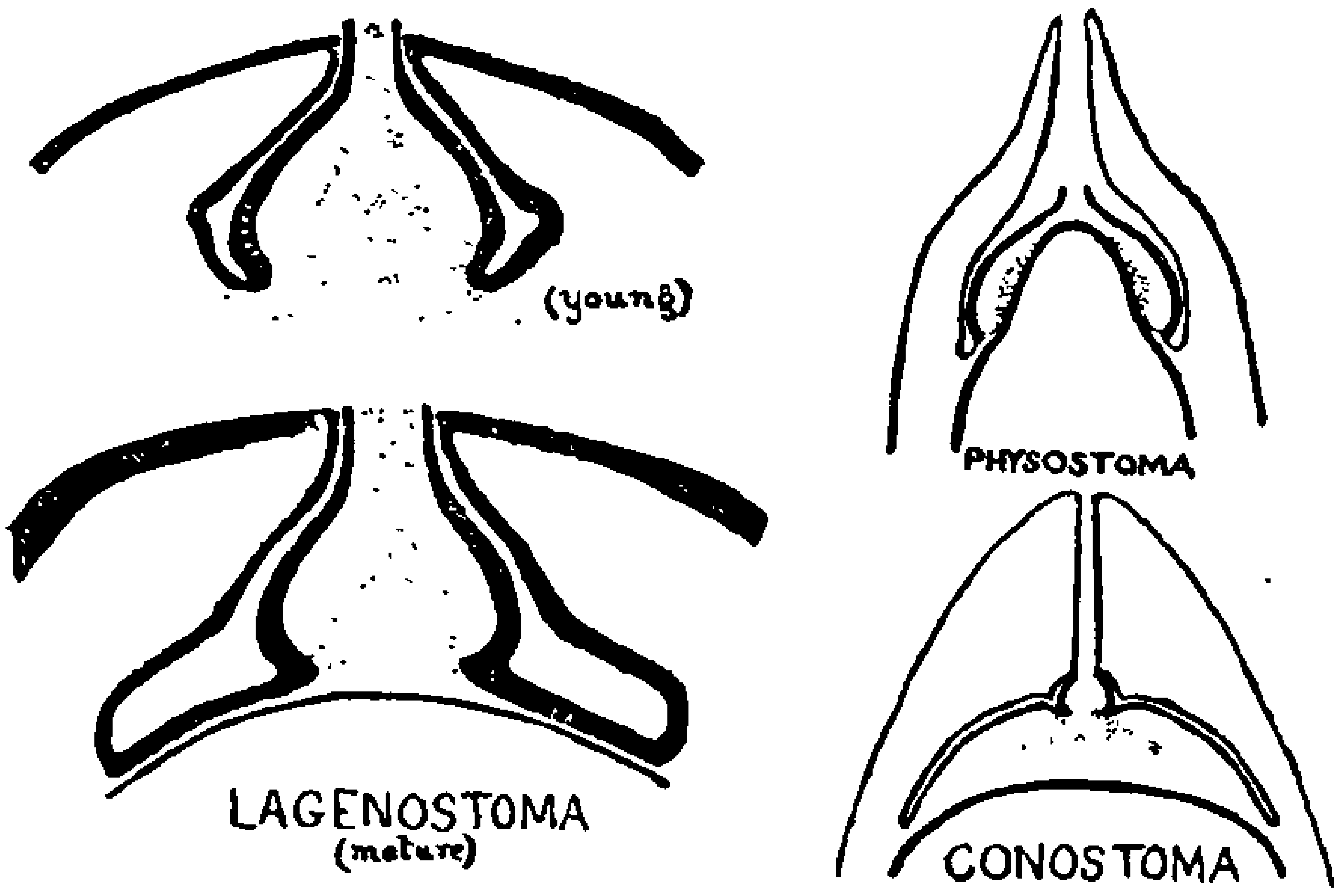
[1] The course followed here of including this seed as a second species of *Conostoma* perhaps demands a word of explanation. The peculiar character of the ribbing, with alternation of major and minor ribs, would go far to justify the creation of a new genus, particularly when regard is had to the relative importance of the testa as a diagnostic character in fossil seeds. Earlier workers in this field have repeatedly founded genera on equally trivial characters, e.g. Brongniart in his Graines silicifiées. Our motive in refraining for the present from raising *C. anglo-germanicum* to generic rank is to emphasize the fact of the essential identity of its internal organization with that of *C. oblongum*.

concerned in the reception and storage of pollen. Briefly stated, these mechanisms were as follows:—

1. The unjoined but approximated lobes of the integument surrounded and overtopped a relatively large lagenostome which bore an orifice seated on a low central papilla. At the time of pollination it is probable that these lobes collectively formed a tube or funnel narrowing towards the mouth of the lagenostome. If so, this type possessed a functional micropyle which played its part in the passage of the pollen (Text-fig. 12, *Physostoma*). This type may be termed a fimbriated micropyle.

2. A relatively massive canopy of united segments was perforated by a long micropyle which led down to a small, included lagenostome, the cavity of which became confluent with that of the plinth below by deliquescence of the filling tissues. The pollen-grains which traversed the micropyle and lagenostome were received into the plinth cavity, where they doubtless underwent maturation. This type is marked by a plinth of considerable vertical extension, an organ not conspicuously developed in type 1 (Text-fig. 12, *Conostoma*).



TEXT-FIG. 12. Diagrams to show the relations of lagenostome, plinth, and canopy in *Lagenostoma*, *Physostoma*, and *Conostoma*. The regions where soft-filling tissue occurs are dotted, i.e. the central cone of the lagenostome in *Lagenostoma*, a shallow cushion resting on the flanks of the intrusive apex of the megaspore chamber in *Physostoma*, and a lens-shaped cushion below the lagenostome in *Conostoma*. Two stages of *Lagenostoma* are shown.

3. The lobes of the integument were fused into a compact canopy which closely invested the conical lagenostome, the orifice of which reached to the outer surface of the seed. In this type the lagenostome must have been directly pollinated without the intervention of the micropyle. A plinth was present, but had only a trifling vertical extension (Text-fig. 12, *Lagenostoma*).

So far as efficiency in the collection of pollen-grains was concerned, each type appears to have been perfectly satisfactory. The presence of much pollen in the lagenostome of *Lagenostoma*, and especially in the species *L. ovoides*, has already been a matter of comment,[1] whilst in *Physostoma* no fewer than eighty grains have been counted in a single section that recently passed through our hands—a number that may safely be trebled to get an approximation to the full number. In *Conostoma*, with its long micropyle, tiny lagenostome, and plinth cavity, the evidence shows that an abundance of large pollen-grains found their way into the plinth cavity.

When regard is had to the relations of the parts in these three types, it seems evident that, assuming them to be derived from a common ancestral group, the reception of pollen was originally independent of the integument. If the free lobing of the integument of *Physostoma* is an archaic character, then in so far as these lobes collectively assisted at pollination this pristine method of pollen reception has been lost and an approach made to the entire micropyle as found in *Conostoma* and *Gnetopsis*.

In marked contrast with these types was *Lagenostoma*, where the lagenostome had kept pace with the investing members and, by means of its elongated neck, retained to itself the function of pollen reception. The persistence of this exserted type of lagenostome, a rare condition, may perhaps be regarded as a kind of conservatism which militated against the surrender to the investing structure of the receptive and conductive functions—a conservatism which finds further illustration in *Gnetum*, where the inner integument projects far beyond the envelopes exterior to itself.

This at any rate seems clear, the arrangements which prevailed in the Conostoma type, with its intercalated plinth, had as a result the carriage of the pollen deep into the heart of the seed. The double functions of reception and storage relinquished by the lagenostome were taken over by the micropyle and plinth cavity respectively, the lagenostome persisting as a sort of inner vestibule—a mere piece in an elaborate though doubtless very perfect mechanism. The very smallness of the lagenostome, whose diameter never exceeded 150 $\mu$ in the known representatives of this type—a dimension barely equalling the length of two pollen-grains as we know them in the plinth cavitity—fully accords with this vestigial phase upon which the lagenostome would appear to have entered.

Passing on to the seeds of other groups, we come first to members of the Medulloseae, of which *Trigonocarpus*, *Stephanospermum*, and a number of the French Permo-carboniferous seeds afford the best known examples. In these, so far as information is available, there existed a prominent nucellar beak which engaged with the base of the micropyle. The pollen was received by this tubular beak from the micropyle and passed into a deeper lying 'pollen-chamber' below, perhaps comparable to the plinth cavity of *Conostoma*. The flattened seeds usually referred to the Cordaiteae appear to be in substantial agreement, whilst the same remark holds good of the living genera of Cycads and of *Ginkgo*.

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[1] Oliver and Scott: loc. cit., p. 214.

In this connexion it is interesting to note that in *Stangeria* and *Ginkgo*, as figured respectively by Lang[1] and Hirasé,[2] the apical papilla of the nucellus which becomes perforated is limited by a prominent epidermis, as to which Lang remarks, 'The superficial cells of the pointed tip seen in Fig. 12 have their walls thickened and form a very definite boundary to the sides of the chamber, suggesting a close comparison with the corresponding region of certain fossil gymnospermous seeds.'[3] The actual place which the pollen reached—the 'pollen-chamber'—is found at a deeper level, a statement also holding good of the fossil seeds to which passing reference has been made. Thus, whilst the facts in so far as they are known are consistent with an elaboration of the nucellus, on lines analogous to *Conostoma*, in the seeds of the Medulloseae, Cordaiteae, recent Cycads, and *Ginkgo*, to say that the beak of the nucellus in these seeds corresponds with a vestigial lagenostome, and the pollen-chamber with a plinth cavity, would be premature if not erroneous. Much fuller details of ovular development than are yet available are required before we can advance further.

Before leaving this part of the subject reference may be made to the presence in several siphonogamous Gymnosperms of examples of ovules of which the nucellus undergoes spontaneous disintegration at the apex before the arrival of the pollen. Whilst this procedure would appear to be the rule in the three genera of Gnetales, in *Ephedra*[4] and *Gnetum*[5] it was carried so far that definite excavations or 'pollen-chambers' were produced. The functional significance of this peculiarity in plants whose fertilization is accomplished by the agency of pollen-tubes is far from evident, and we must await new light from current or future investigations. We would only remark in this connexion that the past history of the Gnetales and of such Conifers as show analogous arrangements[6] may be the determining factor in the possession of a mechanism which has somewhat the appearance of being an anachronism.

## VII. GENERAL DISCUSSION ON THE TESTA.

The ribbing, which is so general a character of these and allied seeds, is broadly an indication of a multiple origin of their integuments. Whatever the nature of the members which coalesced to form this organ, it seems reasonable to assume that primitively each of the coalescing members had its own vascular strand, and that the correspondence which usually obtains, both in number and in position, between the ribs and bundles, is an expression of one and the same fact, viz. the multiple origin. In *Physostoma*

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[1] W. H. Lang: Ann. of Bot., vol. xiv, Pl. XVII, Fig. 15.

[2] S. Hirasé: Journ. Coll. Sci. Tokyo, vol. xii, Pl. IX, Figs. 31 and 32.

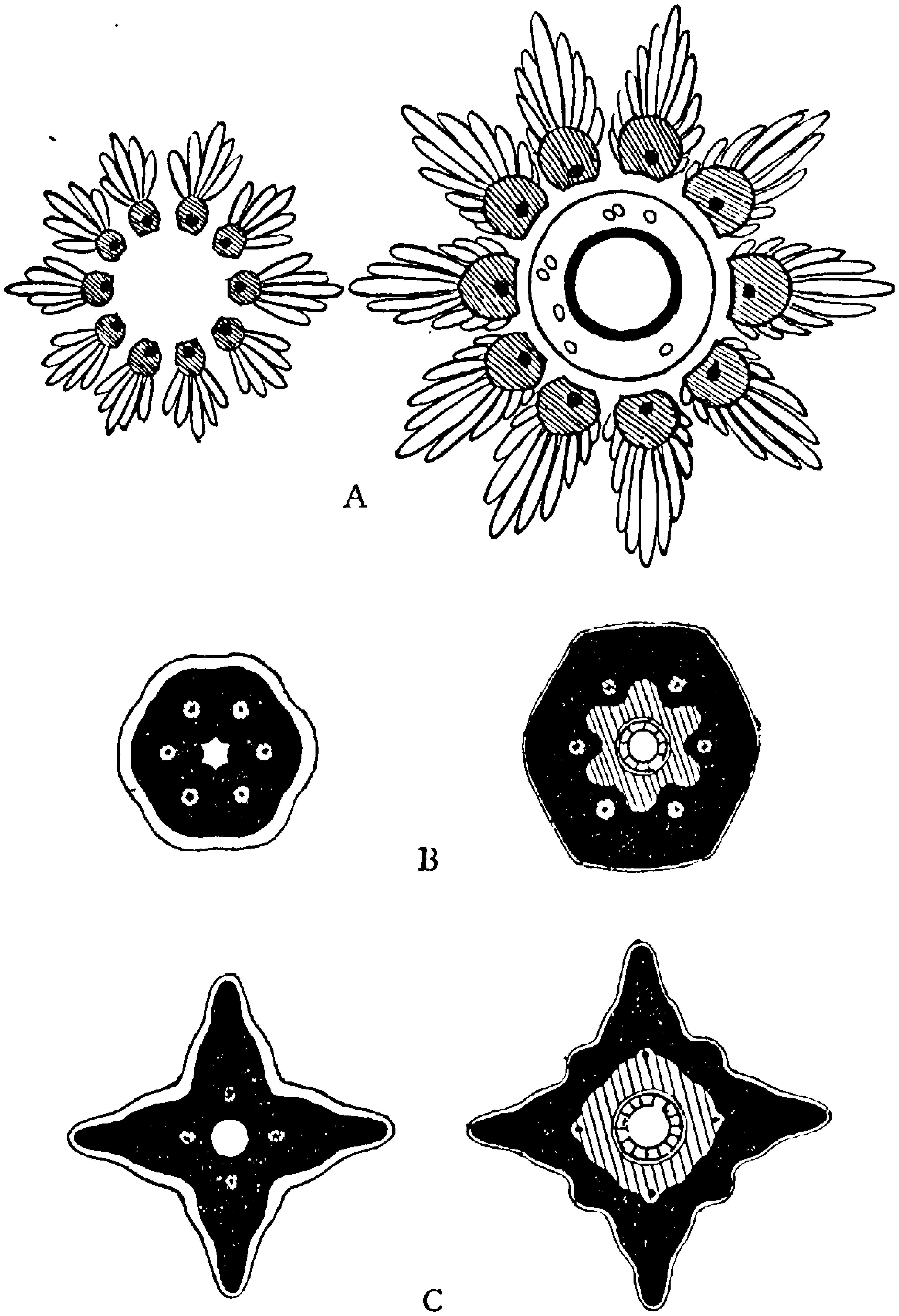
[3] Lang: loc. cit., p. 286.

[4] W. J. G. Land: Bot. Gaz., vol. xxxviii, Pl. V, Fig. 44.

[5] Lotsy: Ann. Jard. Bot. Buitenzorg, vol. xvi, Pl. V, Fig. 35.

[6] e. g. *Sciadopitys verticillata*; see Lawson, Ann. of Bot., vol. xxiv, Pl. XXIX, Fig. 13.

the ribs passed out into free tentacles at the apex, each with its own vascular bundle, and in the young seed the conjunctive tissue between the ribs was much less developed than in mature specimens, perhaps an ontogenetic recapitulation of phylogeny.[1] This is still further borne out by the gradual



TEXT-FIG. 13. Transverse sections (diagrammatic) passing through the apex and the lagenostome of *Physostoma* (A), *Conostoma oblongum* (B), and *Conostoma anglo-germanicum* (C). Parenchyma shaded: testa in black: 'blow-off' white.

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[1] Oliver: Ann. of Bot., vol. xxiii, p. 100, Pl. VII, Fig. 29.

elimination of members as we pass from those seeds in which the lobes are partially free to those in which they are almost completely fused. In *Physostoma*, where the multiple integument is most marked, the number is ten; in *Lagenostoma Lomaxii*, which has a slightly lobed apex, nine; and in *Conostoma oblongum*, where the lobes are internally almost obliterated, six (Text-fig. 13).

The primitive condition of each member was, we think, that seen in *Physostoma*, where the tissue of each tentacle consists of undifferentiated parenchyma. As we pass along the series, we find progressive sclerization proceeding inwards from the whole periphery of each member, thus tending towards the final obliteration of the parenchyma which formed the 'loculi' of the canopy, the sclerization having its inception historically before the fusion of the constituent members. In this way the alternate loculi in *Conostoma anglo-germanicum* have disappeared, though still represented exteriorly by the minor ribs. This gradual decrease in the number of bundles may have culminated in their total suppression, resulting in a condition similar to that in the integument of present-day Phanerogams.

With the more complete fusion of the component members came a gradual loss of vascular tissue. This diminution of the vascular supply of the ovule was restrained in those forms where, as in Cycads, the motile sperms are still retained, but elsewhere, as in most Gymnosperms and the whole of the angiospermic series, where siphonogamy has replaced zoidiogamy, the vascular supply tends to become reduced to a mere basal cup with rare indication of its distal extensions. Thus this view, which has already been put forward, seems to find in these seeds two more links in the chain of evidence.[1]

It seems not improbable that, as already suggested, the prominent ribbing in *C. anglo-germanicum* has a definite mechanical value, for the seed is an exceptionally long one as compared with its width, whilst the testa between the ribs is even thinner than in the much shorter seed of *C. oblongum*. This suggestion seems to find corroboration in *Polylophospermum*, where, too, there is pronounced ribbing associated with a thin sclerotesta and great length.[2] From the integumental standpoint we can then regard *C. anglo-germanicum* as a late stage of the series, in which only four members remain as such, the peripheral portions of all the members still being retained as ribs in relation to their mechanical value; whilst *Gnetopsis*, with four ribs only, probably forms its culmination.

In the medullosean series of forms there is a similar relation existing between ribs and bundles. The latter are, however, situated within the sarcotesta and *exteriorly* to the ribs. In *Trigonocarpus Parkinsonii*, Br.,

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[1] Oliver: On the Ovules of the Older Gymnosperms. Ann. of Bot., vol. xvii, 1903, p. 451.

[2] Oliver: Notes on *Trigonocarpus* and *Polylophospermum*. New Phyt., vol. iii, No. 4, 1904, p. 96.

there are three principal ribs, three secondary, and six tertiary. The six bundles subtend the last.

In *Polylophospermum stephanense*, Br., there are six major ribs and six minor, each with a bundle.

If the origin of the integument here was similarly multiple, we must assume that there was complete fusion of the individual members before the inception of sclerization. This latter extended along the inner surface of the fused organs. The ribs may have been purely mechanical and utilitarian in origin, and their relation to the bundles of a similar nature to that which is exemplified in the leaf of a Cordaitean such as *C. angulostriatus*, where sclerization has proceeded at both surfaces and produced prominent ribs at each bundle, and between each pair of bundles a secondary rib and two symmetrically placed tertiary ribs on either side. In modern Cycads, such as *Macrozamia spiralis* and *Encephalartos Altensteinii*, the bundles in the outer flesh overlie the ribs of the sclerotesta.[1] If the integument here be double, as some hold,[2] it could only be homologized on this view by the assumption that sclerization took place, in time, subsequent to the fusion of the outer and inner integuments.

A further point of general interest as regards the testa, and perhaps of some considerable significance, is the flattening observed in the seed of *Conostoma oblongum*; this platyspermy is even further developed in *Gnetopsis elliptica*, where it is associated with a reduction of the number of bundles to four (Text-fig. 11). The appearance of the transverse section of the latter seed could be readily obtained from the former if we suppose the two major ribs to have lost their bundles and the corresponding angles to have been flattened to a gentle curve. These facts, taken together with the general tendency exhibited in the group towards the reduction in number of the vascular strands accompanied by a corresponding reduction in the number of ribs or angles, point to the possibility of this tendency having been carried still further, resulting in the production of a seed with only two vascular strands and a testa exhibiting a bilateral symmetry comparable to that of *Cardiocarpus*. But whether such a seed definitely referable to this chain of affinity be found or not, the facts seem to indicate that, whilst the terms 'radiospermic' and 'platyspermic' have a definite use as morphological distinctions, our attitude towards them as criteria of taxonomic importance may require readjustment.

The presence in *Conostoma* and *Gnetopsis* of the highly specialized layer we have termed the 'blow-off' seems to call for some explanation. Probably to be regarded as homologous with the peg-producing layer of *Lagenostoma* and the epidermis with its mucilage-containing hairs in *Physostoma*, its

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[1] M. C. Stopes: Beiträge zur Kenntnis der Fortpflanzungorgane der Cycadeen. Flora, 1904, p. 474.

[2] Coulter and Chamberlain, p. 158, Morphology of Spermophytes, 1901; M. C. Stopes, loc. cit.

secretory nature may be due to the same internal causes that have so frequently rendered vestigial structures secretory among living plants. The 'blow-off' layer and the soft apical tissue of *Conostoma oblongum* may be the remnant of a once much more extensive tissue comparable to the sarcotesta of the medullosean series. The closest analogy which modern plants offer appears to be the megaspore of *Pilularia*. Here the mucilaginous layer which invests the megaspore serves to attract and retain the sperms; above the archegonium the mucilage forms a deep funnel, which becomes filled with spermatozoids.[1] In *Conostoma* the mucilage layer, as in *Pilularia*, reaches its maximum development at the apex. In *Conostoma oblongum* the epidermis split up the flanks of the free apical lobes, as is seen in Pl. I, fig. 6, *bl.*; the expanding mucilage must thus have found its way into the micropyle and in the space between the apical lobes. If the seeds were retained till after pollination this mucilage may well have acted as a drop mechanism comparable to that of the present-day *Taxus*. If, however, as might have been the case, the seeds were first shed, perhaps the mucilage played a part analogous to *Pilularia* in capturing and nourishing the male cells. Our knowledge, however, of the functions of mucilage, even in recent plants, is so incomplete as to render the problem in fossil plants extremely difficult.

In *Conostoma anglo-germanicum* and *Gnetopsis* the 'blow-off' is not exfoliated even in specimens showing pollen-grains. We probably have then in all these seeds to deal with a common physiological cause, and any value the layer may have had in certain cases is to be regarded as a secondary adaptation.

## VIII. CONCLUSION AND SUMMARY.

The facts recorded in the foregoing paper go to prove that the seeds of the palaeozoic epoch showed, within certain well-defined limits, a considerable degree of diversity in mechanism.

When regard is had to the dominance which seed-possessing plants afterwards attained, it is hardly surprising that the seeds of Coal Measure times should have shown unmistakable indications of modification and elaboration in a variety of different directions.

This diversity, as it affected the apex of the seed, is fully illustrated in Text-figs. 12 and 13. Whilst the actual parts involved are in fundamental agreement—lagenostome, plinth, and a compound integument—the detailed relations of these parts are altogether different. In *Physostoma* the large lagenostome was enveloped in the lobes of the integument, which collectively formed what may well have been the precursor of the micropyle in this group of seeds. In *Lagenostoma* these arms were united into a chambered 'canopy', which whilst investing the lagenostome, was overtopped by the orifice of the latter, which thus had direct access to the sur-

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[1] Campbell: Mosses and Ferns, p. 425, 1905.

face of the seed. The other extreme is afforded by *Conostoma*, where the minute lagenostome lay at the foot of a long and specialized micropyle which traversed a canopy in which the unit parts, though more highly modified than in *Lagenostoma*, were still recognizable.

A peculiar organ, the plinth, claims special attention in *Conostoma*, not merely from its dimensions, but also on account of the part which it played in the reception of pollen. Though this zone or region is represented in all three types, it is only in *Conostoma*, and the probably related *Gnetopsis*, that it attained to any special significance. To what extent the nucellus of existing Gymnosperms—especially Cycads—may have undergone analogous elaboration cannot be stated with any confidence owing to the defective state of our knowledge of the developmental history of the ovules.

The ribbing and angling of these seeds also raises matters of interest dealt with in the body of the paper (p. 41). In these ribs there appear to be presented traces of what may be regarded, in the light of *Physostoma*, as the original segments or lobes of the ancestral integument. As these show considerable variety, even in allied seeds, in the relative prominence and in the presence or absence of accompanying vascular strands, it is evident that no great reliance can be placed on these characters for diagnostic purposes —especially where the larger groups are concerned. Incidentally, it may also be remarked that incipient stages in the passage from radial to bilateral symmetry appear to be illustrated by both *Conostoma oblongum* and *Gnetopsis elliptica*. This shows, if further proof be needed, that the old provisional distinction of palaeozoic seeds into radiospermic and platyspermic types had little or no significance as a guide to affinity.

Though allusion has been made to the modification and elaboration in different directions which the seed underwent, it would be premature hastily to suppose that our different types had necessarily diverged from a common *seed-possessing* ancestor. In these days when the doctrine of polyphylesis is steadily gaining ground, the alternative view that (to take a concrete case) *Physostoma*, *Lagenostoma*, and *Conostoma* had been separately derived from as many related but distinct *cryptogamic* types will certainly have to be considered. On that view, then, the differences between our seeds would depend not only on such divergences as arose after the establishment of the seed habit, but they would be, in part at least, determined by inherited differences already present (or latent) in the several ancestors.

Moreover, the coming of the seed habit must, from the evolutionary point of view, have marked a relatively active period ; for, even if we suppose the qualifications for seed-bearing to have been acquired in cryptogamic days, there must have been a transitional period during which the less immediately serviceable portion of the cryptogamic inheritance was either eliminated or underwent functional change.

These considerations may perhaps serve to indicate some of the difficulties which beset the allocation to their exact place in phylogeny of the various structures and mechanisms which collectively constitute the seed.

In the foregoing paper, the subject-matter of which is set forth in the table of contents (p. 1), we describe in detail two palaeozoic seeds, *Conostoma oblongum*, Will., and *C. anglo-germanicum*, sp. nov.; these, with *Gnetopsis*, are provisionally placed in a separate group, the Conostomeae, ranking with the Physostomeae and Lagenostomeae as subdivisions of the larger class Lagenostomales. The seeds of the Conostoma type are compared with related forms, whilst diagnoses of the species and provisional diagnoses of the groups are given. In the more general parts of the paper especial attention is drawn to the arrangements for the reception and maturation of pollen found in the various seed types and to the peculiarities of the testa.

UNIVERSITY COLLEGE, LONDON,
*November*, 1910.

## IX. GLOSSARY OF TERMS EMPLOYED.

**'Blow-off.'** An epidermal layer of presumed mucilage-containing cells, forming the outermost investment of the testa (p. 14).

**Canopy.** The apical portion of the hard testa consisting of a varying number of more or less fused members surrounding the free portion of the nucellus.

**Cupule.** A free sheathing structure arising from the peduncle and investing one or more seeds.

**Doubly oblique** or **Assymetrically oblique.** Applied to a section which is oblique both to any plane of symmetry and to the axis of the structure cut (p. 12).

**Flange.** A ring-like projection of the integumental lining of the micropyle (p. 14).

**Lagenostome.** A differentiated chamber at the apex of the nucellus formed by modification of the epidermis. The lagenostome is either *included* where the integumental micropyle forms an intermediate passage between its orifice and the exterior, as in *Conostoma*, or *exserted* where by upward extension of the lagenostome it communicated with the exterior direct, e. g. *Lagenostoma*.

**Lens.** The contracted tissue of the plinth which frequently remained attached to the base of the lagenostome (p. 20).

**Loculus.** A chamber present in the canopy usually represented by a space, but probably filled with parenchymatous tissue continuous with the soft part of the integument lining the seed cavity, and into which the vascular strand passed.

**Major rib** or **angle.** Applied to the large ribs or angles of a seed irrespective of their vascularity (p. 28).

**Minor rib** or **angle.** Applied to the lesser ribs or angles of a seed where these latter fall into two categories only; in other cases the terms secondary and tertiary are employed.

**Micropyle.** The passage to the nucellar apex formed by the integument, which may be of three kinds, viz. a fimbriated micropyle of non-fused members, as in *Physostoma*; an entire micropyle, as in *Conostoma*; or an investing micropyle, as in *Lagenostoma.*

**Micropylar funnel.** The lower portion of the micropylar tube where it expands to join the seed cavity (lagenostome jacket).

**Micropylar tube.** The passage formed by the micropyle.

**Micropylar membrane.** The integumental epidermis lining the micropyle—often found separated.

**Oblique.** Applied to a section of which the plane is at right angles to a plane of symmetry but oblique to the axis of the structure cut.

**Pad.** The central portion of the lens (p. 20).

**Plinth.** The free portion of the nucellus supporting the lagenostome (p. 16).

**Plinth jacket.** The epidermis of the soft integument surrounding the plinth.

**Shoulder.** A term applied to that part of a structure where it begins to curve inwards towards the apex.

**Sinus.** The space between the free portion of the nucellus and the integumental lining or the gaps in a fimbriated micropyle.

**Tapetal septum.** The septum separating the megaspore cavity from the apex of the nucellus.

**Tent pole.**[1] A raised central portion of the apex of the prothallus.

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## XI. EXPLANATION OF PLATES I-III.

Illustrating Messrs. Oliver and Salisbury's paper on Conostoma group of Palaeozoic Seeds.

U. C. L., R., and Q. = University College London Collection.
J. = Dr. Jongmans' Collection.
W. = Mr. D. M. S. Watson's Collection.

### PLATE I.

FIGS. 1-11 (Photographs).

Fig. 1. Nearly longitudinal section through seed, showing the boat-shaped outline. The cushion (*ls.*) is in position just beneath the lagenostome (*lg.*), and the micropylar membrane (*m.m.*) has contracted from the hard testa (*t.*). U. C. L., R. 111 (Shore). × 12 (see p. 10).

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[1] S. Hirasé: Études sur la fécondation, etc., du *Ginkgo biloba.* Journ. Coll. Sci. Japan, vol. xii, p. 113.

Fig. 2. Apex of young seed cut obliquely, showing the plinth jacket (*pl. j.*) and wall of plinth (*pl.*) in close contact. The cells of the testa (*t.*) show contents, and the plinth tissue is slightly displaced from the base of the lagenostome (*lg.*). U. C. L., R. 114 (Halifax). × 80 (see pp. 12, 14).

Fig. 3. Apex of young seed cut tangentially. The 'blow-off' layer (*bl.*) is in position on the left, but on the right has exfoliated. The cells of the soft apical tissue (*st.*) are well shown and pass gradually into the hard tissue below (*t.*). U. C. L., R. 122 (Shore). × 70 (see pp. 12 and 15).

Fig. 4. Oblique section through winged base of seed, showing basal portions of the cell-walls of the 'blow-off' layer still attached (*bl.w.*) to the prominent wings of the base ($r^1$, $r^5$, $r^6$). U. C. L., R. 110 (Dulesgate). × 36 (see p. 15).

Fig. 5. Transverse section through middle region of seed. The somewhat flattened outline is well shown and the structure of the testa with outer palisade (*pa.*) and inner fibrous layers (*fb.*). *ma.* and *mi.*, major and minor angles. U. C. L., R. 119 (Shore). × 26 (see p. 10).

Fig. 6. Oblique section through apex, showing three lobes of 'blow-off' (*bl.*). The cells of the cushion (*ls.*) are well preserved. *lg.* lagenostome wall; *m.m.*, micropylar membrane; *pl.*, plinth. U. C. L., R. 116 (Shore). × 70 (see p. 18).

Fig. 7. Median longitudinal section through apex of same specimen as Fig. 1, showing the micropylar membrane (*m.m.*) cut obliquely and consisting above of superimposed tiers of cells. The lagenostome (*lg.*) is cut tangentially. *bl.*, 'blow-off' layer; *ls.*, lens or residue of plinth tissue. U. C. L., R. 111 (Shore). × 100 (see p. 14).

Fig. 8. Oblique section through micropyle, showing the soft tissue at the apex (*s.t.*) separating from the testa below (*t.*); the loculus of the canopy on the right (*loc.*) shows the vascular bundle (*v.b.*). *m.m.*, micropylar membrane. W. 267 (Shore). × 64 (see p. 12).

Fig. 9. Transverse section of base of seed, showing seven wings. *bl.*, 'blow-off'; *scl.*, sclerenchymatous cells; *v.b.*, vascular bundles; *c.s.*, central space; *s p.*, one of the secretory passages. U. C. L., R. 113 (Halifax). × 40 (see p. 15).

Fig. 10. Somewhat oblique longitudinal section through seed passing out above the stalk; seven ribs are present ($r^1$, $r^2$, . . .), two of them with their vascular bundles preserved (*v.b.*$^5$, *v.b.*$^7$). *s.*, sinus; *lg.*, lagenostome; *ls.*, lens; *pd.*, pad. U. C. L., R. 110 (Dulesgate). × 18 (see p. 12).

Fig. 11. Doubly oblique section through seed, showing contained prothallus (*pr.*) with 'tent-pole' (*t.p.*); the shoulders of the plinth cavity (*pl.c.*) are exaggerated by the direction of the section. *bl.*, 'blow-off'; $r^1$ and $r^3$, ribs asymmetrically cut. U. C. L., R. 119 (Shore). × 30 (see p. 12).

## PLATE II.

Figs. 12–20 (Photographs).

Fig. 12. Oblique section of seed above the lagenostome, showing the soft apical tissue above (*s.t.*) and with 'blow-off' (*bl.*) exterior to it. The micropyle is in the centre of the figure, its lining membrane (*m.m.*) is seen as a fluted layer. At the top of the figure are two somewhat displaced lobes of the canopy (*l.*, *l.*) with a sinus (*s.*) between. W. 268 (Shore). × 70 (see p. 13).

Fig. 13. Portion of apex of seed given in Pl. I, Fig. 1, showing the outer edge of the testa 'blow-off' raised up by pegs of mucilage beneath (*pe.*); *m.m.*, micropylar membrane. U. C. L., R. 111 (Shore). × 195 (see p. 15).

Fig. 14. Median longitudinal section through lagenostome, plinth, and adjacent parts. *lg.*, lagenostome with apparently two wall layers; *pl.*, wall of plinth; *pl.j.*, plinth jacket; *s.*, foot of sinus between plinth and plinth jacket; *ls.*, remains of plinth tissue ('lens') adhering to lagenostome; *pd.*, pad resting on tapetum; *v.b.*, position of vascular strand. U. C. L., R. 110 (Dulesgate). × 85 (see p. 20).

Fig. 15. Central part of Fig. 16 enlarged. *pd.*, central pad resting on remains of plinth tissue (*pl.t.*); *p.g.*, pollen-grains, the upper right-hand one with internal cells. U. C. L., R. 117 (Shore) × 182 (see p. 20).

Fig. 16. Longitudinal section of upper part of seed, showing testa (*t.*), and base of micropyle (*mc.*), lagenostome (*lg.*), plinth (*pl.*), and remains of tissue of plinth (*pl.t.*) resting on the tapetal septum (*tap.*); part of the tapetum has separated as a blister. Around the pad are several pollen-grains (*p.g.*). *loc.*, loculus of canopy; *s.*, base of sinus between plinth and plinth jacket. Photographed by Mr. W. Tams. U. C. L., R. 117 (Shore . × 38 (see p. 20).

Fig. 17. Longitudinal section of lower end of seed, showing testa (*t.*), and tapetum (*tap.*) several cell layers deep. U. C. L., R. 121 (Shore). × 80.

Fig. 18. Lagenostome enlarged from specimen given in Fig. 16. *lg.o.*, outer layer of wall, *lg.i.*, inner layer of wall of lagenostome; *pl.*, wall of plinth; *pl.j.*, plinth jacket; *u.f.*, upper flange, *l.f.*, lower flange of lagenostome. U. C. L., R. 117 (Shore). × 125 (see p. 7).

Fig. 19. Median section of apex of seed with prothallus (*pr.*); the asymmetry of the internal ribbing of micropyle wall shown. *i.r.*, internal rib; *m.t.*, micropylar tube; *m.f.*, micropylar funnel; *lg.*, lagenostome; *pl.*, plinth cavity; *ls.*, tissue of plinth ('lens'); *p.g.*, pollen-grain; *t p.*, 'tent pole'; *tap.*, tapetum. U. C. L., R. 125 (Deighton, Yorks.). × 75 (see p. 20).

Fig. 20. Longitudinal section of micropylar tube (*m.t.*) and lagenostome; the wall of the lagenostome is cut tangentially, the cells showing conspicuous reticulated sculpturing. U. C. L., R. 115, 1 (Shore). × 182 (see p. 18).

## PLATE III.

Fig. 21. Transverse section through base of the megaspore cavity, showing the basal wings formed by the major ribs ($R^1$, $R^2$, $R^3$, $R^4$), three of which have corresponding vascular bundles, and the minor ribs ($r^1$, $r^2$, $r^3$, $r^4$), which have no vascular elements. *tap.*, tapetum; *bl.*, 'blow-off' layer. U. C. L., R. 140 *d* (Langendreer). × 27 (see p. 29).

Fig. 22. Transverse section from the same series as above through the middle region. Major ribs ($R^1$, $R^2$, $R^3$, $R^4$); minor ribs ($r^1$, $r^2$, $r^3$, $r^4$). U. C. L., R. 140 *b* (Langendreer). × 27 (see p. 28).

Fig. 23. Section from the same series through the apex; the four minor ribs have died out. The four major $R^1$, $R^2$, $R^3$, $R^4$) are pierced by the canopy loculi (*loc.*), in which the black dots, seen in two, are the vascular bundles. *mc.*, micropyle; *bl.*, 'blow-off'. U. C. L., R. 140 *a* (Langendreer) × 27 (see p. 28).

Fig. 24. Longitudinal section through the same seed as in Fig. 26. Micropyle (*mc.*) showing the concave upper edges of the major ribs ($R^1$ *e*, $R^3$ *e*). The lagenostome (*lg.*) is cut tangentially. *p.g.*, pollen-grains; *pl.*, plinth; *pl.j.*, plinth jacket; *s.*, sinus; *t.s.*, tapetal septum; *ls.*, tissue of plinth. J. 12 (Duisburg). × 42 (see p. 28).

Fig. 25. Longitudinal section of plinth and lagenostome, enlarged from Fig. 28. *mc.*, micropyle; *m.m.*, micropylar membrane, still adhering to the testa; *lg.*, lagenostome with cells preserved on the left; *pl.*, plinth cavity; *ls.*, lens, slightly displaced; *p.g.*, pollen-grains. J. 9 (Duisburg). × 100 (see p. 30).

Fig. 26. The same section as Fig. 24, through micropyle (*mc.*), showing mucronate apex of seed. $R^1$, $R^3$, major ribs; *m.co.*, micropylar cone; *s.*, sinus. J. 12 (Duisburg). × 17 (see p. 28).

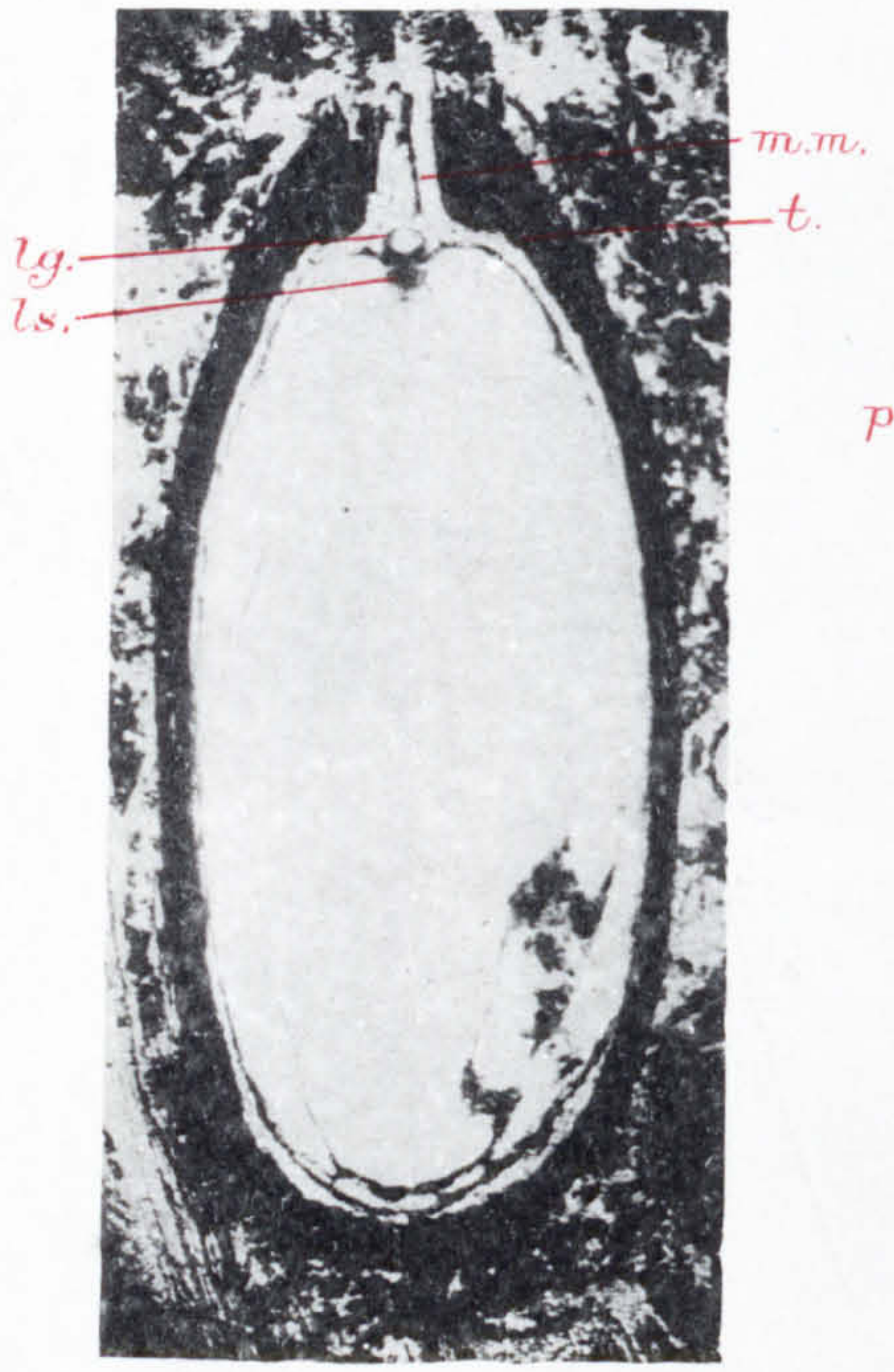
Fig. 27. Oblique transverse section near base of seed, showing the four vascular bundles (*v.b.*) corresponding to the major ribs ($R^1$, $R^2$, $R^3$, $R^4$), minor ribs $r^1$, $r^2$, $r^3$, $r^4$). *bl.*, 'blow-off'. Q. 18 (Shore). × 28 (see p. 29).

Fig. 28. Same seed as in Fig. 25, showing the lagenostome (*lg.*), plinth jacket (*pl.j.*), the lens (*ls.*), plinth (*pl.*). J. 9 (Duisburg). × 25.

Fig. 29. Longitudinal section of nucellar apex and testa, showing two loculi (*loc.*) of major ribs, 'blow-off' layer (*bl.*), lagenostome (*lg.*). *pl.j.*, plinth jacket; *pl.*, plinth; *s.*, sinus; *ls.*, lens; *pd.*, pad of tissue on tapetal septum. J. 3 (Duisburg). × 72 (see p. 29).

Fig. 30. Nearly longitudinal section passing out through two major ribs at the apex in which the loculi are cut obliquely (*loc.*); the lens (*ls.*) is seen in position with the descended pad (*pd.*). *bl.*, 'blow-off'; *v.b.*, vascular bundle; *pl.j.*, plinth jacket; *s.*, sinus; *lg.*, lagenostome; *pl.*, plinth. J. 3 (Duisburg). × 17 (see p. 30).

Fig. 31. Section tangential to seed and doubly oblique. The upper lateral ribs ($r^1$, $R^2$) are rendered obtuse, the terminal ribs ($R^1$, $r^2$) are exaggerated, and the basal laterals ($r^3$, $R^4$) have become cuspidate, through the plane of section. *v.b.*$^2$, *v.b.*$^3$, *v.b.*$^4$, vascular bundles; *bl.*, 'blow-off'; *pl.j.*, plinth jacket. J. 6 (Duisburg). × 17 (see p. 30).



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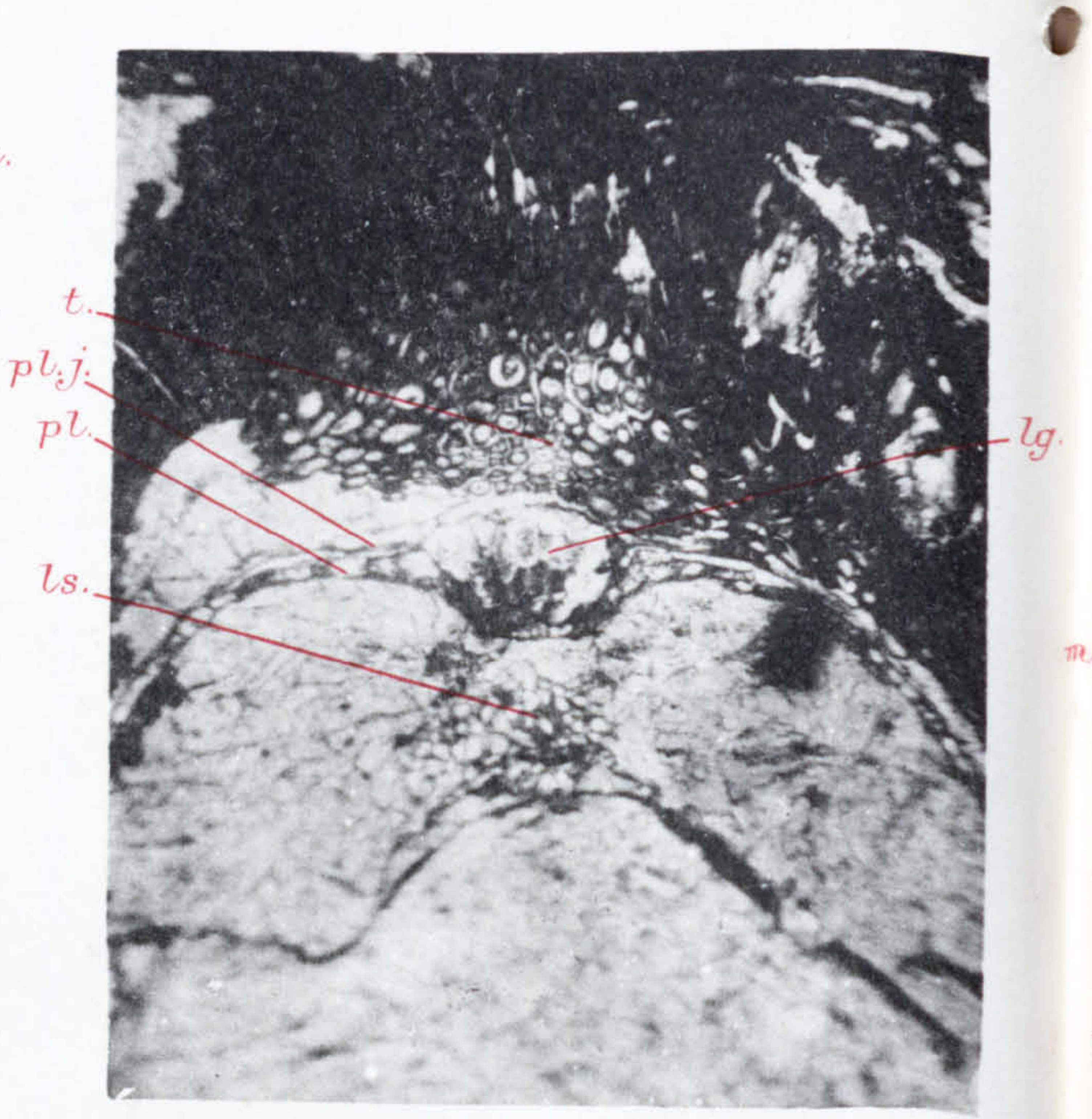

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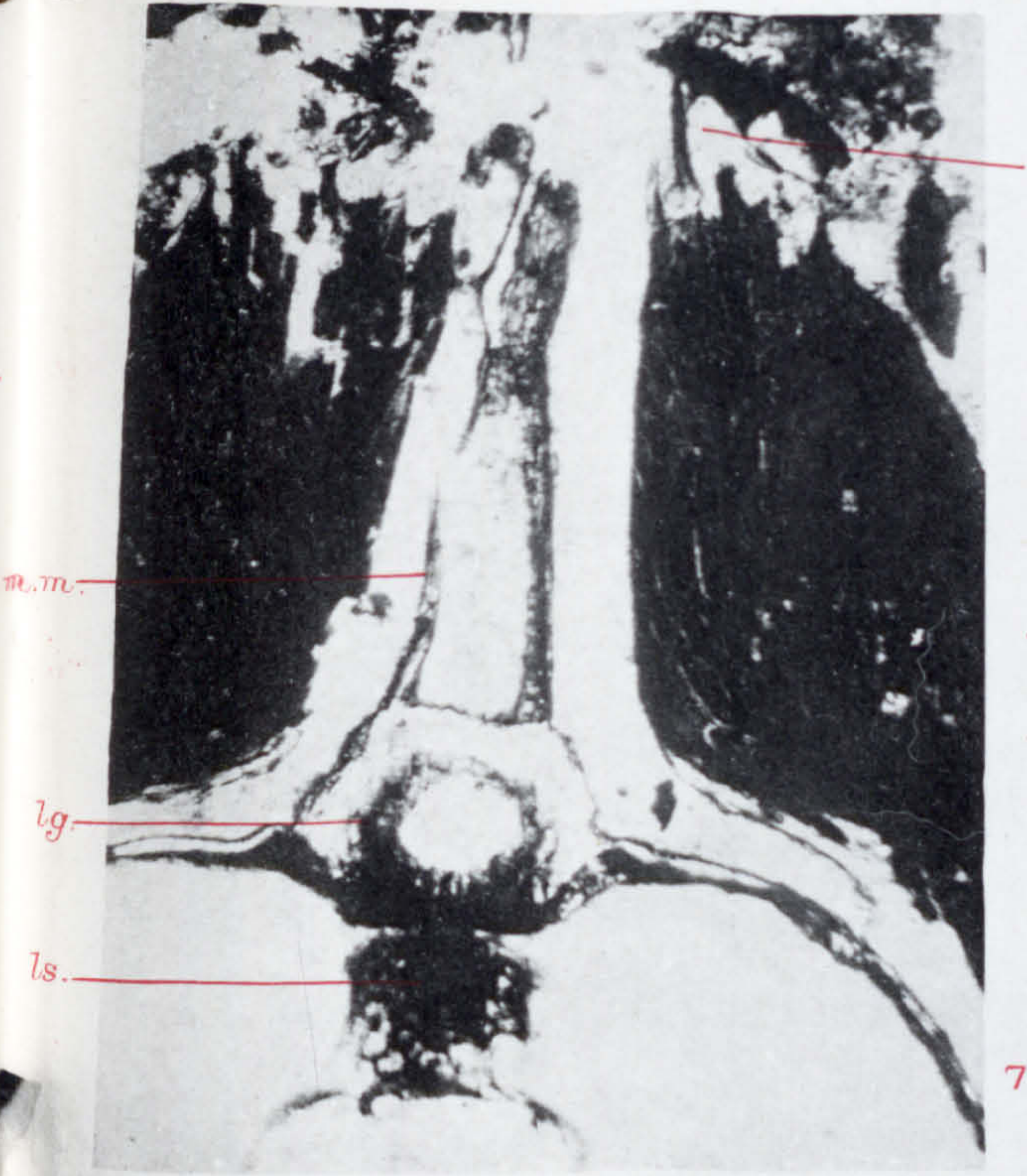

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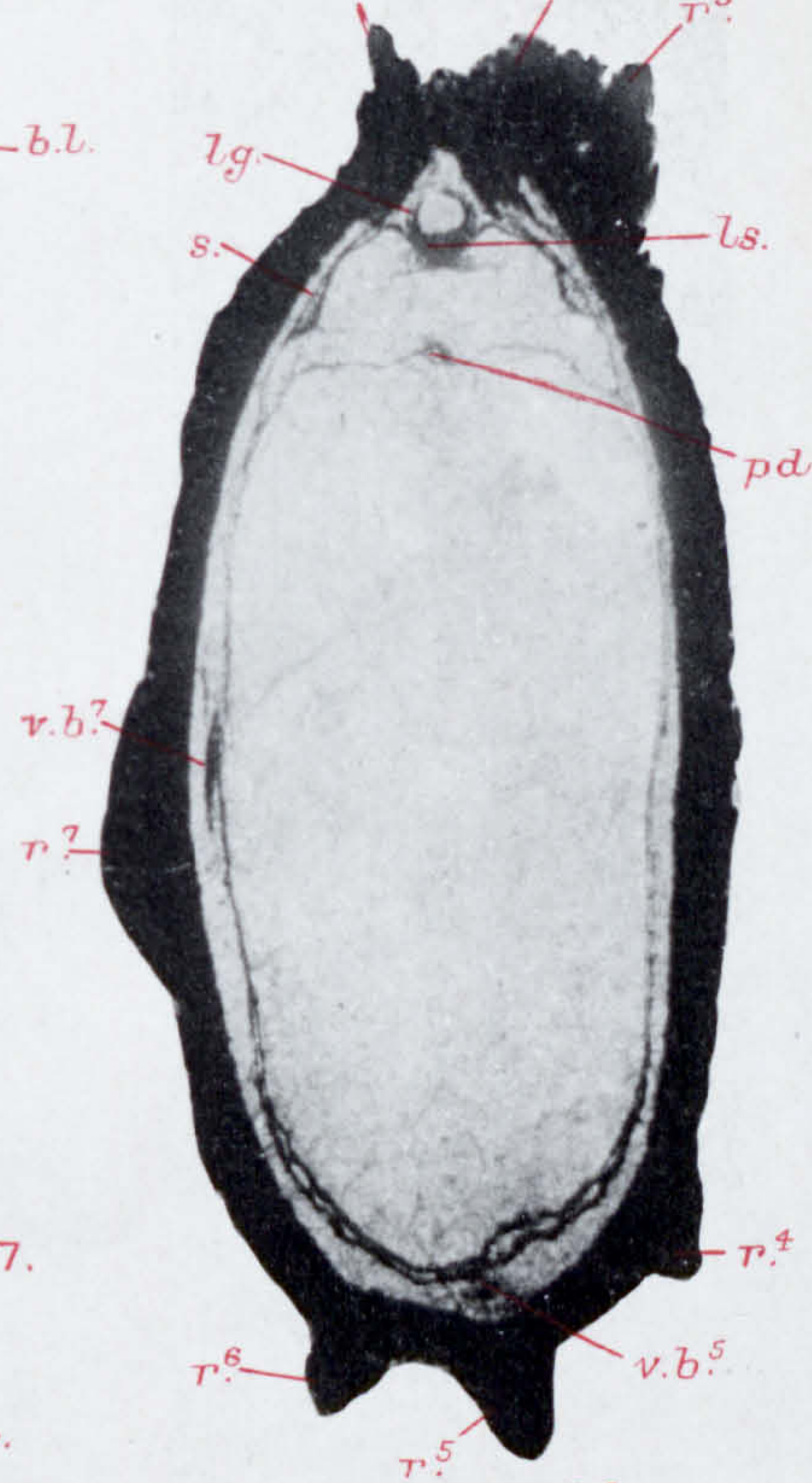

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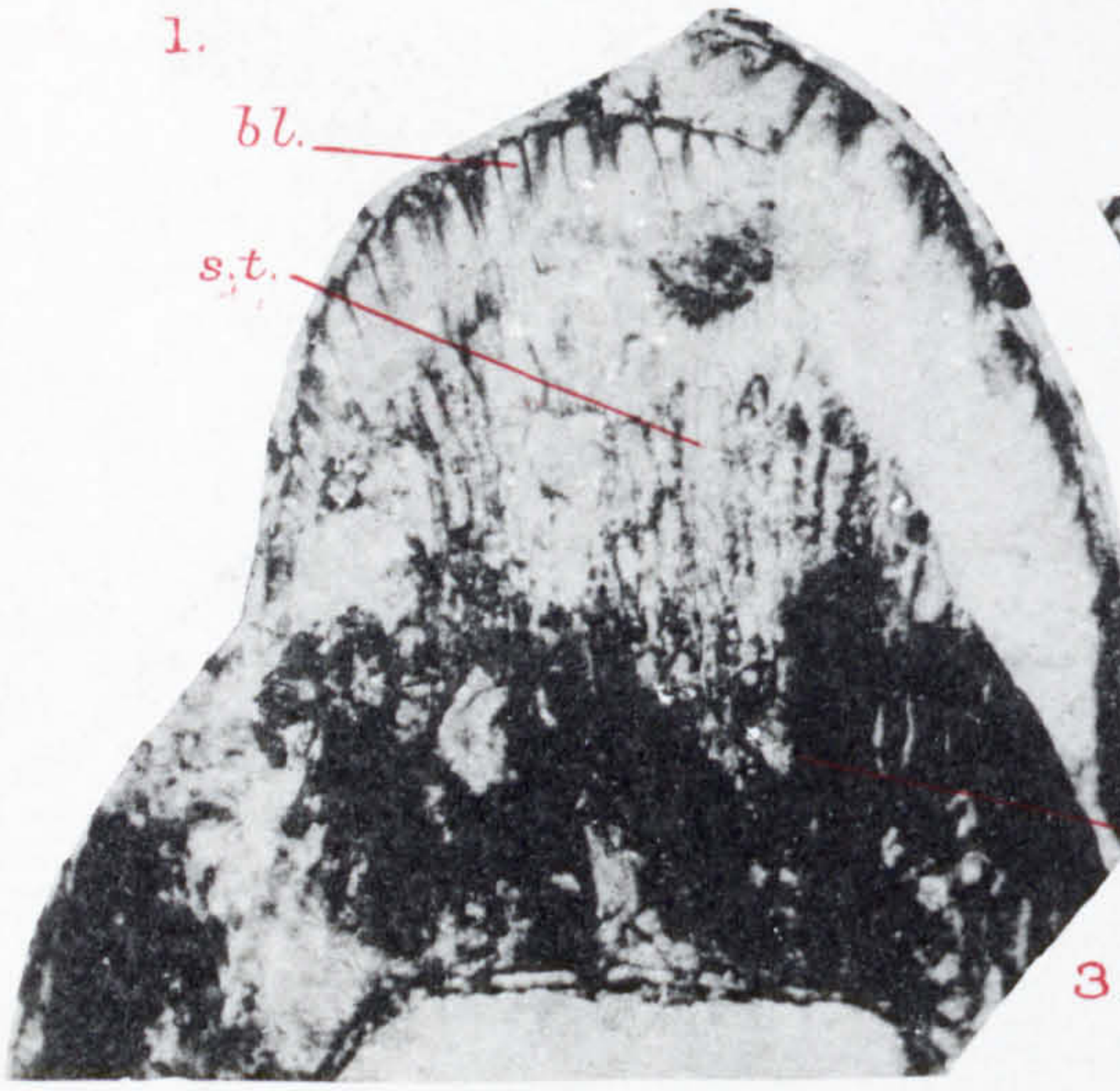

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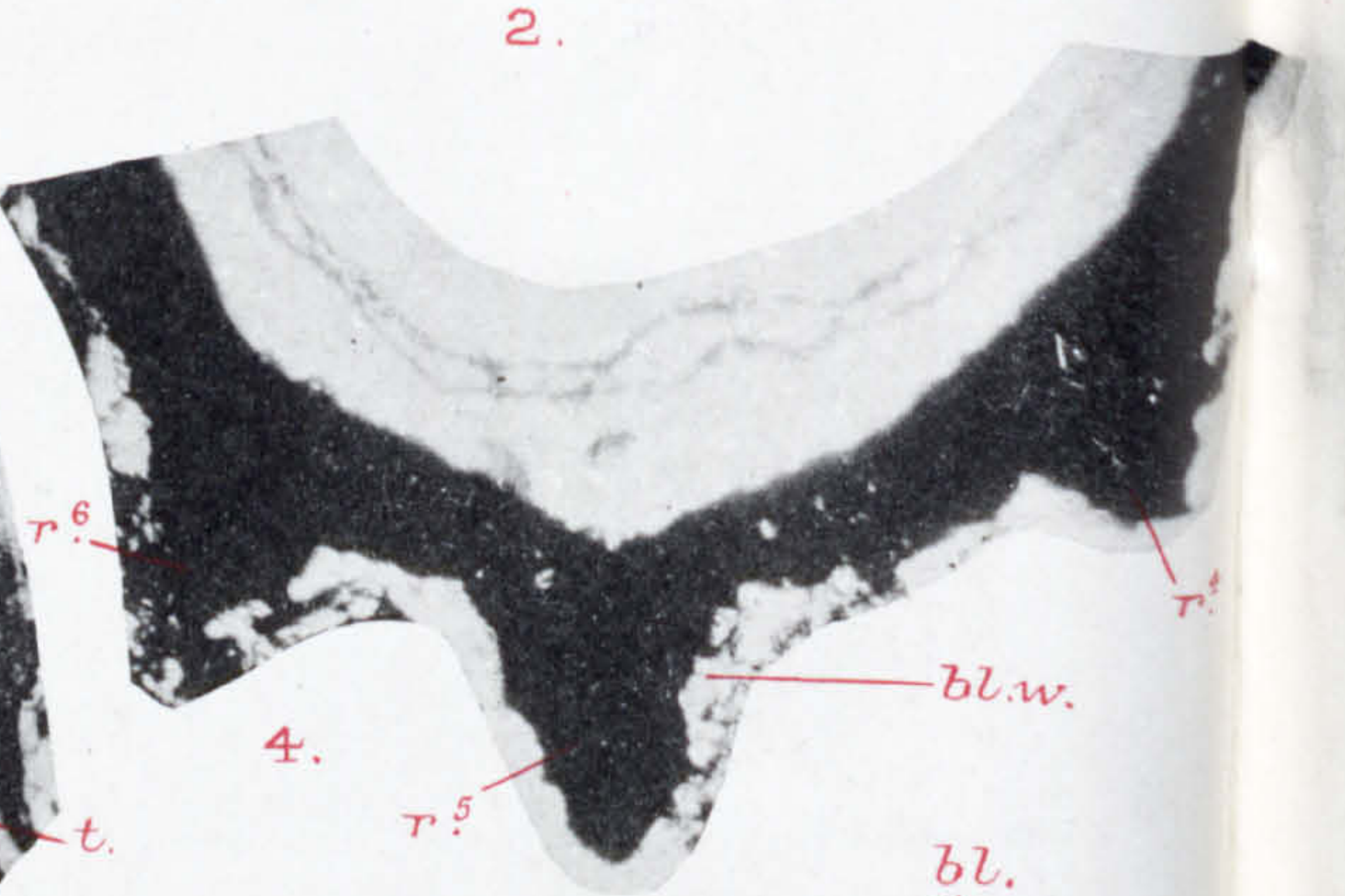

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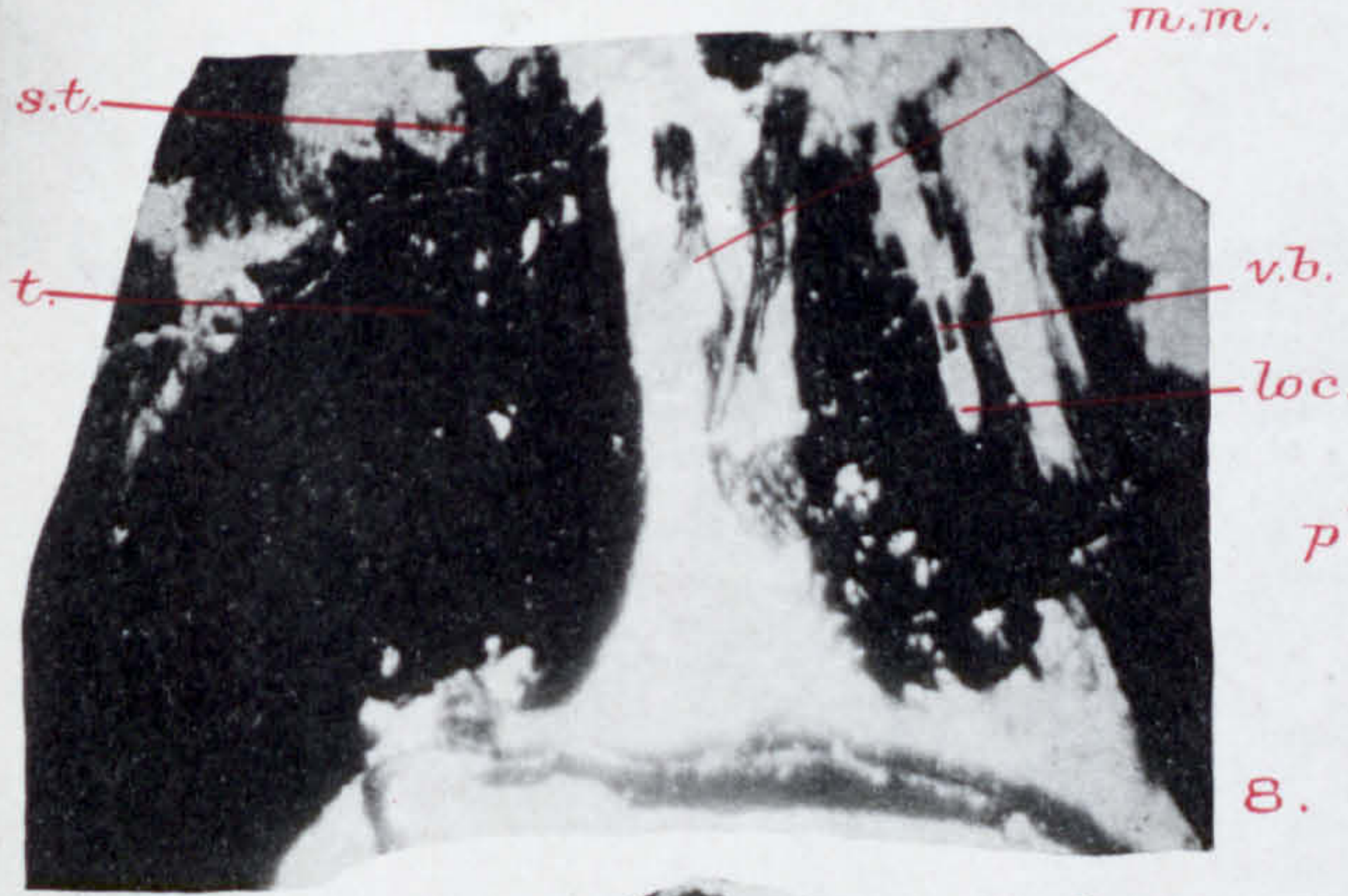

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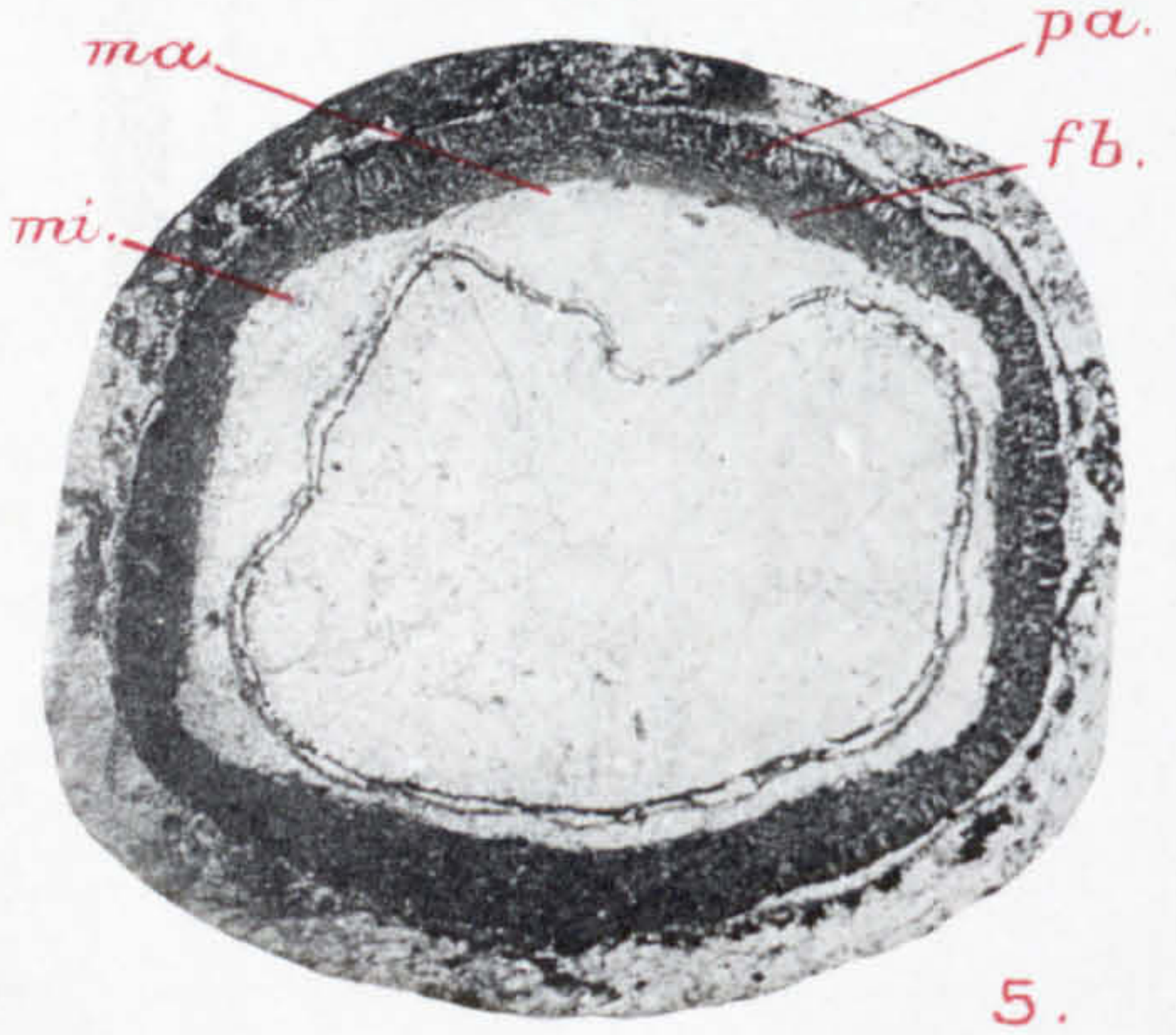

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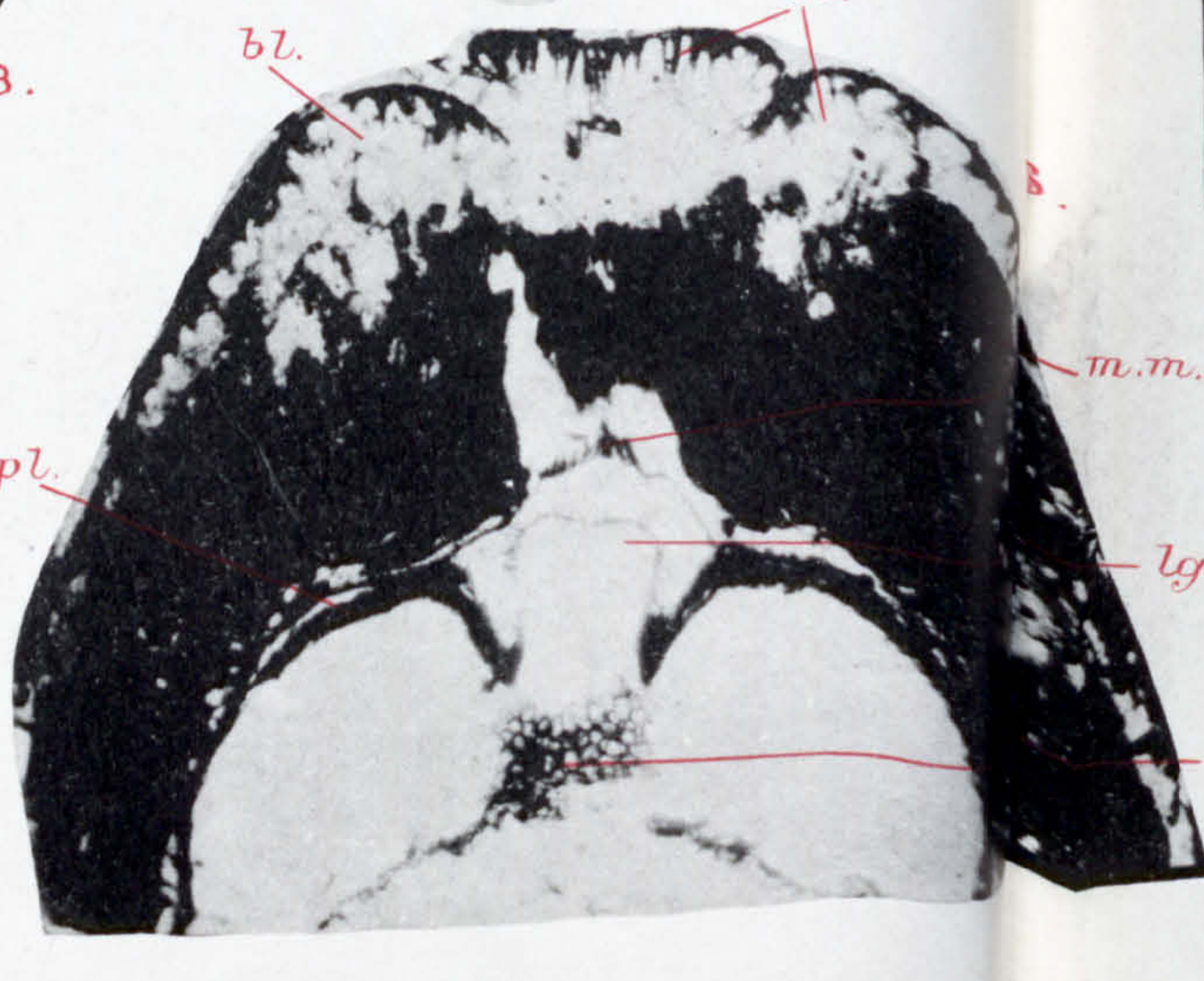

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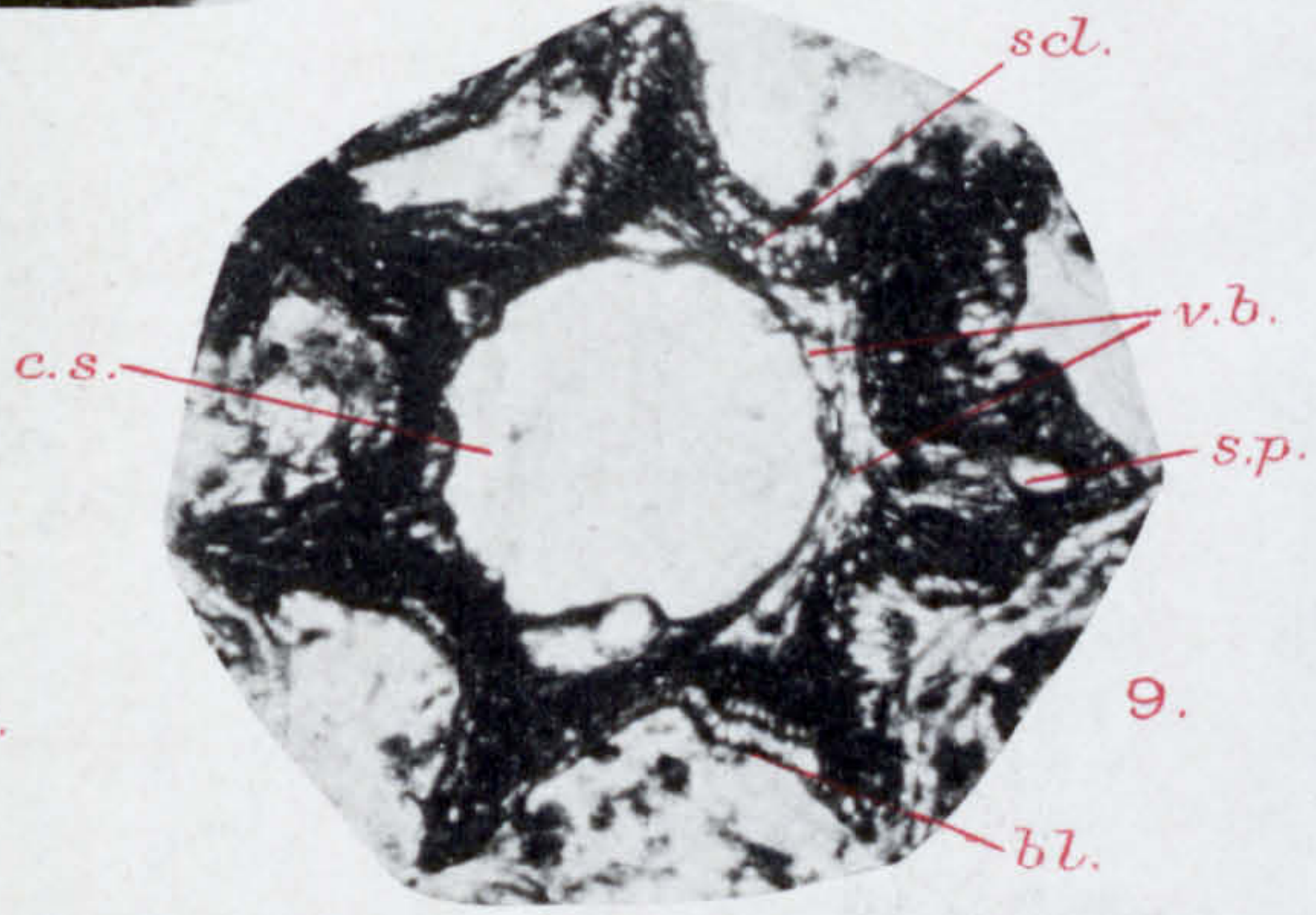

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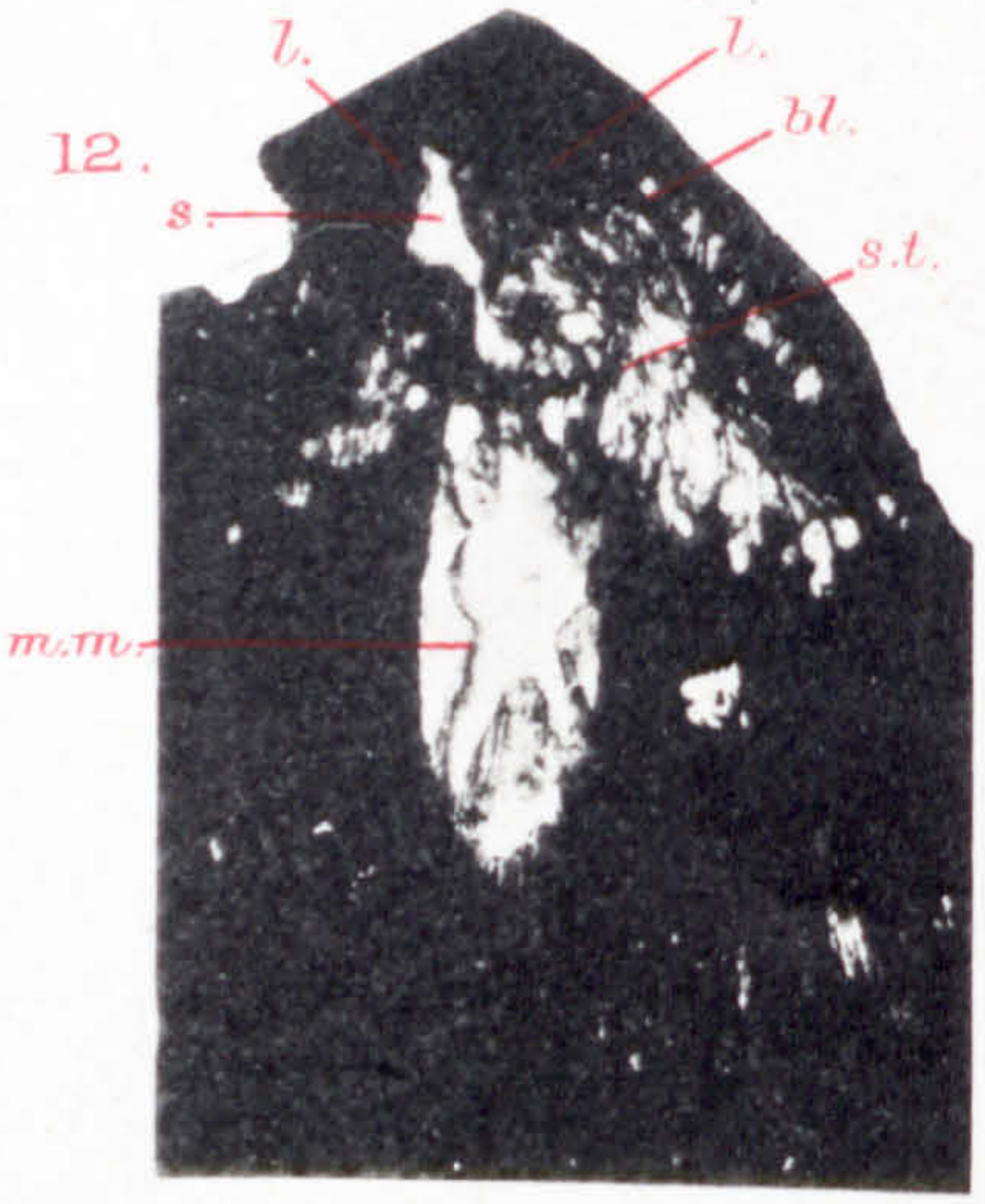
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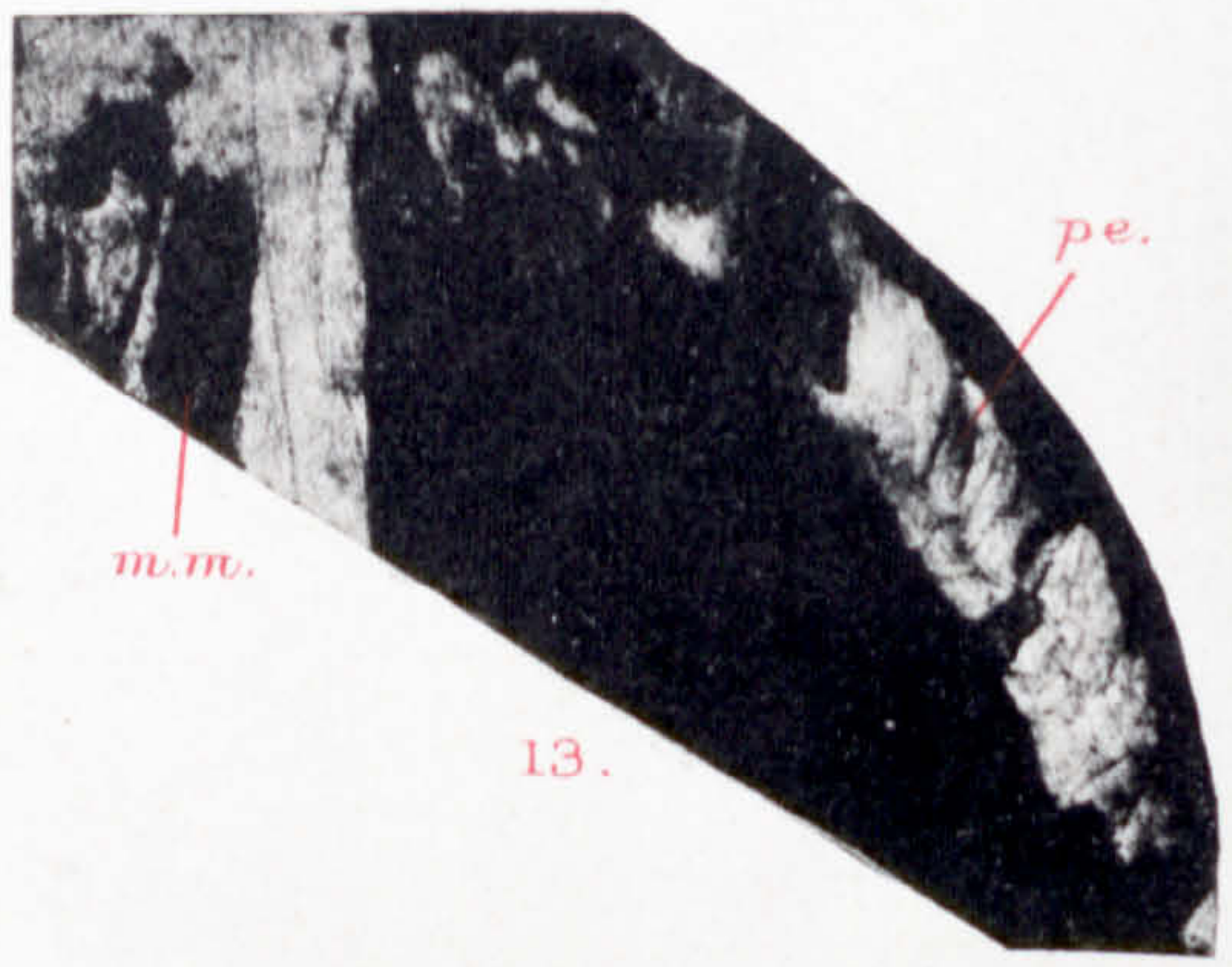
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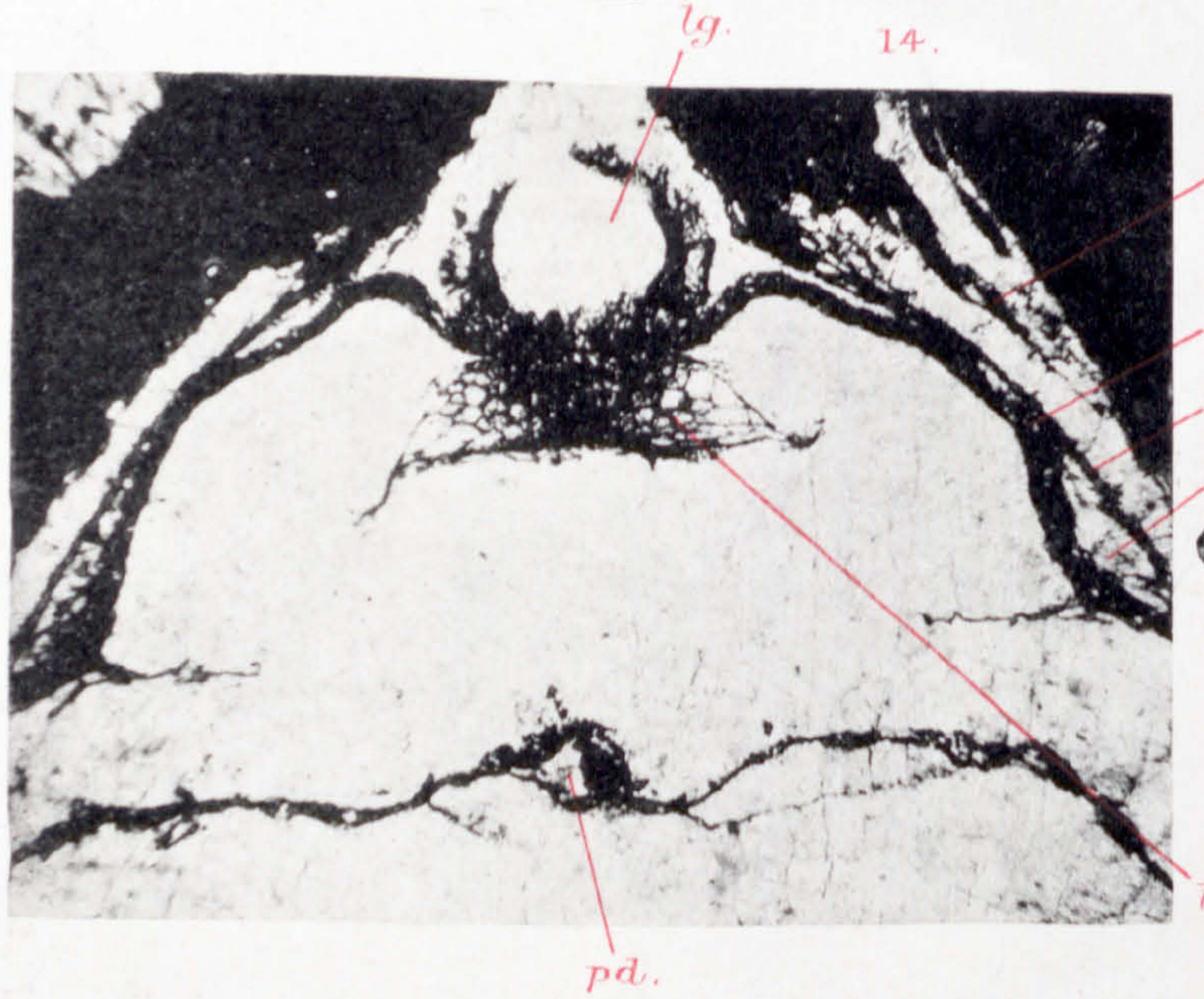
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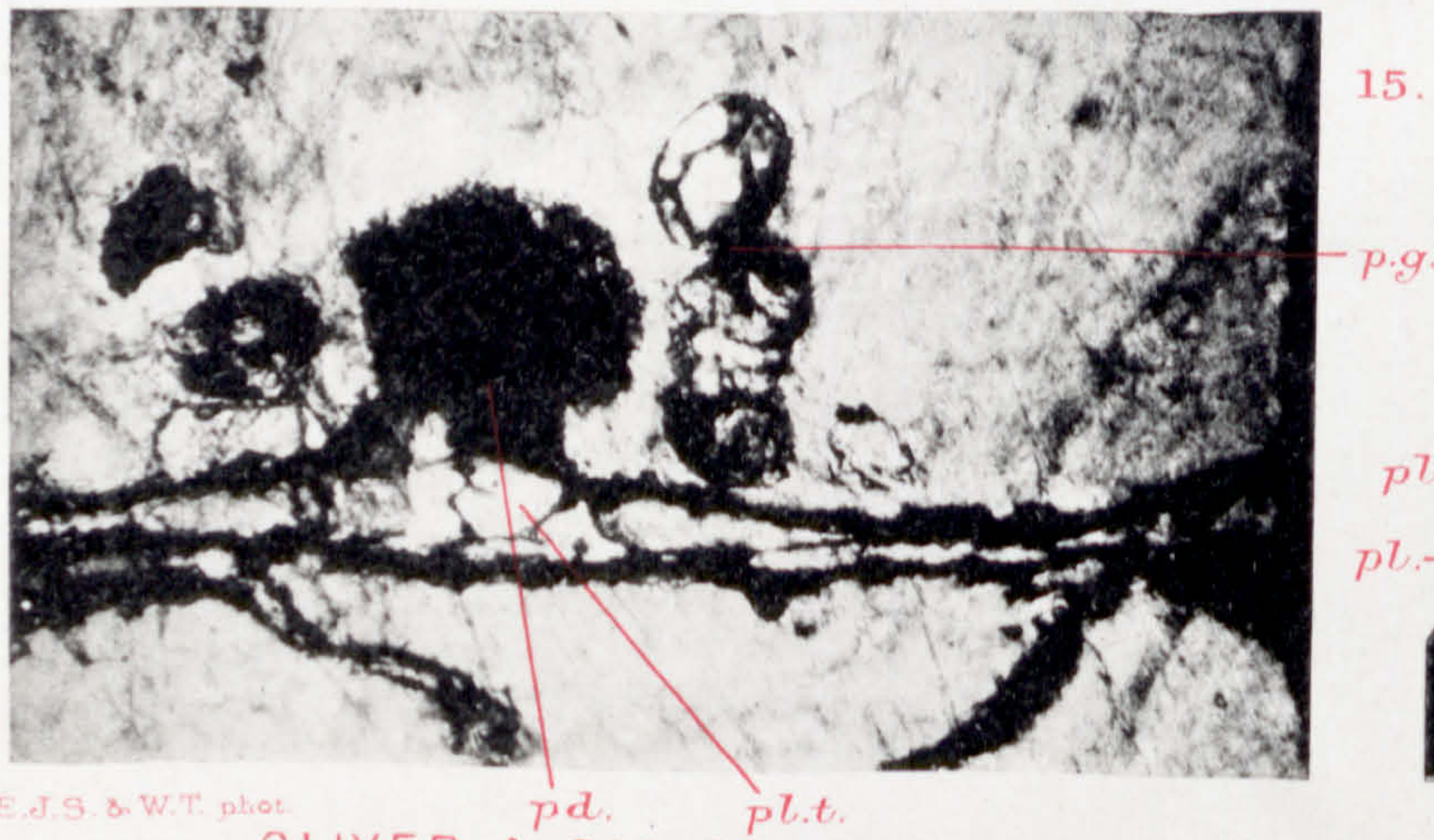
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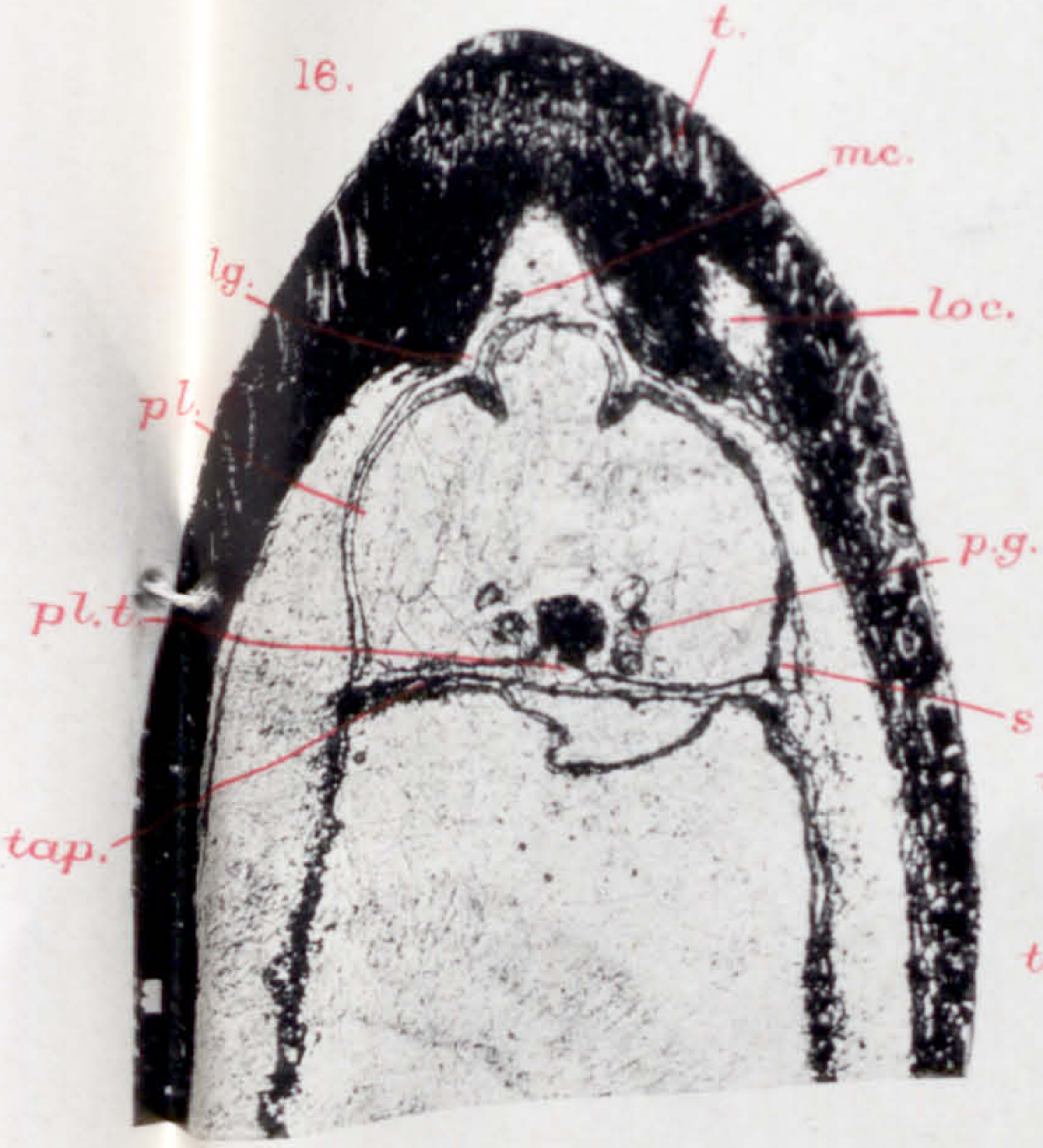
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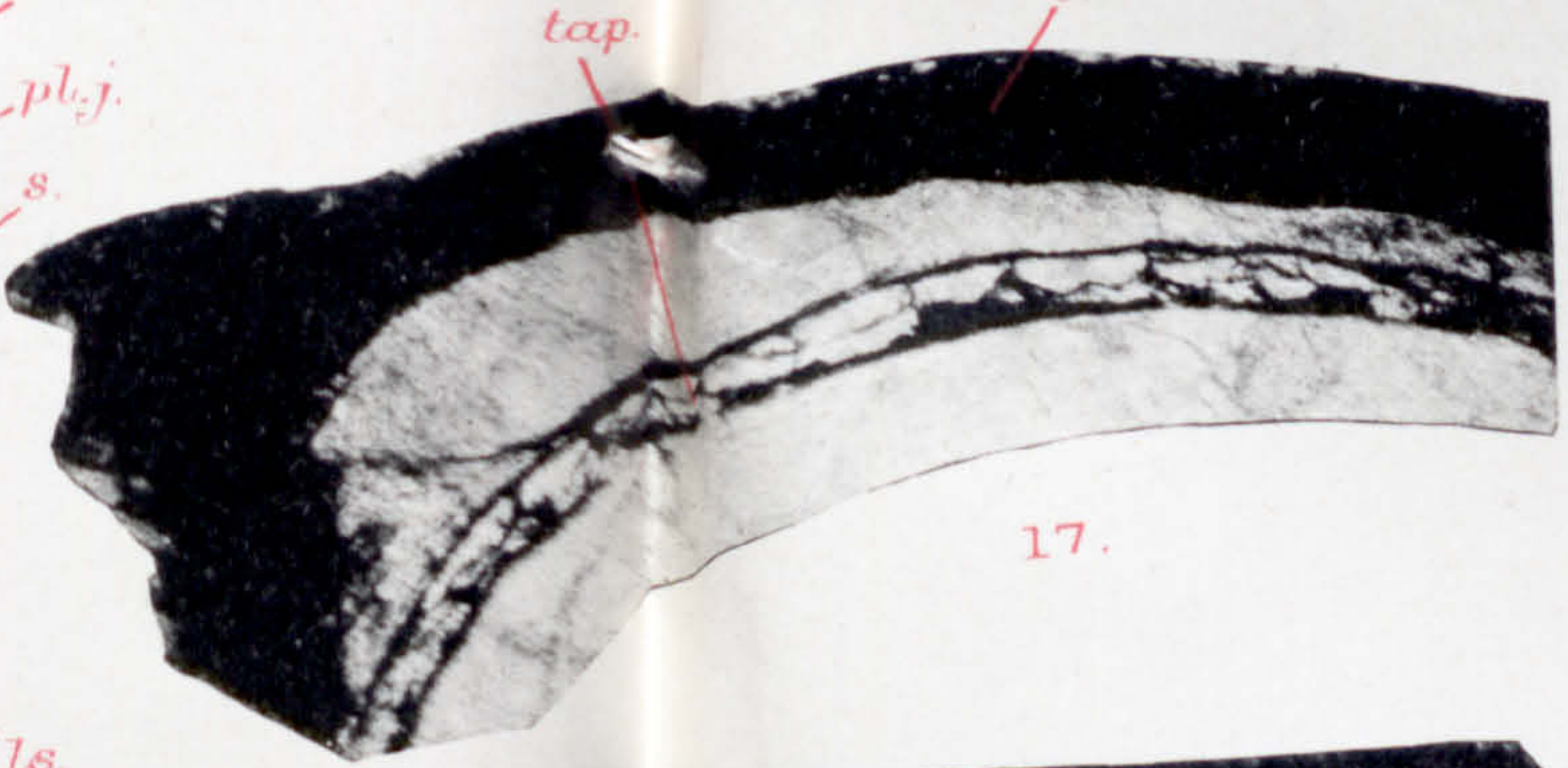
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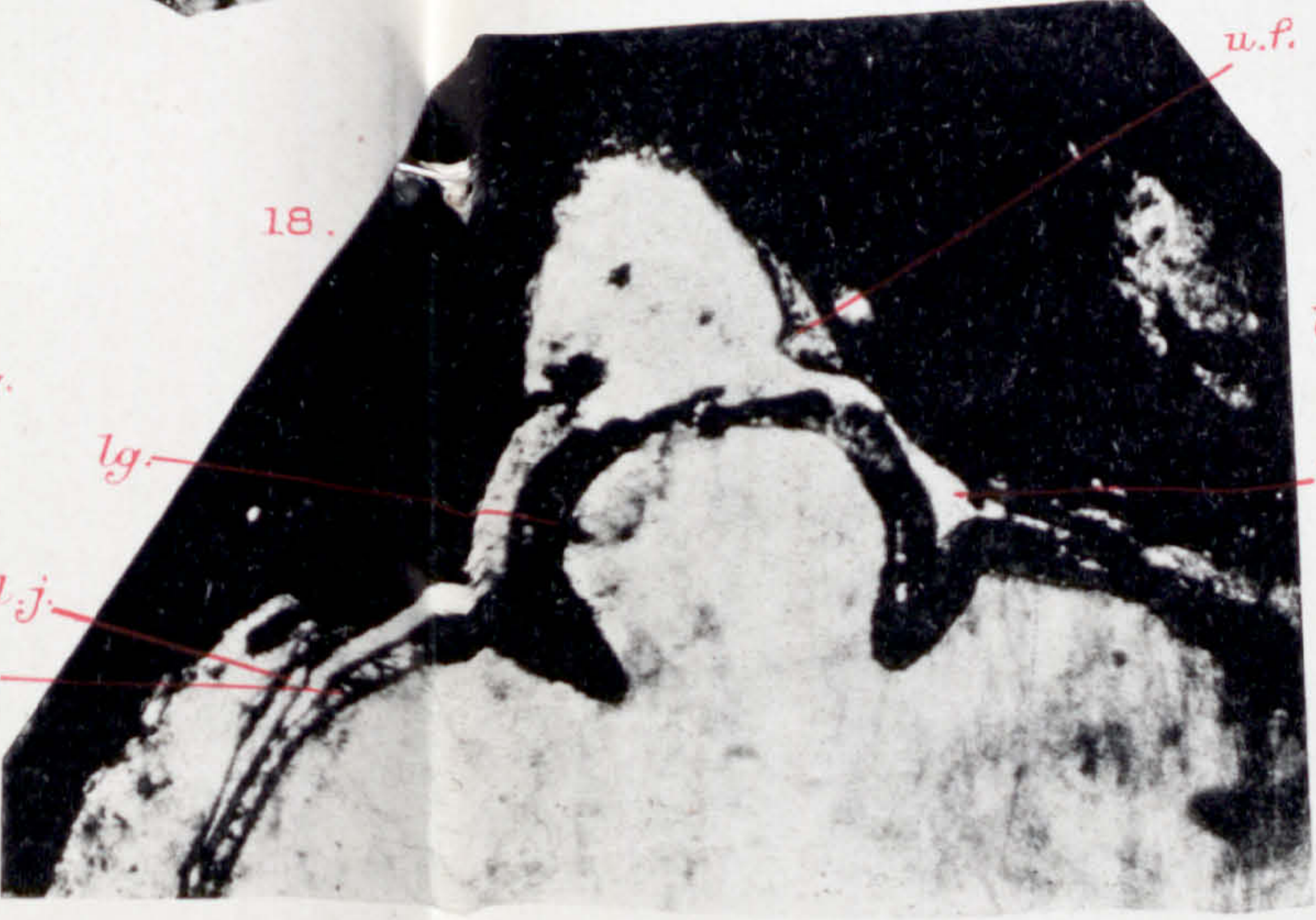
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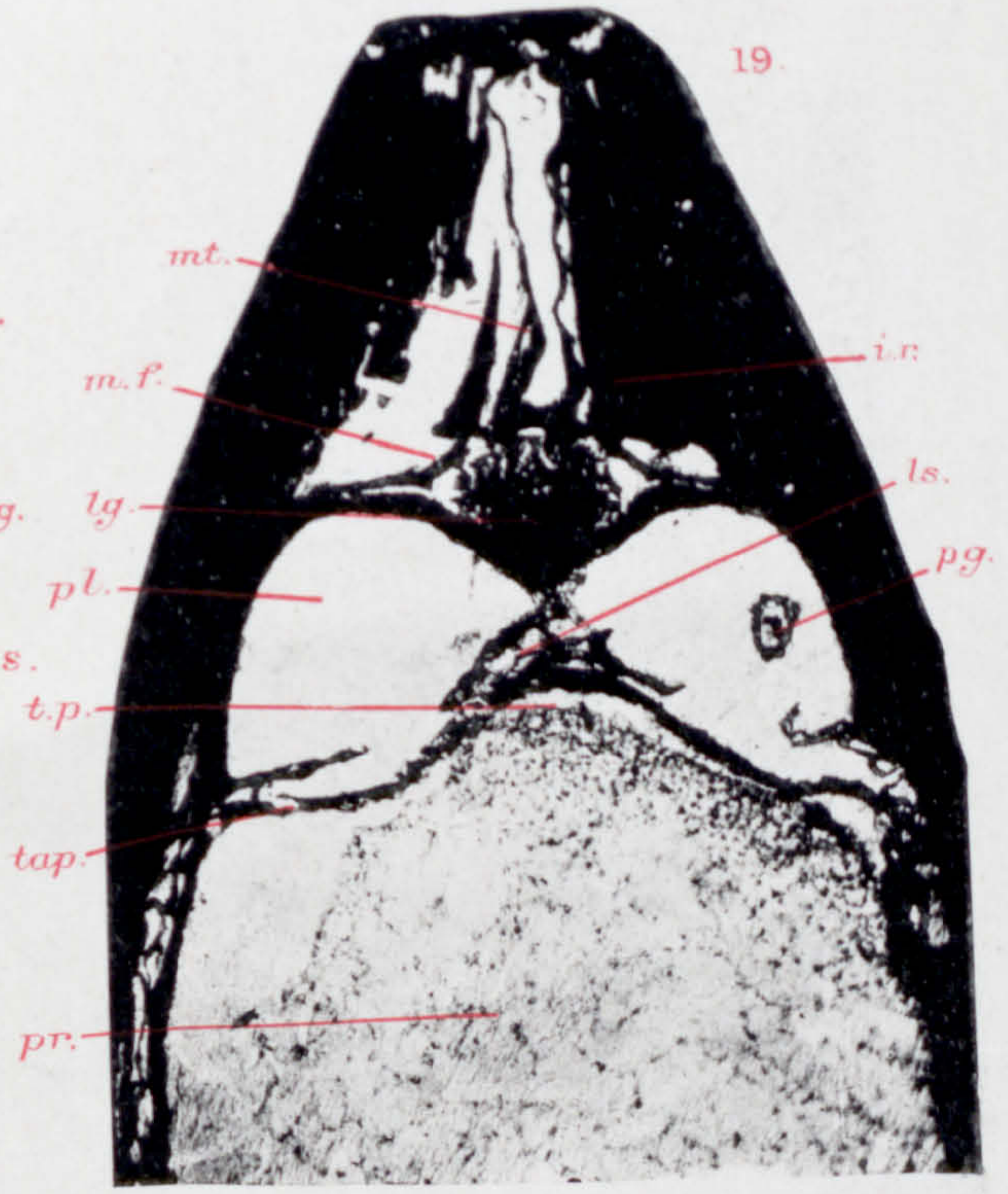
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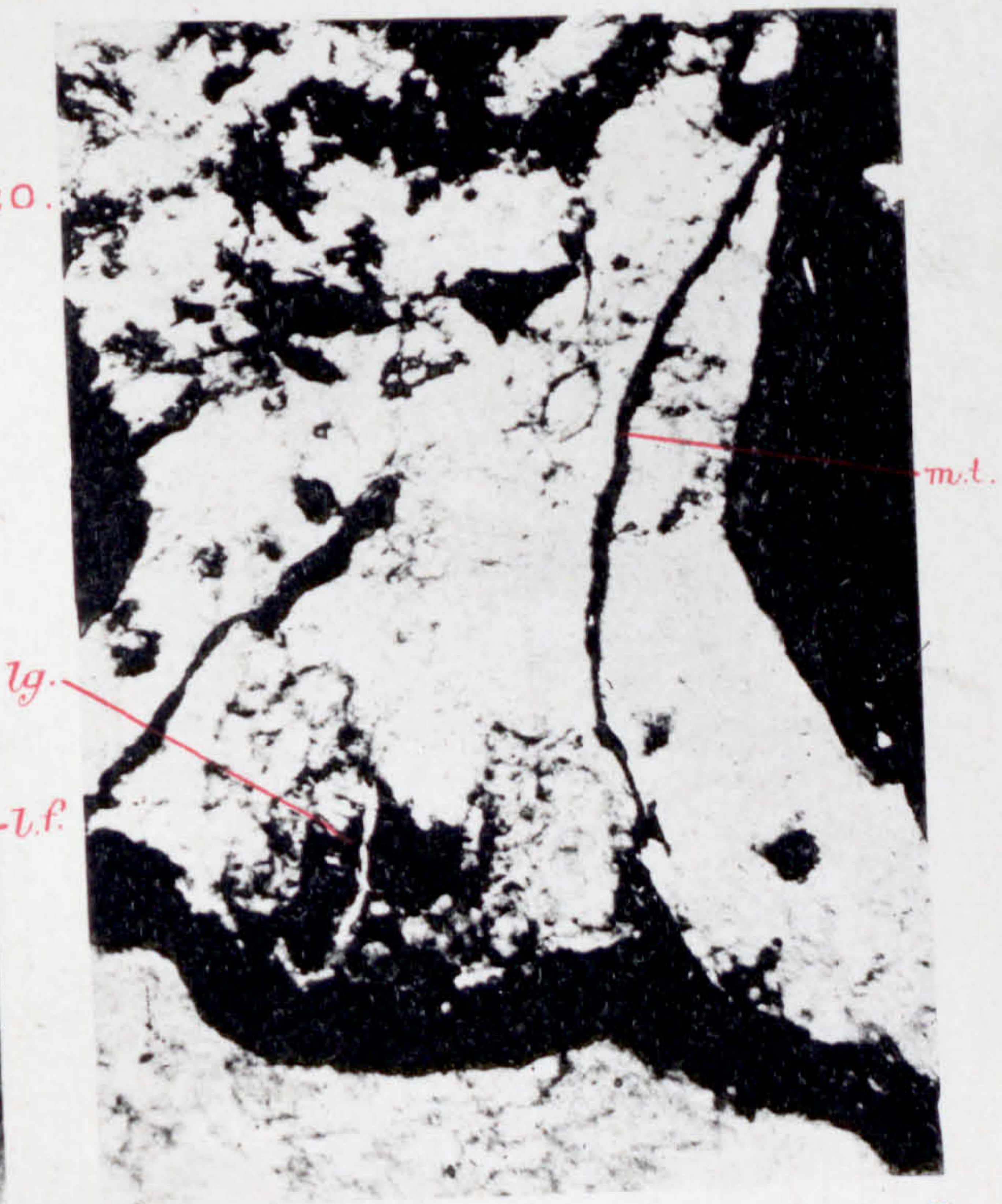
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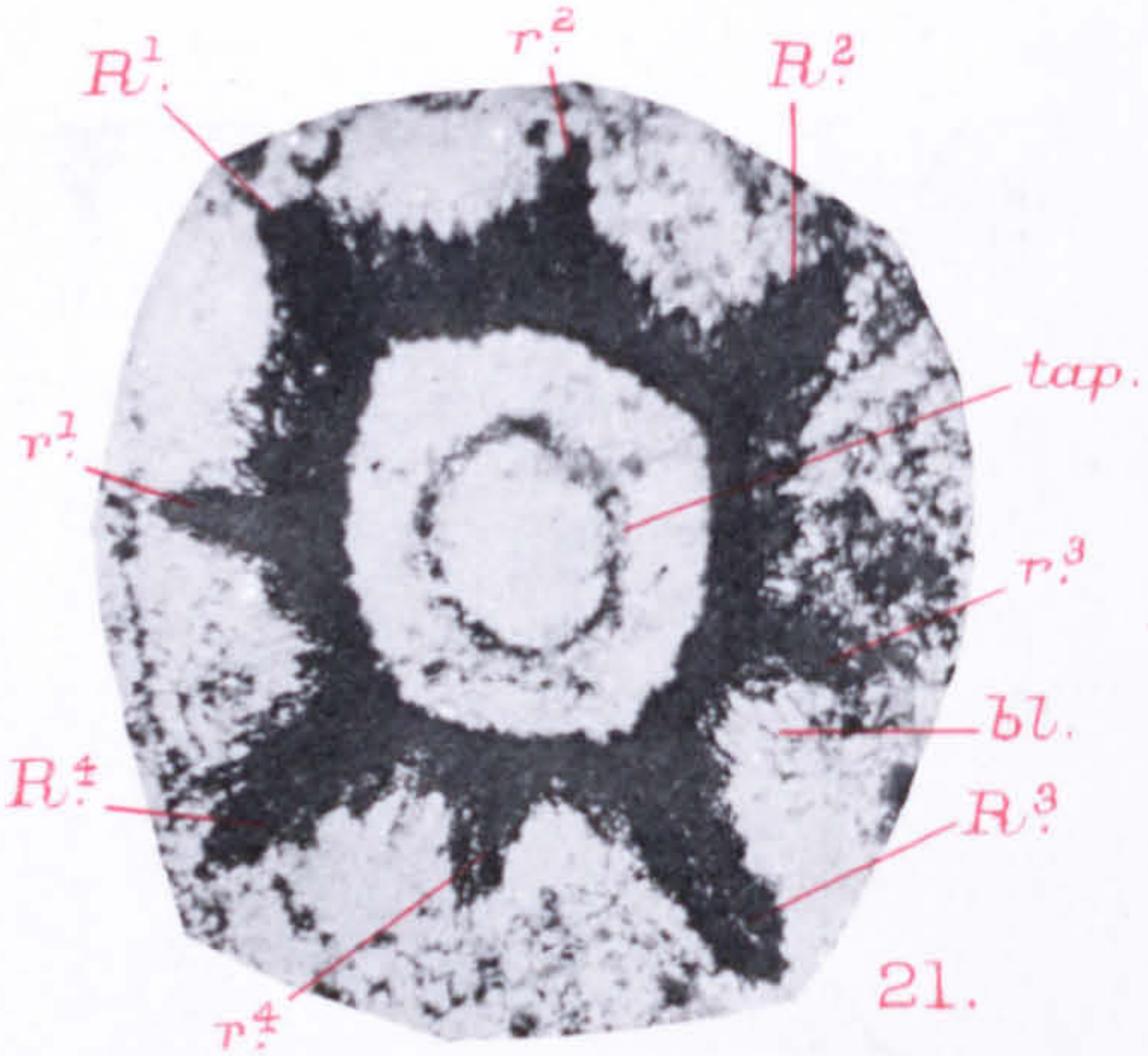

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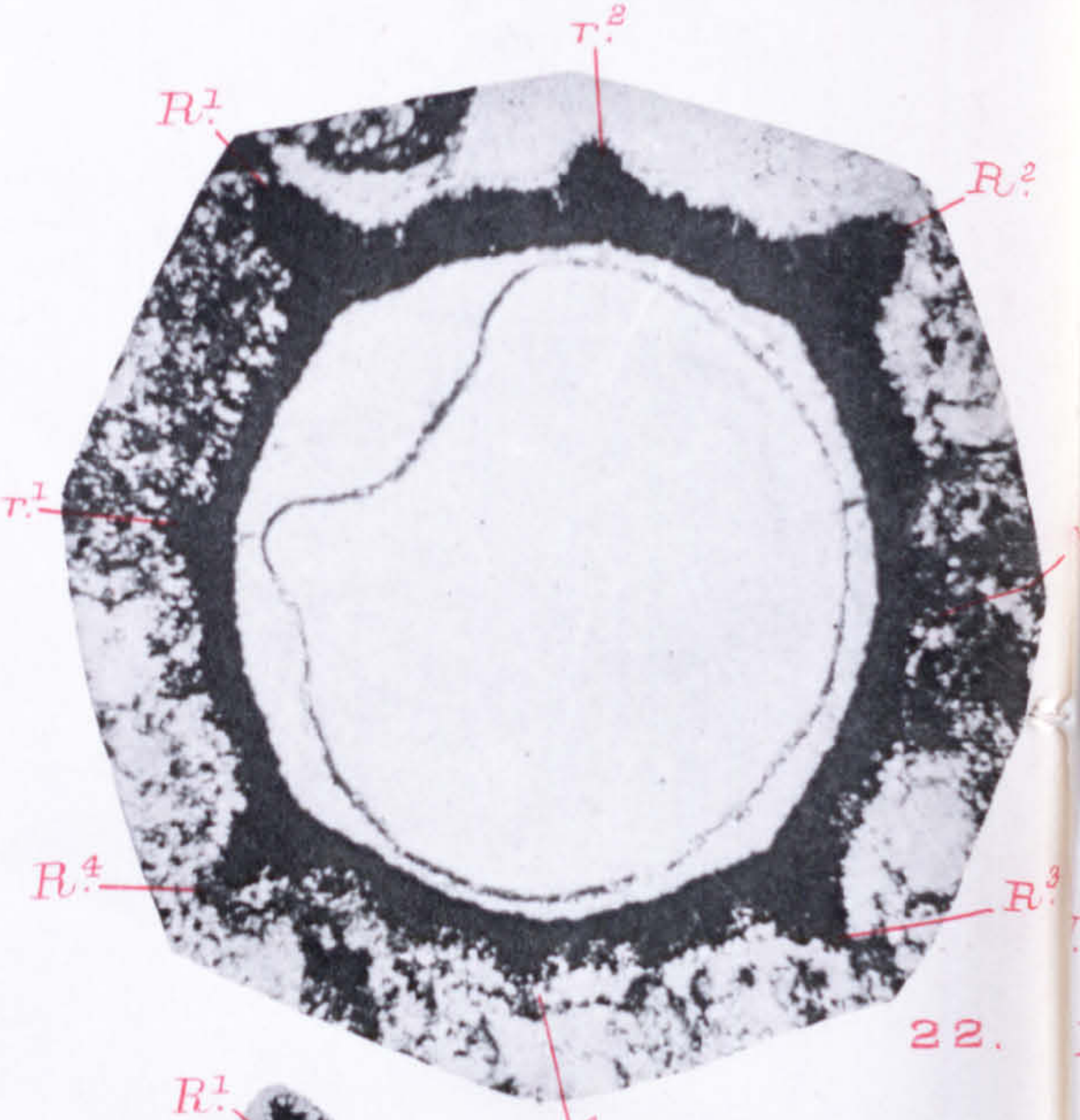

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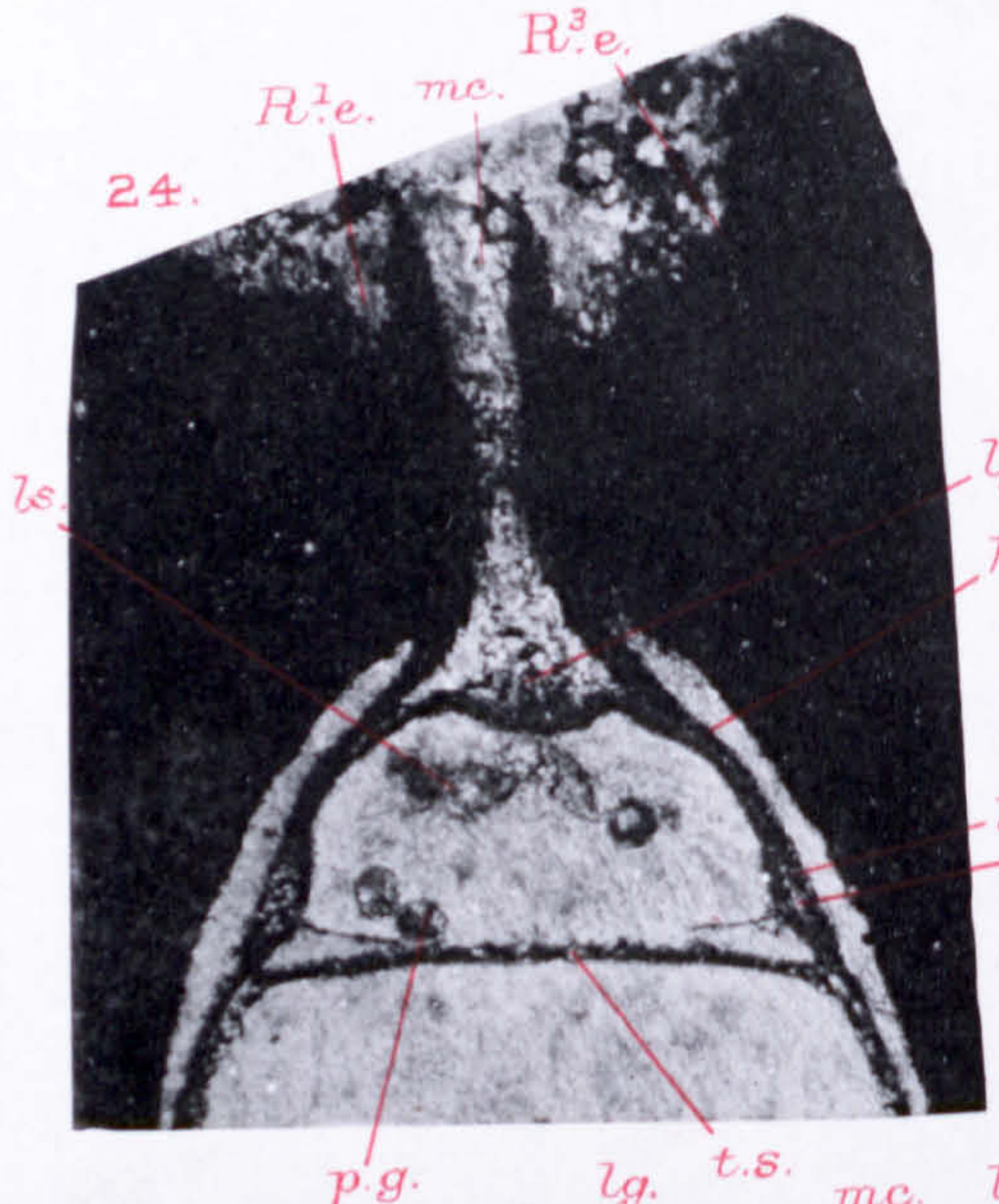

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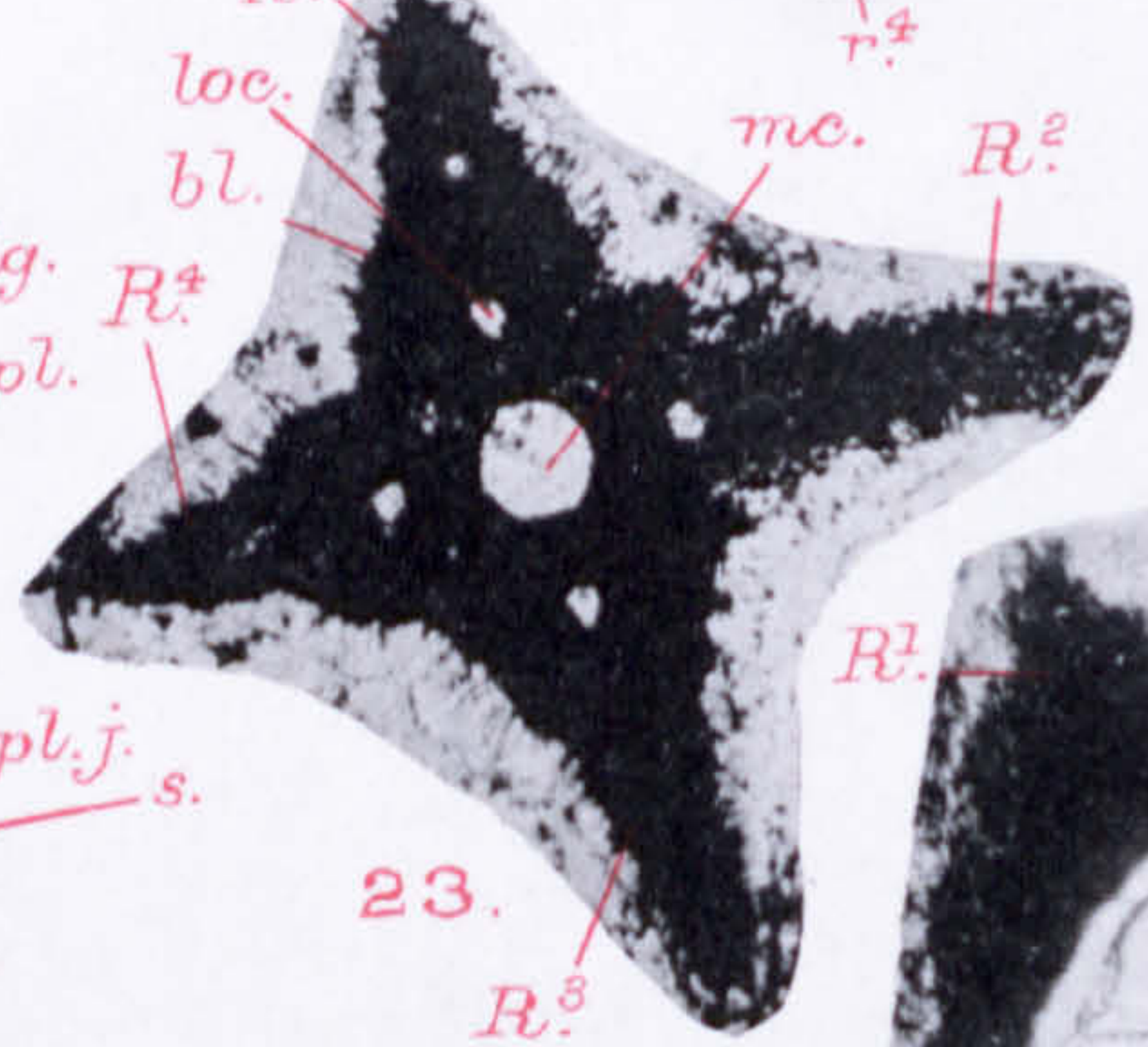

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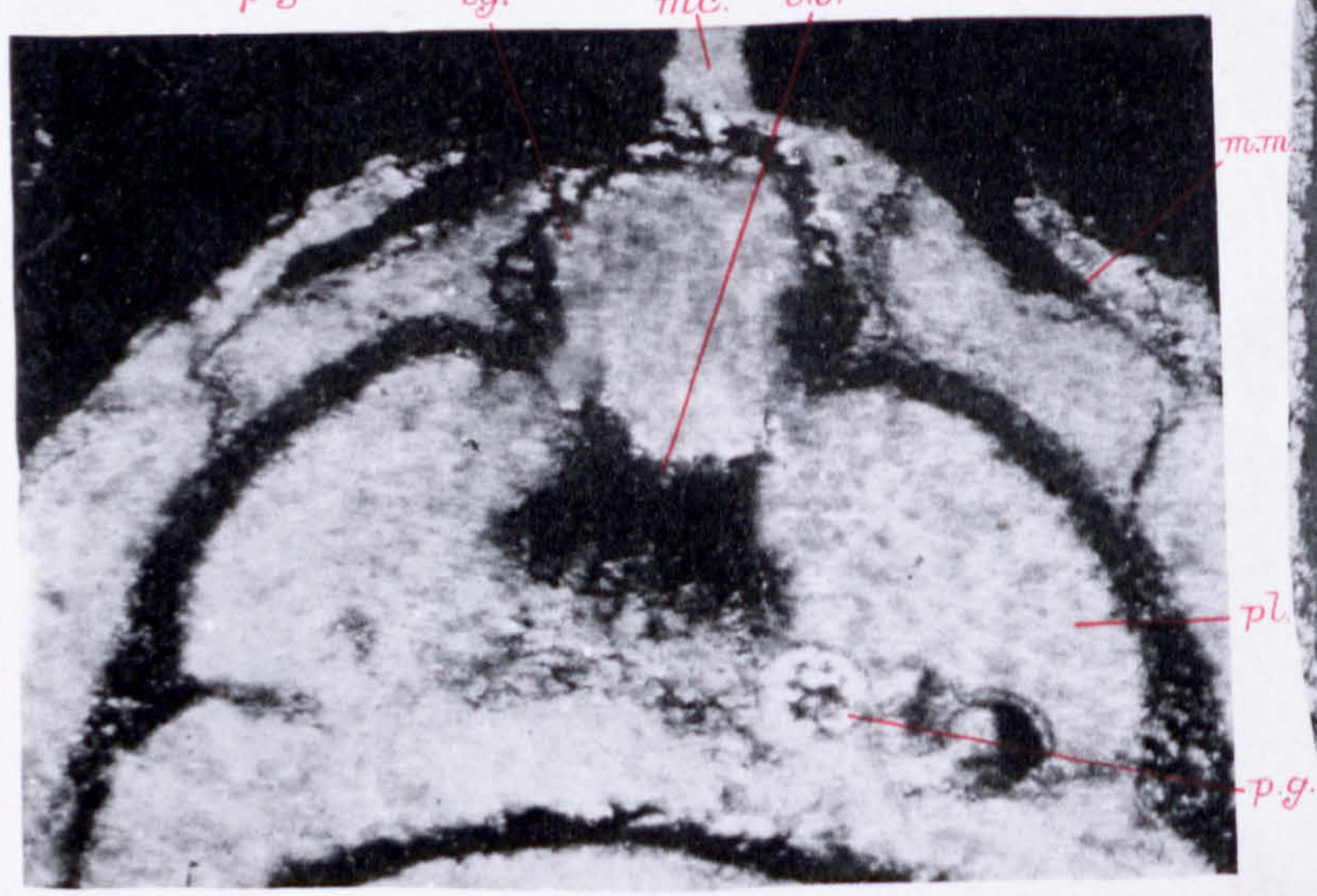

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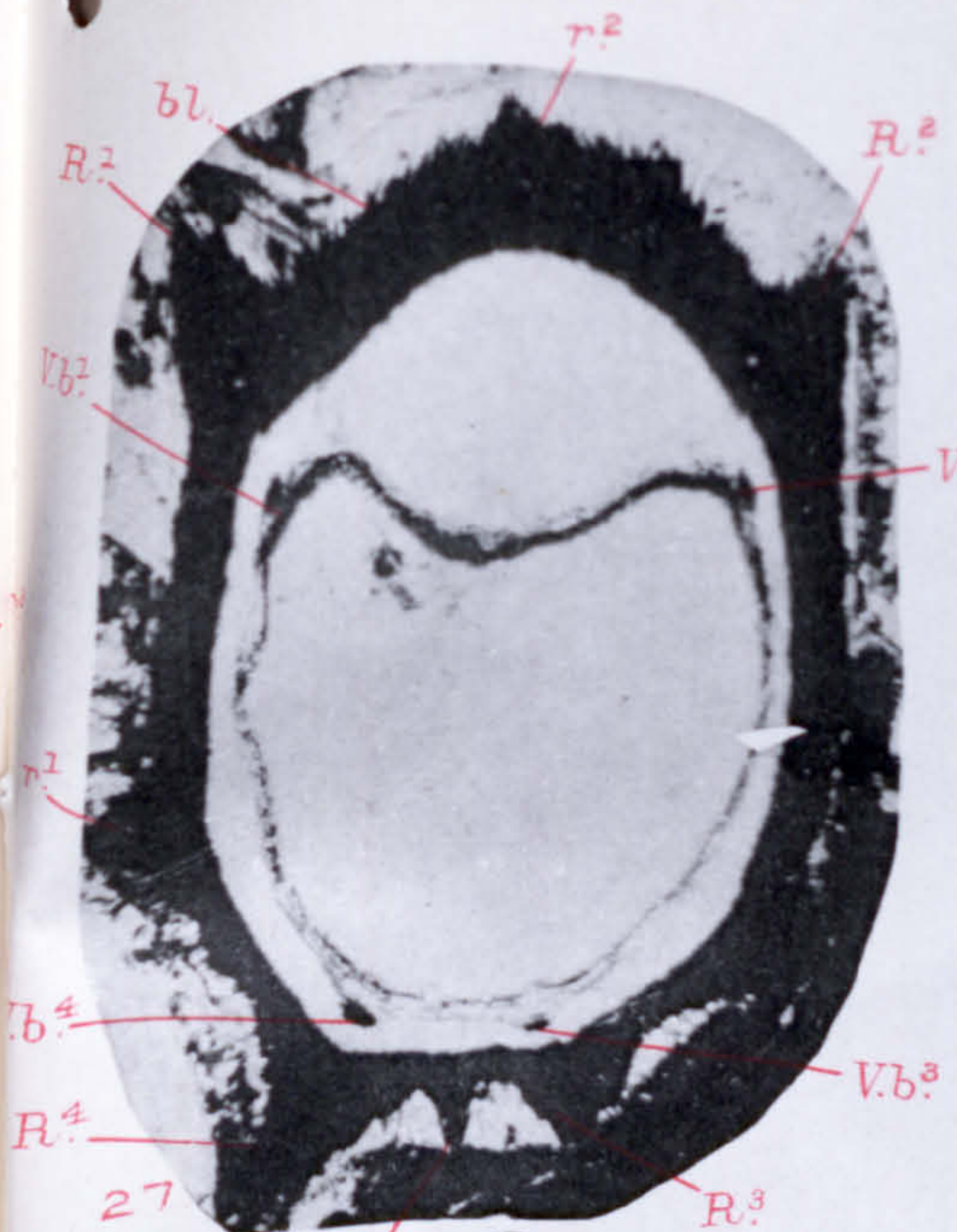

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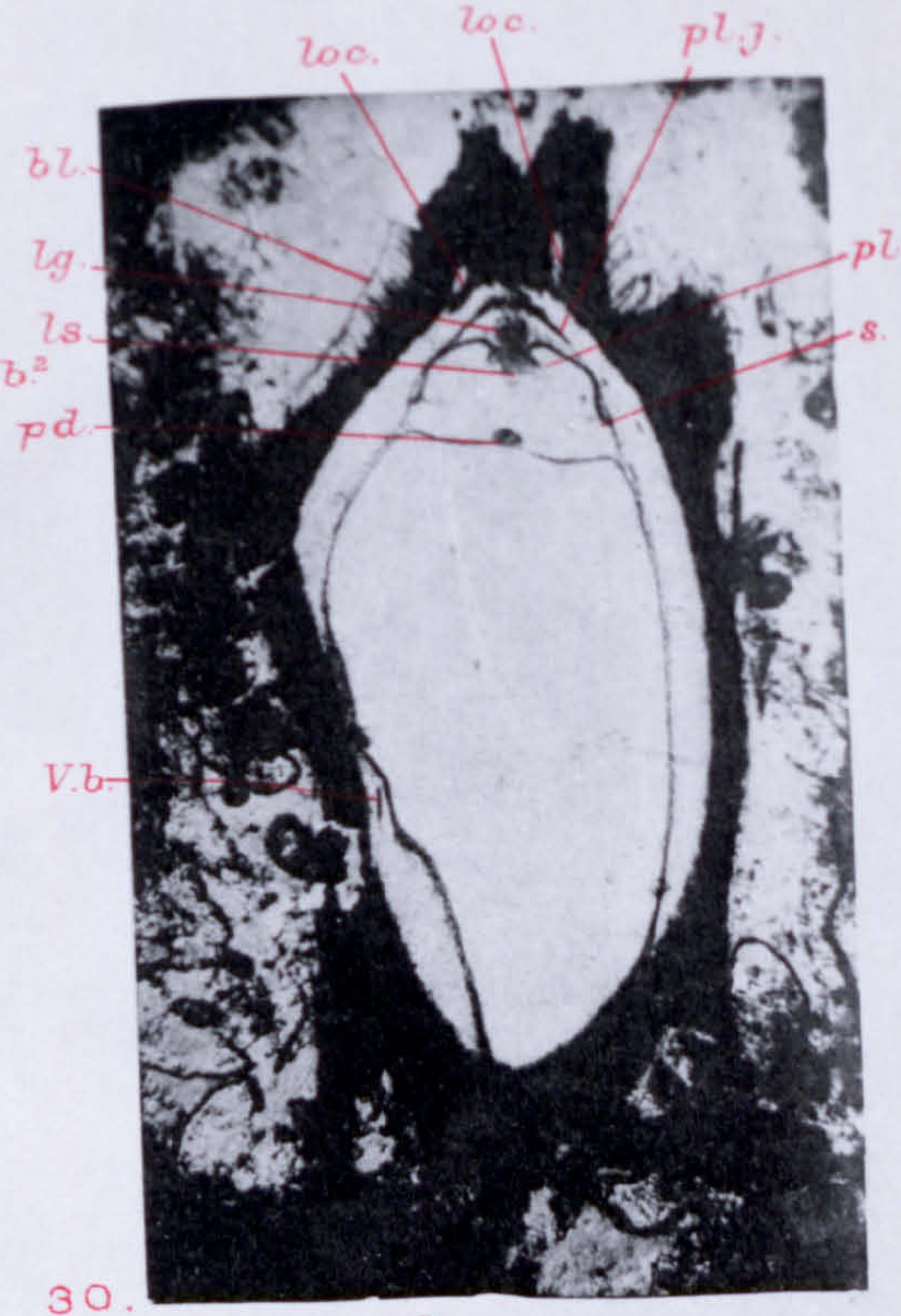

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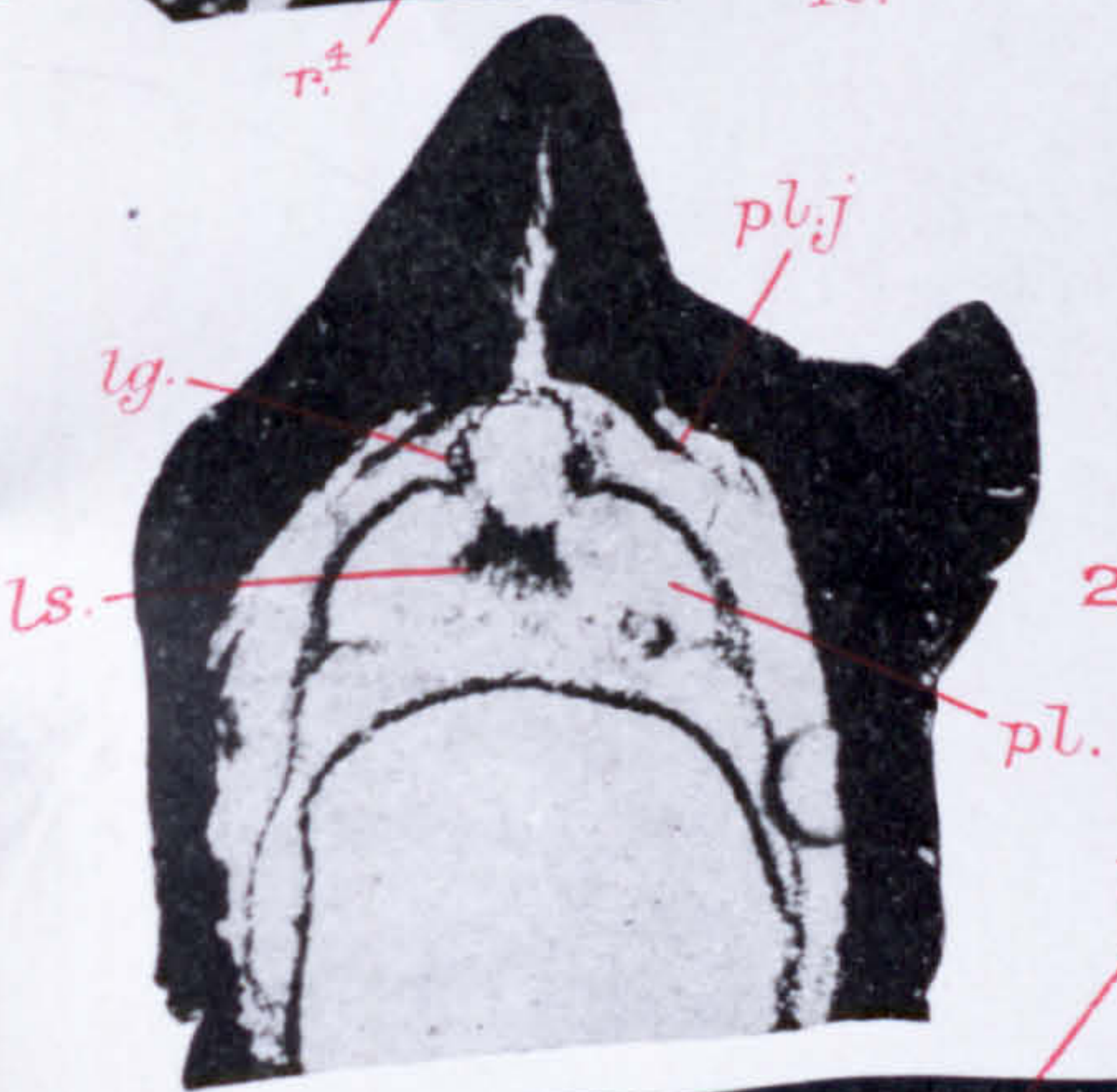

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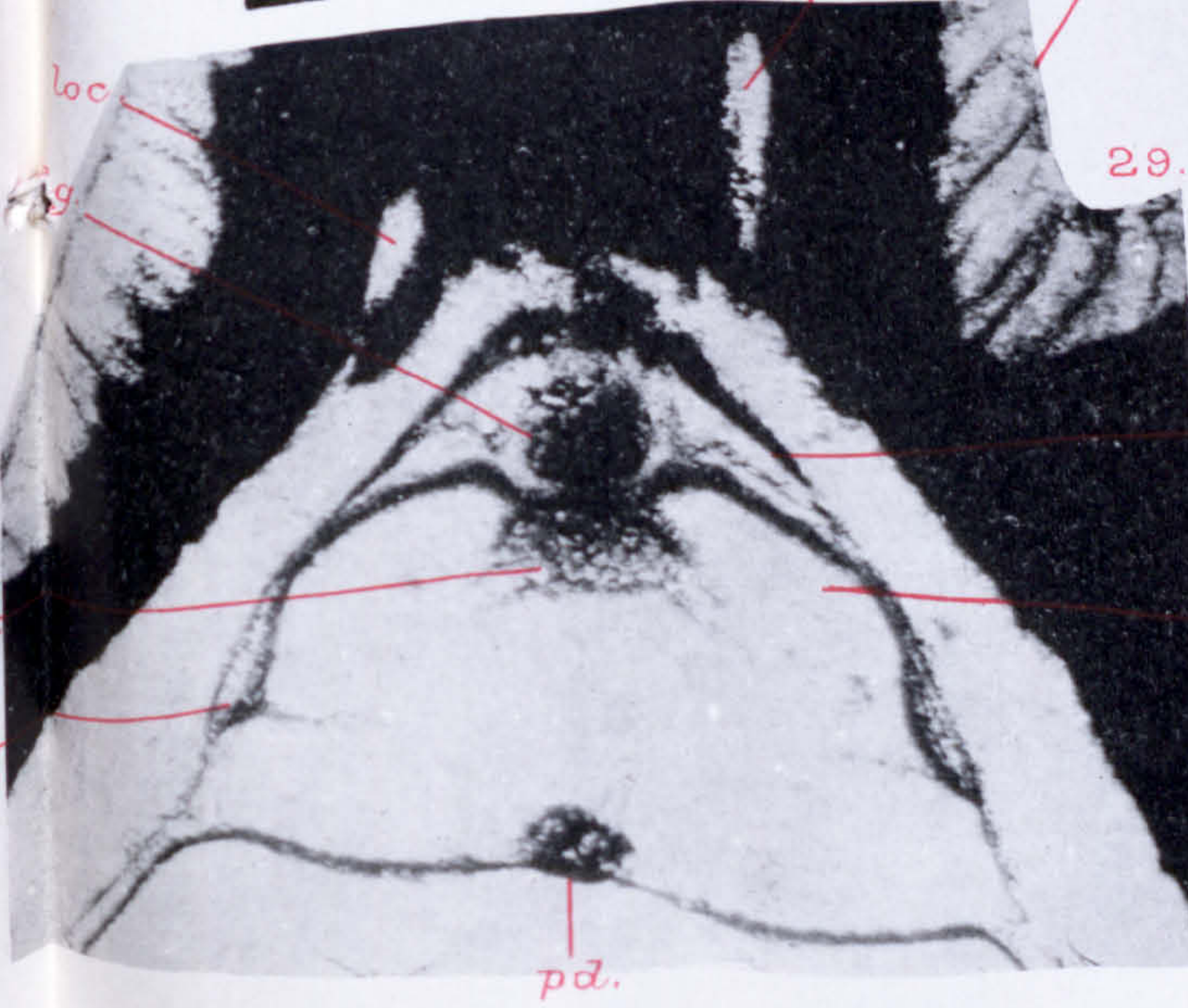

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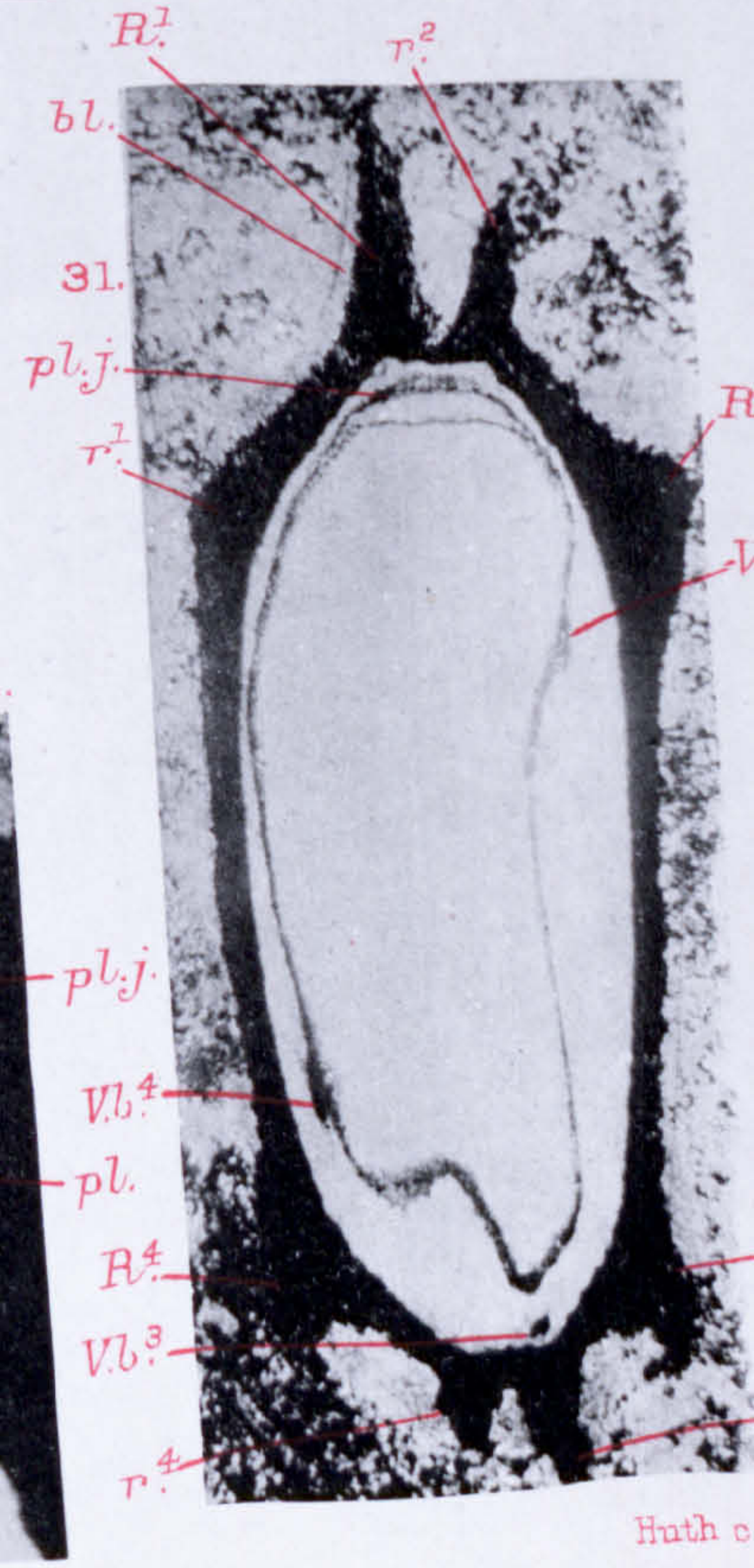

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OLIVER & SALISBURY — CONOSTOMA ANGLO-GERMANICUM.

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# SALISBURY

# ON TRIGONOCARPUS SHORENSIS, SP. NOV.

D. Sc. (Botany.) 1914.
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# On the Structure and Relationships of Trigonocarpus Shorensis, sp. nov:

## A New Seed from the Palaeozoic Rocks.[1]

BY

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**With Plates IV and V and eight Figures in the Text.**

## CONTENTS.

## I. INTRODUCTION.

THE bulk of the material which forms the basis of this communication was placed in my hands for investigation by Prof. F. W. Oliver; and I gladly take this opportunity of expressing my deep indebtedness to him for much helpful advice and criticism, and also for putting at my disposal such slides of the University College Collection as I have had occasion to consult.

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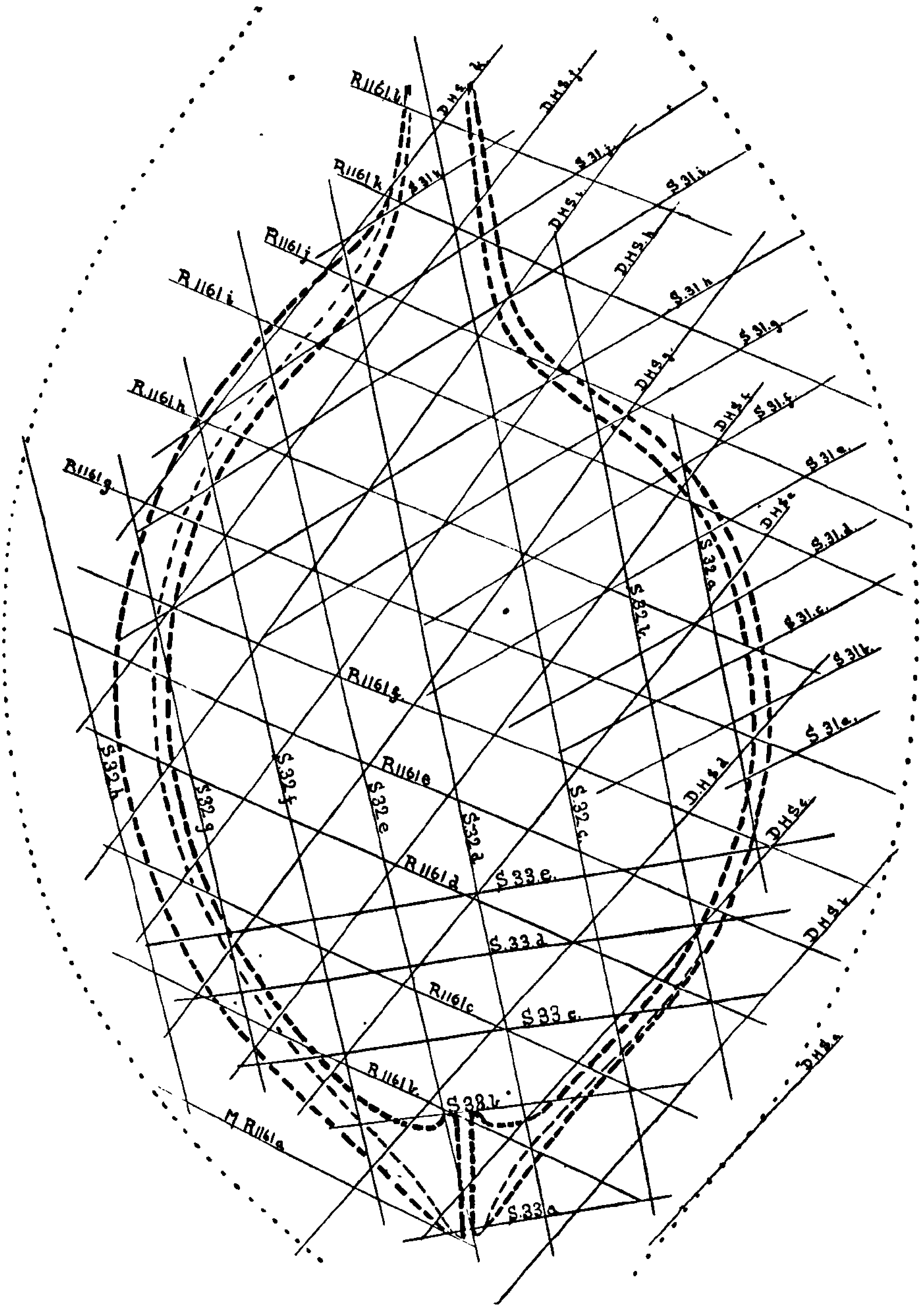
[1] Thesis approved for the degree of Doctor of Science in the University of London.

[Annals of Botany, Vol. XXVIII. No. CIX. January, 1914.]



TEXT-FIG. 1. Plottings on an ideal median longitudinal section showing the planes of all the preparations. D.H.S. = Dr. Scott's series; R. = Owens College, Manchester, series; S. = University College, London, Collection.

My thanks are also due to Dr. D. H. Scott and to Prof. F. E. Weiss for the loan of preparations. To Dr. Scott I am also indebted for permitting me to examine the more important sections in his unique collection of *Trigonocarpus Parkinsoni*, without which an adequate comparison between the two seeds would not have been possible.

The same methods have been employed in the reconstruction of the present seed as were used in the investigation of *Conostoma oblongum* and *C. anglo-germanicum*.[1] These have been recently described in a separate article[2] and need not be recapitulated here.

The sections that furnish data for the following account are all cut from seam nodules obtained from the well-known locality at Shore Littleborough, re-opened through the generosity of the late Mr. Sutcliffe. To mark its origin it has been thought appropriate to designate this seed by the specific name of *Shorensis*.

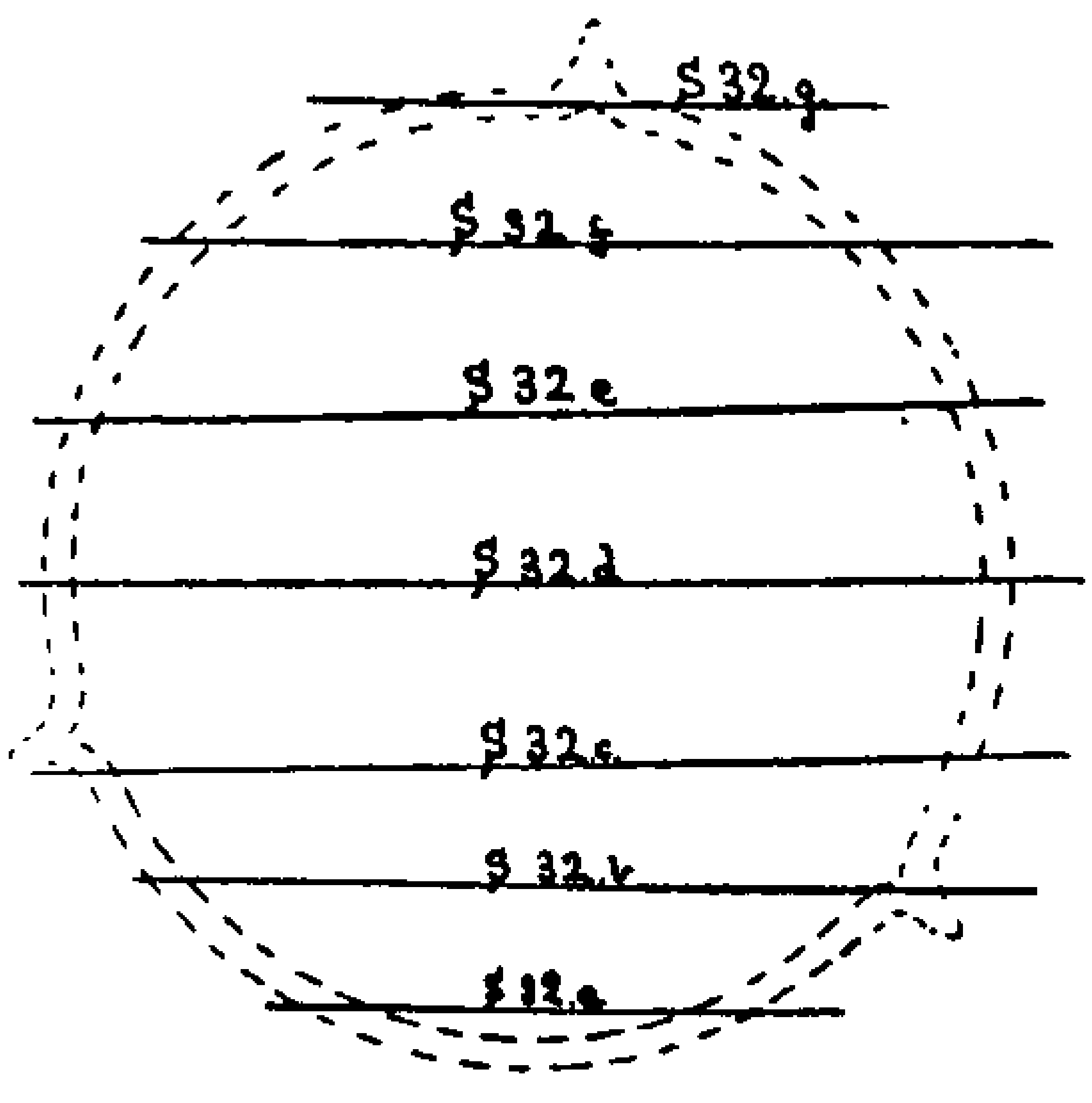
## II. GENERAL FEATURES.

The seed with which the present investigation deals was of large size, approximately elliptical in form, and circular in transverse section. The exact limits at either end cannot with certainty be determined, but the total length was probably considerably over four centimetres. In breadth the seed attained a maximum diameter, about half-way up, of nearly two and a half centimetres.

Although specimens showing the actual attachment of the seed are wanting, the chalazal end certainly tapered towards its insertion and, judging from the general direction of the surface curvature, followed a more gentle curve inwards to the apex.

The testa comprised three or perhaps four layers, the two outer of which constituted a broad sarcotesta remarkable for the presence of a number of scattered secretory sacs and representing nearly one-third of the total width of the seed.

Within the sarcotesta was a hard sclerized shell bearing three salient ridges which extended from the base to the apex. These ridges were symmetrically placed around the body of the seed, and from the chalazal end to about a third the height of the sclerotestal shell were present three more ribs much less pronounced than the former, and occupying positions intermediate between them.



TEXT-FIG. 2. Plottings on the transverse section of the S. 32 series.

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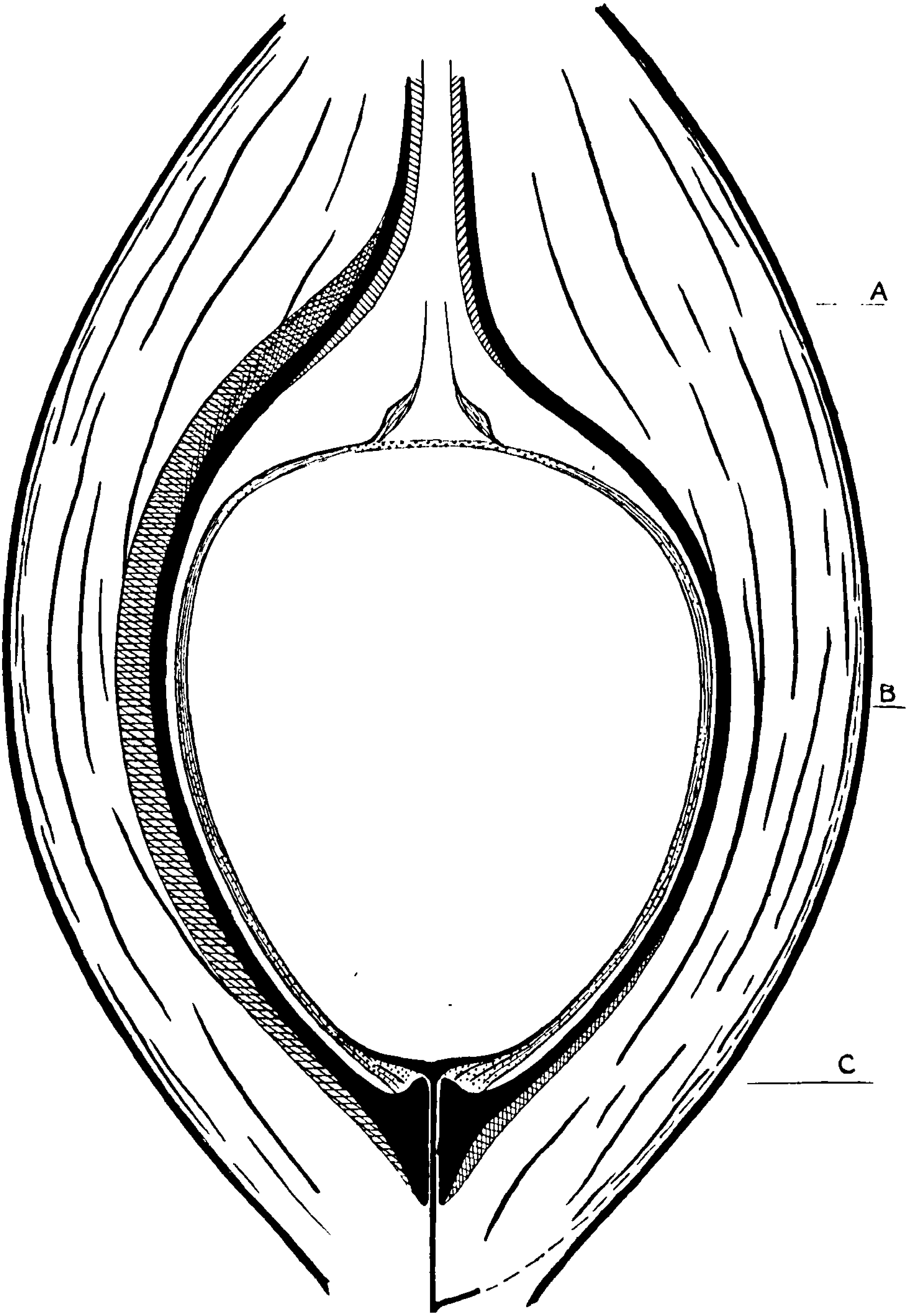
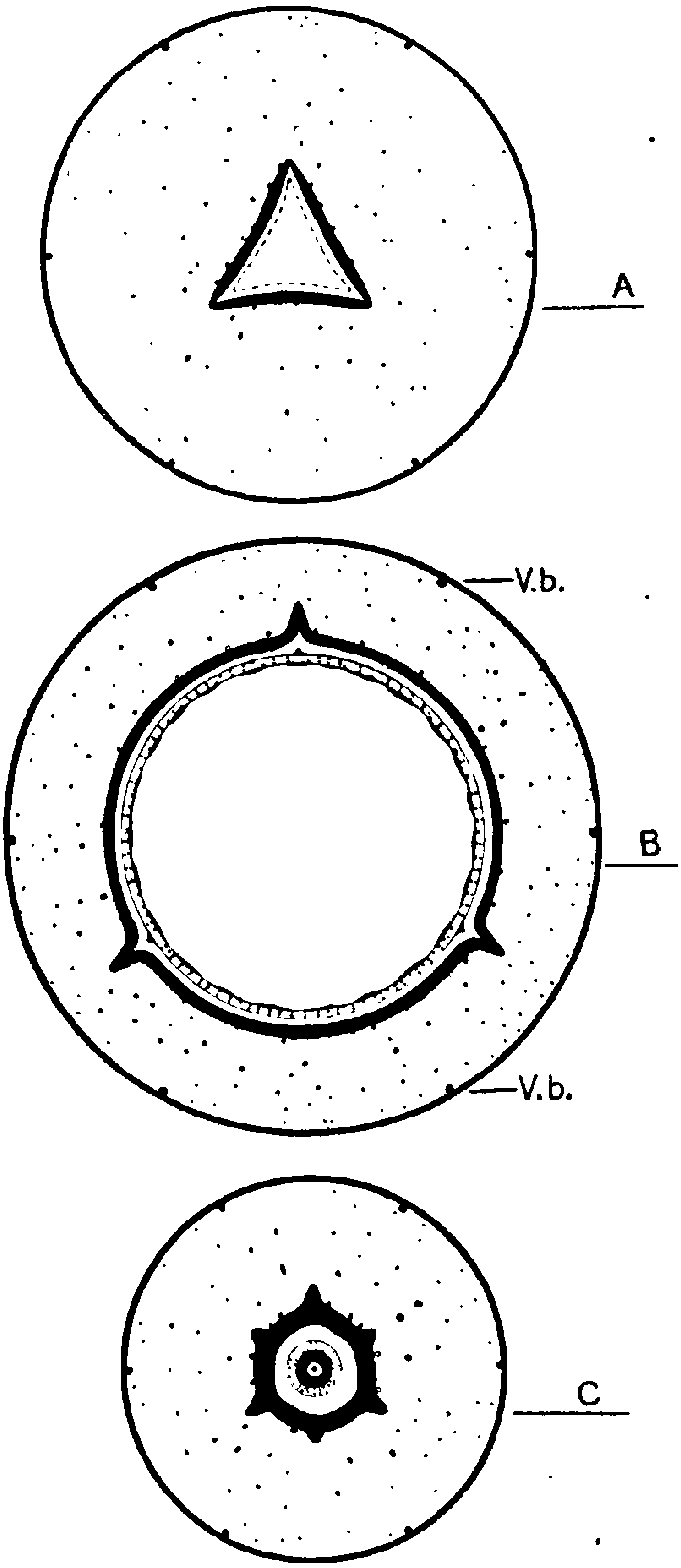
[1] Oliver and Salisbury: On the Structure and Affinities of the Palaeozoic Seeds of the *Conostoma* group. Ann. Bot., vol. xxv, 1911.

[2] Ann. Bot., vol. xxvii, No. cvi, 1913.



TEXT-FIG. 3. Diagrammatic restoration of an ideal median longitudinal section of *Trigonocarpus Shorensis* passing through a primary and secondary rib. The sclerotesta and limiting layers of the sarcotesta are shown in black; the ribs are cross-hatched, and the inner flesh, the extent of which is hypothetical, is represented by diagonal shading. The branching of the chalazal bundle is based on analogy with *T. Parkinsoni*, and the direction of one of the sarcotestal strands is also shown as a dotted line, though not actually present in the plane of section. Nucellar tissue dotted, secretory sacs black.



TEXT-FIG. 4. Transverse restorations of *Trigonocarpus Shorensis* at the levels A, B, C in Fig. 3. Tissues represented as in the previous diagram. The six sarcotestal strands are represented by large black dots, and the secretory sacs by smaller.

In the chalazal region there were thus six ribs, of which three soon die out, whilst the remaining three persist.

In general form the sclerotesta was ovoid, the pointed end corresponding to the chalazal region, whilst the blunt end was surmounted by a triangular micropylar tube, the angles being continuations of the ribs lower down, into which they pass by a hollow curve.

Within the sclerotic tissue was a fourth layer, probably confined to the micropylar region and representing the 'inner flesh' of related seeds.

The megaspore cavity was much less pointed at the base than was the hard shell around, and through this divergence of the two surfaces a chalazal cushion of sclerotic tissue was formed from which arose a nucellus, that stood up erect and free within the seed cavity, surmounted at its apex by a large pollen-chamber.

The nucellus was bounded at the exterior by a well-differentiated epidermis, and within was a tracheal sheath forming the upward continuation of a single vascular strand which pierced the chalazal cushion.

The vascular organisation was essentially similar to that of other seeds of this group, and consisted of a sarcotestal system of bundles without and a nucellar system within.

Neither pollen nor prothallus are preserved in any of our sections, which may indicate that all our specimens were abortive ovules, though the presence of numerous fungal spores within the megaspore cavity may indicate its former occupation by an organized tissue which served as nourishment to the saprophytic organisms.

## III. THE TESTA.

### 1. The Sclerotesta.

The obovoid sclerotesta had an average thickness of about 0·5 mm. and bore, as we have seen, six longitudinal ribs, of which the three major persisted as far as the triangular beak. At the apex these ribs pass gradually into the three angles of the micropyle, and, except at the base, are commissured. The major ribs from the base of the micropyle to within some 6 mm. of the chalazal extremity have about the same radial extent, but exhibit varying development in the different specimens (0·75 mm. from surface in S. 33, *a–e*, to 1·4 mm. in S. 31, *a–k*). The three minor ribs alternated with the three major, were without commissures, and attained their greatest extent (0·4 mm.) about 2 mm. from the base, above which point they gradually diminished and finally died out some 8 mm. from the chalaza. At the base of the seed the sclerotesta formed a solid inverted cone about 3·5 mm. high, perforated by a narrow canal through which the single vascular bundle passed to the floor of the nucellus. The base of this cone projected upwards as a dome-shaped papilla about 0·5 mm. high and 1·5 mm. in diameter, and its margin served as the place of attachment for the nucellar epidermis. As the ribs, both major and minor, approached the chalazal end they became gradually smaller till at the extremity all indication of ribbing had disappeared. The cavity within the sclerotesta was, owing to the sclerotic papilla, much blunter than the external form, and from the base of the micropylar canal measured some 19 mm. with a diameter in its broadest part of slightly over 14 mm.

Sections through the micropyle (Pl. IV, Fig. 2) show that the sclerized sides of the triangular canal about half-way up, formed of four layers of longitudinally directed fibres, were from 0·13 to 0·14 mm. in thickness and distinctly concave, the internal diameter of the canal measured from the apex of an angle to the middle of one of the sides being just over 2 mm. In the highest of our sections (Pl. IV, Fig. 5), viz. Man. Coll. R. 1161, *b*, the limit between sclerotesta and sarcotesta is indefinite and the diameter of the micropyle is reduced to 1·4 mm. On that side of this oblique section which is at the higher level the sclerized layer is seen to be even less developed than on the lower, and the concavity of the flanks has resolved itself into a slight double convexity (thickness between the angles 0·10 mm. and at the convexities 0·16 mm.) (Pl. IV, Fig. 8, *m, c*).

Although this section is broken there is evidence that the sclerotesta towards the apex segregated into three distinct portions separated at the angles by intervening soft tissue and each itself composed of two parts fused in the median plane.

Except for the slight local thickening, both here and in the preceding section, there is a thinning down of the sclerotic beak which, if maintained at the same rate, must have resulted in its complete elimination at a level not far above that at which our section was cut.

From these facts it would appear that the beak was comparatively short (probably not more than 8 mm. in length), although the extensive development of the sarcotesta at this level and the curve which successive sections show its surface to have followed indicate a much further persistence of that tissue. So that in this respect our seed resembled most closely the condition that obtains in present-day Cycads.

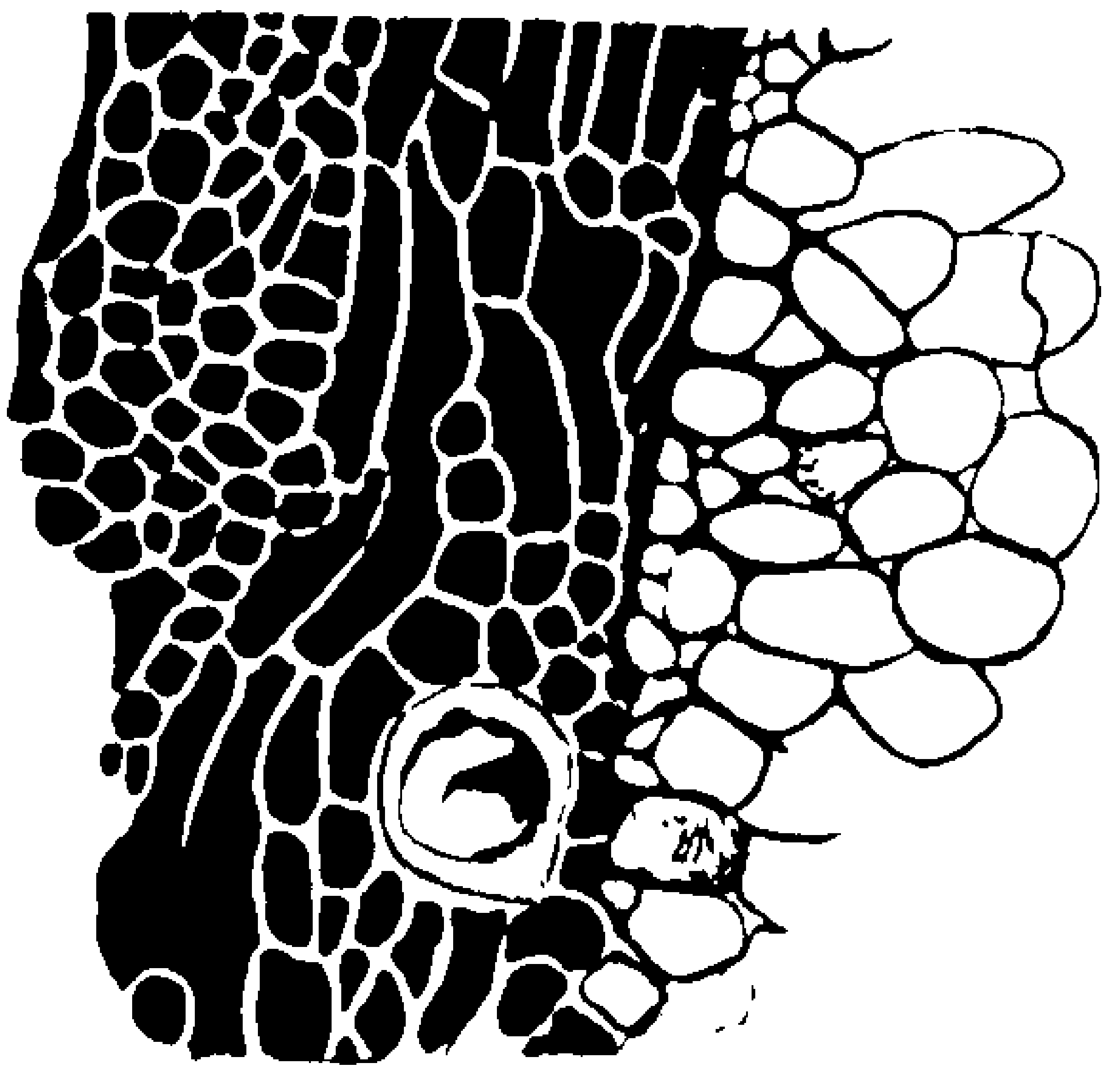
*Histology of the Sclerotesta.* The sclerotesta was formed of from 14 to 15 layers of thickened fibrous elements, of which the inner, and most of those forming the ribs, were longitudinally directed. In the best-preserved specimens the innermost layer is seen to have been composed of radially flattened fibres which form a smooth internal surface, and negative the suggestion of a more interior tissue. In transverse sections the fibres appear rounded or polygonal (28–42 $\mu$) with dark contents separated by a thin membrane (? middle lamella), on either side of which is a translucent yellow zone about 3·5 $\mu$ in width perhaps representing the cell-wall. The fibres consisted of superposed cells which can be traced for over 1·5 mm.

The sclerotic fibres, 5–9 deep, forming the outer layers behave as aggregates or bands, each of from one to two elements in the radial direction and of a very variable number in the tangential (Text-fig. 5). For a time each band follows the longitude of the seed, and then almost abruptly all the fibres bend, some to the right and others to the left, or all of them in the same direction, so that their course is at a very narrow angle with the horizontal plane, and in transverse sections they appear cut obliquely or almost longitudinally for some distance. Where the members of a band are in one layer they appear to all bend in a similar manner, but where the band is more than one element in thickness those of each layer probably bend in opposing directions, but it cannot be definitely ascertained whether or no they again take up a longitudinal direction.

The extreme irregularity of the course of the fibres is shown by the inconstant numerical relation between those cut obliquely and transversely, and, to still further complicate the structure, the bands do not always remain in the same vertical plane.

Owing to this complex interlacing of the outer elements of the sclerotesta, it presents a plait-like appearance when cut by sections tangential to the surface, as is seen in Pl. IV, Fig. 3.

Eventually the thickened elements of the sclerotesta pass obliquely outwards by a well-marked transition into the sarcotesta.



TEXT-FIG. 5. A portion of the sclerotesta as seen in transverse section, showing the vertically directed fibres at the interior and the almost horizontal direction at the periphery; a single secretory sac is also present.

In the outer part of the sclerotesta, and there only, elongated secretory elements partially or entirely immersed in the sclerotic tissue are present, which pass out into the sarcotesta at one point and occasionally into the sclerotesta again at another (Pl. IV, Fig. 6, *m.s.*). In all respects these secretory elements resemble those present in the sarcotesta.

For convenience of description the sclerotesta has been treated as consisting of two parts, the plane at which the different structure is assumed being variable. There is, in fact, little doubt that the outer zone represents the terminations of a large portion and perhaps even all of the longitudinally directed fibres, and cannot possibly be regarded as the region of fusion of two morphological surfaces, as has been suggested for the stony layer of the Cycadean ovule.[1]

## 2. The Sarcotesta.

(*a*) *General Structure.* The sarcotesta in the living state must have been the most pronounced feature of this seed, for even as petrified it invests the sclerotic shell in the middle region to a thickness of over 4 mm.

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[1] Stopes: The Double Nature of the Cycadean Integument. Ann. Bot., vol. xix, 1905.

At the base this decreased to under 2 mm., but the almost sudden concavity of the sclerotesta at the micropyle gives the sarcotesta in that region a maximum thickness of nearly 6 mm. Although our highest sections pass not far below the apex no flattening is exhibited, but the sarcotesta curves inwards equally on all sides. This is in conformity with the impressions of seeds attached to *Neuropteris heterophylla* and *Neuropteris obliqua* described by Kidston[1] and Kidston and Jongmans.[2]

The junction of the sclerotesta with the sarcotesta, composed as the latter was of thin-walled cells, appears superficially as a sudden change, but the innermost cells of the sarcotesta can be recognized as direct continuations of the rows of sclerized elements. It is only in tangential or longitudinal sections that this transition can be properly seen, since the innermost sarcotestal cells, which are elongated and tubular (0·15 mm.–0·25 mm. x 0·033–0·049 mm.), are directed obliquely outwards and upwards (Pl. IV, Fig. 5). Owing to this the transition, which was of equal gradation throughout, appears much more sudden in transverse sections through the middle region than in those through the base or apex, where the surface is cut obliquely. This may perhaps be true also of the similar observations of Scott and Maslen[3] for *T. Parkinsoni.*

Very frequently cells comprising the innermost layer of the sarcotesta are seen cut longitudinally, also in tangential sections (Pl. IV, Fig. 5, *st. c.*) these cells alter their direction in a similar sinuous manner to those of the outer sclerotesta. Here and there slight thickening of the walls can be detected, and the intercellular spaces are either very minute or completely absent. It is clear, then, that the structure of the cells and architecture of the innermost tissue of the sarcotesta were essentially the same as in the outer layers of the sclerotesta—a continuity of structure which can only be reconciled with a homogeneity of origin. As we pass further outwards the intercellular spaces become more and more pronounced, and the constituent cells, at first tubular, very quickly become more rounded, and *pari passu,* as we pass to the exterior, develop irregularities in the form of projections which connect on to those of adjacent cells and give an almost stellate structure to the tissue (Text-fig. 6).

Owing to the rounded character of the middle sarcotestal cells, the intercellular spaces between them were of more or less equal dimensions in every direction. At a very little distance out, however, the cells were slightly flattened, and tend, especially at the periphery, to form short vertical series separated from one another by elongated lacunae. Sections in this plane also show that the arms or projections of successive cells were often superposed, so that each large lacuna is frequently without trabeculae,

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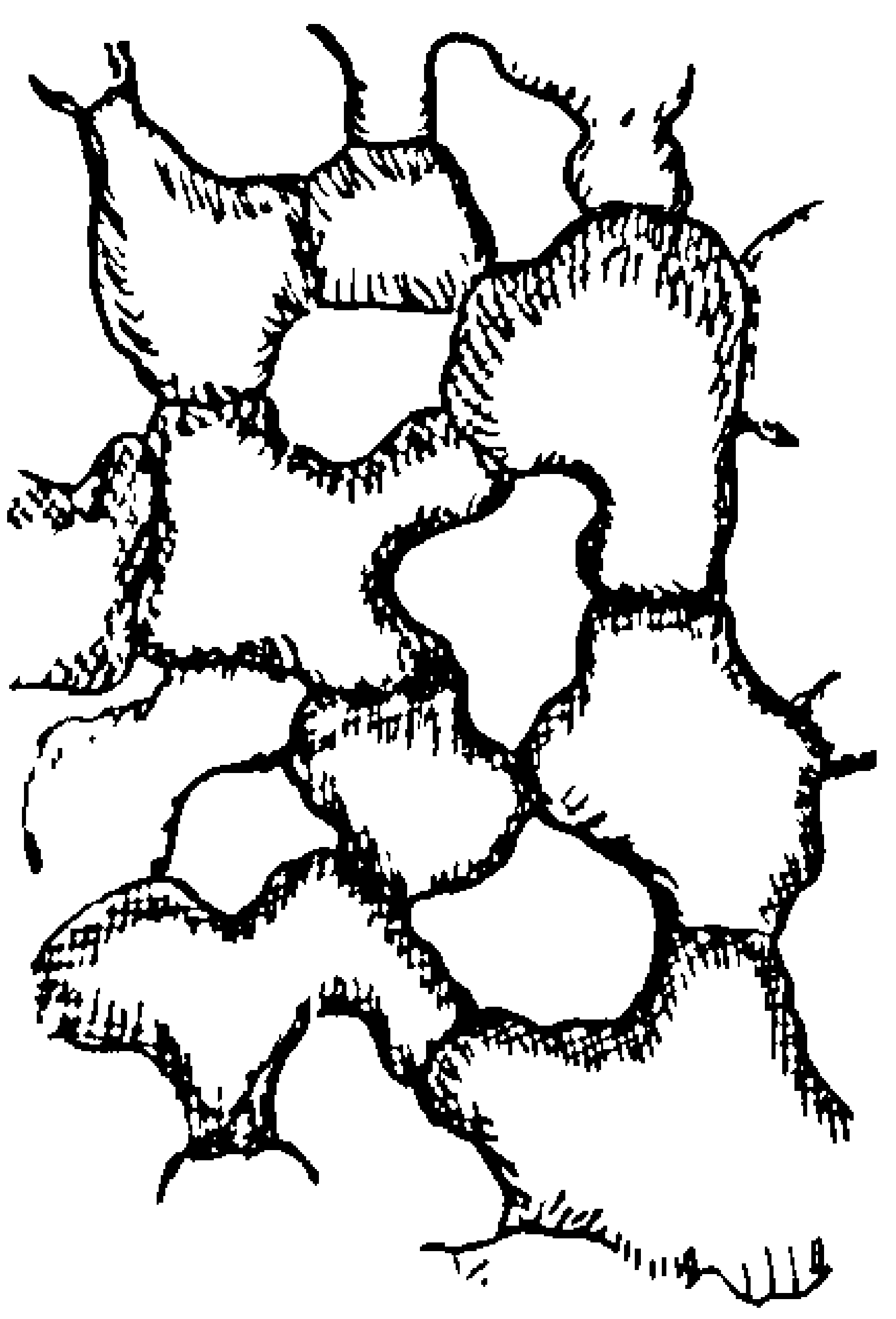
[1] On the Fructification of *N. heterophylla.* Proc. Roy. Soc. London, vol. cxcvii, 1904, p. 1.

[2] Archives néerlandaises d. sci. exactes et naturelles, sér. iii, B, tome i, 1911, p. 25.

[3] Ann. Bot., vol. xxi, No. lxxxi, 1907.

and the projections themselves often appear as narrow vertical series partially or completely separating adjacent intercellular spaces (Pl. IV, Fig. 10). Although the above fundamentally expresses the arrangement of the cells in this region, it was subject to great irregularity.

In the living condition this tissue must therefore have been remarkably light and spongy, and if these seeds were shed into water would render them of great buoyancy. Several seeds of this affinity, e.g. *Trigonocarpus Parkinsoni*,[1] *Pachytesta*,[2] and *Aethiotesta elliptica*,[3] exhibit a lacunar sarcotesta, and the suggestion put forward by Renault for *Aethiotesta* that this served as a mechanism for dispersal by water may well have been true also in the present instance, all the more that the method of occurrence of fossilized vegetable remains favours the view that they were in part components of water-borne drift.



Text-fig. 6. A small portion of the outer sarcotesta, showing the large intercellular spaces.

(*b*) *The Peripheral Zone.* At the exterior the sarcotesta was bounded by a very ill-preserved layer of thin-walled cells (1·5 $\mu$–3 $\mu$ tangential × 2 $\mu$ radial). Beneath this epidermis there were numerous sclerized fibres between which a soft-walled parenchymatous tissue was most likely present originally, though all except a few remnants of walls have become disintegrated.

The total width of this peripheral zone where there is no evidence of crushing or contraction is about 0·3 mm. In most cases the sclerized elements appear irregularly scattered, probably due to post-mortem changes, as in several places, where this zone has almost retained what was probably its original width, they are seen to be grouped together to form somewhat irregular radial plates (Pl. V, Fig. 19). Each plate was formed of from 2 to 6 elements, the higher number probably being the more usual, whilst tangentially the groups generally form either a single or a double row.

Not infrequently there were considerable local aggregations tangential to the surface, forming broad bands which may well have arisen through the lateral fusion of a number of the sclerotic plates. In outline each broad band formed a continuous hypodermal layer of sclerotic elements, with occasional projections inwards. Owing to crushing and contraction, many of the sclerotic bands have come to occupy an oblique or even tangential direction, causing irregularity and superposition of the originally radial plates

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[1] Scott and Maslin, loc. cit., p. 101.

[2] Renault: Bassin houiller et permien d'Autun et d'Épinac, vol. iv, p. 390, and Pl. LXXXIII, Fig. 10.

[3] Renault: Mém. Soc. d. Sci. nat. d. Saône-et-Loire, p. 1, 1887.

The individual sclerotic fibres were roughly rectangular, with a slight flattening in the radial direction, and usually about 2·5 × 4·5 μ. The wall was much thickened (about 0·8 μ) and formed of an outer transparent, yellowish layer and an inner and slightly thicker brown layer, both of which show clearly defined lamellation.

The longitudinal sections do not show the outer region of the sarcotesta preserved. The maximum longitudinal dimension in oblique sections is a quarter of a millimetre, and no doubt the real length was much greater.

The width of the intervals between successive plates is usually fairly regular, but rarely they are seen in very close proximity even where there is no evidence of displacement, and these are, perhaps, like the larger aggregations, to be interpreted as due to anastomoses.

Irregularly interspersed amongst the sclerotic cells are numerous secretory sacs, some 7·5 μ in diameter, which were no doubt situated in the soft parenchyma between the sclerotic plates, and become very numerous just beneath this zone.

Here and there the secretory sacs occur two or three together, arranged radially, and it is possible that these too, as in the nucellus, formed rows alternating with those of the sclerized elements.

Where cut obliquely, the secretory cells show fine longitudinal striation of the external surface of their walls; in one section, which is especially well preserved, this wall is seen cut transversely as a series of dark beads separated by clear spaces of about equal width. Surrounding the carbonized contents is a clear space which probably represents a thick sclerotic wall: the elements, in fact, were almost identical in appearance with the thick-walled mucilage sacs found in the sporophylls and testa of present-day Cycads.

In favourable cases, four or five connexions at more or less regular intervals can be seen between the dark central mass and the thin external wall. They probably represent radial pittings of the cell-wall, but must not be confused with the numerous and much finer and fainter radial striations, which are doubtless a matrix effect.

Occasionally the secretory sacs were situated at one or other end of the sclerotic plates, or even in the middle, replacing the sclerotic elements themselves.[1]

The presence of the numerous hard plates in the peripheral zone of the sarcotesta must have given to that region considerable rigidity, and the dark layer often seen between it and the soft underlying tissue is no doubt to be interpreted as originating through the compression of the outer cells of this latter.

(*c*) *The Secretory System.* The sarcotesta is not only distinguished from that of other seeds by its extreme development, but also by the

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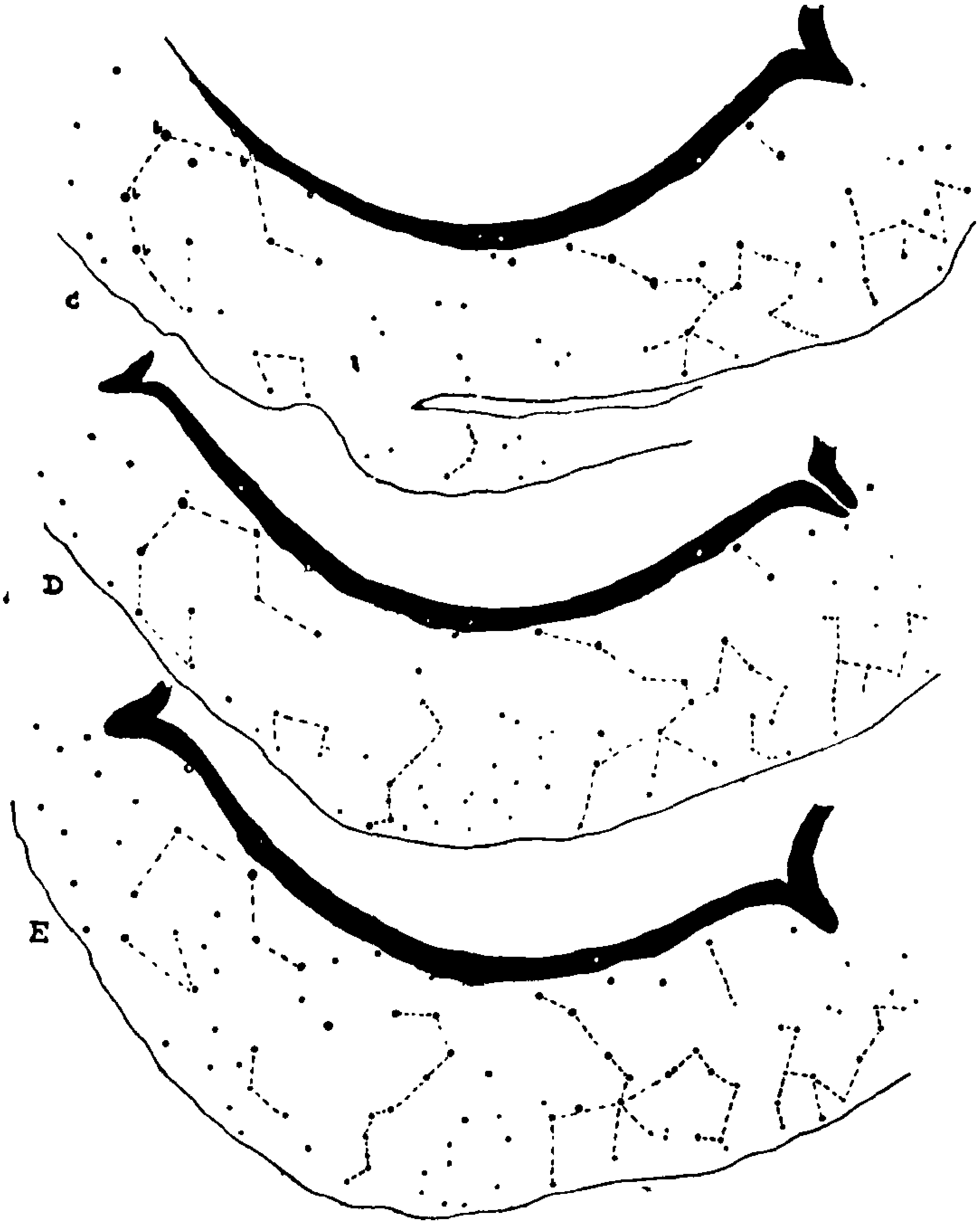
[1] Cf. Petiole of *Medullosa.* Scott's Studies in Fossil Botany, Fig. 176.

numerous secretory sacs which permeate it throughout (Pl. IV, Fig. 2, *m.s.*). In all respects the secretory elements of the interior appear to agree with those of the periphery.

Each secretory sac is sheathed by a continuous layer of parenchymatous cells, which separate it off from the surrounding lacunar tissue. Component cells of this sheath are seen in tangential sections to have been vertically elongated and to have reached a length of some five times their width.



TEXT-FIG. 7. Plottings of the secretory sacs in three successive sections. In order to make the corresponding sacs more clear, they have been connected up by means of dotted lines.

By carefully mapping the distribution of the secretory sacs between the same pair of ribs in successive sections of a series, one can recognize, from the relative positions which they occupy to one another, that the same sacs often extend for a considerable distance (Text-fig. 7).

In the subjoined table an analysis of the results obtained from S. 31, *b–i*, is given; the vertical series show the number of sacs in each section which can be traced back as far as that of which the designating letter heads the column. In Section *f* the sarcotesta is much broken, hence the figure for *g* is probably double its real value. If this be the case, then the number of additional sacs appearing at any given level is about twenty-one, or sixty-three for the whole circumference. The whole interval included between S. 31, *b* and S. 31, *i* is about 14 mm., and out of the total of 195 separate secretory elements encountered, not more than eight persist throughout. A few are only present in one section, whilst the greater number extend into the next (an interval between sections of about 2 mm.) with a falling off in each successive section.

| S. 31. | | *b* | *c* | *d* | *e* | *f* | *g* | *h* | *i* | *Total.* |
|---|---|---|---|---|---|---|---|---|---|---|
| Section S. 31. | *c* | 46 | 23 | | | | | | | 69 |
| ” | *d* | 45 | 15 | 26 | | | | | | 86 |
| ” | *e* | 35 | 12 | 24 | 22 | | | | | 93 |
| ” | *f* | ? | ? | ? | ? | 10 + | | | | ? |
| ” | *g* | 23 | 6 | 2 | 8 | 10 | 37 | | | 86 |
| ” | *h* | 20 | 5 | 2 | 7 | 6 | 32 | 11 | | 83 |
| ” | *i* | 8 | 4 | 2 | 6 | 6 | 13 | 5 | 20 | 64 |

The level of *k* in the Manchester series is the base of the micropyle, and of *c* that at which the nucellus is attached to the chalazal cushion. The number of secretory sacs in each case represents approximately one-third of the total at that level.

| | | | | | |
|---|---|---|---|---|---|
| Man. Coll. | *c* | 34 | Man. Coll. | *h* | 101 |
| ” | *d* | 46 | ” | *i* | 92 |
| ” | *e* | 65 | ” | *j* | 93 |
| ” | *f* | 82 | ” | *k* | 109 |
| ” | *g* | 98 | | | |

A study of the two series shows that, in spite of irregularities, there was a decrease in number both towards the apex and base. From a comparison of the same sacs cut at different levels, they are seen to have tapered gradually both above and below, so that where cut across near their terminations they are of very small size and, where the surrounding wall is disclosed, very closely resemble developmental stages in the formation of secretory canals, the surrounding sheath simulating an epithelium, which may perhaps be the explanation of the similar appearances described by Professor Seward in the medullosean petiole *Rachiopteris Williamsoni*.[1]

A single secretory element, as seen in one section, is in several instances replaced by two in intimate contact in the succeeding section (Pl. V, Fig. 12); the fact that both are usually of nearly the same cross-section seems to favour the view that this is due to branching.

The normal course followed by the secretory elements was slightly sinuous and approximately parallel to the direction of the surface, with an outward tendency exhibited by the more interior. The distribution was irregular, with a marked increase—especially of the smaller—towards the periphery; whilst the largest (0·124–0·166 mm.) are found midway between the sclerotesta and the external surface (cf. Text-fig. 3, p. 42).

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[1] Ann. Bot., vol. viii, No. xxx, 1894.

### 3. The Inner Flesh.

All those sections which pass through the body of the seed, even where the preservation of soft tissues is excellent, show no indications of an inner flesh. It is certainly true that in most of the preparations the internal surface of the sclerotesta exhibits an irregular outline, but in the transverse series S. 33, *a*–S. 33, *d*, in which the internal preservation is almost perfect, the inner margin of the sclerotesta in some places forms a perfectly even surface. This latter affords positive evidence of far more value than the negative evidence of a ragged surface, and still more so since we find in the badly preserved material that the sclerotesta does show signs of superficial disintegration.

In dealing with the nucellus we shall find that it was possessed of a highly differentiated and probably strongly cuticularized epidermis, and there is evidence that it was in close contact with the sclerotic tissue.

Having due regard to all these facts, one is forced to the conclusion that in this species of *Trigonocarpus* an inner flesh was not present in the middle part of the seed cavity.

When we come, however, to about the level of the insertion of the micropyle, the zone of sclerization begins as it were to shift slightly outwards, and we thus find within the sclerotesta several layers of cells which, though possessing thick walls, have not the dark brown contents of the sclerotic fibres themselves, and, moreover, become thinner-walled as we pass inwards. This tissue reached its maximum thickness, of some four layers, midway between the angles, and on its inner margin exhibits a broken surface that here might well indicate a greater extent of probably more parenchymatous elements (Pl. IV, Fig. 8, *i.f.*).

Even then, if we regard this micropylar lining as homologous with the inner flesh of other Trigonocarpeae, our seed is as extreme a member on the one hand, as *Pachytesta* on the other.

## IV. THE VASCULAR ORGANIZATION.

### (*a*) *The Chalazal Bundle and Nucellar System.*

The lowest of our transverse sections yields us no information as to the vascular structure, but from S. 33, *b*, Man. R. 1161, *b*, and the longitudinal section S. 32, *e*, we find that a single vascular bundle entered the chalazal end of the seed. This passed up to the base of the nucellus, at which level it is cut by the section S. 33, *b* (Pl. V, Fig. 16). The bundle is there seen to have been a solid mass of xylem very slightly triangular in outline, the angles corresponding in position with the three main ribs of the seed. It was formed of from sixty to seventy elements, and attained a diameter of about 0·18 mm. The larger tracheae are situated mostly at the periphery

(Pl. V, Fig. 16), and in their radial dimension (30–40 μ) considerably exceed their width (75μ–0·025 mm., average about 0·015 mm.). The central elements are polygonal in form and from 0·015 mm. to 0·02 mm. in diameter. The bundle therefore has the appearance in transverse section of a central core surrounded by a single layer of radially flattened elements.

The smallest tracheae, measuring some 0·8μ in diameter, lie just within this outer layer and appear to form six not very clearly defined groups, two corresponding to each of the three angles. That these are the protoxylem elements is rendered the more probable by an examination of the single longitudinal section passing through the chalazal bundle (S. 32, *e*). From this we find that the majority of the elements were scalariform or densely spiral (Pl. V, Fig. 18), whilst separated by one such element from the periphery of the bundle there appear to be one or two narrow elements with distant spiral thickenings.

The xylem is completely surrounded by a ring of parenchymatous tissue (Pl. V, Fig. 16, *p.s.*) composed of three to five layers of thin-walled elements which together attain a width of about 0·05 mm. In the longitudinal section this tissue is seen to have consisted of narrow, vertically elongated components, perhaps undifferentiated phloem. The whole bundle, including this delicate sheath, was surrounded by larger-celled and thin-walled nucellar tissue in which were numerous secretory sacs. One element exhibits parallel markings, and may be a transfusion tracheide comparable perhaps to those found by Scott and Maslen between the bundles of the sarcotesta of *T. Parkinsoni* (loc. cit., p. 114 and Pl. XIV, Fig. 25, *st.*).

The single bundle passed through the base of the nucellus, where it expanded in a cup-like manner and formed a tracheal investment (1–4 elements) to the megaspore cavity. This is well seen in section D of Dr. Scott's series, which passes obliquely through the base of the megaspore cavity, and shows the continuous and several-layered tracheal cup around its base.

As seen in transverse section, the tracheal mantle appears to be built up of broad, laterally fused, bands traversing the longitudinal direction which are thickest in the middle and gradually diminish towards the sides. As can be seen from the plottings (Fig. 1), the section S. 33, *c* is slightly oblique to the axis of the seed, and it is on the higher side of the section that this grouping of the tracheides is the more marked.

Presumably, then, the vascular tissue between the level of this section and the base of the megaspore cavity consisted of a uniform zone of tracheides, which on the upper side became incompletely segregated into bands. The number of these latter cannot be ascertained with certainty, owing to the oblique direction of our most nearly transverse sections, but if we assume the slight indications of thinning on the lower side to mark the lateral limits of vascular aggregations, then there were probably twelve such bands, the width of the more clearly delimited varying between 1 mm. and 1·3 mm.

The internal diameter of the megaspore cavity, as seen in section S. 33, *c*, from which the above data were obtained, is 4·4 mm., which represents a periphery of approximately 13·8 mm. If we assume each band to have been of equal width, this gives us 1·15 mm. as the measurement of each if their number were twelve. This figure is sufficiently close to the actual measurements to support the belief that this was the actual total of the bands. Unfortunately, none of our other preparations furnish any corroborative data, but it is worthy of note that the repeated hexamerous character of the seed-structure again recurs in this figure.

The next section (S. 33, *d*), though ill preserved, shows the tracheides were completely segregated into lenticular strands which were much narrower (0·25 mm.-0·5 mm.) and more numerous than at the preceding level (probably over twenty).

These strands were probably mesarch in structure, of from four to five elements in the radial plane, diminishing both in number and size on either side. In some cases, tracheides at the edge of the xylem bands can be seen passing horizontally, as is the case in *Trigonocarpus Parkinsoni*,[1] but actual connexions were not observed.

Tangential sections show that the individual tracheides were often oblique or curved, and the appearance of horizontally directed elements, in the slightly oblique transverse sections, might easily be accounted for in this way. In spite of the excellent preservation, no indication of phloem has been observed in relation to the nucellar strands.

The final section of the transverse series only contributes confirmatory evidence that the bands of xylem were disconnected, and that their smallest elements were centrally placed.

For the further course of the bundles only longitudinal and oblique sections are available. In these, the bands of tracheides can be traced to what must have been a level close to the floor of the pollen chamber. Only two sections, viz. S. 32, *c* and Section I of Dr. Scott's series, actually pass through this structure; neither of these shows any tracheides within, but the internal preservation of the latter section is very poor, whilst the former has a broken and ill-preserved floor.

The vascular elements of the nucellar system appear to be very uniform in structure (0·022–0·03 mm.), and exhibit scalariform thickenings which occasionally show anastomoses between adjacent horizontal bars. (Interval between bars, 0·0015–0·003 mm.)

From the above description it will be seen that the internal vascular system is almost identical with that described by Scott and Maslen for *Trigonocarpus Parkinsoni* (loc. cit., pp. 120–1), and it may be of some

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[1] Scott and Maslen, loc. cit., Pl. XIV, Fig. 13.

significance that in neither species has the nucellar system been traced beyond the plane of insertion of the pollen chamber.

### (*b*) *The Sarcotestal System.*

In several sections of the University College series S. 31 *a*–S. 31, *k*, and perhaps in section R. 1161, *h* of the Manchester series, bundles in various conditions of preservation are to be found at the extreme periphery of the sarcotesta proper, where the outermost lacunar tissue abuts upon the limiting layers containing the radial sclerotic plates. The only parallel amongst nearly allied seeds to so external a position is to be found in *Pachytesta*,[1] where, however, if we regard the exotesta as representing sarcotesta and sclerotesta combined,[2] the bundles are only far out if considered in relation to the testa as a whole.

Owing to the incomplete preservation of the periphery, it is hardly surprising that in no slide are more than three sarcotestal bundles present at one and the same time. In several of the University College series, S. 31, *a*–S. 31, *k*, two bundles are cut in successive sections, and both of these are fortunately situated between the same pair of major ribs, and also occupy the same positions relative to them. Altogether, four distinct bundles can be distinguished in this series, and two possible bundles are also recognizable in one of the Manchester sections (R. 1161, *h*). In every case these sarcotestal vascular strands are situated in the radial plane midway between a major and a minor rib, and though the bundles are not present, in any one of our specimens, on all three faces, yet the occurrence of two, and two only, in several successive sections between the one pair of major ribs seems to point conclusively to the total number as being six, symmetrically disposed around the circumference of the seed.

The sarcotestal system was then identical as to the number of its components, and almost so as to their arrangement, with that which has been described for *Trigonocarpus Parkinsoni* and *Polylophospermum*,[3] only differing in the latter respect with regard to the proximity of the bundles to the sclerotic shell.

The structure of an individual strand is shown in S. 31, *i* (Pl. V, Fig. 17), where, owing to the curvature of the surface, the section which is oblique to the axis of the seed passes transversely through a sarcotestal bundle exhibiting extraordinarily perfect preservation. As can be seen from the figure, the bundle is slightly more extended in the tangential than in the radial direction (0·29 mm. × 0·17 mm.) and consists of some seventy xylem elements, of which the smallest occupy the central region (Pl. V, Fig. 17, *pt.x*). The latter, which probably represent the protoxylem, comprise some

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[1] Renault, loc. cit.

[2] Oliver: On Gymnospermous Seeds, New Phytologist, vol. i, No. 7, 1902, p. 148.

[3] Oliver, Ann. Bot., vol. xxi, No. lxxxii, 1907, pp. 303–4.

four tracheides (0·0075 mm. x from 0·0075 mm.–0·015 mm.) with thicker walls than those around. From the mesarch protoxylem there extends in the centrifugal direction an irregular fan-shaped group (Pl. V, Fig. 17, *cf.x.*), the elements of which, though larger than those of the protoxylem, are distinctly smaller than both those which lie on their flanks and those on the inner side of the bundle.

The centripetal xylem (Pl. V, Fig. 17, *cp.x.*) exhibits a further distinction in that the elements here are mostly cut more or less obliquely, so that the scalariform or reticulate sculpturing of their walls can be seen. A single layer of xylem elements on the centripetal side of the bundle immediately next the protoxylem do not show this character, although they exhibit the increased dimension.

The bulk of the centripetal wood evidently then consisted of short tracheides, such as are frequently present in centripetal xylem that is becoming obsolete, as is exemplified in *Lepidodendron vasculare*[1] or *Osmundites Kolbei.*[2]

### (*c*) *Additional Facts as to the Vascular System of Trigonocarpus Parkinsoni.*

The course of the sarcotestal bundles at the base of the seed of *Trigonocarpus Shorensis* cannot be traced, as the peripheral portion is lacking in the sections which pass through that region.

Two sections probably belonging to *Trigonocarpus Parkinsoni*, viz. S. 34, *a* and S. 34, *b* of the University College collection, have however recently come to hand, which Prof. Oliver has also placed at my disposal for description, and which, owing to their excellent preservation, add considerably to our knowledge of the vascular structure in this region. The absence of similar data regarding our own seed, and the essential similarity between the vascular systems of the two species, are sufficient justification for inclusion here.

The first section, viz. S. 34, *a*, just passes through the lower limit of the sclerotesta, and the second, parallel to the first, obliquely through the seed base, but without traversing the megaspore cavity. In this latter section eight ribs can be distinguished, of which three are doubtless the primary ribs, and from the distribution of the remaining five it seems likely that the seed was twelve-angled, the missing ribs having become obliterated either by obliquity or in consequence of the lower level at which the seed is cut on one side. A further point of importance is that this seed was evidently blunt at the base and not tapering,

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[1] Hovelacque, M.: Recherches sur le *Lepidodendron selaginoides*, Sternb. Mém. Soc. Linn. Normandie, vol. xvii.

[2] Kidston and Gwynne-Vaughan: On the Fossil Osmundaceae, Pt. IV. Trans. Roy. Soc. Edinburgh, 1910.

as shown by the great difference in the area of sclerotesta sectioned at the two successive levels. These facts, taken together with the position of the sarcotestal bundles, seem to justify the assumption that the seed was *Trigonocarpus Parkinsoni.*

In both of the sections a few secretory sacs can be seen. Dr. Scott has permitted me to examine his best preparations of *T. Parkinsoni* with the sarcotesta preserved, and particularly Wild's section S. 1952, figured by Scott and Maslen,[1] in which there are present some dark bodies surrounded by a clear space 0·045 mm.–0·052 mm. in diameter. Neither for these nor for similar bodies in the other preparations can one definitely assign a secretory nature, but a comparison with ill-preserved secretory sacs of *T. Shorensis* discloses a striking similarity between them. Probably, then, secretory sacs were present in *T. Parkinsoni*, both at the base and apex of the sarcotesta, but in very much smaller numbers than in *T. Shorensis.*

The central region of the lowest of the two sections cuts the single main chalazal bundle obliquely, at the level where the sclerotesta begins to be differentiated.

The general outline of the vascular bundle was very slightly triangular, with a diameter of about 0·3 mm., the angles corresponding in position to the secondary ribs. From each of the two upper of these angles (Pl. V, Fig. 14, *v.b.*) a strand is seen in process of being given off into the sarcotesta.

The main bundle is surrounded by a thin-walled parenchymatous tissue (*par.*) consisting of vertically elongated elements. In the centre is a solid mass of xylem, throughout which are scattered short tracheides horizontally directed, exhibiting scalariform or pitted thickenings. The section is sufficiently oblique to show that the longitudinally directed tracheides were scalariform.

In the centre of the xylem a single secretory cell can be detected (Pl. V, Fig. 14, *m.s.*).

The periphery of the bundle is formed of a band of short tracheides 1–2 elements in width, which for the most part are separated from the central xylem mass by what appears to have been parenchymatous tissue similar to that surrounding the bundle as a whole. But this tissue is interrupted at several points by junctions between the outer and inner tracheides. The smallest xylem elements lie mostly at the periphery of the central core, but others are situated more interiorly.

From an examination of the angle which is cut at the highest level, it can be seen that from this peripheral zone pass out the xylem elements of the sarcotestal bundles. In this particular case, the portion has partially separated off from the central mass, and the corresponding bundle, owing to the double obliquity of the section, is again cut further

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[1] Loc. cit., Pl. XII, Fig. 11.

out in the sarcotesta. What was doubtless the second half of this strand is seen at the edge of the bundle cavity, and clearly shows that the course of the two halves was divergent.

In the next section, viz. S. 34, *b*, which is nearly parallel to the former, five sarcotestal bundles can be distinctly recognized, whilst the position of a sixth is marked by a lacuna.

Where the bundles are cut on the lower side of this section, the level is only about one-third of a millimetre above that at which the central bundle is cut in the previous slide, so that the distance is scarcely sufficient for other bundles to have been given off.

It would appear then, from these two preparations, that three bands of xylem in continuity with the peripheral part of the chalazal strand were given off simultaneously, each of which then almost immediately underwent bifurcation into two divergent halves.

The soft parenchymatous tissue which surrounded the bundle consisted of cells which, when cut transversely, appear more or less polygonal and isodiametric: where cut longitudinally they measure about 0·12 mm. x 0·022 mm., and are separated by slightly oblique transverse walls. This tissue may perhaps have served the purpose of phloem, though apparently quite undifferentiated; that it had some definite function is supported by its sharp delimitation from the surrounding tissue, even where this too was parenchymatous in nature. A similar sheath accompanied each of the six sarcotestal strands in this, the basal region of the seed.

As seen in S. 34, *b* (Pl. V, Fig. 15) the central part of each bundle was occupied by a strand of elongated scalariform tracheides (*n.tr.*), and around this was a complete ring of much shorter and stouter spiral or slightly reticulate elements (*s.tr.*). Separating the outer zone from the central core, was a narrow space from which the bulk of the tissue has perished, but here and there can be seen patches of elongated parenchymatous elements similar to those forming the bundle-sheath, and no doubt they originally constituted a complete ring.

Each sarcotestal bundle was then essentially similar to that supplying the chalaza. An examination of the bundles of Dr. Scott's section 626 of *T. Parkinsoni* through the same region as S. 34, *b*, though exhibiting far less perfect preservation, seems to agree with the description here given.

Before leaving these sections it should be said that, though the type of preservation is the same as that of the bulk of the specimens of *T. Shorensis*, in none of the secretory elements present was I able to find the longitudinal striation characteristic of the wall in that species, though this feature is exhibited by well-preserved ducts in the stems of *Medullosa anglica*.

## V. THE NUCELLUS.

The total length of the free nucellus, from the point of junction with the testa to the base of the pollen chamber, was about 18 mm., and its diameter in the widest region about 11 mm. As the cavity in this part was some 15 mm. in width, there is left a space of 2 mm. all round for which to account. The question of an inner flesh has already been discussed, but in any case these dimensions for the nucellus are probably much too small, owing to post-mortem contraction.

The general outline of the nucellus conformed closely to that of the cavity within which it stood, following the same lines until near the base of the micropyle, where the nucellar tissue curved sharply inwards to the insertion of the pollen chamber.

Disregarding this latter structure, the conformation was that of a sharply pointed egg with its narrower end directed downwards and attached to the sclerotesta, whilst the blunt free end was surmounted by the pollen chamber.

The nucellar tissue is in most cases either lacking altogether or ill preserved, but fortunately, in the transverse series S. 33, *a* to S. 33, *d*, the structure is beautifully shown, though considerably contracted. In the uppermost of the series the nucellus occupies a one-sided position which is in part due to the slight obliquity, but no doubt in the main to displacement through asymmetrical shrinkage.

In the second of this series the nucellar tissue is seen surrounding the chalazal bundle. As already described, this consists of parenchymatous tissue, of which the cells are thin-walled and vary in size from about 0·01 to 0·050 mm., interspersed with secretory ducts, the largest of which are at the periphery and measure about 0·07 mm. in diameter. This ring of tissue is only 0·2 mm. in width, but from its ragged edge was evidently much more extensive in life.

Owing to the shrinkage of the soft underlying tissue, the much less contractable epidermis is thrown into numerous folds, but the projections thus formed do not, as in *Trigonocarpus Parkinsoni*, correspond to underlying vascular strands,[1] but to radial files of secretory elements (Pl. V, Fig. 20, *m.s.* and *n.r.*). Taking the distance from the edge of the megaspore cavity to the summit of these ridges as the basis of our estimate, the thickness of the nucellar tissue must have been, near the chalazal end of the seed, at least 0·3 mm., though above this level it diminished slightly and then remained of constant width up to the base of the pollen chamber. At the outside there was a very strongly defined epidermis, (S. 33, *c*, Pl. V, Fig. 20, *n.e.*), the cells of which (0·05 mm. radial x 0·03 mm. tangential) stand out all the more clearly since their contents are preserved as dark carbonaceous masses that have contracted away from the cell walls. Where, owing to the contortions

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[1] Scott and Maslen, loc. cit., p. 119.

of the surface, the longitudinal dimension can be estimated, it is about three times as great as the width (0·09 mm.). As seen in this view, the cells are more or less oblong in shape, whilst cut transversely they appear distinctly convex on the external face, a feature which seems to point to the absence of close contact with an inner flesh.

Under the best conditions of preservation, the epidermal cells resemble very closely the secretory sacs and, like them, have the appearance of possessing a thickened wall. In several places the outer layer of the exterior walls, together with part of the middle lamellae from between each pair of the component cells, has split away, so that in transverse section it appears as a thin membrane with pegs projecting inwards. Evidently this outer layer was of a durable character, as it can occasionally be recognized even where the interior tissue has decayed away, and is much less subject to contraction, suggesting that it may probably have been a cuticularized layer such as we find with similar pegs amongst modern plants.

Such a specialized epidermis we should hardly expect to find in a completely enclosed structure like the nucellus, if it were in close contact with a soft inner flesh.

Between the epidermis and the tracheal sheath there intervened a zone of soft parenchymatous elements in which numerous secretory cells were present. The ground-tissue was without intercellular spaces and formed of polygonal cells with very thin walls (0·03 mm. to 0·08 mm. × 0·15 mm.). The secretory cells were embedded in this ground-tissue, and where they did not occur singly, formed radial plates of varying extent and usually consisting of a single row of secretory elements, though more rarely at the base of the seed of two such rows. The greatest number of secretory cells which were present in any one radial plane appears to have been five. The proximity of the radial plates and the number of elements in each decreased as the apex of the seed was approached, so that some two-thirds from the base of the pollen chamber the plates were about a third of a millimetre apart and reduced to one, two, or at the most three elements. The secretory sacs themselves (0·06–0·09 mm.) exhibit much the same structure as those of the sarcotesta, but with thinner walls. In the longitudinal direction the carbonized contents show segmentation into short lengths, but the septation thus produced probably bore no relation to transverse walls.

In two of the seeds (viz. S. 31, U. C. Coll., and Man. R. 1161), besides the longitudinal ridges already referred to, others more pronounced are present, occupying positions opposite to the commissural ribs, and bear no relation to contained radial files of secretory elements. In the series S. 33, U. C. Coll., with its excellently preserved nucellus, no such ridges are however to be seen, which may be correlated with the fact that this seed was probably in an immature condition, judging from its relatively small size, the thinness of the testa, and the slight development of the ribs. In S. 31, *g*, such ridges, corresponding to both the major ribs preserved, can be distinguished. Such commissural ridges,[1] of which an example is figured in Pl. V, Fig. 13, *n.f.*, from section S. 31, *e*, furnish the strongest evidence that the nucellar surface was in the mature condition in close contact with the sclerotic testa, a point which the well-developed cuticle further emphasizes.

## VI. THE POLLEN CHAMBER.

Our information respecting the structure of the pollen chamber is extremely meagre, as only two sections furnish data of any importance. The general form of the pollen chamber, as seen in S. 32, *c*, is rectangular, with longer sides forming the roof and floor (3 mm. wide × 1·26 mm. high). As will be seen from the diagram, the direction of the section passes tangentially through the pollen chamber in a plane slightly oblique to that of a minor rib.

The central part of the roof in this section shows a triangular, blunt-ended, upward projection of the epidermis, which may be the base of the micropylar tube.

The epidermis of the pollen chamber is continuous with that of the nucellus, and the component cells up to about half its height are of the same form in both. Beyond this point they become much larger (0·066 mm. radial by 0·04 to 0·08 mm. vertical), with thinner walls, and do not possess the black carbonaceous contents present in the lower part. The increased size is especially noticeable where the sides curve inwards to form the roof; these shoulders project somewhat laterally, partly owing to the larger size of the epidermal cells and partly to the slightly greater internal diameter (Pl. V, Fig. 11). The blunt apex of the angular projection is formed of cells which are much narrower in the tangential direction, 0·005 mm. Interiorly, the sides of the pollen chamber were occupied by a soft parenchymatous tissue, consisting of elongated cells with tapering ends. This is most pronounced in the shoulders, and the appearance presented very closely resembles that described and figured for other seeds of this affinity, as for example *T. Parkinsoni*,[2] *T. pusillus*,[3] *Aethiotesta*,[4] and *Stephanospermum*.[5]

In S. 32, *h*, the pollen chamber exhibits a prominent angle corresponding in position to a major rib, and also in Section I of Dr. Scott's series the shoulders appear double-angled, the lower of the four angles being the true

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[1] Cf. Renault: Angling of Nucellus in *Trigonocarpus pusillus*. Flore fossile d'Autun et d'Épinac, pt. 2, p. 398.

[2] Scott and Maslen, loc. cit., p. 121.

[3] Oliver: New Phyt., vol. iii, 1904, Pl. II, Fig. 3.

[4] Renault: Mém. Soc. d. Sci. Nat. de Saône-et-Loire, 1887, Pl. XVI, Fig. 3.

[5] Oliver: Trans. Roy. Soc. Lond., p. 370, Pl. XLII, Figs. 11 and 18.

shoulders, and the upper again coinciding with the positions of major ribs. There seems little doubt, then, that the pollen chamber was three-angled in correspondence with the projections of the nucellus lower down.

## VII. COMPARISON WITH OTHER TYPES.

### 1. *Trigonocarpus Parkinsoni*, Brongniart.

It is hardly necessary to recapitulate in detail the many points of general resemblance which *Trigonocarpus Parkinsoni* and *Trigonocarpus Shorensis* have in common. The main structural plan in both seeds is essentially the same, but this only serves to throw into greater prominence the many differences of their more minute structure.

We note the entire absence in *Trigonocarpus Shorensis* of tertiary ribs subtending the vascular bundles, and though the behaviour of the primary sutured ribs is alike in each, the beak into which they pass is short in *T. Shorensis* and long in *T. Parkinsoni.*

The secondary ribs of the latter seed are subject to considerable variation, sometimes being almost absent; but usually they persist to near the apex, where they die out before the micropylar beak is reached, an earlier disappearance of the secondary ridges which is still more pronounced in *T. Shorensis.* Scott and Maslen give the thickness of the stony layer in *T. Parkinsoni* as from 1 to 1·5 mm. (loc. cit., p. 106), which is two to three times the corresponding dimension for our seed. Probably this added thickness and the increased number of ribs are to be correlated with the small extent of the sarcotesta, as compared with that of *T. Shorensis*, necessitating greater mechanical strength in the layer beneath; or perhaps, put more correctly, the broad sarcotesta in the latter species, with its peripheral sclerotic system, had not involved the necessity for development of such mechanical strength in the sclerotesta.

The most interesting comparison between these two seeds is afforded by the sarcotestal structure. This tissue was in *T. Parkinsoni* bordered at the exterior by a narrow epidermis, followed by a thickened palisade-like hypodermis (Scott and Maslen, loc. cit., p. 102). As we have seen, the limiting layers in the present seed were much more complex, and formed a, probably anastomosing, complex of radial plates, accompanied by numerous secretory elements present also further in, which, though represented, were extremely few in *T. Parkinsoni.* Now the occurrence of radial sclerotic plates at the periphery, and of secretory elements both within these and interiorly, are characteristic features of the vegetative organs of Medulloseae, and especially of their petiolar structure,[1] so that *T. Shorensis* in this respect would appear to be far more primitive than its congener. The absence of the prolonged

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[1] Scott, D. H.: On *Medullosa anglica.* Phil. Trans., B, vol. cxci, p. 101, and Pl. VIII, Fig. 18, 1899.

sclerotic beak and secondary ridges opposite the bundles also point to a lesser degree of specialization.

A further striking difference is the tapering insertion of the seed of *T. Shorensis* as compared with its abrupt insertion in *T. Parkinsoni*; the former is probably a relatively older type than the latter, just as the horizontal departure of the leaf-trace characterizes the modern plant, in contradistinction to the oblique insertion, as found in the more ancient.

Analogy with *Physostoma elegans*[1] would seem to suggest that the presence of a secretory system in the nucellar tissue is a more primitive feature than its absence. If this has any significance, and the close relationship between the Trigonocarpeae and Lagenostomales supports such an assumption, then in this respect *T. Shorensis* stands in the same relation to *T. Parkinsoni* as does *Physostoma* to the other known members of the latter group.

We have shown good reason for believing that *T. Shorensis* was without a definite inner flesh, except in so far as we can apply that term to the lining of the micropylar canal. Such a tissue would, however, appear to have been present in *T. Parkinsoni*. Perhaps at first sight this might seem to be a pronounced distinction between the two, but the extreme peripheral situation of the sclerized layer in *Pachytesta*, surrounding an extensive inner flesh, coupled with the undoubtedly close relationship of the two genera, indicate that the position taken up by the region of sclerization was subject to considerable fluctuation in the group as a whole, and therefore of no great significance when exhibited in a smaller degree by members of the same genus.

The well-defined nucellar epidermis, even more pronounced than that of *T. Parkinsoni*, indicates a stage less far removed from the condition in which the nucellus was a naked sporangium unprotected by a surrounding integument; and probably the production of an inner flesh is likewise correlated with a phylogenetically more prolonged contact between the two surfaces, which functionally have become internal.

As previously indicated, the vascular organization of the two seeds was essentially similar, perhaps the most outstanding distinction between them being the much more peripheral position occupied by the sarcotestal strands in *Trigonocarpus Shorensis*. On the whole, the internal vascular system of our seed probably shows a somewhat more pronounced tracheal investment at the base of the nucellus, whilst the separate strands into which this passed were broader, though this may well be an outcome of the larger nucellus they supplied. If, as may have been the case, the Trigonocarpeae were derived from fern-like plants having sporangia with a complete internal tracheal investment, then it would appear from Scott and Maslen's description that in this respect *Trigonocarpus Parkinsoni* was more primitive than

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[1] Oliver: Ann. Bot., vol. xxiii, p. 73.

*T. Shorensis*, for in the latter anastomoses, if they existed, were probably of infrequent occurrence.

### 2. *Trigonocarpus Oliveri; its systematic position.*

This seed was described and figured by Scott and Maslen in 1907,[1] from a series of four sections through a single seed, and the diagnosis there given is as follows:

'Length nearly 2 cm., diameter about 0·9 cm., characteristically coffin-shaped in vertical sections. Base flattened. Sclerotesta produced around the base of the seed in the form of a circular ridge enclosing the stalk of the seed. Longitudinal ridges of the sclerotesta acute-angled, not rounded as in *Trigonocarpus Parkinsoni*.'

The number of longitudinal ridges which the seed bore is not explicitly stated, but, presumably from the description given, was assumed to have been six.

The writer has carefully examined the preparations and employed for their interpretation the methods recently described.[2] The conclusions arrived at differ essentially from those of Scott and Maslen, who evidently did not fully recognize the marked effects of obliquity in this seed, which are so clearly brought out by the modelling method.

As can be seen, the first section (S. 28, *d*)[3] is tangential to the surface of the seed and passes at unequal depths through two ribs, the divergent axes of which, towards the upper part, indicate that the plane was below the middle region, sloping away from the chalaza. The next section (S. 28, *c*) shows the more deeply cut of these ribs sectioned nearer the axis, and consequently represented by two angular projections, one at the apex and the other at the base. This section cuts the seed so far in that two lateral ribs, one on either side, are also encountered; where these are cut near the apex they appear as angular projections, whilst near the base they exhibit a curious truncated outline, but are unequal in size, owing to the obliquity which was also manifested in the previous section. It is these two lateral ridges at the base which have been interpreted as a circular ridge, though the true character where sectioned near the apex was recognized. In order to explain the peculiar form of the lower projections, the assumption was made that they were incomplete. The objections against such an interpretation furnished by this section alone are, that if a chalazal ring were present, it is highly improbable that the central rib would extend below it and the lateral ribs be in no way represented; whilst this difficulty cannot be overcome, since the interpretation of the median ridge as a part of the stalk is inadmissible, owing to the plane of section.

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[1] The Structure of the Palaeozoic Seeds *Trigonocarpus Parkinsoni* and *Trigonocarpus Oliveri*. Ann. Bot., vol. xxi, No. lxxxi, 1907.

[2] Salisbury: Methods of Palaeobotanical Reconstruction. Ann. Bot., April, 1913.

[3] Loc. cit., Pl. XIII.

On the interpretation here put forward no difficulties are involved, since converging ribs cut in a plane at a narrow angle with that which they themselves follow would necessarily acquire in section the square-ended form which they actually present.

In the section just described, one notes that the region of attachment of the nucellus is cut through, so that since in the next preparation the nucellus shows as a complete oval membrane it is clear that this section passes right across the axis of the seed, cutting through a rib on either side almost vertically, and it is the slight angling of the cavity corresponding to these which, as in similar sections of *Conostoma oblongum*, results in the coffin-shaped appearance.

At the apex of S. 28, *b*, we see the three ribs represented in S. 28, *c*, and at the lower end three other ribs sectioned almost transverse to their direction, so that the triangular form is preserved. If, on the other hand, they were really a chalazal ring, a section in this plane should render them convergent, not divergent, and furthermore, their size on that view is incompatible with the projections in the previous section, especially if the latter are to be regarded as incomplete.

*T. Oliveri* was then an eight-angled seed, and, until further specimens are obtained with better-preserved internal tissues, its systematic position, except for inclusion in the vague group of the Radiospermeae, must for the present remain uncertain. The removal of this seed from the genus *Trigonocarpus* makes it therefore unnecessary to institute any comparison between it and *Trigonocarpus Shorensis.*

### 3. Fructifications of *Neuropteris heterophylla* and *Neuropteris obliqua.*

Attention has already been called to the tapering and the abrupt insertion found within the genus *Trigonocarpus*, both of which are represented in the fructifications found attached to Neuropteridian foliage. Three specimens of *Neuropteris heterophylla* have been described by Dr. Kidston with attached seeds,[1] in which the abrupt insertion of the *Parkinsoni* type is clearly exhibited. More recently, Kidston and Jongmans[2] have described fructifications attached to the fronds of *Neuropteris obliqua*, in which the seed tapers towards its insertion on a bifurcated axis, thus conforming to the second type as represented by *T. Shorensis.* Owing to the incomplete preservation of the latter at the apex, its longitudinal extent cannot be exactly estimated, but nevertheless the comparison of the approximate dimensions of the two types of impressions and petrifactions given below shows that broadly the resemblances of insertion are accompanied by an approximately similar ratio in size.

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[1] Phil. Trans. Roy. Soc., ser. B, vol. cxcvii, 1904, p. 1.

[2] Archives néerlandaises d. sci. exactes et nat., sér. iii, B, tome i, 1911, p. 25.

| *Species.* | *Length.* | *Breadth.* |
|---|---|---|
| *T. Parkinsoni* | 4–5 cm. | 2 cm. |
| *N. heterophylla* | 3 cm. | 1·1–1·4 cm. |
| *T. Shorensis* | Over 4 cm. | 2·4 cm. |
| *N. obliqua* | About 6 cm. | 2·25 cm. |

A further feature that the fructifications of *N. obliqua* and *T. Shorensis* have in common is found in the marked striation exhibited by the surface of the former, and attributed by the authors cited above to the presence of a large number of sclerenchymatous strands of tissue near the surface of the seed. These are no doubt identical with the numerous radial sclerotic plates which we have described as a prominent feature in the peripheral layers of the sarcotesta in *T. Shorensis.*

In view of the occurrence of the seeds of *N. obliqua* in pairs on a bifurcated axis, it may be of some significance that in one of our series a portion of a second seed is present, having approximately the same orientation as the more complete specimen close to which it lies.

These considerations render it likely that our seed was itself borne on a plant possessing foliage of the *Neuropteris* type, and almost certainly belonged to the same subsection of the genus as Kidston and Jongman's specimens.

### 4. *Trigonocarpus corrugatus.*

Amongst the casts of Trigonocarpean seeds, none approach so closely to *Trigonocarpus Shorensis* as that described by Renault under the name *Trigonocarpus corrugatus.* The following is the diagnosis given by that author:

'Graines trigones, dilatées un peu au-dessus du milieu de leur hauteur, longues de 22 millimètres et larges dans la partie renflée de 12 millimètres, marquées de trois côtes saillantes qui vont jusqu'au sommet de la graine sans produire de point. Entre ces trois côtes on remarque trois plissements en relief qui s'étendent à peu près jusqu'à mi-hauteur.'[1]

From the above we see that the dimensions of the seed, though smaller than those of our own species, bear very nearly the same ratio for the corresponding parts of the sclerotesta.

| *Species* | *Width (max.)* | *Length.* | *Ratio Length, Width.* |
|---|---|---|---|
| *T. corrugatus* | 12 mm. | 22 mm. | 1·83 |
| *T. Shorensis* | 15 mm. | 28 mm. | 1·86 |

The presence of the three secondary ribs extending for only a part of the total length of the hard shell, though persisting for a greater distance than in *T. Shorensis*, also the absence of a beak (a description that might easily in this type of preservation be consistent with the presence of a very short structure of such a character), and the tapering base, still further strengthen the resemblance between the two seeds.

[1] B. Renault, Bassin houiller et permien d'Autun et d'Épinac, p. 399.

## 5. Comparison with Cycads.

Recent work on the Cycadean ovule,[1] and the additional facts regarding the structure of *Trigonocarpus* here brought forward, serve to emphasize the unmistakable relationship between the two groups. In the organization of the integument, differentiated into three layers, the agreement is extremely close, even as regards the broad structure of the stony layer which in Cycads as well as in *Trigonocarpus* is formed of longitudinally directed fibres on the inside, which at the outside become interwoven with horizontally directed elements.[2] Also, in the vascular organization and the structure of the pollen chamber[3] the resemblances are particularly evident.

The chief interest of the present work in this connexion results from the recognition of the short Cycadean type of sclerotic beak within the genus *Trigonocarpus*, and the presence of secretory elements situated in the sarcotesta of the latter, and resembling very closely the mucilage sacs of the modern group.

The tendency for the non-vascular ribs to die out, of which an early stage is shown by *T. Shorensis*, reaches its culmination in the Cycadean family, where, too, the development of ribs in relation to the sarcotestal bundles, as found in *T. Parkinsoni*, likewise constitutes a prominent feature of certain genera.

The absence of a nucellar system in the Lagenostomales is probably correlated with the fusion between testa and nucellus. How, then, are we to account for the retention of this same system under similar conditions in the Cycadean ovule? The explanation seems to be found in the isolation of the nucellar and integumental systems from one another by the intervening sclerotesta, which thus prevents the latter from performing the functions of both.

The suggestion advanced by Worsdell[4] that the fused integument and nucellus was brought about by a congenital fusion rather than that it arose as an intercalated zone of growth, as suggested by F. W. Oliver,[5] seems the more probable, both on the grounds there adduced and in view of the absence of any evidence in Cycads, comparable to that found in the Lagenostomales, of such having taken place.

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[1] Kershaw: Structure and Development of the Ovule of *Bowenia spectabilis*. Ann. Bot., vol. xxvi, No. 103, 1912.

[2] Stopes: On the Double Nature of the Cycadean Integument. Ann. Bot., vol. xix, 1905, p. 564; Chamberlain: The Ovule and Female Gametophyte of *Dioon*. Bot. Gaz., vol. xlii, 1906, p. 332.

[3] Kershaw, loc. cit., p. 643.

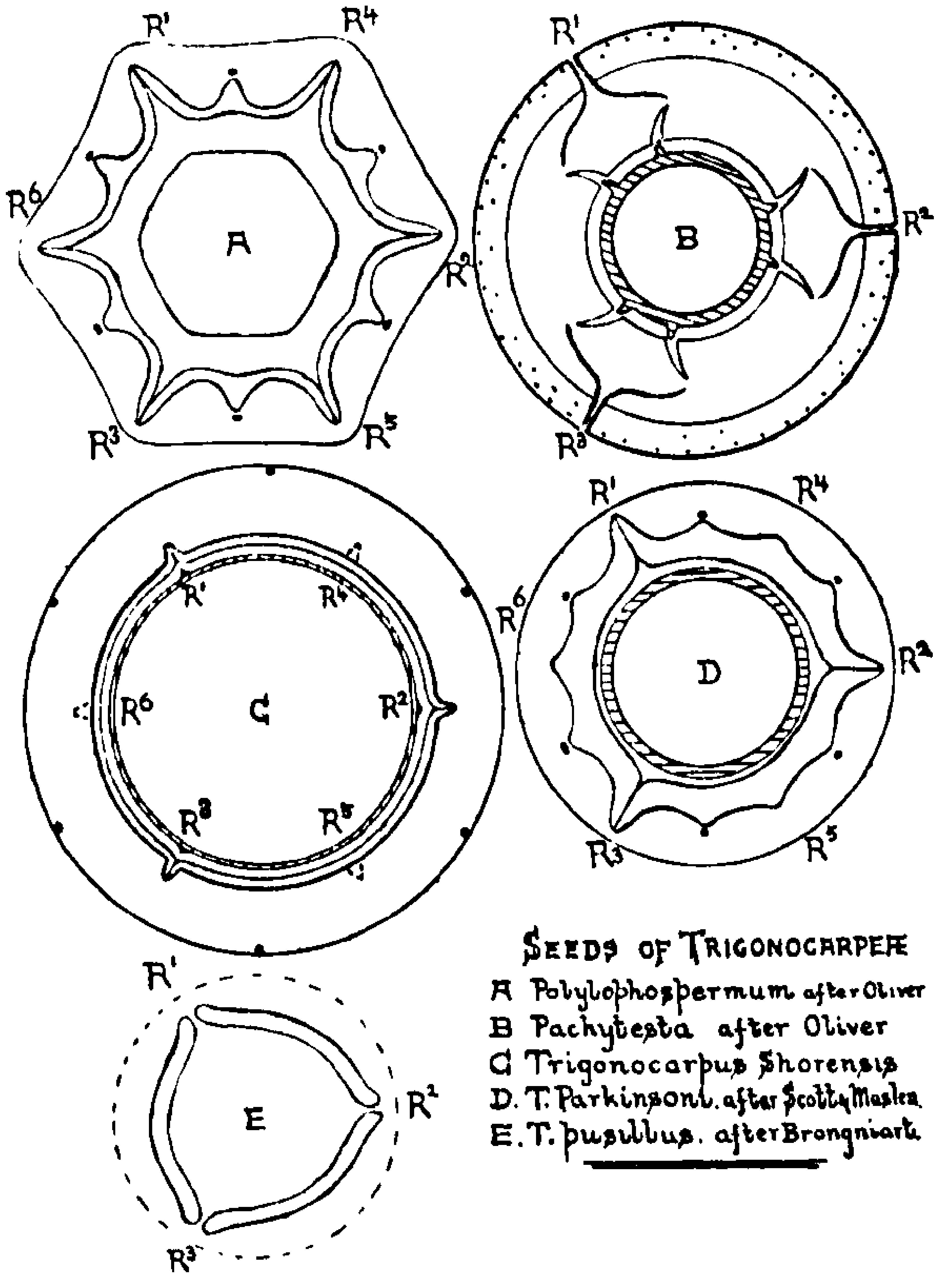
[4] Fasciation, its Meaning and Origin. New Phyt., vol. iv, 1905, p. 38.

[5] The Ovules of the Older Gymnosperms. Ann. Bot., vol. xvii, 1903.

## VIII. GENERAL DISCUSSION OF THE TESTA.

### 1. The Multiple Origin of the Integument in the Trigonocarpeae.

The general facts supporting the theory of a multiple origin for the integument of the Lagenostomales are well known,[1] and in the Trigonocarpean series the integument is also composed of several equivalent units, which may well have had a similar origin. We shall therefore briefly review the chief testal features which the members of this group exhibit.



TEXT-FIG. 8. Transverse sections of the seeds of various Trigonocarpeae. Corresponding ribs are in each case marked R¹, R², &c.

In the genus *Trigonocarpus* itself *T. Parkinsoni* had twelve ribs, three primary and fissured, three secondary and non-fissured, and six tertiary, opposite which the sarcotestal bundles were situated (Text-fig. 8, D).

In *T. corrugatus*[2] and *T. Shorensis* six ribs only were present, of which the three non-commissured died out, about half-way up in the former seed and one-third in the latter (Text-fig. 8, C).

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[1] Oliver and Salisbury: Palaeozoic Seeds of *Conostoma*. Ann. Bot., vol. xxv, 1911, p. 41.

[2] Renault, loc. cit.

In *T. pusillus*[1] the ribs had almost become obsolete and the sclerotesta was nearly circular in outline, with three commissured ribs only very slightly projecting (Text-fig. 8, E).

*Polylophospermum*[2] possessed twelve ribs, of which six were fissured, the alternating and non-fissured ribs corresponding to the radial planes of the six sarcotestal bundles (Text-fig. 8, A).

*Ptychotesta* and *Hexapterospermum.*[3] Six-angled seeds with very prominent ribs, all of which in the case of the former were fissured (perhaps also in the latter) and enlarged at the ends, owing to the separation of the two parts in that region.

*Polypterospermum.*[4] An hexagonal seed with six acute ribs at the angles of the testa, and alternating with them six others which were short and blunt.

*Pachytesta.*[5] A circular seed, but exhibiting, like *T. pusillus*, three commissures. The bundles had undergone considerable branching, so that not only are they numerous tangentially, but also form two concentric series, a complexity of vascular organization that goes hand in hand with an elaborate internal structure (Text-fig. 8, B).

*Stephanospermum.*[6] The two species were circular, and all vestiges of ribbing have disappeared. The sarcotesta is usually only represented by the tissue occupying the apical cup, so that its vascular structure is unknown.

The species of *Trigonocarpus*, we see, thus form a consecutive series involving the gradual elimination of the secondary ribs.

The production of ribs in relation to bundles is a phenomenon of widespread occurrence, met with elsewhere in the seeds of Dicotyledons, Gnetales, and Cycadales, as well as in the vegetative organs of many plants. They are probably an expression of mechanical utility, and, except from the taxonomic standpoint, the absence of such ribs from the seeds of *T. Shorensis* and *T. corrugatus* is a point of little importance.

Disregarding the vascular ribs, the general sclerotestal structure in *Trigonocarpus Shorensis* and *T. Parkinsoni* is identical. Scott and Maslen[7] remarked on the variability in development of the secondary ribs in the latter species, which always die out before the primary, and in some cases are so slightly developed as to be practically absent. The two species *T. corrugatus* and *T. Shorensis* constitute further stages in the reduction series, for in the former these ribs only extend for half the length of the seed, and in the latter are mere chalazal vestiges. In *T. Noeggerathi* only the primary ribs are present. And, finally, in species such as *T. pusillus* and *T. elongatus* all indication of the secondary ribs is lost, which applies almost equally to the primary ones also. It is evident that the secondary ridges in the genus *Trigonocarpus* were in an obsolescent condition, which would fully account for the absence of commissures if such did, as the writer believes, originally exist.

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[1] F. W. Oliver, New Phyt., vol. iii, 1904, pp. 96–104.

[2] F. W. Oliver, Ann. Bot., vol. xxi, 1907, pp. 303–4.

[3] Brongniart, Comptes rendus, tome lxxviii, 1874, pp. 15a, 16.

[4] Brongniart, loc. cit., p. 16.

[5] F. W. Oliver, New Phyt., vol. i, No. 7, 1902.

[6] Oliver, Trans. Linn. Soc. Bot., vol. vi, 1904.

[7] Loc. cit., p. 107.

F. W. Oliver has called attention to the remarkable resemblance between the plans of *T. Parkinsoni* and *Polylophospermum*,[1] one which is rendered complete if we assume that the secondary ribs of the former were the representatives of originally commissured structures. The conclusion, then, seems warranted that the six ribs of *T. Shorensis* and the non-vascular ribs of *T. Parkinsoni* are homologous with the six commissured ribs of *Polylophospermum* (in other respects, of course, this seed is specialized). It is, moreover, probable that the sutures themselves represent the planes of lateral fusion between six originally free members—a view which is further supported by the recognition of six component units in the micropylar region of *T. Shorensis.*

Newberry[2] has figured a cast showing the apex of a *Trigonocarpus* with its sarcotesta preserved, and in which the micropylar canal is seen as a star-shaped opening surrounded *by six small but free sarcotestal lobes.*

We have noted how, in the genus *Trigonocarpus*, ribs have become completely eliminated and each pair of units fused laterally, so that three sutures only remain. This condition obtains in the genus *Pachytesta*, and further reduction might well result in the production of a non-commissured seed, as in *Stephanospermum.*

The remaining genera cited above are either six- or twelve-ribbed seeds, and in the latter case the additional members may well correspond to the six vascular ribs of *Polylophospermum.*

Other genera there are, belonging to the Radiospermeae, which nevertheless possess ribs that in number are some multiple of two, e.g. *Eriotesta*, *Codonospermum.* Our review has, however, shown that there existed a group of seeds agreeing in their internal structure and consistent with our hypothesis in their sclerotestal plan, moreover including all those forms in which an undoubtedly Trigonocarpean organization has been established.

The possible origin of dimerous from trimerous forms is considered in the sequel, but the Radiospermeae is doubtless an artificial aggregate of which the Trigonocarpeae is one of the included natural groups; a statement that is borne out by the constant association with these seeds of the Neuropteridian type of foliage.[3]

None of these genera militate, then, against the theory that the integument originated as a whorl of six free members, each with a single vascular bundle, which subsequently became laterally fused. Such an interpretation necessitates the recognition of the sarcotesta and sclerotesta as constituting a phylogenetically homogenous structure, and in the next section will be given data that amply warrant that conclusion.

A striking feature of the Trigonocarpeae is not only the occurrence

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[1] Ann. Bot., vol. xxi, 1907, pp. 303-4.

[2] Rep. Geol. Survey of Ohio, vol. i, Pt. 2, 1873, p. 336 and Pl. XLII, Fig. 5.

[3] See M. Grand' Eury, Comptes rendus, vol. cxxxix, 1904, p. 3.

throughout of the hexamerous type, but also the absence of variation in the individual species. This stereotyped character suggests analogy with present-day Monocotyledons, and is in marked contrast to the variability exhibited by the Lagenostomales, not only as between different genera and species, but also as between individuals. For example, in *Physostoma*[1] nearly 50 per cent. of the seeds had ten ribs, but the remainder exhibited from nine to twelve. In *Conostoma* the number was six or eight according to the species, with one recorded variant of *Conostoma oblongum* possessing seven.[2] In *Lagenostoma Lomaxi* the normal number was nine,[3] and for *L. ovoides* eight, with variation from six to nine.[4] Finally, in *Gnetopsis elliptica* the number of ribs was four, with perhaps two others vestigial.[5] In this series we see that there is almost every variation from four up to twelve, and whilst a multiple of three is by no means infrequent—a reminiscence perhaps of relationship to the Trigonocarpeae—the more normal feature is some multiple of two.

Our knowledge of the structure of *Conostoma* and *Gnetopsis* has shown how narrow is the dividing line between radiospermy and platyspermy.[5] Also the recent discoveries of *Aneimites fertilis*[6] and *Pecopteris Plukeneti*,[7] together with the obvious relationships between Pteridosperms and the Cordaiteae, render it necessary to consider the possibility of deriving bilateral forms from a trigonous group. The fact that the fructification *Pecopteris Plukeneti* was borne on a Medullosean type of foliage certainly indicates such a change, so that the analogy afforded by examples from the carpellary structures of the present-day Flora may not be without value. The *Carices* are represented in the British Flora by about fifty species, of which over thirty possess three stigmas associated with a triangular nutlet; the remaining species mostly have two stigmas, and the nut is either bilaterally symmetrical or plano-convex. In a few species with two stigmas the nut is slightly trigonous, and in *Carex paludosa*, Good., the stigmas vary from three to two, accompanying which the nut is either trigonous or lenticular.

As an example from the Dicotyledonous series, the Polygonaceae furnish us with a group in which triangular fruits are the rule. In part of the genus *Polygonum*, and in the genus *Rumex*, a triangular nut is associated with three stigmas. In the section *Persicaria* of the genus *Polygonum*, and in *Oxyria*, the fruit is lenticular and composed of only two carpels, as shown by the pair of stigmas.

To come much nearer, the fructifications of *Ginkgo biloba* have been

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[1] Oliver: Ann. Bot., 1909.

[2] Oliver and Salisbury: Ann. Bot., vol. xxv, 1911.

[3] Oliver and Scott: Phil. Trans. Roy. Soc., vol. v, 1903, p. 197.

[4] Prankerd, T. L.: Jour. Linn. Soc. Bot., vol. xl, No. 278, p. 463.

[5] Oliver and Salisbury, loc. cit.

[6] Dr. David White: The Seeds of *Aneimites*. Smithsonian Misc. Coll., vol. xlvii, pt. 3.

[7] M. Grand' Eury, Comptes rendus, vol. cxl, p. 920.

found with three ribs in place of two, a variation that may even be a reversion.

Such examples suffice to show that the assumption of an originally hexamerous integument (later becoming trimerous in some forms) for the Trigonocarpeae does not preclude the origin of closely allied genera possessing bilaterally symmetrical structures. (The position of the tetramerous Radiosperms awaits details of their internal structure.)

In view of the frequent association in the monocotyledonous series of trimerous flowers with a triangular stem structure, an expression probably of similar mechanical relations, it is of interest to note that the general outline of the stems both of *Medullosa anglica* and *Sutcliffia insignis* was broadly triangular,[1] though the character does not of course hold for other species of the former genus.

Before leaving this subject it is of interest to note that Drs. Stopes and Fuji regarded *Yezostrobus Oliveri* as more nearly approaching to *Trigonocarpus* than any other known fossil or recent group,[2] and therefore, on the foregoing hypothesis, the triangular outline which this seed exhibits in transverse section[3] may have a phylogenetic significance.

## 2. The Question of a homogeneous or dual Phylogeny.

The question at once arises in relation to the integument: was this structure of uniform origin or was it dual, as suggested by Stopes for Cycads?[4] The close agreement of the two groups makes the assumption of a double nature for the one almost necessitate its acceptance for the other. The main grounds on which this theory is based are, briefly, the presence of two series of bundles, both supposed to be integumental, and the resemblances that exist between *Lagenostoma* with its cupule on the one hand, and the Cycadean ovule with its sarcotesta on the other. The recent work of Miss Kershaw[5] on *Bowenia spectabilis* has shown that in this species at least the inner vascular system is nucellar. On the other hand, Dr. Stopes traced some members of the inner vascular system of Cycads into the integument beyond the free part of the nucellus, and unless future work should show that it is only the accessory branches from the integumental system that behave in this manner, the evidence as to the nature of the inner bundles must remain in its present contradictory state. But in view of the diverse data at present available, we are not warranted in attaching any great importance to the occurrence of two systems, even should they prove to be both integumental in certain cases. The branched

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[1] Scott, Phil. Trans. Roy. Soc., B, vol. cxci, 1899; and Scott: On *Sutcliffia insignis*. Trans. Linn. Soc. Bot., vol. iii, 1906, Pt. 4, ser. 2.

[2] Phil. Trans. Roy. Soc., ser. B, vol. cci, 1909. More recently, however, Prof. Fuji has come to regard the nearest living relatives of this plant as being the Araucarieae.

[3] Loc. cit., Fig. 14.

[4] On the Double Nature of the Cycadean Integument. Ann. Bot., 1905.

[5] Ann. Bot., vol. xxvi, No. 103, 1912, p. 636.

and double system of integumental strands in *Pachytesta* evinces a tendency that might well have subsequently developed, and its origin in consequence have gradually become obscured.

With regard to the second argument in relation to *Lagenostoma*, recent work has shown that, in spite of the free nucellus exhibited by the Trigonocarpeae, they agree both in the structure of their fructifications and stem anatomy much more closely with the modern group than do the Lagenostomales.[1]

When we turn to *Trigonocarpus Shorensis* we find that the evidence for a homogeneous origin for the whole integument is abundantly clear. Such inner flesh as is present is but the unsclerized internal lining of the hard shell, and this latter, though broadly composed of an outer and inner part, is formed from one and the same tissue by the different course which its elements pursue.

The sarcotesta on its inner periphery shows a complete transition from the outer sclerotestal cells, so there is no zone to which we can point as possibly representing the fusion plane of two morphological units. And if further evidence were necessary it is furnished by the course of the secretory elements which pass from sclerotesta to sarcotesta irrespective of the differences of texture which, in the mature fruit, these regions present.

## IX. THE ORIGIN OF THE INTEGUMENT IN THE TRIGONOCARPEAE AND THE LAGENOSTOMALES.

The addition of yet another Trigonocarpean seed, showing a well-defined nucellar epidermis, adds to the certainty that the group was characterized by the possession of an extensive free region of the nucellus, to which part the megaspore cavity was almost entirely confined. This would seem to be a fundamental difference separating them off from the other members of the Pteridospermeae.

The considerable resemblances which the Trigonocarpeae bear to the Lagenostomales, both as regards the general organization of their seeds and the broad features of anatomy, in the few stems which have been allocated to fructifications, indicate that the two must have had a closely allied ancestry, either in some semi-Pteridospermic group which possessed a generalized type of fructification, giving rise to the characters of both; or in two parallel developments arising independently from the Pteridophytic stock.

The theory of intercalated growth put forward by F. W. Oliver in a similar connexion[2] to homologize modern with fossil forms, applied in the manner indicated below, seems to offer the best explanation of both the resemblances and differences which these two groups exhibit.

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[1] Kershaw, loc. cit.; and de Fraine: On *Sutcliffia insignis*. Ann. Bot, vol. xxvi, 1912.

[2] The Ovules of the Older Gymnosperms. Ann. Bot., vol. xvii, 1903.

In *Physostoma*, the most archaic type of the Lagenostomales, the megaspore cavity projects into the free portion of the nucellus, the plinth being only slightly developed.

In the more advanced *Lagenostoma*, the plinth exhibits intercalary growth, so that there is a greater extent of free nucellus in the older than in the younger phase, whilst in *Conostoma* the plinth reaches its greatest extent.

These facts seem to indicate that the free apical portion of the nucellus was in this series a phylogenetically late development, resulting from a zone of intercalated growth.

On various grounds *Physostoma* is regarded as the most primitive seed yet known,[1] therefore it is of greater significance as being the only member of the Lagenostomales exhibiting a free apex of the nucellus into which the megaspore cavity projects. We may therefore suppose that the potentiality for the development of a free nucellus was possessed by the ancestors of *Physostoma*; but was only exhibited by the majority of the group in the intercalated growth of the region *above* the contained megaspore, resulting in the elaboration of the plinth.

Probably, then, the common ancestors which gave rise to the Lagenostomales on the one hand and the Trigonocarpeae on the other possessed a nucellus unenclosed at the apex, and round the base of which were fused a whorl of members with free apical portions, affording protection to the sporangium, in which the prothallus was now retained. With the inception of the seed habit came an increase in the size of the megaspore cavity, accompanying enlargement of the nutritive prothallus. Here is where the divergence in the two lines of descent arose. In the one case there was an upward extension of the megaspore cavity and the surrounding free pro-integumental lobes, resulting in the production of a free nucellus which may either have had its origin in an already vascularized sporangium,[2] or the nucellar system may have arisen in relation to the greater demands upon the water-supply now created.

Along the line of the Lagenostomales the increased dimensions were brought about by a similar phylogenetic intercalation of growth, which took place, however, in the lower part where the whorl of protective members constituting the pro-integument was laterally fused to form a ring around the base of the sporangium. The close proximity of the integumental bundles would account either for the suppression or non-development of a special nucellar system. Such a view would not only explain the intermediate characters exhibited by the archaic *Physostoma*, but it further accords with the broad features of the testa as seen in the two groups.

A marked characteristic throughout the Lagenostomales is that at the

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[1] Oliver: Ann. Bot., 1909.

[2] Oliver: A Vascular Sporangium. New Phytologist, vol. i, 1902, p. 60.

apex of the seed the multiple nature of the integument exhibits itself with almost sudden clearness after it becomes free from the nucellus. In the seeds of the Trigonocarpeae, on the other hand, the component units of the testa are in general equally distinct at the base as at the apex, or even throughout their length. These two conditions seem only explicable on the hypothesis that in the one group lateral fusion was simultaneous throughout, representing in fact the elongation of the free parts, and in the other took place in the 'canopy' and body of the seed at phylogenetically distinct periods.

Our investigation of the present seed has shown us that the external periphery of the integument was circular in outline throughout; in other words, the lobing is only shown superficially at the internal periphery, where it extends from near the base to the apex, though in the body of the seed the six lobes manifest near the chalaza, and reappearing at the micropyle, had become reduced to three.

What is true of this species was, judging from impressions with sarcotesta preserved, true also for its congeners, and may well have been a group character. The Trigonocarpeae were then characterized by an internal lobing almost to the base of the seed, whereas in the Lagenostomales such internal lobing is only to be found in the apical region, so that superficially as well as internally the major part of the integument in the one is to be homologized with the distal extremity in the other.

We have assumed that the ancestral fructification of the two groups possessed a whorl of surrounding members fused at the base between themselves. In both *Trigonocarpus Shorensis* and *Trigonocarpus Parkinsoni* the sutures of the primary ribs disappear a little before the floor of the seed cavity is reached.

The structural facts therefore justify the assumption that in both groups there was a phylogenetically earlier lateral fusion of the pro-integumental members at the base, followed later by their fusion at the apex.

The congenital fusion of the integument with the contained nucellus was but a matter of time, naturally evinced first in the basal region or zone of earlier lateral fusion. This latter, in the Trigonocarpeae, is wellnigh vestigial, so that a free nucellus resulted, whilst in the Lagenostomales it represents the greater part of the seed body.

Later on in the history of the Trigonocarpeae and their descendants, congenital fusion followed in the upper part, giving us the condition in modern Cycads; though here, as in the more recent Lagenostomales, the apical region has remained permanently free in relation to its specialized structure and functions.

## X. RELATION TO VEGETATIVE ORGANS.

In two of our series of sections there occur, associated with the seed structures, Medullosean petioles of which portions of as many as three are present in one and the same preparation. This fact would, in the light of present knowledge,[1] appear of itself significant, and, added to this, numerous secretory elements are present in these petioles which agree in structure with those found in the sarcotestal tissue of *Trigonocarpus Shorensis*. Each is enclosed by a sheath-like layer of somewhat flattened cells, and the wall surrounding the dark carbonaceous mass in the centre exhibits externally the characteristic longitudinal striations. Both of these features are also exhibited in the stems and petioles of *Medullosa anglica*.

The individual bundles are collateral in structure, the phloem being represented by an empty space upon which the smallest protoxylem elements abut. The xylem is surrounded by a band of sclerotic fibres in close contact with the tracheides. The xylem exhibits no admixture of parenchymatous elements, so that in all respects the bundles are distinct from those of *Rachiopteris Williamsoni*,[2] but agree very closely with those of *Myeloxylon*.[3] If, then, the petioles above described really belonged to the plant which bore our seed, the petrifaction known as *Myeloxylon* probably represents an aggregate of petiolar structures corresponding to at least two species of Trigonocarpean fruits, and possibly in both cases having as their stem a structure of the *Medullosa anglica* type. In any case, the evidence at present available is against any suggestion that *Trigonocarpus Shorensis* was the fructification of *Sutcliffia insignis*, though the above association may be entirely without significance.

The presence of numerous secretory ducts is a feature shared by both the known British Medullosean stems. In the structure of the chalazal bundle, whilst the protoxylems of *Trigonocarpus Shorensis* appear to be grouped in pairs (a feature of *Sutcliffia insignis*), in the presence of internal parenchyma and a secretory duct within the xylem our sections of *Trigonocarpus Parkinsoni* show a closer agreement with that stem.

## XI. DIAGNOSIS.

### *Trigonocarpus Shorensis*, sp. nov.

**Locality**: Shore Littleborough.
**Horizon**: Lower Coal Measures.

A radially symmetrical obovoid seed tapering to its insertion and circular in transverse section. Length over 4 cm., width 2·4 cm.

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[1] Scott, Progressus Rei Botanicae, vol. i, p. 206.

[2] Seward, Ann. Bot., vol. viii, No. 30, 1894, p. 208.

[3] Ibid., vol. vii, 1893, p. 1.

Testa differentiated into two parts:

(*a*) **Sclerotesta** (length 2·8 cm., width 1·5 cm.) produced at the apex into a short triangular beak and bearing six ribs, viz. three principal and commissured extending throughout, and three minor and non-sutured reaching to some 8 mm. from the base. (*b*) **Sarcotesta** about 4 mm. in thickness, lacunar in structure with numerous secretory sacs, and six peripherally situated vascular bundles alternating in position with the ribs. Limiting layers containing sclerotic strands. **Nucellus** free, containing vertically directed secretory sacs, and limited within by vascular tissue forming a continuous lining at the base but above passing into separate bundles.

## XII. SUMMARY.

In the foregoing pages a detailed description is given of the Palaeozoic seed *Trigonocarpus Shorensis*, of which the chief diagnostic features are summarized in the preceding section.

The sclerotesta differed principally from that of the well-known species in its obovoid form and tapering insertion, the absence of ridges in relation to the vascular bundles, and in the relatively short beak. In the early disappearance of the secondary ribs it resembled closely the external cast of *Trigonocarpus corrugatus.*

Both sarcotesta and sclerotesta showed considerable complexity, with nevertheless a well-marked transition, such as can only be reconciled with differentiation of the same organic unit. The sclerotesta was built up of fibrous elements longitudinally directed within and without, intertwined in a complex manner. The sarcotesta was unusually broad, lacunar in structure, and contained numerous secretory sacs comparable to those of Cycads.

The limiting layers were formed of a ground-tissue of parenchyma containing a system of probably anastomosing and tangentially flattened strands of fibres, with secretory sacs like those of the interior. The whole structure in this region approached much more nearly to that of the peripheral layers of a Medullosean petiole than in *Trigonocarpus Parkinsoni.*

The sarcotesta exhibited no flattening, but was circular in form throughout, whilst an inner flesh was probably only present as an inconspicuous layer within the micropyle.

The vascular system comprised two parts, viz. a sarcotestal and a nucellar.

The most notable feature of the former is the extreme peripheral position occupied by the six mesarch vascular bundles.

The single chalazal bundle had the protoxylem groups just within the periphery, and expanded at the base of the nucellus into a tracheal cup, which was probably formed of twelve laterally fused bands that gradually increased in number to form numerous mesarch lenticular bundles lining the inner limit of the nucellus.

The nucellus was attached at the base to a sclerotic papilla, but was otherwise free from the testa, and its outstanding features were—a well-developed and thick-walled epidermal layer; the occurrence of three longitudinal flanges, corresponding with the commissures; and the presence of numerous secretory sacs in the ground-tissue, arranged in radial files.

Two sections of *Trigonocarpus Parkinsoni* are described which indicate that the chalazal bundle gave off three branches simultaneously, which almost immediately bifurcated to form the six sarcotestal strands.

A comparison with Cycads and allied types leads to the conclusion that *Trigonocarpus Shorensis* is in several respects a relatively more primitive type than its congeners. In this connexion *Trigonocarpus Oliveri* is shown to have been an eight-angled seed, and is therefore probably to be excluded from the Trigonocarpeae.

In the general discussion on the testa, the evidence for its homogenous origin is set forth, and the theory is advanced that it had its inception in the lateral fusion of a whorl of six originally free members. The testal structure of the various genera is discussed in the light of this theory.

The resemblances and differences between the Trigonocarpeae and Lagenostomales are shown to be explicable on the hypothesis of intercalated growth, followed by subsequent congenital fusion between the nucellus and integument.

Medullosean petioles associated in the coal-balls with *Trigonocarpus Shorensis* are briefly described, and resemble *Myeloxylon.*

## EXPLANATION OF PLATES.

Illustrating Mr. Salisbury's paper on *Trigonocarpus Shorensis.*

R = Owens College, Manchester, Collection; S = University College Collection; D.H.S. = Dr. Scott's Collection.

### PLATE IV.

Figs. 1–10, photomicrographs.

Fig. 1. Nearly transverse section through the middle of the seed, showing the three commissural ridges ($R^1$, $R^2$, $R^3$) and the extensive sarcotesta (*st.*). The nucellus is seen in part on the right with a ridge near the commissure slightly displaced (*n.f.*). The black dots in the sarcotesta are the carbonaceous contents of the mucilage sacs. R. 1161, *h.* × about 4.

Fig. 2. Slightly oblique section through the micropyle, showing sarcotesta with secretory sacs (*m.s.*). Within the triangular sclerotesta the inner flesh can be faintly seen. R. 1161, *k.* × 2·5.

Fig. 3. Tangential section through the outer sclerotesta. The band-like aggregates of fibrous cells are seen overlapping in a plait-like manner (*f.b.*) and passing in different directions. S. 32, *g.* × 60.

Fig. 4. Slightly oblique transverse section near base of seed; on one side a small projection is seen, representing the termination of a minor rib ($r^1$). Within is the contracted nucellus (*nu.*) with secretory sacs in radial files, over which the contracted epidermis has formed ridges. S. 33, *c.* × 2.

Fig. 5. A tangential section through the zone of transition between the sclerotesta (*scl.*) and the sarcotesta (*st. c.*). The slightly thickened walls, the elongated form, and the sinuous course of the inner sarcotestal cells are here seen. S. 32, *g.* × 90.

Fig. 6. An oblique section through the base of the micropyle, showing the extensive unflattened sarcotesta with limiting layers at *l.l.*, and secretory sacs in outer sclerotesta (*m.s.*). S. 31, *i.* × 5.

Fig. 7. Obliquely longitudinal section through chalazal end of the seed, showing vascular bundle (*v.b.*), chalazal papilla (*c.p.*), and the tapering base of seed. S. 32, *e.* × 2½.

Fig. 8. Section through extreme apex of sclerotic beak. The sclerotesta is seen to be thinning out rapidly, and at the higher level on the right is only some three elements in width. The sides show a median constriction (*m.c.*) resulting in a six-lobed structure (*m.l.*). The inner flesh (*i.f.*) shows a gradual transition from the sclerotic tissue. R. 1161, *e.* × 28.

Fig. 9. Oblique section through the base of the seed, passing through all six ribs ($R^1$, $R^2$, $R^3$, and $r^1$, $r^2$, $r^3$). At *c.p.* the chalazal papilla is seen perforated by the single vascular bundle (*v b.*). R. 1161, *b.* × 4.

Fig. 10. Tangential section through the periphery of the sarcotesta, showing the lacunae (*lac.*) separated in places by the superposed peg-like projections of the stellate cells (*p.*), and elsewhere by the cells proper. S. 32, *h.* × 90.

## PLATE V.

Figs. 11–20, photomicrographs.

Fig. 11. Vertical section through the pollen-chamber wall (*p.w.*), from which the cuticle has become separated (*cu.*). The shoulder is occupied by thin-walled parenchymatous tissue (*sh.*). The oval bodies are fungal spores (*sp.*). S. 32, *c.* × 50.

Fig. 12. Transverse section through the sarcotesta with two secretory elements, probably derived by branching, in close contact (*m.s.*). S. 31. × 60.

Fig. 13. A portion of a transverse section to show the nucellar flange, consisting of parenchymatous tissue (*n.f.*) and corresponding in position to a commissural rib (*com.*). A lenticular nucellar strand is seen on the left (*v.b.*). S. 31, *e.* × 30.

### *Trigonocarpus Parkinsoni.*

Fig. 14. Transverse section through the chalazal bundle of *Trigonocarpus Parkinsoni* at the level at which the sarcotestal strands (*v.b.*) are given off. At the top one of these has branched into two. The central xylem mass (*c. xy.*) is surrounded by a discontinuous sheath of parenchyma (*par.*), exterior to which more tracheides (*tr.*) are seen. A single secretory element (*m.s.*) occupies a position within the xylem mass. In the space between the bundle and the sclerotesta several more secretory elements are seen and remains of parenchymatous tissue. S. 34, *a.* × 90.

Fig. 15. A single sarcotestal bundle from near the base of *Trigonocarpus Parkinsoni*, showing the dual nature of the xylem. The centre of the strand is occupied by narrow tracheides (*n.tr.*) surrounded by a parenchyma sheath (*par.*), and this again is followed by a zone of short broad tracheides (*s.tr.*). S. 34, *b.* × 90.

### *Trigonocarpus Shorensis.*

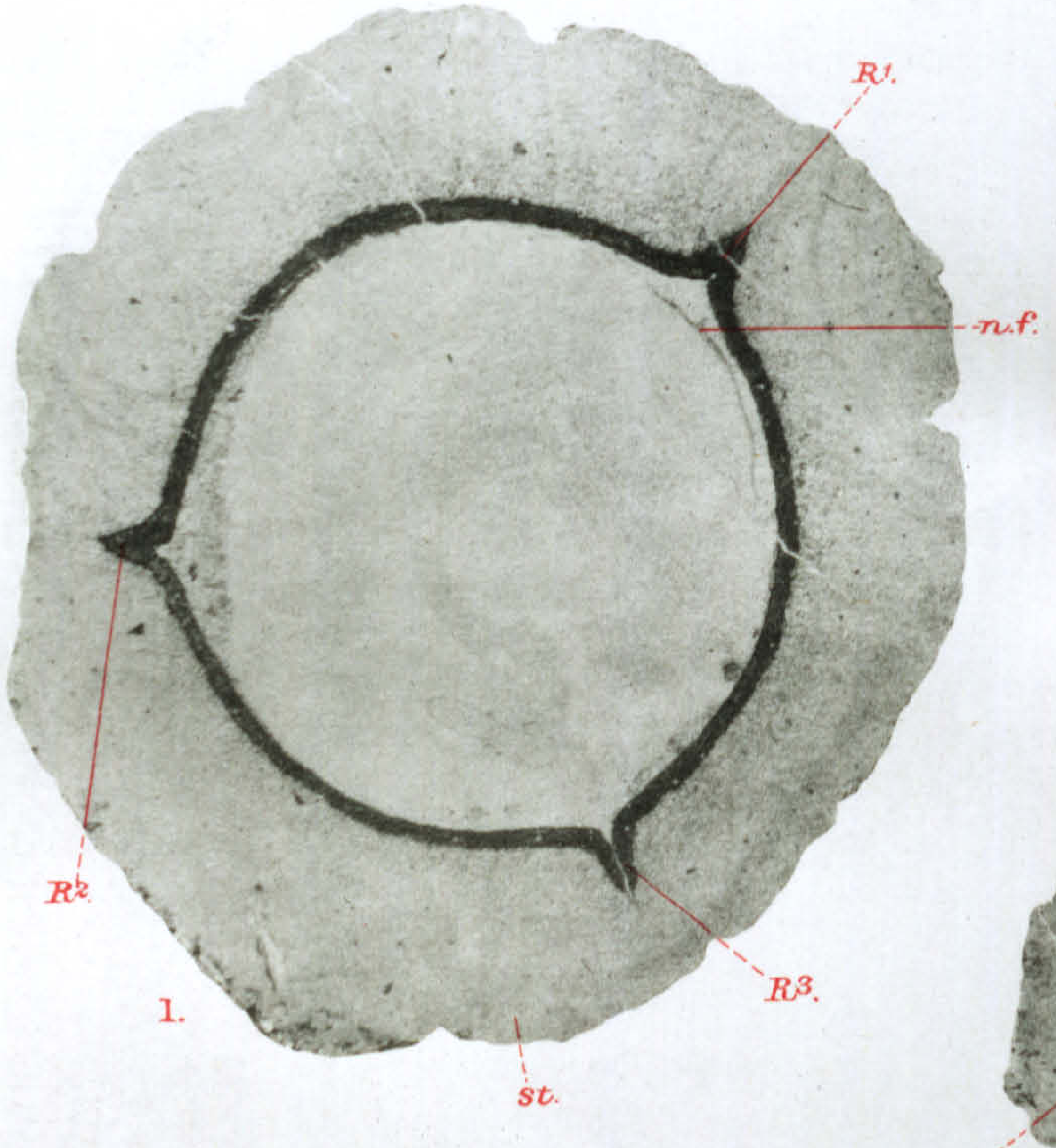
Fig. 16. Transverse section through the chalazal bundle of *T. Shorensis.* The parenchyma sheath (*p.s.*) around the bundle and the radially extended tracheides of the outer zone are clearly seen. The protoxylems are seen occupying a position just within these latter. *m.s.*, mucilage sacs. S. 33, *b.* × 100.

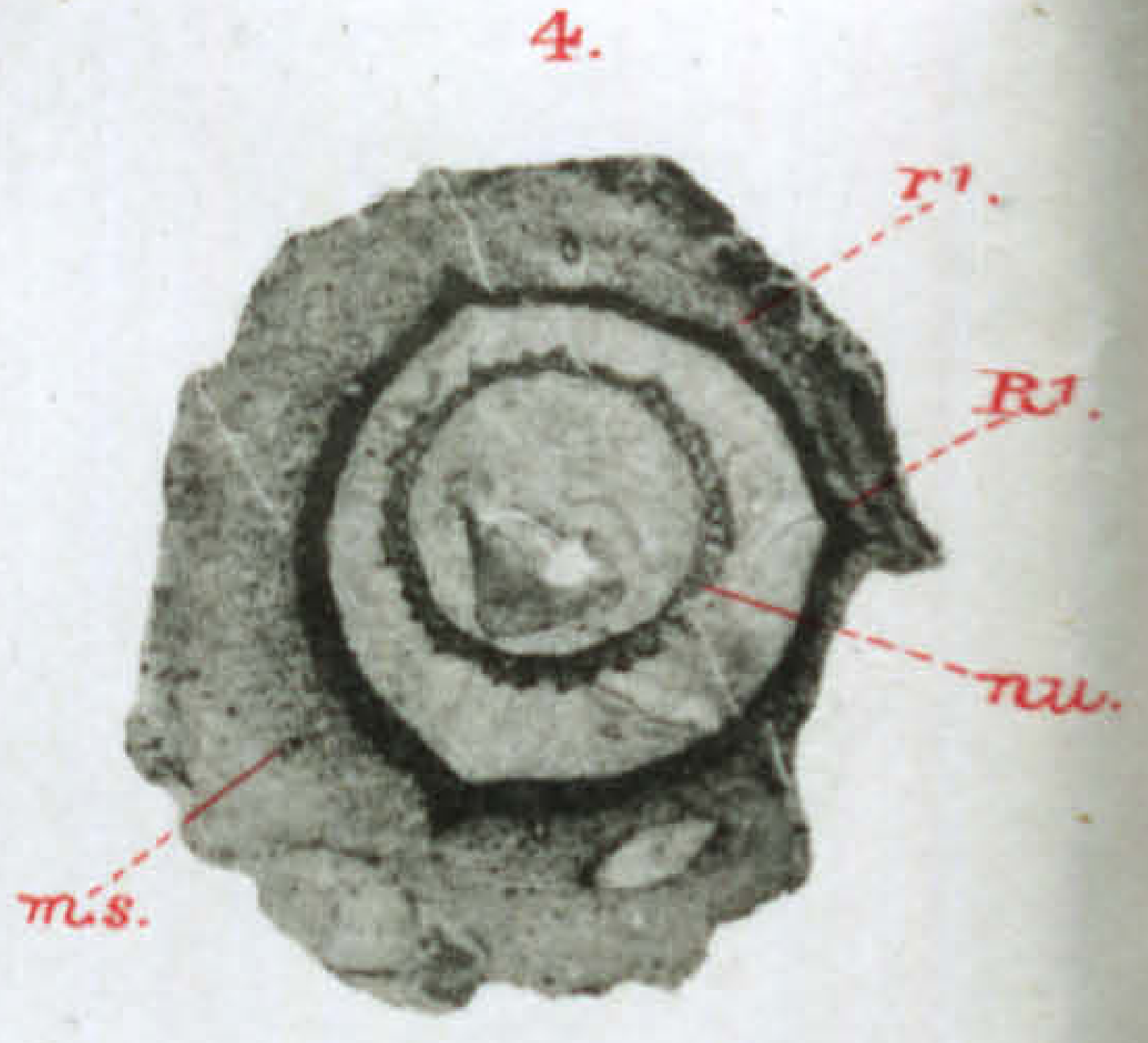
Fig. 17. Transverse section through a sarcotestal bundle, showing the thick-walled protoxylem elements (*pt.x.*), the small elements of the centrifugal xylem (*cf.x.*), and the large short tracheides comprising the centripetal (*cp.x.*). Touching the bundle on the right is a sclerotic strand of the limiting layers. *m.s.*, mucilage sac. S. 31, *i.* × 100.

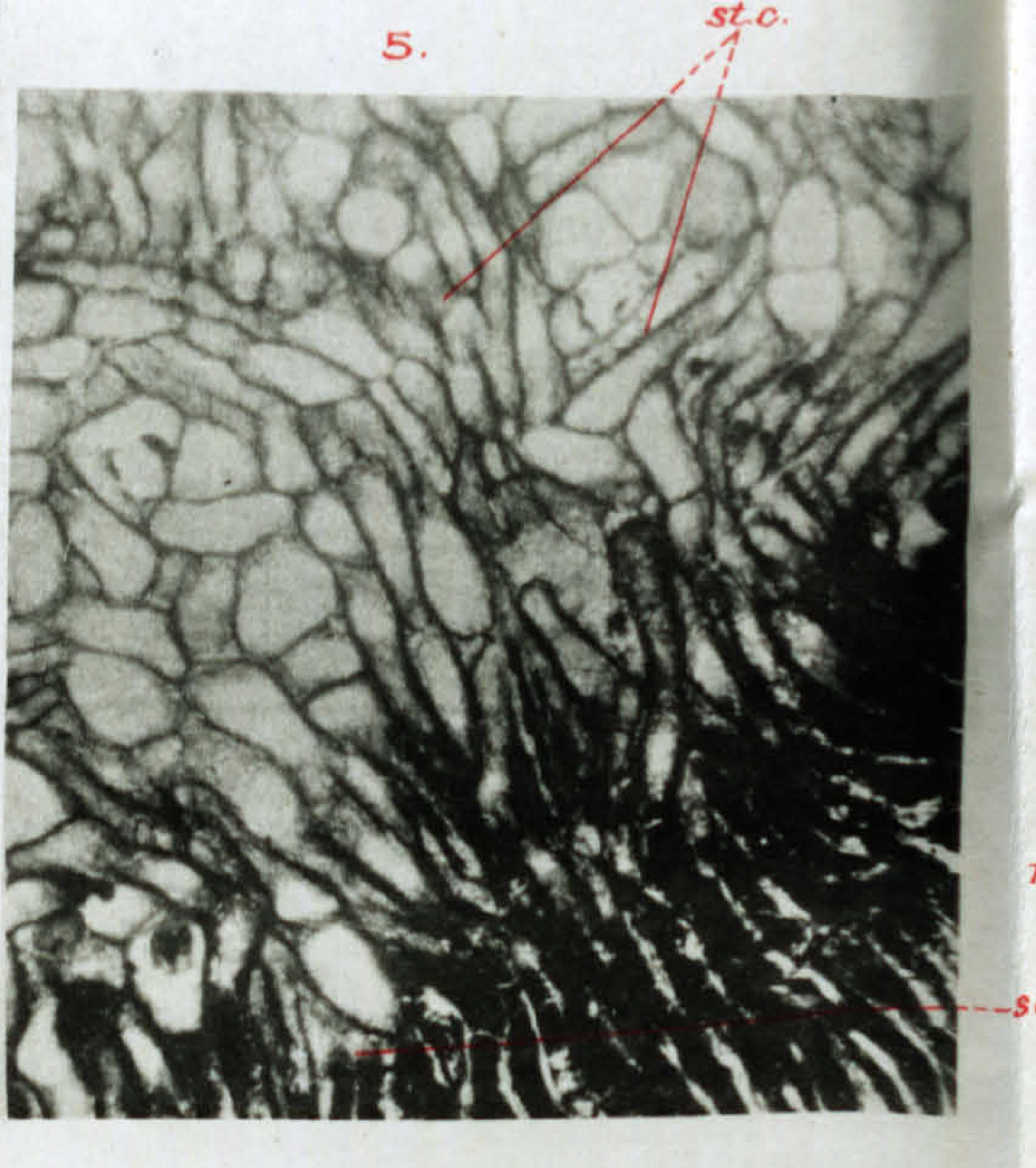
Fig. 18. Oblique section through the chalazal bundle, from the same preparation as Fig. 7, showing the scalariform thickenings of the tracheides (*tr.*). *scl.*, sclerotesta. S. 32, *e.* × 80.

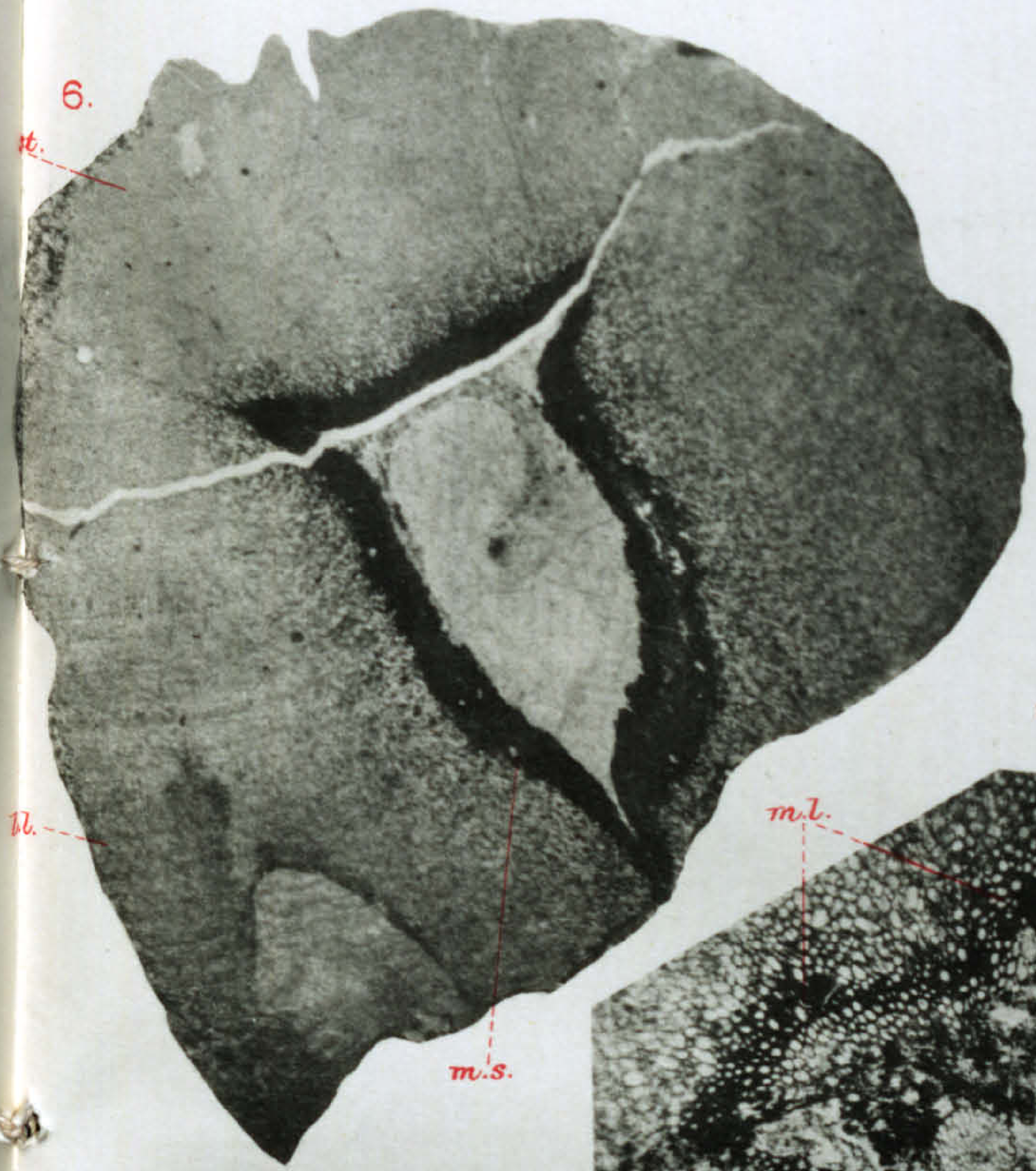
Fig. 19. Transverse section through the limiting layers of the sarcotesta, occupied by several radially extended sclerotic strands (*scl.p.*) partially displaced by contraction. The sclerotic plate on the extreme left is interrupted by a medianly placed mucilage sac, and both here and in the other here present (*m.s.*) the thickened wall stands out clearly as a transparent zone around the dark contents. S. 31, *i.* × 100.

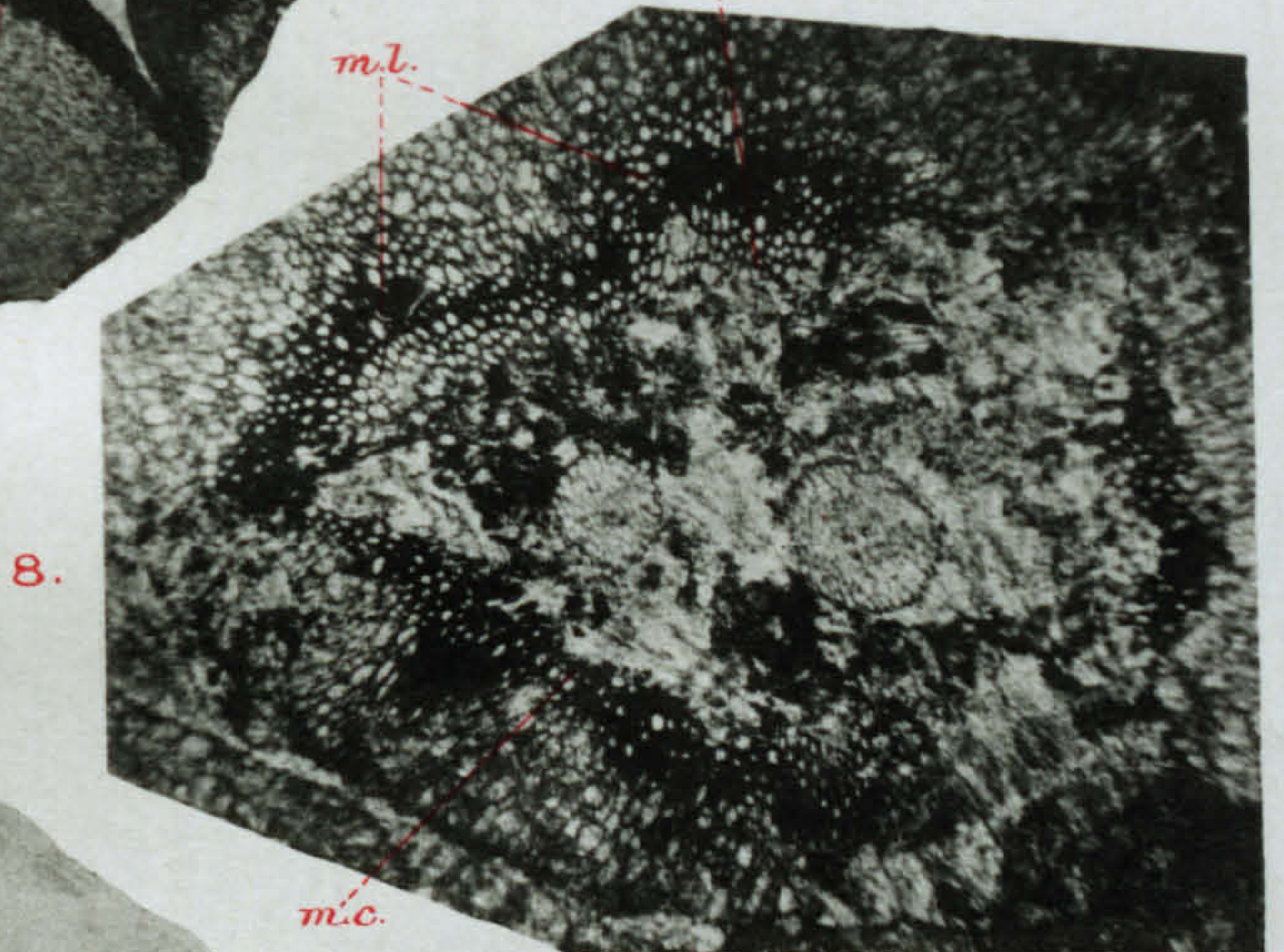
Fig. 20. Transverse section through the nucellus from the same preparation as Fig. 4. The radial files of mucilage sacs (*m.s.*) are clearly seen, causing corresponding ridges (*n.r.*) upon the surface of the contracted nucellar epidermis (*n.e.*). The ground-tissue is occupied by thin-walled parenchymatous tissue (*par.*), and the inner limit is marked by a zone of tracheides (*tr.*). S. 33, *c.* × 120.

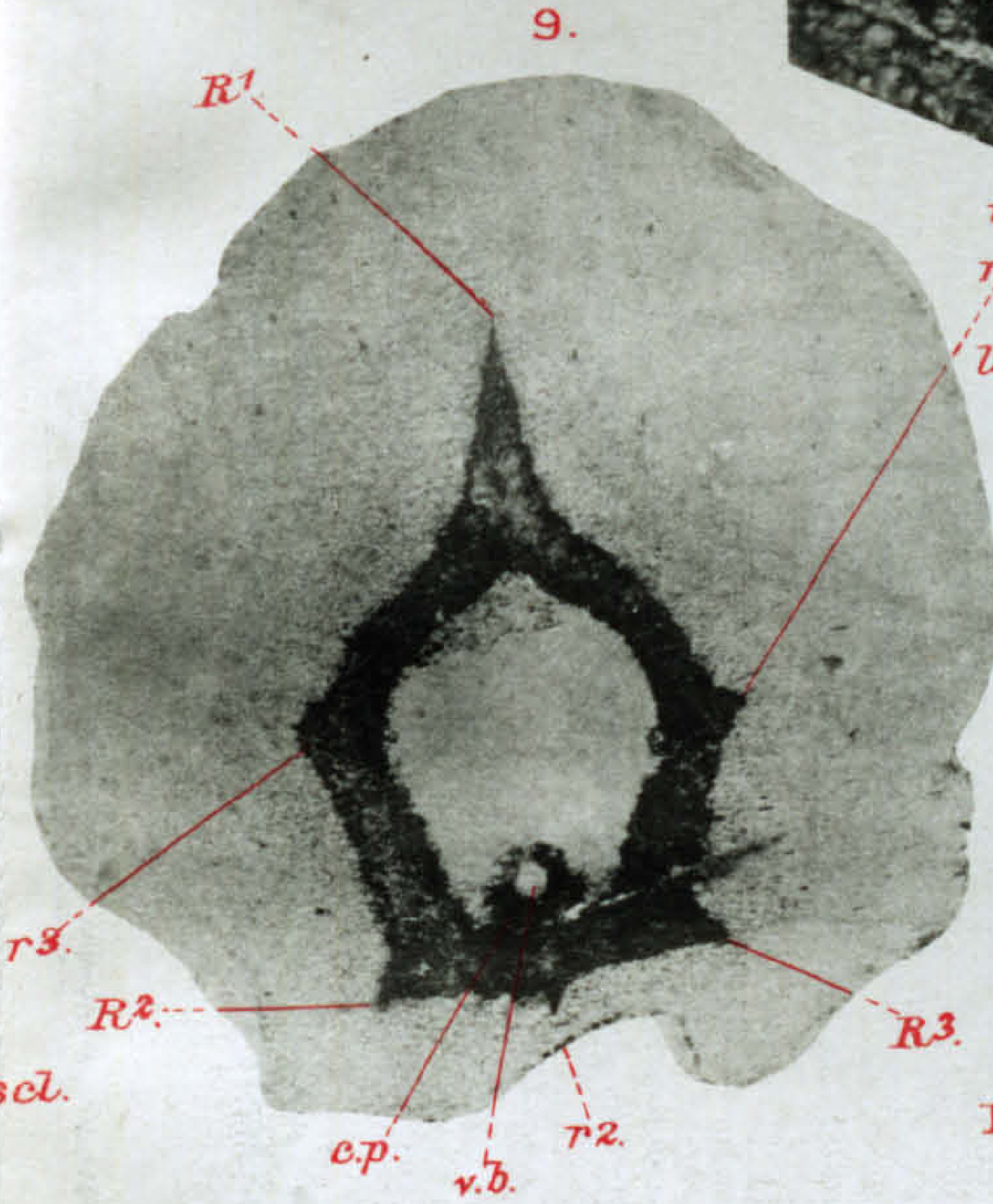


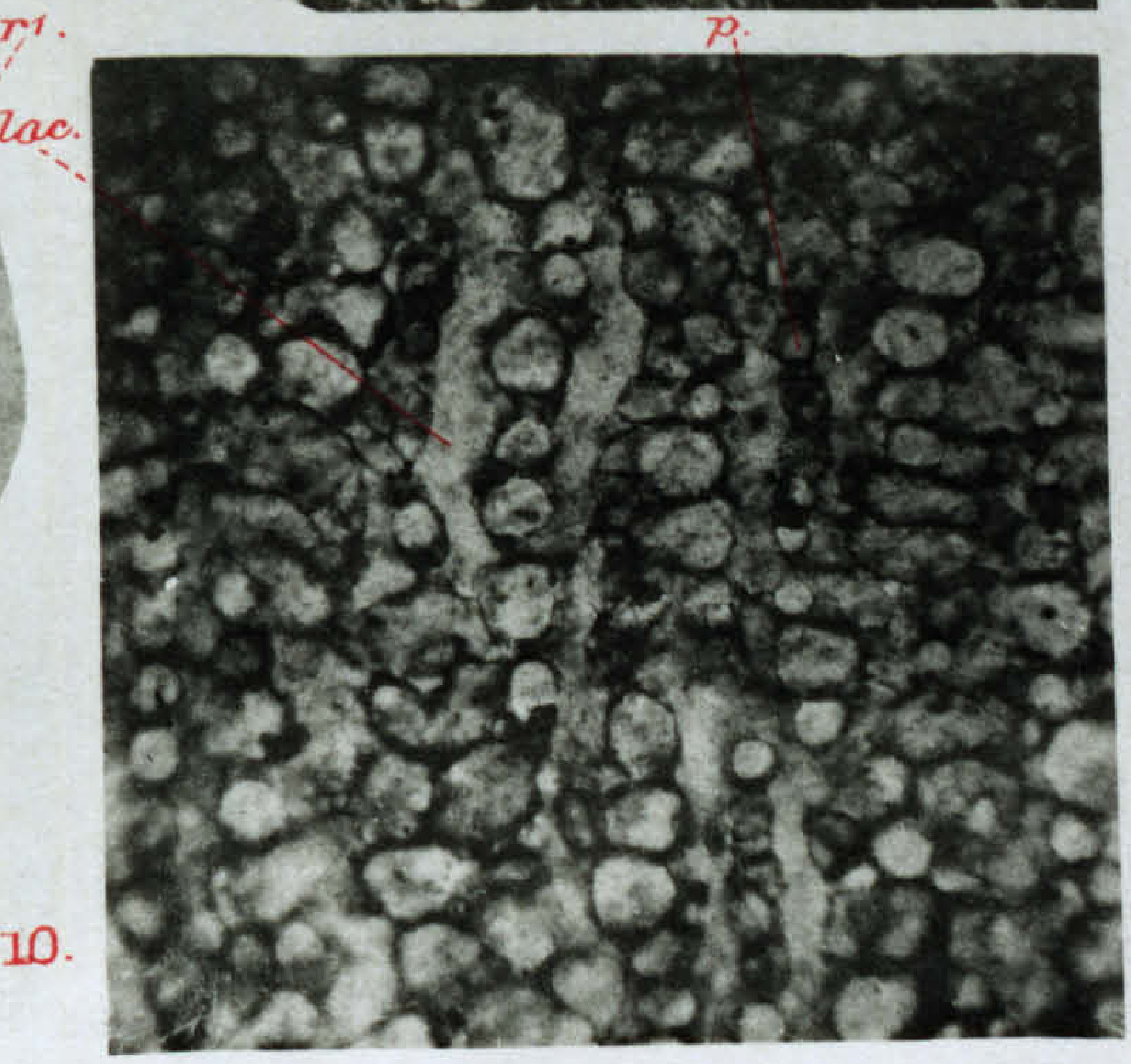












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SALISBURY—TRIGONOCARPUS SHORENSIS.

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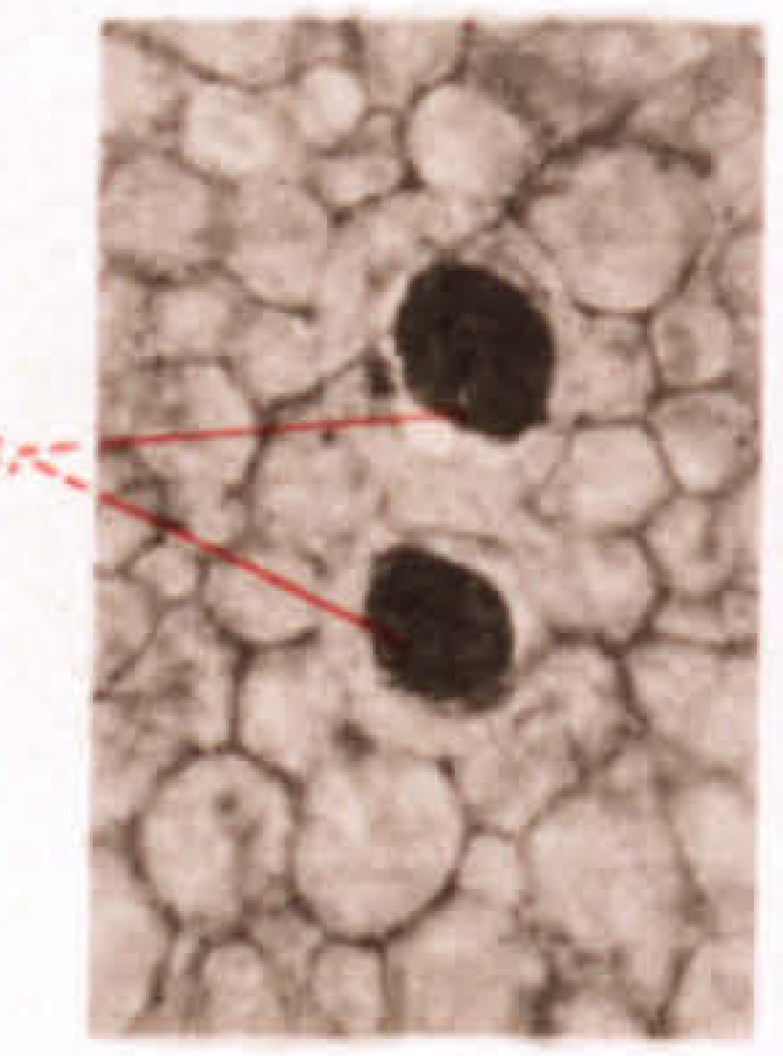

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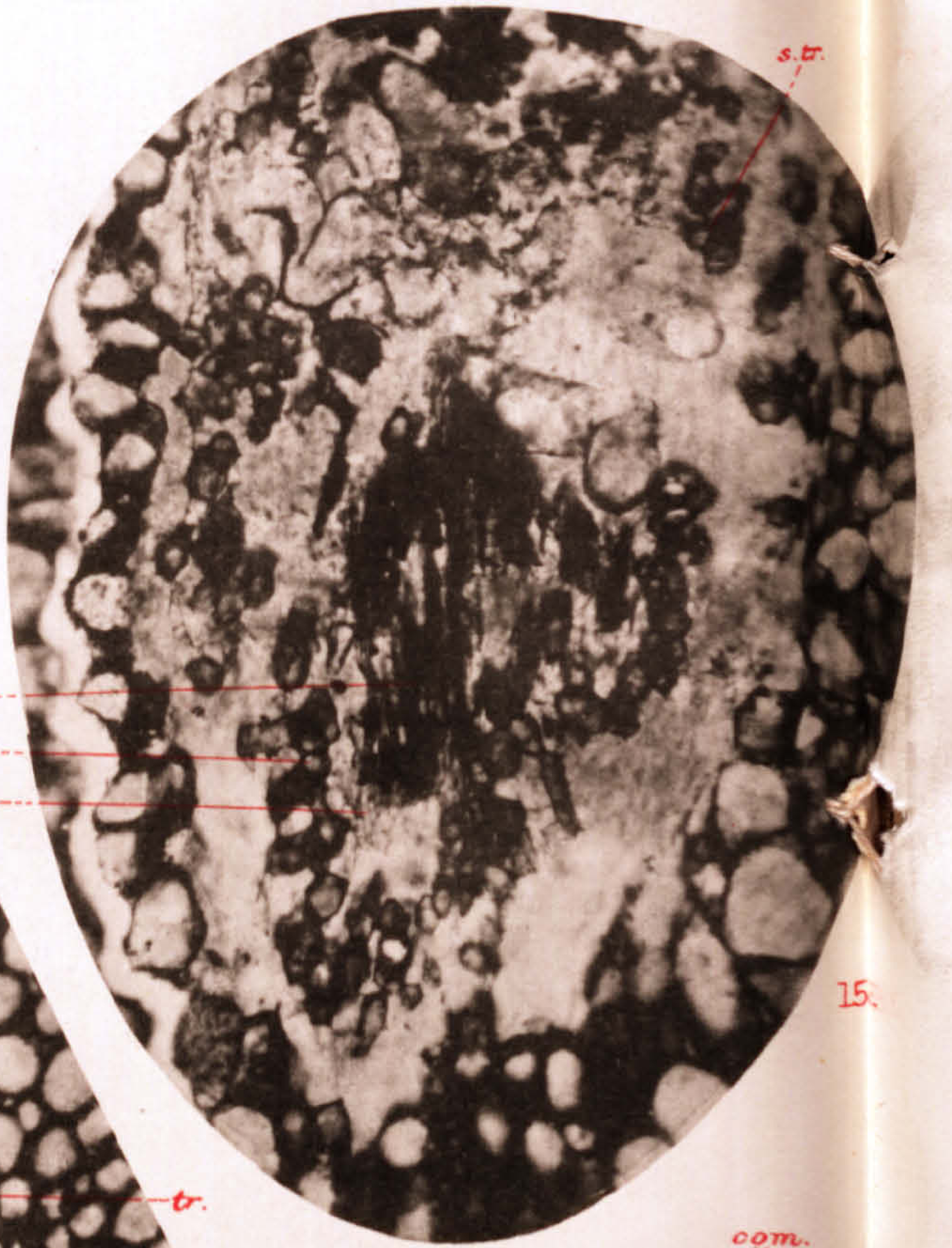

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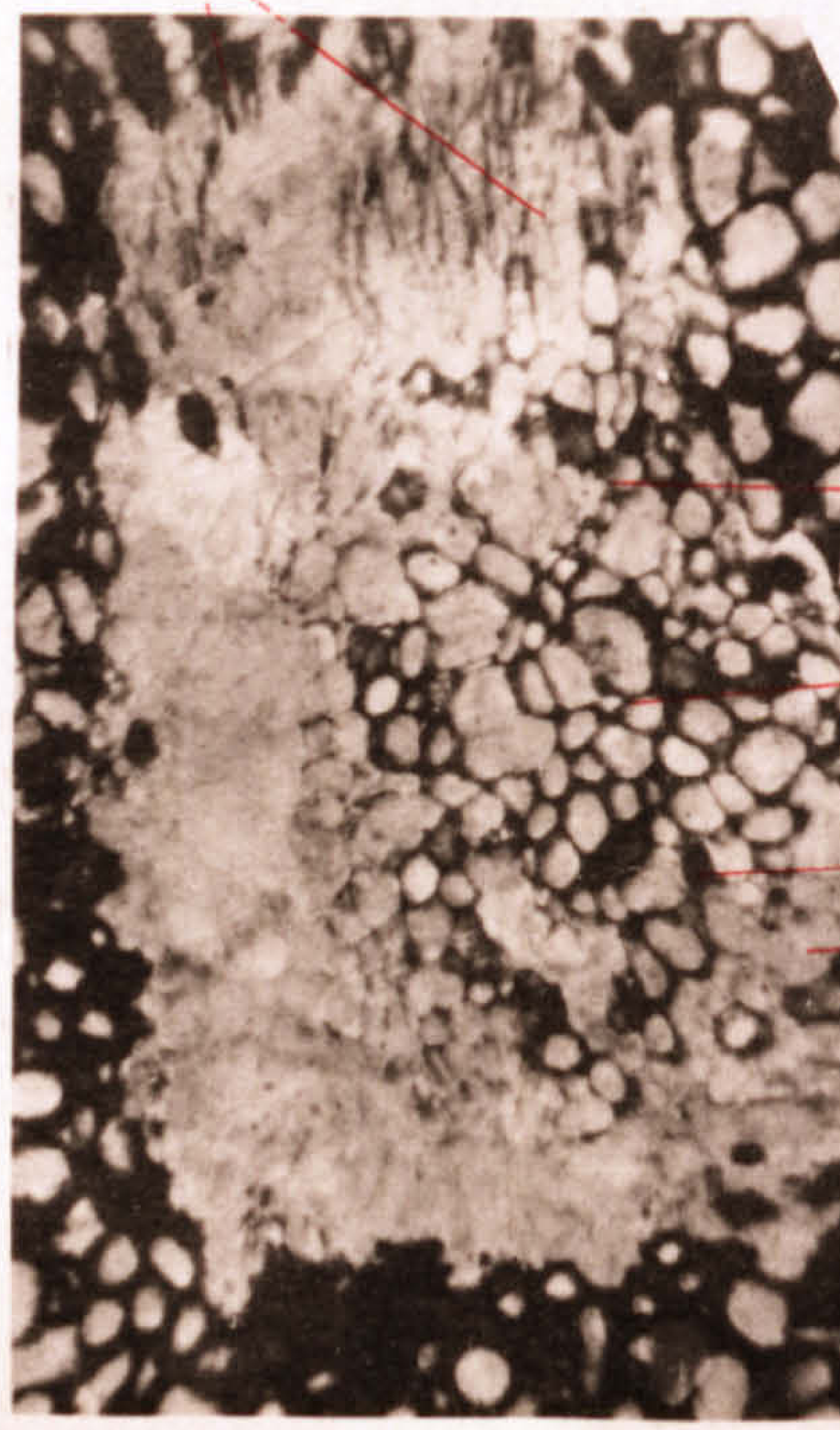

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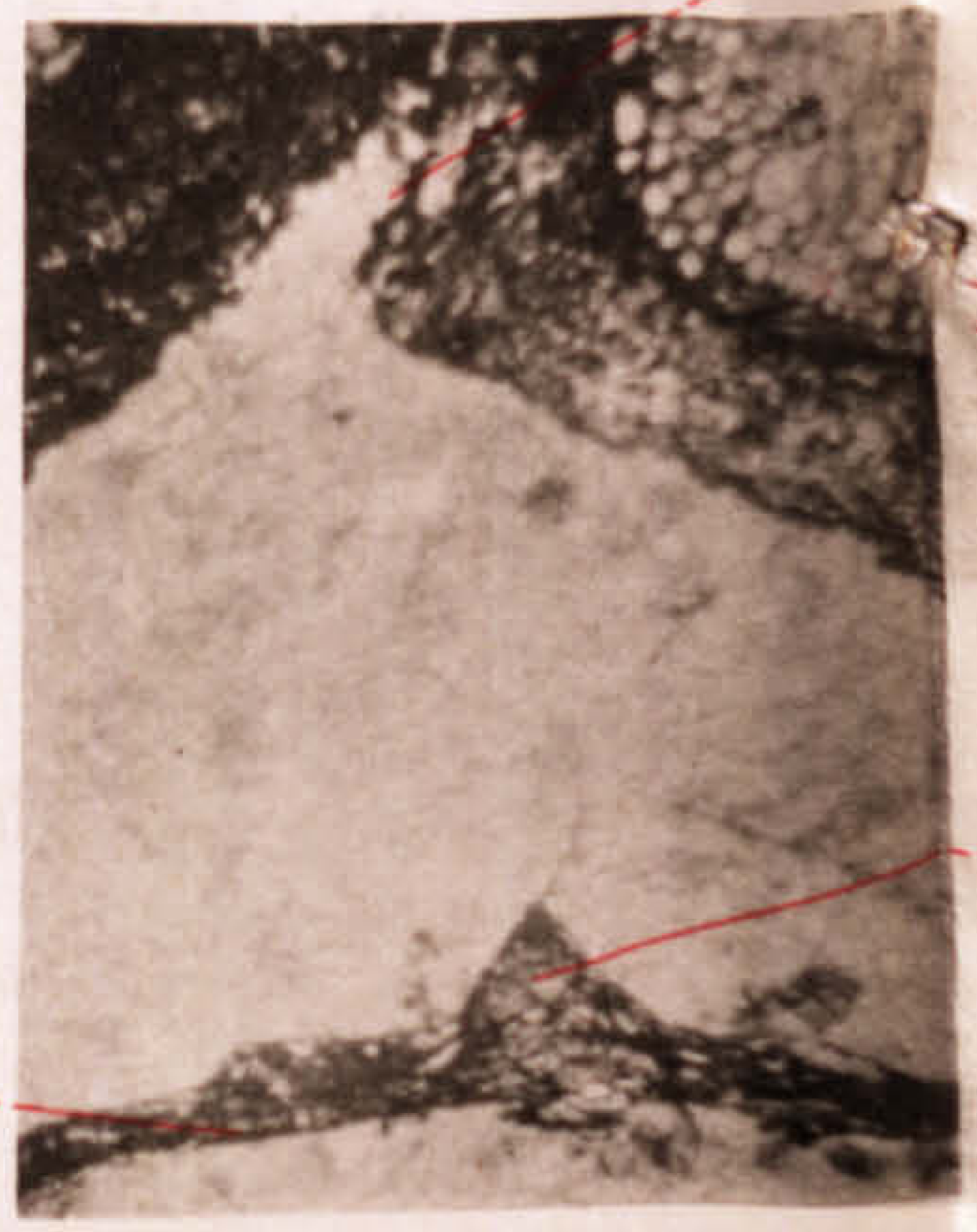

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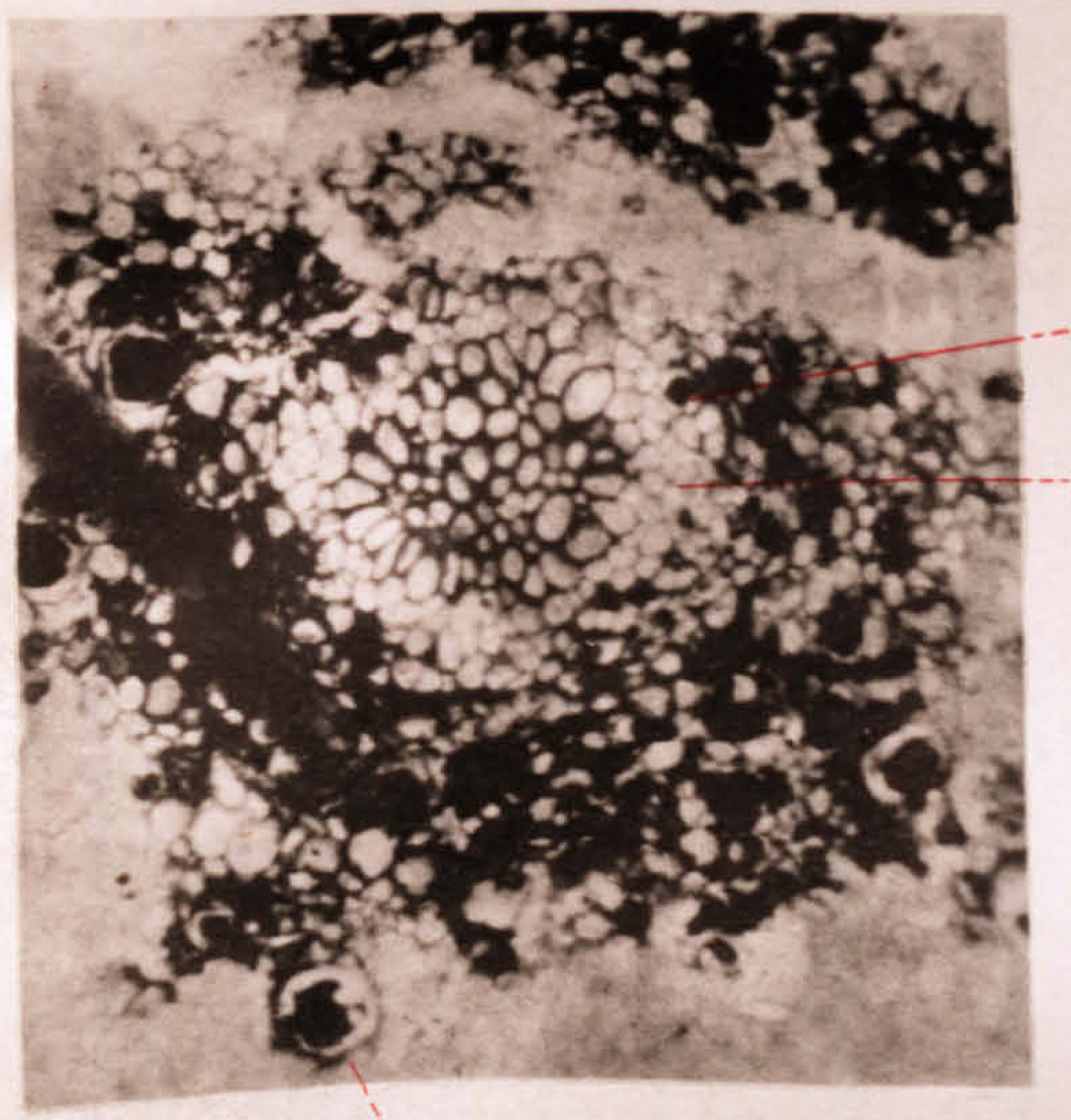

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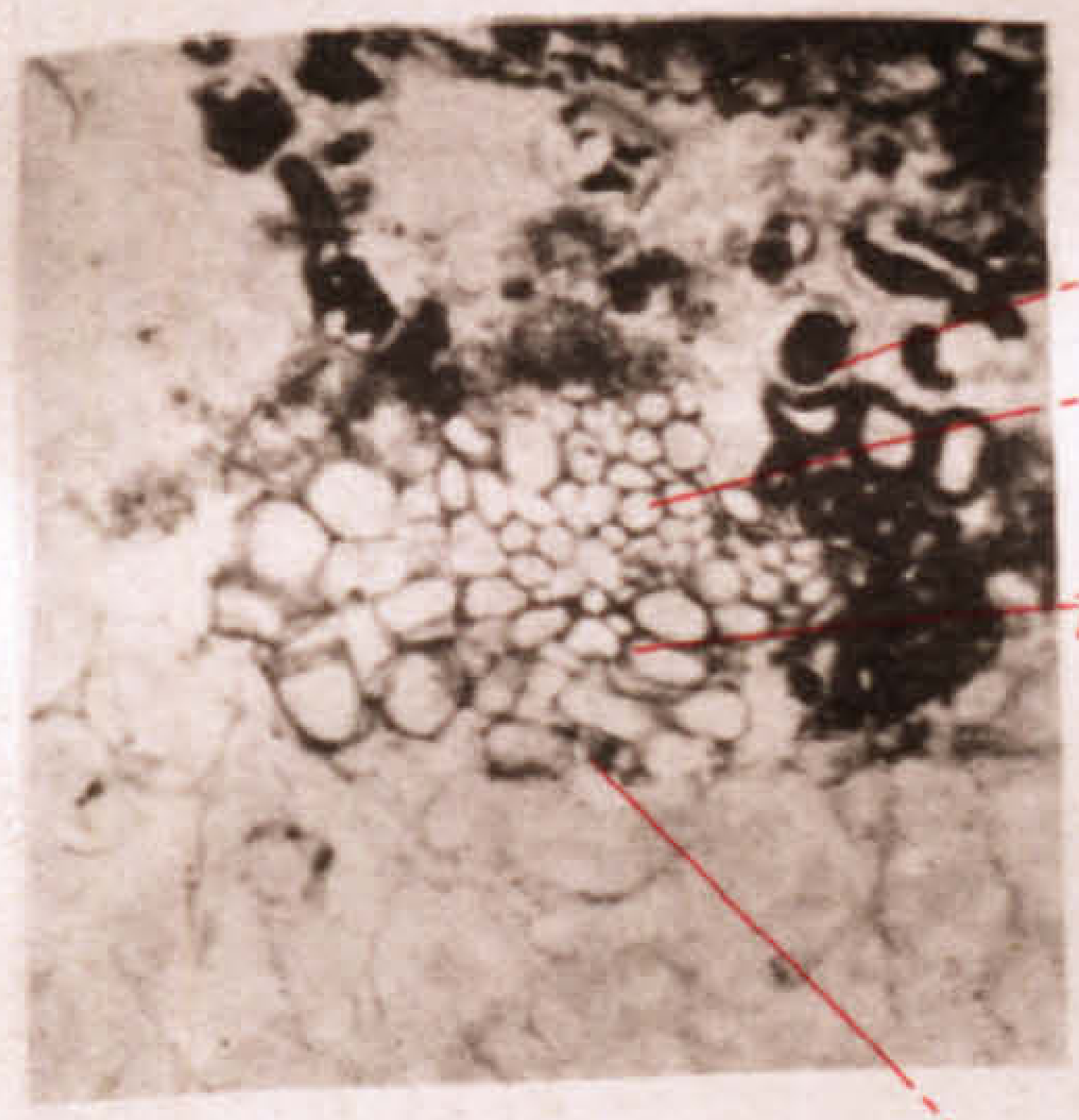

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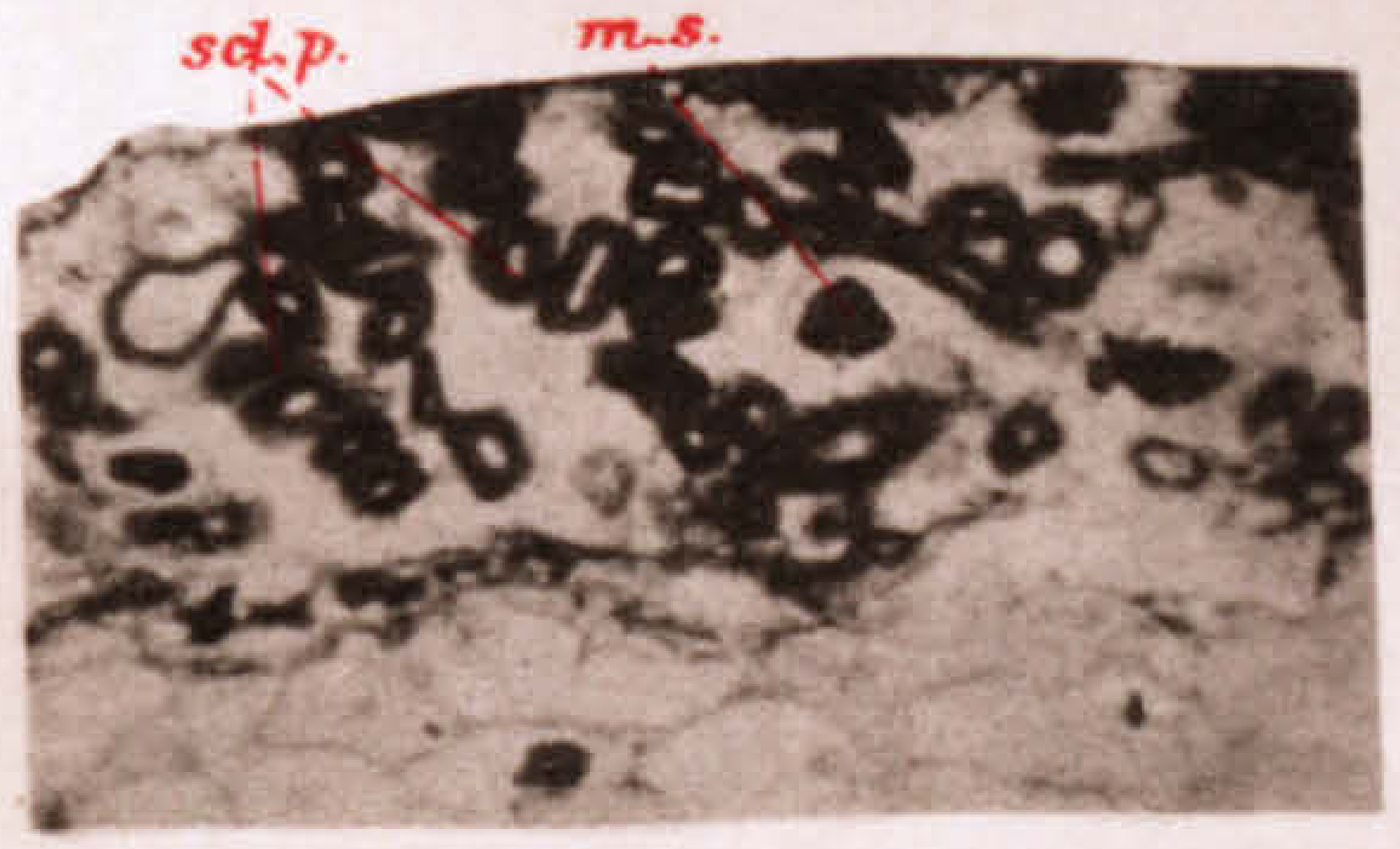

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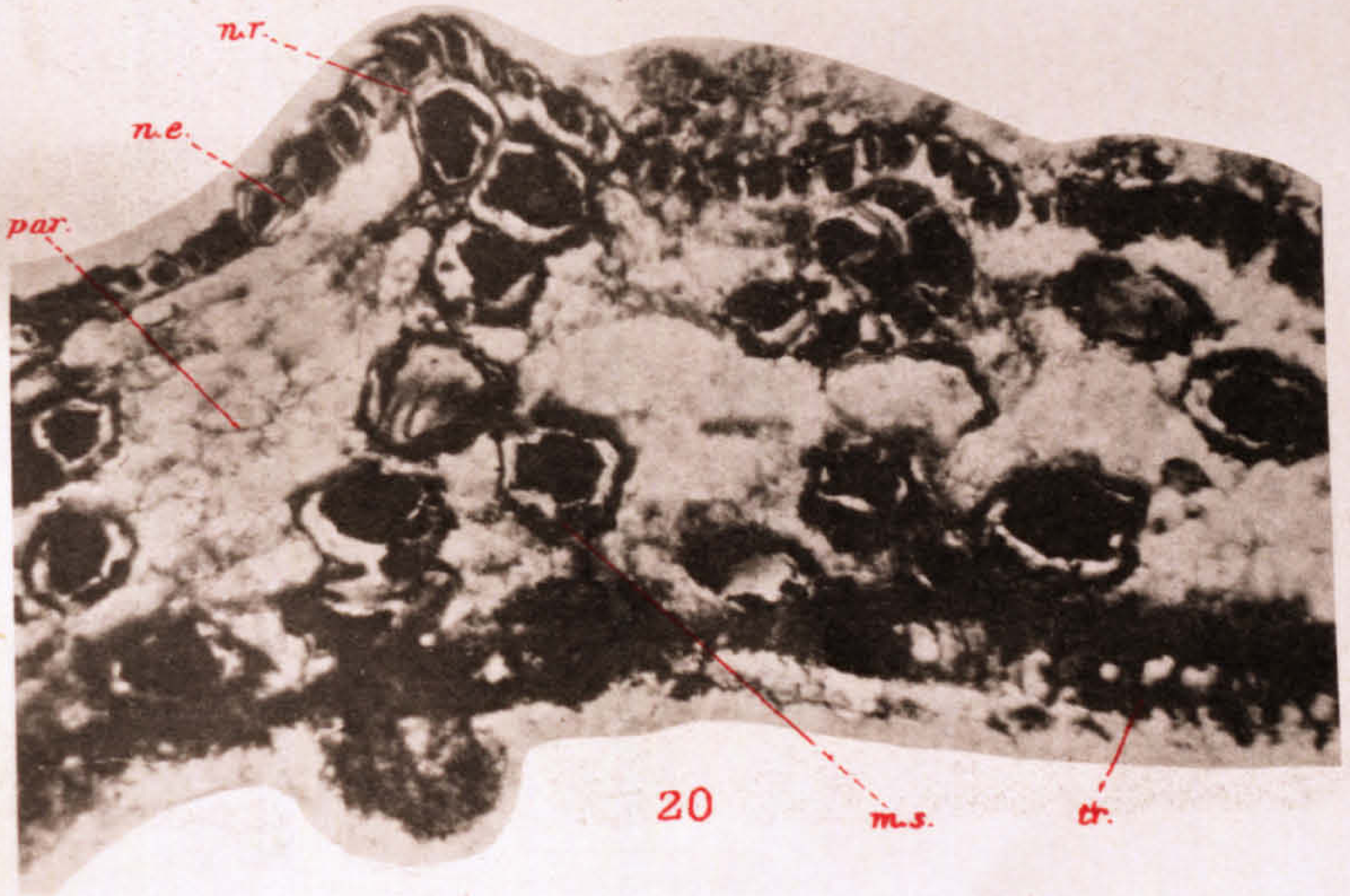

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SALISBURY—TRIGONOCARPUS SHORENSIS.

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# ON TRIGONOCARPUS SHORENSIS, SP. NOV.

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# On the Structure and Relationships of Trigonocarpus Shorensis, sp. nov.

## A New Seed from the Palaeozoic Rocks.[1]

BY

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**With Plates IV and V and eight Figures in the Text.**

## CONTENTS.

## I. INTRODUCTION.

THE bulk of the material which forms the basis of this communication was placed in my hands for investigation by Prof. F. W. Oliver; and I gladly take this opportunity of expressing my deep indebtedness to him for much helpful advice and criticism, and also for putting at my disposal such slides of the University College Collection as I have had occasion to consult.

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[1] Thesis approved for the degree of Doctor of Science in the University of London.

[Annals of Botany, Vol. XXVIII. No. CIX. January, 1914.]

My thanks are also due to Dr. D. H. Scott and to Prof. F. E. Weiss for the loan of preparations. To Dr. Scott I am also indebted for permitting me to examine the more important sections in his unique collection of *Trigonocarpus Parkinsoni*, without which an adequate comparison between the two seeds would not have been possible.

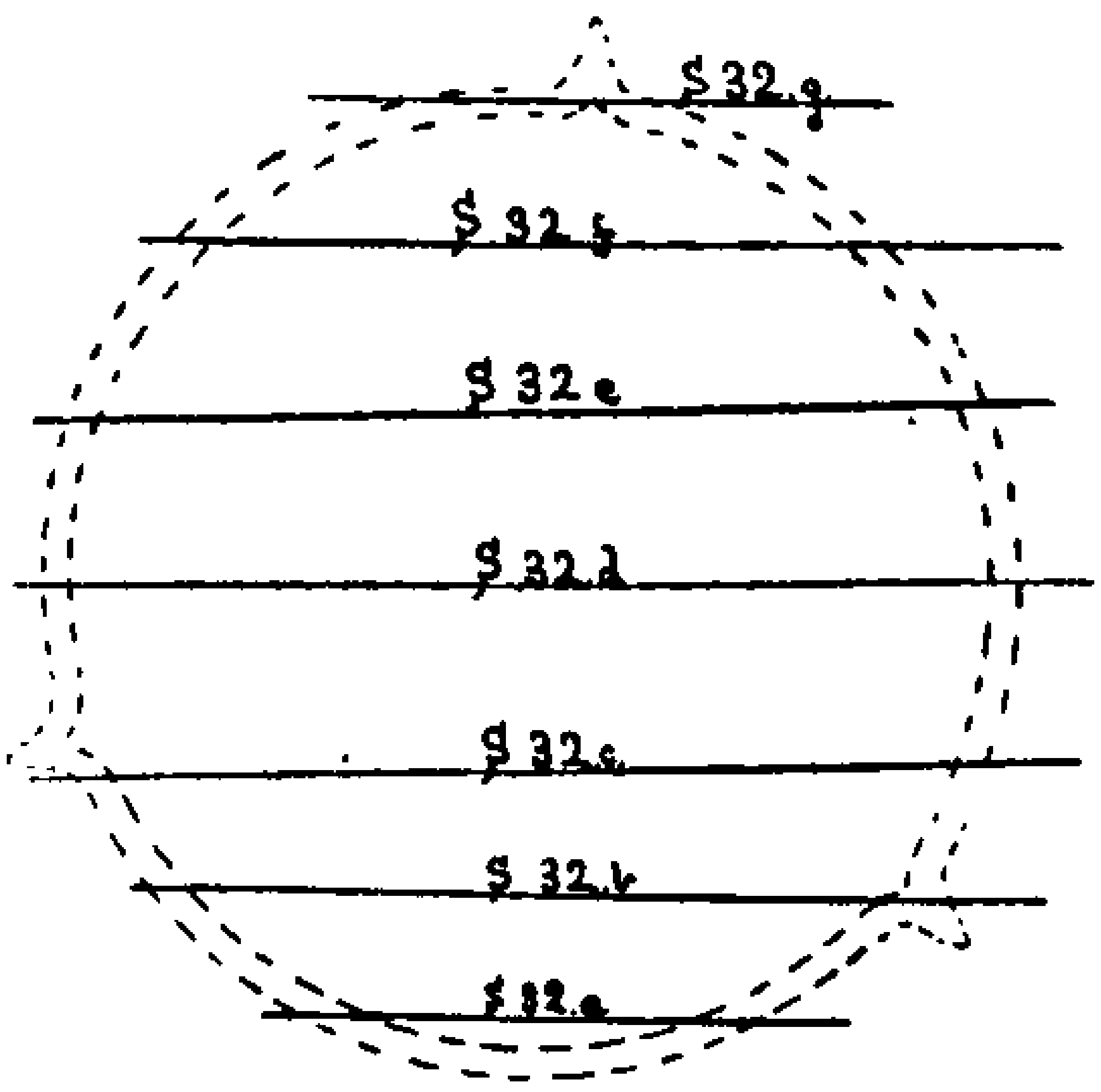
The same methods have been employed in the reconstruction of the present seed as were used in the investigation of *Conostoma oblongum* and *C. anglo-germanicum*.[1] These have been recently described in a separate article[2] and need not be recapitulated here.

The sections that furnish data for the following account are all cut from seam nodules obtained from the well-known locality at Shore Littleborough, re-opened through the generosity of the late Mr. Sutcliffe. To mark its origin it has been thought appropriate to designate this seed by the specific name of *Shorensis*.

## II. GENERAL FEATURES.

The seed with which the present investigation deals was of large size, approximately elliptical in form, and circular in transverse section. The exact limits at either end cannot with certainty be determined, but the total length was probably considerably over four centimetres. In breadth the seed attained a maximum diameter, about half-way up, of nearly two and a half centimetres.

Although specimens showing the actual attachment of the seed are wanting, the chalazal end certainly tapered towards its insertion and, judging from the general direction of the surface curvature, followed a more gentle curve inwards to the apex.



TEXT-FIG. 2. Plottings on the transverse section of the S. 32 series.

The testa comprised three or perhaps four layers, the two outer of which constituted a broad sarcotesta remarkable for the presence of a number of scattered secretory sacs and representing nearly one-third of the total width of the seed.

Within the sarcotesta was a hard sclerized shell bearing three salient ridges which extended from the base to the apex. These ridges were symmetrically placed around the body of the seed, and from the chalazal end to about a third the height of the sclerotestal shell were present three more ribs much less pronounced than the former, and occupying positions intermediate between them.

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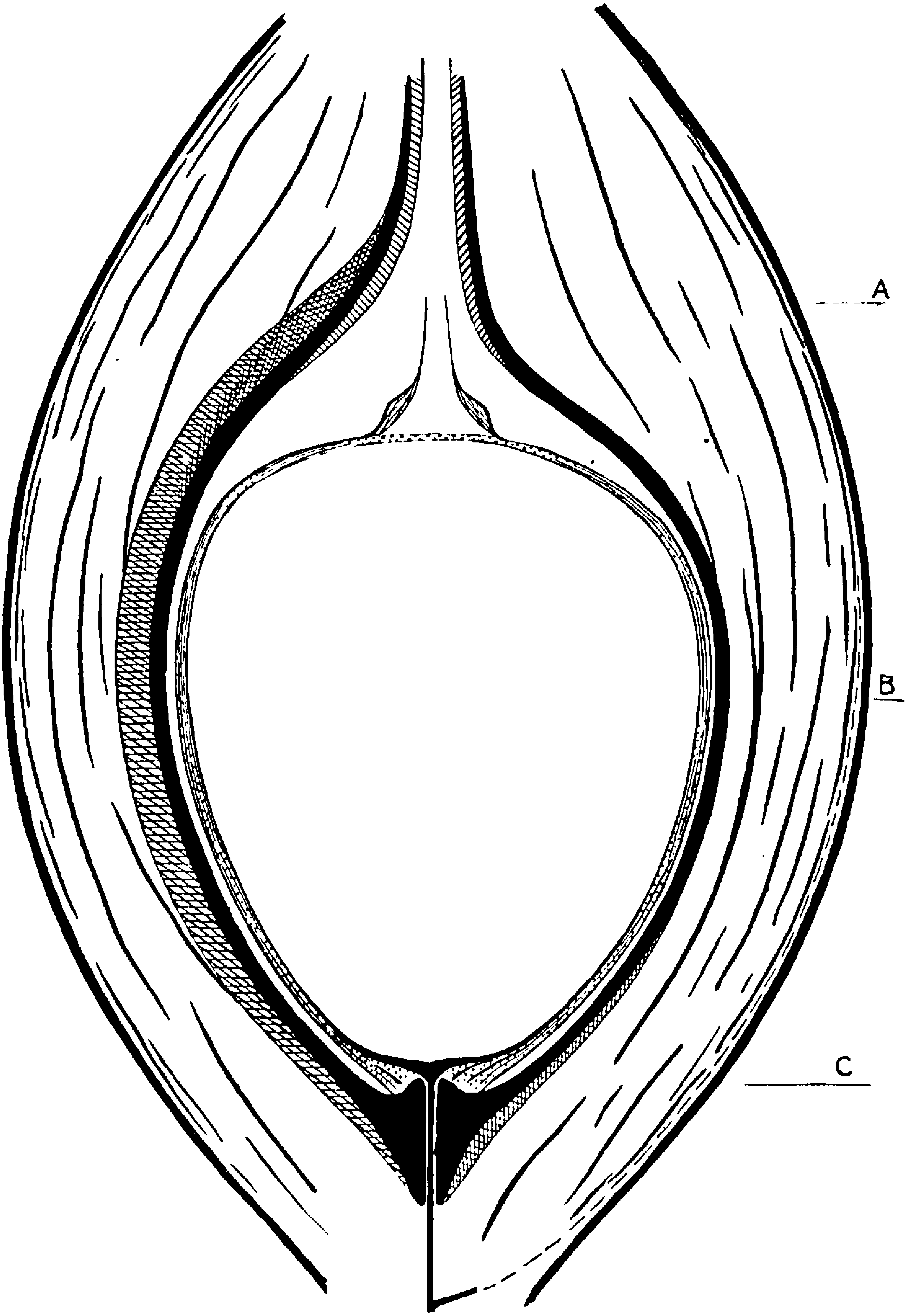
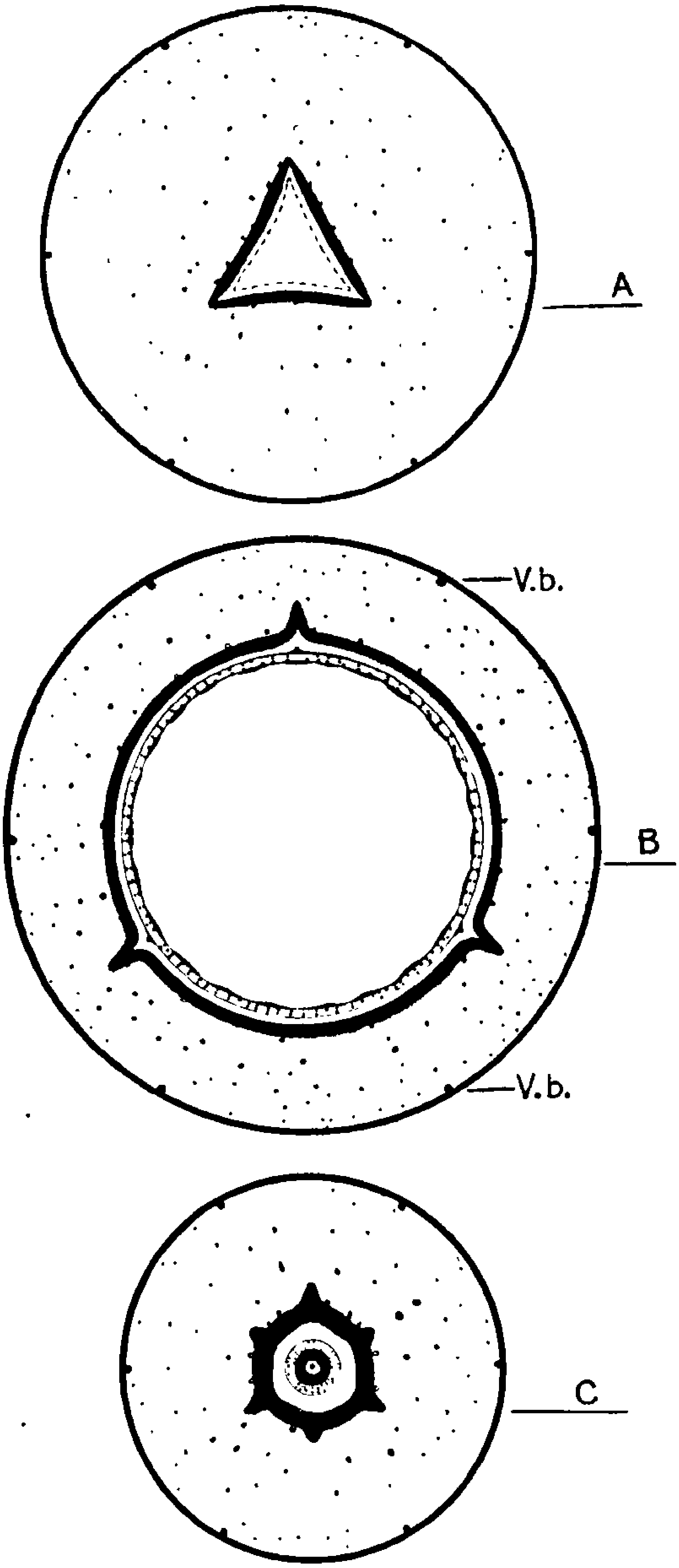
[1] Oliver and Salisbury: On the Structure and Affinities of the Palaeozoic Seeds of the *Conostoma* group. Ann. Bot., vol. xxv, 1911.

[2] Ann. Bot., vol. xxvii, No. cvi, 1913.



TEXT-FIG. 3. Diagrammatic restoration of an ideal median longitudinal section of *Trigonocarpus Shorensis* passing through a primary and secondary rib. The sclerotesta and limiting layers of the sarcotesta are shown in black; the ribs are cross-hatched, and the inner flesh, the extent of which is hypothetical, is represented by diagonal shading. The branching of the chalazal bundle is based on analogy with *T. Parkinsoni*, and the direction of one of the sarcotestal strands is also shown as a dotted line, though not actually present in the plane of section. Nucellar tissue dotted, secretory sacs black.



TEXT-FIG. 4. Transverse restorations of *Trigonocarpus Shorensis* at the levels A, B, C in Fig. 3. Tissues represented as in the previous diagram. The six sarcotestal strands are represented by large black dots, and the secretory sacs by smaller.

In the chalazal region there were thus six ribs, of which three soon die out, whilst the remaining three persist.

In general form the sclerotesta was ovoid, the pointed end corresponding to the chalazal region, whilst the blunt end was surmounted by a triangular micropylar tube, the angles being continuations of the ribs lower down, into which they pass by a hollow curve.

Within the sclerotic tissue was a fourth layer, probably confined to the micropylar region and representing the 'inner flesh' of related seeds.

The megaspore cavity was much less pointed at the base than was the hard shell around, and through this divergence of the two surfaces a chalazal cushion of sclerotic tissue was formed from which arose a nucellus, that stood up erect and free within the seed cavity, surmounted at its apex by a large pollen-chamber.

The nucellus was bounded at the exterior by a well-differentiated epidermis, and within was a tracheal sheath forming the upward continuation of a single vascular strand which pierced the chalazal cushion.

The vascular organisation was essentially similar to that of other seeds of this group, and consisted of a sarcotestal system of bundles without and a nucellar system within.

Neither pollen nor prothallus are preserved in any of our sections, which may indicate that all our specimens were abortive ovules, though the presence of numerous fungal spores within the megaspore cavity may indicate its former occupation by an organized tissue which served as nourishment to the saprophytic organisms.

## III. THE TESTA.

### 1. The Sclerotesta.

The obovoid sclerotesta had an average thickness of about 0·5 mm. and bore, as we have seen, six longitudinal ribs, of which the three major persisted as far as the triangular beak. At the apex these ribs pass gradually into the three angles of the micropyle, and, except at the base, are commissured. The major ribs from the base of the micropyle to within some 6 mm. of the chalazal extremity have about the same radial extent, but exhibit varying development in the different specimens (0·75 mm. from surface in S. 33, *a–e*, to 1·4 mm. in S. 31, *a–k*). The three minor ribs alternated with the three major, were without commissures, and attained their greatest extent (0·4 mm.) about 2 mm. from the base, above which point they gradually diminished and finally died out some 8 mm. from the chalaza. At the base of the seed the sclerotesta formed a solid inverted cone about 3·5 mm. high, perforated by a narrow canal through which the single vascular bundle passed to the floor of the nucellus. The base of this cone projected upwards as a dome-shaped papilla about 0·5 mm. high and 1·5 mm. in diameter, and its margin served as the place of attachment for the nucellar epidermis. As the ribs, both major and minor, approached the chalazal end they became gradually smaller till at the extremity all indication of ribbing had disappeared. The cavity within the sclerotesta was, owing to the sclerotic papilla, much blunter than the external form, and from the base of the micropylar canal measured some 19 mm. with a diameter in its broadest part of slightly over 14 mm.

Sections through the micropyle (Pl. IV, Fig. 2) show that the sclerized sides of the triangular canal about half-way up, formed of four layers of longitudinally directed fibres, were from 0·13 to 0·14 mm. in thickness and distinctly concave, the internal diameter of the canal measured from the apex of an angle to the middle of one of the sides being just over 2 mm. In the highest of our sections (Pl. IV, Fig. 5), viz. Man. Coll. R. 1161, *b*, the limit between sclerotesta and sarcotesta is indefinite and the diameter of the micropyle is reduced to 1·4 mm. On that side of this oblique section which is at the higher level the sclerized layer is seen to be even less developed than on the lower, and the concavity of the flanks has resolved itself into a slight double convexity (thickness between the angles 0·10 mm. and at the convexities 0·16 mm.) (Pl. IV, Fig. 8, *m*, *c*).

Although this section is broken there is evidence that the sclerotesta towards the apex segregated into three distinct portions separated at the angles by intervening soft tissue and each itself composed of two parts fused in the median plane.

Except for the slight local thickening, both here and in the preceding section, there is a thinning down of the sclerotic beak which, if maintained at the same rate, must have resulted in its complete elimination at a level not far above that at which our section was cut.

From these facts it would appear that the beak was comparatively short (probably not more than 8 mm. in length), although the extensive development of the sarcotesta at this level and the curve which successive sections show its surface to have followed indicate a much further persistence of that tissue. So that in this respect our seed resembled most closely the condition that obtains in present-day Cycads.

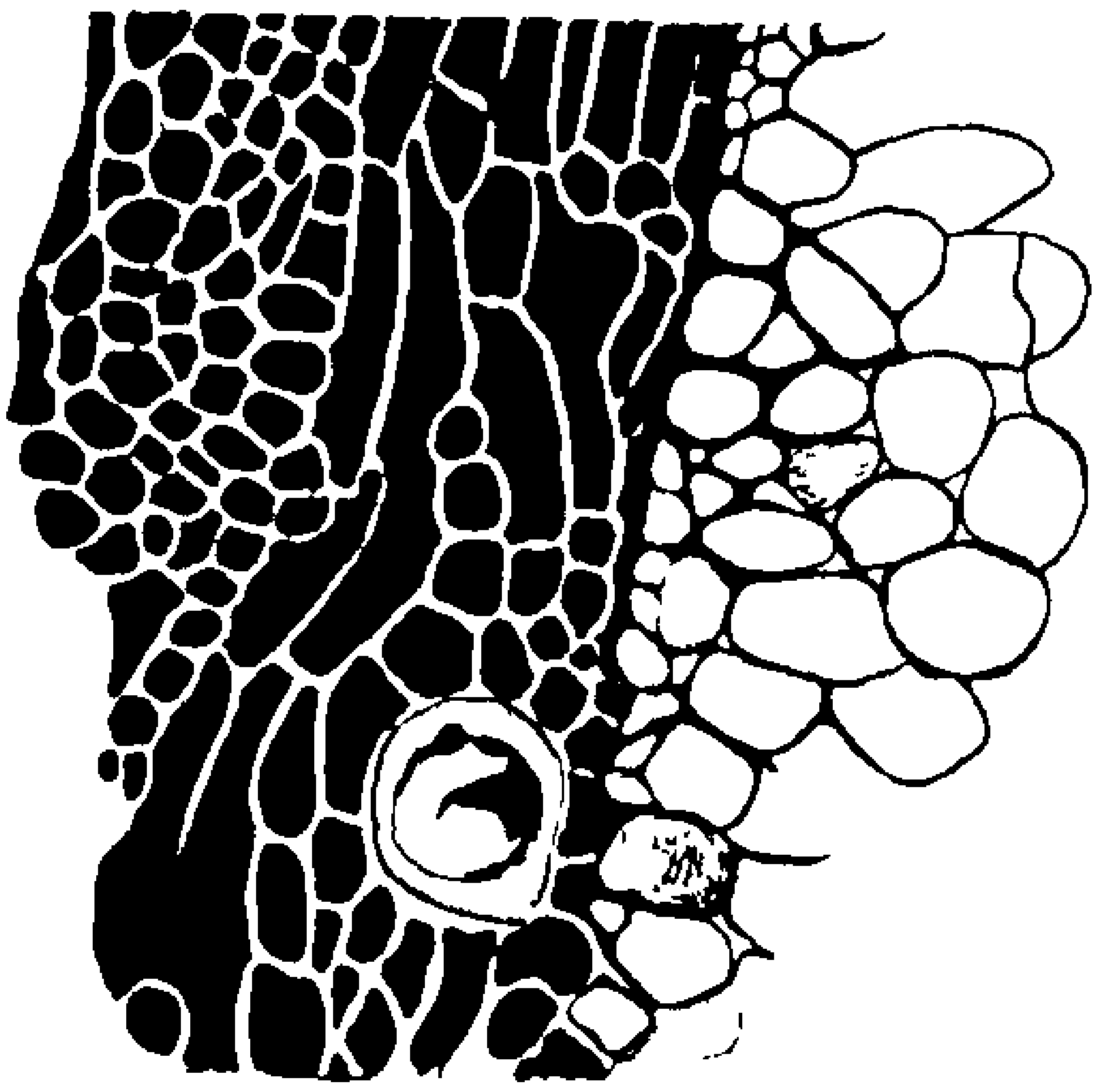
*Histology of the Sclerotesta.* The sclerotesta was formed of from 14 to 15 layers of thickened fibrous elements, of which the inner, and most of those forming the ribs, were longitudinally directed. In the best-preserved specimens the innermost layer is seen to have been composed of radially flattened fibres which form a smooth internal surface, and negative the suggestion of a more interior tissue. In transverse sections the fibres appear rounded or polygonal (28–42 μ) with dark contents separated by a thin membrane (? middle lamella), on either side of which is a translucent yellow zone about 3·5 μ in width perhaps representing the cell-wall. The fibres consisted of superposed cells which can be traced for over 1·5 mm.

The sclerotic fibres, 5–9 deep, forming the outer layers behave as aggregates or bands, each of from one to two elements in the radial direction and of a very variable number in the tangential (Text-fig. 5). For a time each band follows the longitude of the seed, and then almost abruptly all the fibres bend, some to the right and others to the left, or all of them in the same direction, so that their course is at a very narrow angle with the horizontal plane, and in transverse sections they appear cut obliquely or almost longitudinally for some distance. Where the members of a band are in one layer they appear to all bend in a similar manner, but where the band is more than one element in thickness those of each layer probably bend in opposing directions, but it cannot be definitely ascertained whether or no they again take up a longitudinal direction.

The extreme irregularity of the course of the fibres is shown by the inconstant numerical relation between those cut obliquely and transversely, and, to still further complicate the structure, the bands do not always remain in the same vertical plane.

Owing to this complex interlacing of the outer elements of the sclerotesta, it presents a plait-like appearance when cut by sections tangential to the surface, as is seen in Pl. IV, Fig. 3.

Eventually the thickened elements of the sclerotesta pass obliquely outwards by a well-marked transition into the sarcotesta.



TEXT-FIG. 5. A portion of the sclerotesta as seen in transverse section, showing the vertically directed fibres at the interior and the almost horizontal direction at the periphery; a single secretory sac is also present.

In the outer part of the sclerotesta, and there only, elongated secretory elements partially or entirely immersed in the sclerotic tissue are present, which pass out into the sarcotesta at one point and occasionally into the sclerotesta again at another (Pl. IV, Fig. 6, *m.s.*). In all respects these secretory elements resemble those present in the sarcotesta.

For convenience of description the sclerotesta has been treated as consisting of two parts, the plane at which the different structure is assumed being variable. There is, in fact, little doubt that the outer zone represents the terminations of a large portion and perhaps even all of the longitudinally directed fibres, and cannot possibly be regarded as the region of fusion of two morphological surfaces, as has been suggested for the stony layer of the Cycadean ovule.[1]

## 2. The Sarcotesta.

(*a*) *General Structure.* The sarcotesta in the living state must have been the most pronounced feature of this seed, for even as petrified it invests the sclerotic shell in the middle region to a thickness of over 4 mm.

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[1] Stopes: The Double Nature of the Cycadean Integument. Ann. Bot., vol. xix, 1905.

At the base this decreased to under 2 mm., but the almost sudden concavity of the sclerotesta at the micropyle gives the sarcotesta in that region a maximum thickness of nearly 6 mm. Although our highest sections pass not far below the apex no flattening is exhibited, but the sarcotesta curves inwards equally on all sides. This is in conformity with the impressions of seeds attached to *Neuropteris heterophylla* and *Neuropteris obliqua* described by Kidston[1] and Kidston and Jongmans.[2]

The junction of the sclerotesta with the sarcotesta, composed as the latter was of thin-walled cells, appears superficially as a sudden change, but the innermost cells of the sarcotesta can be recognized as direct continuations of the rows of sclerized elements. It is only in tangential or longitudinal sections that this transition can be properly seen, since the innermost sarcotestal cells, which are elongated and tubular (0·15 mm.–0·25 mm. × 0·033–0·049 mm.), are directed obliquely outwards and upwards (Pl. IV, Fig. 5). Owing to this the transition, which was of equal gradation throughout, appears much more sudden in transverse sections through the middle region than in those through the base or apex, where the surface is cut obliquely. This may perhaps be true also of the similar observations of Scott and Maslen[3] for *T. Parkinsoni.*

Very frequently cells comprising the innermost layer of the sarcotesta are seen cut longitudinally, also in tangential sections (Pl. IV, Fig. 5, *st. c.*) these cells alter their direction in a similar sinuous manner to those of the outer sclerotesta. Here and there slight thickening of the walls can be detected, and the intercellular spaces are either very minute or completely absent. It is clear, then, that the structure of the cells and architecture of the innermost tissue of the sarcotesta were essentially the same as in the outer layers of the sclerotesta—a continuity of structure which can only be reconciled with a homogeneity of origin. As we pass further outwards the intercellular spaces become more and more pronounced, and the constituent cells, at first tubular, very quickly become more rounded, and *pari passu*, as we pass to the exterior, develop irregularities in the form of projections which connect on to those of adjacent cells and give an almost stellate structure to the tissue (Text-fig. 6).

Owing to the rounded character of the middle sarcotestal cells, the intercellular spaces between them were of more or less equal dimensions in every direction. At a very little distance out, however, the cells were slightly flattened, and tend, especially at the periphery, to form short vertical series separated from one another by elongated lacunae. Sections in this plane also show that the arms or projections of successive cells were often superposed, so that each large lacuna is frequently without trabeculae,

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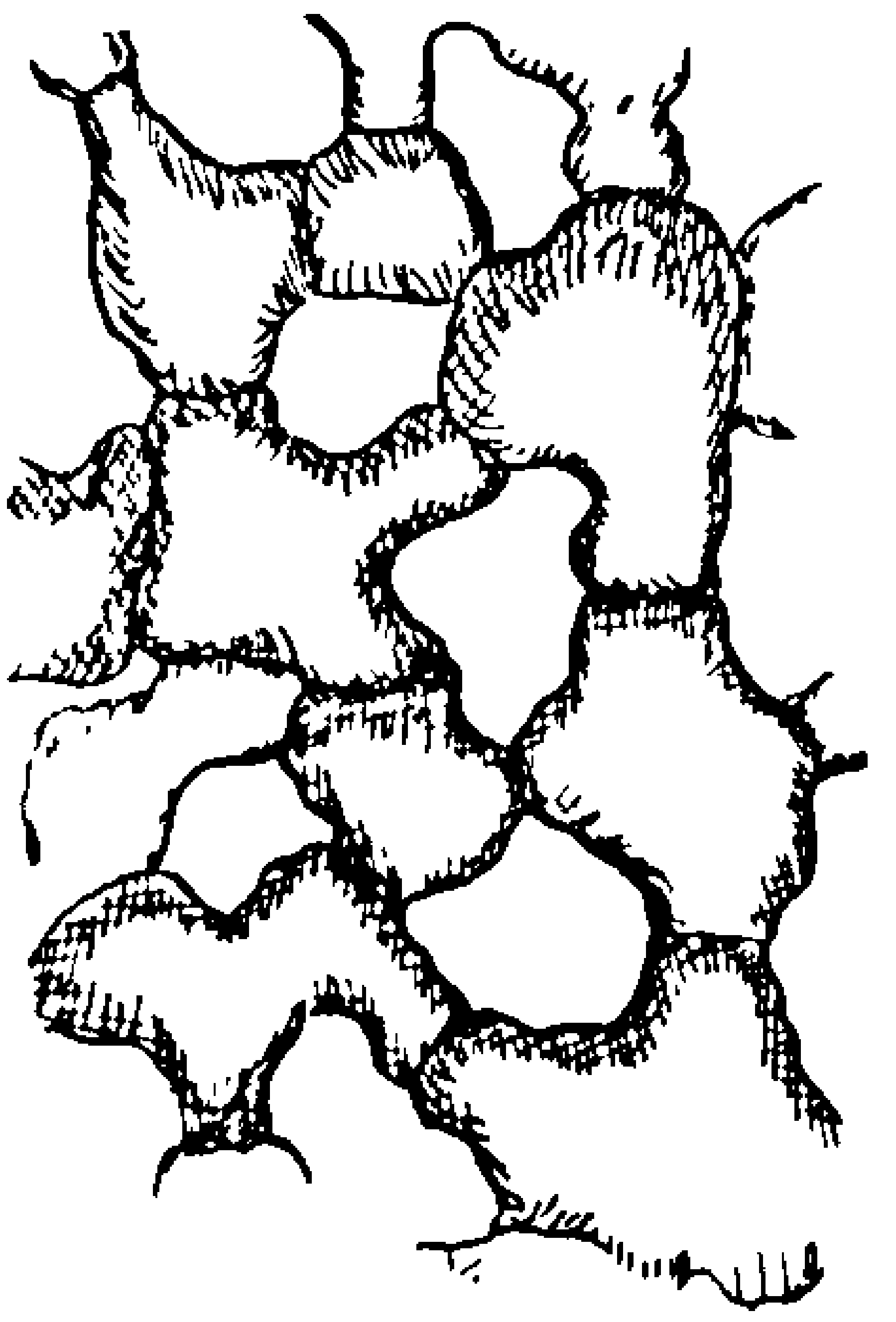
[1] On the Fructification of *N. heterophylla*. Proc. Roy. Soc. London, vol. cxcvii, 1904, p. 1.

[2] Archives néerlandaises d. sci. exactes et naturelles, sér. iii, B, tome i, 1911, p. 25.

[3] Ann. Bot., vol. xxi, No. lxxxi, 1907.

and the projections themselves often appear as narrow vertical series partially or completely separating adjacent intercellular spaces (Pl. IV, Fig. 10). Although the above fundamentally expresses the arrangement of the cells in this region, it was subject to great irregularity.

In the living condition this tissue must therefore have been remarkably light and spongy, and if these seeds were shed into water would render them of great buoyancy. Several seeds of this affinity, e.g. *Trigonocarpus Parkinsoni*,[1] *Pachytesta*,[2] and *Aethiotesta elliptica*,[3] exhibit a lacunar sarcotesta, and the suggestion put forward by Renault for *Aethiotesta* that this served as a mechanism for dispersal by water may well have been true also in the present instance, all the more that the method of occurrence of fossilized vegetable remains favours the view that they were in part components of water-borne drift.



TEXT-FIG. 6. A small portion of the outer sarcotesta, showing the large intercellular spaces.

(*b*) *The Peripheral Zone.* At the exterior the sarcotesta was bounded by a very ill-preserved layer of thin-walled cells (1·5 μ–3 μ tangential × 2 μ radial). Beneath this epidermis there were numerous sclerized fibres between which a soft-walled parenchymatous tissue was most likely present originally, though all except a few remnants of walls have become disintegrated.

The total width of this peripheral zone where there is no evidence of crushing or contraction is about 0·3 mm. In most cases the sclerized elements appear irregularly scattered, probably due to post-mortem changes, as in several places, where this zone has almost retained what was probably its original width, they are seen to be grouped together to form somewhat irregular radial plates (Pl. V, Fig. 19). Each plate was formed of from 2 to 6 elements, the higher number probably being the more usual, whilst tangentially the groups generally form either a single or a double row.

Not infrequently there were considerable local aggregations tangential to the surface, forming broad bands which may well have arisen through the lateral fusion of a number of the sclerotic plates. In outline each broad band formed a continuous hypodermal layer of sclerotic elements, with occasional projections inwards. Owing to crushing and contraction, many of the sclerotic bands have come to occupy an oblique or even tangential direction, causing irregularity and superposition of the originally radial plates

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[1] Scott and Maslin, loc. cit., p. 101.

[2] Renault: Bassin houiller et permien d'Autun et d'Épinac, vol. iv, p. 390, and Pl. LXXXIII, Fig. 10.

[3] Renault: Mém. Soc. d. Sci. nat. d. Saône-et-Loire, p. 1, 1887.

The individual sclerotic fibres were roughly rectangular, with a slight flattening in the radial direction, and usually about 2·5 × 4·5 μ. The wall was much thickened (about 0·8 μ) and formed of an outer transparent, yellowish layer and an inner and slightly thicker brown layer, both of which show clearly defined lamellation.

The longitudinal sections do not show the outer region of the sarcotesta preserved. The maximum longitudinal dimension in oblique sections is a quarter of a millimetre, and no doubt the real length was much greater.

The width of the intervals between successive plates is usually fairly regular, but rarely they are seen in very close proximity even where there is no evidence of displacement, and these are, perhaps, like the larger aggregations, to be interpreted as due to anastomoses.

Irregularly interspersed amongst the sclerotic cells are numerous secretory sacs, some 7·5 μ in diameter, which were no doubt situated in the soft parenchyma between the sclerotic plates, and become very numerous just beneath this zone.

Here and there the secretory sacs occur two or three together, arranged radially, and it is possible that these too, as in the nucellus, formed rows alternating with those of the sclerized elements.

Where cut obliquely, the secretory cells show fine longitudinal striation of the external surface of their walls; in one section, which is especially well preserved, this wall is seen cut transversely as a series of dark beads separated by clear spaces of about equal width. Surrounding the carbonized contents is a clear space which probably represents a thick sclerotic wall: the elements, in fact, were almost identical in appearance with the thick-walled mucilage sacs found in the sporophylls and testa of present-day Cycads.

In favourable cases, four or five connexions at more or less regular intervals can be seen between the dark central mass and the thin external wall. They probably represent radial pittings of the cell-wall, but must not be confused with the numerous and much finer and fainter radial striations, which are doubtless a matrix effect.

Occasionally the secretory sacs were situated at one or other end of the sclerotic plates, or even in the middle, replacing the sclerotic elements themselves.[1]

The presence of the numerous hard plates in the peripheral zone of the sarcotesta must have given to that region considerable rigidity, and the dark layer often seen between it and the soft underlying tissue is no doubt to be interpreted as originating through the compression of the outer cells of this latter.

(*c*) *The Secretory System.* The sarcotesta is not only distinguished from that of other seeds by its extreme development, but also by the

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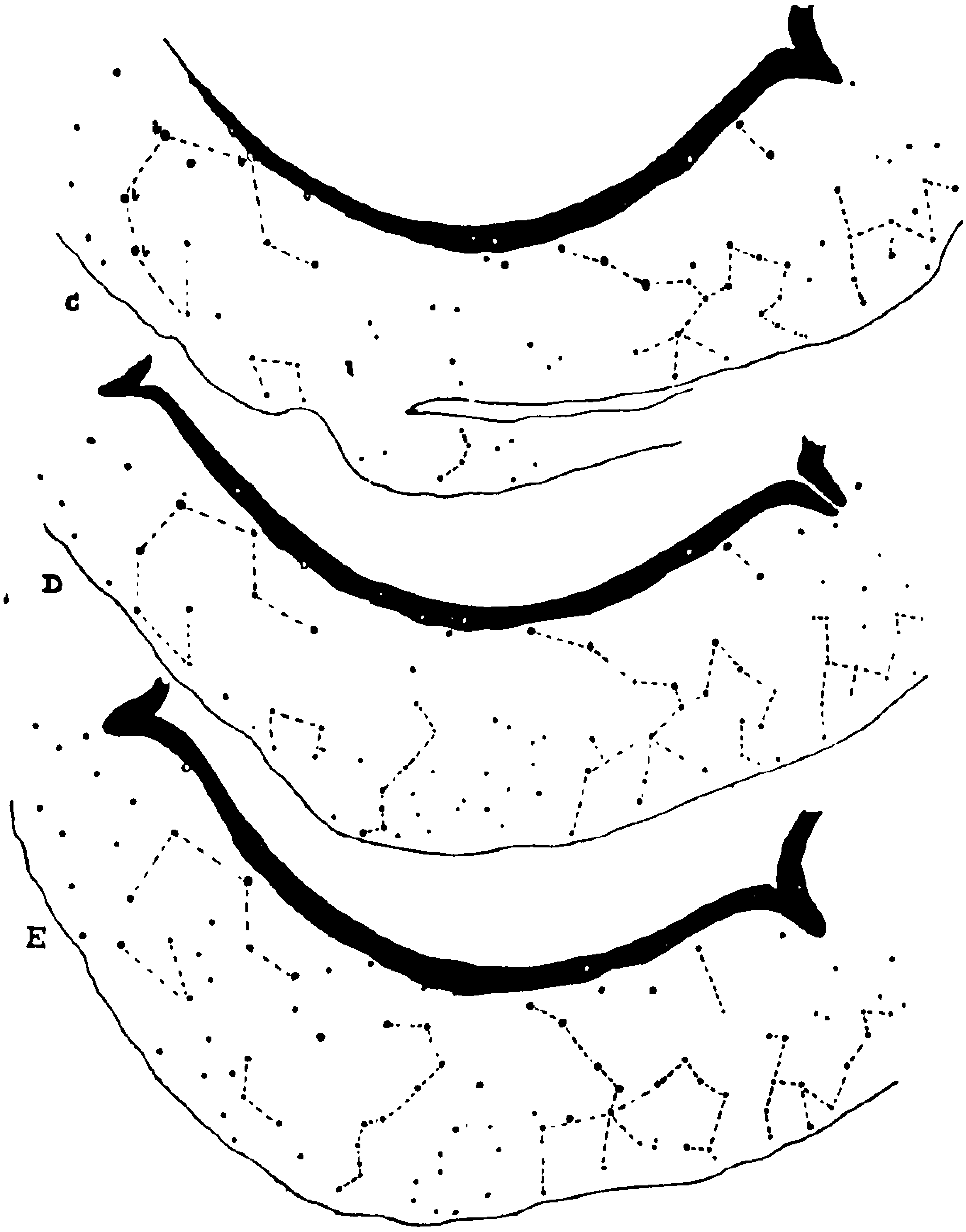
[1] Cf. Petiole of *Medullosa*. Scott's Studies in Fossil Botany, Fig. 176.

numerous secretory sacs which permeate it throughout (Pl. IV, Fig. 2, *m.s.*). In all respects the secretory elements of the interior appear to agree with those of the periphery.

Each secretory sac is sheathed by a continuous layer of parenchymatous cells, which separate it off from the surrounding lacunar tissue. Component cells of this sheath are seen in tangential sections to have been vertically elongated and to have reached a length of some five times their width.



TEXT-FIG. 7. Plottings of the secretory sacs in three successive sections. In order to make the corresponding sacs more clear, they have been connected up by means of dotted lines.

By carefully mapping the distribution of the secretory sacs between the same pair of ribs in successive sections of a series, one can recognize, from the relative positions which they occupy to one another, that the same sacs often extend for a considerable distance (Text-fig. 7).

In the subjoined table an analysis of the results obtained from S. 31, *b–i*, is given; the vertical series show the number of sacs in each section which can be traced back as far as that of which the designating letter heads the column. In Section *f* the sarcotesta is much broken, hence the figure for *g* is probably double its real value. If this be the case, then the number of additional sacs appearing at any given level is about twenty-one, or sixty-three for the whole circumference. The whole interval included between S. 31, *b* and S. 31, *i* is about 14 mm., and out of the total of 195 separate secretory elements encountered, not more than eight persist throughout. A few are only present in one section, whilst the greater number extend into the next (an interval between sections of about 2 mm.) with a falling off in each successive section.

| S. 31. | | *b* | *c* | *d* | *e* | *f* | *g* | *h* | *i* | *Total.* |
|---|---|---|---|---|---|---|---|---|---|---|
| Section S. 31. | *c* | 46 | 23 | | | | | | | 69 |
| ,, | *d* | 45 | 15 | 26 | | | | | | 86 |
| ,, | *e* | 35 | 12 | 24 | 22 | | | | | 93 |
| ,, | *f* | ? | ? | ? | ? | 10+ | | | | ? |
| ,, | *g* | 23 | 6 | 2 | 8 | 10 | 37 | | | 86 |
| ,, | *h* | 20 | 5 | 2 | 7 | 6 | 32 | 11 | | 83 |
| ,, | *i* | 8 | 4 | 2 | 6 | 6 | 13 | 5 | 20 | 64 |

The level of *k* in the Manchester series is the base of the micropyle, and of *c* that at which the nucellus is attached to the chalazal cushion. The number of secretory sacs in each case represents approximately one-third of the total at that level.

| | | | | | |
|---|---|---|---|---|---|
| Man. Coll. | *c* | 34 | Man. Coll. | *h* | 101 |
| ,, | *d* | 46 | ,, | *i* | 92 |
| ,, | *e* | 65 | ,, | *j* | 93 |
| ,, | *f* | 82 | ,, | *k* | 109 |
| ,, | *g* | 98 | | | |

A study of the two series shows that, in spite of irregularities, there was a decrease in number both towards the apex and base. From a comparison of the same sacs cut at different levels, they are seen to have tapered gradually both above and below, so that where cut across near their terminations they are of very small size and, where the surrounding wall is disclosed, very closely resemble developmental stages in the formation of secretory canals, the surrounding sheath simulating an epithelium, which may perhaps be the explanation of the similar appearances described by Professor Seward in the medullosean petiole *Rachiopteris Williamsoni*.[1]

A single secretory element, as seen in one section, is in several instances replaced by two in intimate contact in the succeeding section (Pl. V, Fig. 12); the fact that both are usually of nearly the same cross-section seems to favour the view that this is due to branching.

The normal course followed by the secretory elements was slightly sinuous and approximately parallel to the direction of the surface, with an outward tendency exhibited by the more interior. The distribution was irregular, with a marked increase—especially of the smaller—towards the periphery; whilst the largest (0·124–0·166 mm.) are found midway between the sclerotesta and the external surface (cf. Text-fig. 3, p. 42).

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[1] Ann. Bot., vol. viii, No. xxx, 1894.

### 3. The Inner Flesh.

All those sections which pass through the body of the seed, even where the preservation of soft tissues is excellent, show no indications of an inner flesh. It is certainly true that in most of the preparations the internal surface of the sclerotesta exhibits an irregular outline, but in the transverse series S. 33, *a*–S. 33, *d*, in which the internal preservation is almost perfect, the inner margin of the sclerotesta in some places forms a perfectly even surface. This latter affords positive evidence of far more value than the negative evidence of a ragged surface, and still more so since we find in the badly preserved material that the sclerotesta does show signs of superficial disintegration.

In dealing with the nucellus we shall find that it was possessed of a highly differentiated and probably strongly cuticularized epidermis, and there is evidence that it was in close contact with the sclerotic tissue.

Having due regard to all these facts, one is forced to the conclusion that in this species of *Trigonocarpus* an inner flesh was not present in the middle part of the seed cavity.

When we come, however, to about the level of the insertion of the micropyle, the zone of sclerization begins as it were to shift slightly outwards, and we thus find within the sclerotesta several layers of cells which, though possessing thick walls, have not the dark brown contents of the sclerotic fibres themselves, and, moreover, become thinner-walled as we pass inwards. This tissue reached its maximum thickness, of some four layers, midway between the angles, and on its inner margin exhibits a broken surface that here might well indicate a greater extent of probably more parenchymatous elements (Pl. IV, Fig. 8, *i.f.*).

Even then, if we regard this micropylar lining as homologous with the inner flesh of other Trigonocarpeae, our seed is as extreme a member on the one hand, as *Pachytesta* on the other.

## IV. THE VASCULAR ORGANIZATION.

### (*a*) *The Chalazal Bundle and Nucellar System.*

The lowest of our transverse sections yields us no information as to the vascular structure, but from S. 33, *b*, Man. R. 1161, *b*, and the longitudinal section S. 32, *e*, we find that a single vascular bundle entered the chalazal end of the seed. This passed up to the base of the nucellus, at which level it is cut by the section S. 33, *b* (Pl. V, Fig. 16). The bundle is there seen to have been a solid mass of xylem very slightly triangular in outline, the angles corresponding in position with the three main ribs of the seed. It was formed of from sixty to seventy elements, and attained a diameter of about 0·18 mm. The larger tracheae are situated mostly at the periphery

(Pl. V, Fig. 16), and in their radial dimension (30–40 μ) considerably exceed their width (75μ–0·025 mm., average about 0·015 mm.). The central elements are polygonal in form and from 0·015 mm. to 0·02 mm. in diameter. The bundle therefore has the appearance in transverse section of a central core surrounded by a single layer of radially flattened elements.

The smallest tracheae, measuring some 0·8μ in diameter, lie just within this outer layer and appear to form six not very clearly defined groups, two corresponding to each of the three angles. That these are the protoxylem elements is rendered the more probable by an examination of the single longitudinal section passing through the chalazal bundle (S. 32, *e*). From this we find that the majority of the elements were scalariform or densely spiral (Pl. V, Fig. 18), whilst separated by one such element from the periphery of the bundle there appear to be one or two narrow elements with distant spiral thickenings.

The xylem is completely surrounded by a ring of parenchymatous tissue (Pl. V, Fig. 16, *p.s.*) composed of three to five layers of thin-walled elements which together attain a width of about 0·05 mm. In the longitudinal section this tissue is seen to have consisted of narrow, vertically elongated components, perhaps undifferentiated phloem. The whole bundle, including this delicate sheath, was surrounded by larger-celled and thin-walled nucellar tissue in which were numerous secretory sacs. One element exhibits parallel markings, and may be a transfusion tracheide comparable perhaps to those found by Scott and Maslen between the bundles of the sarcotesta of *T. Parkinsoni* (loc. cit., p. 114 and Pl. XIV, Fig. 25, *st.*).

The single bundle passed through the base of the nucellus, where it expanded in a cup-like manner and formed a tracheal investment (1–4 elements) to the megaspore cavity. This is well seen in section D of Dr. Scott's series, which passes obliquely through the base of the megaspore cavity, and shows the continuous and several-layered tracheal cup around its base.

As seen in transverse section, the tracheal mantle appears to be built up of broad, laterally fused, bands traversing the longitudinal direction which are thickest in the middle and gradually diminish towards the sides. As can be seen from the plottings (Fig. 1), the section S. 33, *c* is slightly oblique to the axis of the seed, and it is on the higher side of the section that this grouping of the tracheides is the more marked.

Presumably, then, the vascular tissue between the level of this section and the base of the megaspore cavity consisted of a uniform zone of tracheides, which on the upper side became incompletely segregated into bands. The number of these latter cannot be ascertained with certainty, owing to the oblique direction of our most nearly transverse sections, but if we assume the slight indications of thinning on the lower side to mark the lateral limits of vascular aggregations, then there were probably twelve such bands, the width of the more clearly delimited varying between 1 mm. and 1·3 mm.

The internal diameter of the megaspore cavity, as seen in section S. 33, *c*, from which the above data were obtained, is 4·4 mm., which represents a periphery of approximately 13·8 mm. If we assume each band to have been of equal width, this gives us 1·15 mm. as the measurement of each if their number were twelve. This figure is sufficiently close to the actual measurements to support the belief that this was the actual total of the bands. Unfortunately, none of our other preparations furnish any corroborative data, but it is worthy of note that the repeated hexamerous character of the seed-structure again recurs in this figure.

The next section (S. 33, *d*), though ill preserved, shows the tracheides were completely segregated into lenticular strands which were much narrower (0·25 mm.–0·5 mm.) and more numerous than at the preceding level (probably over twenty).

These strands were probably mesarch in structure, of from four to five elements in the radial plane, diminishing both in number and size on either side. In some cases, tracheides at the edge of the xylem bands can be seen passing horizontally, as is the case in *Trigonocarpus Parkinsoni*,[1] but actual connexions were not observed.

Tangential sections show that the individual tracheides were often oblique or curved, and the appearance of horizontally directed elements, in the slightly oblique transverse sections, might easily be accounted for in this way. In spite of the excellent preservation, no indication of phloem has been observed in relation to the nucellar strands.

The final section of the transverse series only contributes confirmatory evidence that the bands of xylem were disconnected, and that their smallest elements were centrally placed.

For the further course of the bundles only longitudinal and oblique sections are available. In these, the bands of tracheides can be traced to what must have been a level close to the floor of the pollen chamber. Only two sections, viz. S. 32, *c* and Section I of Dr. Scott's series, actually pass through this structure; neither of these shows any tracheides within, but the internal preservation of the latter section is very poor, whilst the former has a broken and ill-preserved floor.

The vascular elements of the nucellar system appear to be very uniform in structure (0·022–0·03 mm.), and exhibit scalariform thickenings which occasionally show anastomoses between adjacent horizontal bars. (Interval between bars, 0·0015–0·003 mm.)

From the above description it will be seen that the internal vascular system is almost identical with that described by Scott and Maslen for *Trigonocarpus Parkinsoni* (loc. cit., pp. 120–1), and it may be of some

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[1] Scott and Maslen, loc. cit., Pl. XIV, Fig. 13.

significance that in neither species has the nucellar system been traced beyond the plane of insertion of the pollen chamber.

### (*b*) *The Sarcotestal System.*

In several sections of the University College series S. 31 *a*–S. 31, *k*, and perhaps in section R. 1161, *h* of the Manchester series, bundles in various conditions of preservation are to be found at the extreme periphery of the sarcotesta proper, where the outermost lacunar tissue abuts upon the limiting layers containing the radial sclerotic plates. The only parallel amongst nearly allied seeds to so external a position is to be found in *Pachytesta*,[1] where, however, if we regard the exotesta as representing sarcotesta and sclerotesta combined,[2] the bundles are only far out if considered in relation to the testa as a whole.

Owing to the incomplete preservation of the periphery, it is hardly surprising that in no slide are more than three sarcotestal bundles present at one and the same time. In several of the University College series, S. 31, *a*–S. 31, *k*, two bundles are cut in successive sections, and both of these are fortunately situated between the same pair of major ribs, and also occupy the same positions relative to them. Altogether, four distinct bundles can be distinguished in this series, and two possible bundles are also recognizable in one of the Manchester sections (R. 1161, *h*). In every case these sarcotestal vascular strands are situated in the radial plane midway between a major and a minor rib, and though the bundles are not present, in any one of our specimens, on all three faces, yet the occurrence of two, and two only, in several successive sections between the one pair of major ribs seems to point conclusively to the total number as being six, symmetrically disposed around the circumference of the seed.

The sarcotestal system was then identical as to the number of its components, and almost so as to their arrangement, with that which has been described for *Trigonocarpus Parkinsoni* and *Polylophospermum*,[3] only differing in the latter respect with regard to the proximity of the bundles to the sclerotic shell.

The structure of an individual strand is shown in S. 31, *i* (Pl. V, Fig. 17), where, owing to the curvature of the surface, the section which is oblique to the axis of the seed passes transversely through a sarcotestal bundle exhibiting extraordinarily perfect preservation. As can be seen from the figure, the bundle is slightly more extended in the tangential than in the radial direction (0·29 mm. x 0·17 mm.) and consists of some seventy xylem elements, of which the smallest occupy the central region (Pl. V, Fig. 17, *pt. x*). The latter, which probably represent the protoxylem, comprise some

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[1] Renault, loc. cit.

[2] Oliver: On Gymnospermous Seeds, New Phytologist, vol. i, No. 7, 1902, p. 148.

[3] Oliver, Ann. Bot., vol. xxi, No. lxxxii, 1907, pp. 303–4.

four tracheides (0·0075 mm. x from 0·0075 mm.-0·015 mm.) with thicker walls than those around. From the mesarch protoxylem there extends in the centrifugal direction an irregular fan-shaped group (Pl. V, Fig. 17, *cf.x.*), the elements of which, though larger than those of the protoxylem, are distinctly smaller than both those which lie on their flanks and those on the inner side of the bundle.

The centripetal xylem (Pl. V, Fig. 17, *cp.x.*) exhibits a further distinction in that the elements here are mostly cut more or less obliquely, so that the scalariform or reticulate sculpturing of their walls can be seen. A single layer of xylem elements on the centripetal side of the bundle immediately next the protoxylem do not show this character, although they exhibit the increased dimension.

The bulk of the centripetal wood evidently then consisted of short tracheides, such as are frequently present in centripetal xylem that is becoming obsolete, as is exemplified in *Lepidodendron vasculare*[1] or *Osmundites Kolbei*.[2]

### (*c*) *Additional Facts as to the Vascular System of Trigonocarpus Parkinsoni.*

The course of the sarcotestal bundles at the base of the seed of *Trigonocarpus Shorensis* cannot be traced, as the peripheral portion is lacking in the sections which pass through that region.

Two sections probably belonging to *Trigonocarpus Parkinsoni*, viz. S. 34, *a* and S. 34, *b* of the University College collection, have however recently come to hand, which Prof. Oliver has also placed at my disposal for description, and which, owing to their excellent preservation, add considerably to our knowledge of the vascular structure in this region. The absence of similar data regarding our own seed, and the essential similarity between the vascular systems of the two species, are sufficient justification for inclusion here.

The first section, viz. S. 34, *a*, just passes through the lower limit of the sclerotesta, and the second, parallel to the first, obliquely through the seed base, but without traversing the megaspore cavity. In this latter section eight ribs can be distinguished, of which three are doubtless the primary ribs, and from the distribution of the remaining five it seems likely that the seed was twelve-angled, the missing ribs having become obliterated either by obliquity or in consequence of the lower level at which the seed is cut on one side. A further point of importance is that this seed was evidently blunt at the base and not tapering,

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[1] Hovelacque, M.: Recherches sur le *Lepidodendron selaginoides*, Sternb. Mém. Soc. Linn. Normandie, vol. xvii.

[2] Kidston and Gwynne-Vaughan: On the Fossil Osmundaceae, Pt. IV. Trans. Roy. Soc. Edinburgh, 1910.

as shown by the great difference in the area of sclerotesta sectioned at the two successive levels. These facts, taken together with the position of the sarcotestal bundles, seem to justify the assumption that the seed was *Trigonocarpus Parkinsoni*.

In both of the sections a few secretory sacs can be seen. Dr. Scott has permitted me to examine his best preparations of *T. Parkinsoni* with the sarcotesta preserved, and particularly Wild's section S. 1952, figured by Scott and Maslen,[1] in which there are present some dark bodies surrounded by a clear space 0·045 mm.–0·052 mm. in diameter. Neither for these nor for similar bodies in the other preparations can one definitely assign a secretory nature, but a comparison with ill-preserved secretory sacs of *T. Shorensis* discloses a striking similarity between them. Probably, then, secretory sacs were present in *T. Parkinsoni*, both at the base and apex of the sarcotesta, but in very much smaller numbers than in *T. Shorensis*.

The central region of the lowest of the two sections cuts the single main chalazal bundle obliquely, at the level where the sclerotesta begins to be differentiated.

The general outline of the vascular bundle was very slightly triangular, with a diameter of about 0·3 mm., the angles corresponding in position to the secondary ribs. From each of the two upper of these angles (Pl. V, Fig. 14, *v.b.*) a strand is seen in process of being given off into the sarcotesta.

The main bundle is surrounded by a thin-walled parenchymatous tissue (*par.*) consisting of vertically elongated elements. In the centre is a solid mass of xylem, throughout which are scattered short tracheides horizontally directed, exhibiting scalariform or pitted thickenings. The section is sufficiently oblique to show that the longitudinally directed tracheides were scalariform.

In the centre of the xylem a single secretory cell can be detected (Pl. V, Fig. 14, *m.s.*).

The periphery of the bundle is formed of a band of short tracheides 1–2 elements in width, which for the most part are separated from the central xylem mass by what appears to have been parenchymatous tissue similar to that surrounding the bundle as a whole. But this tissue is interrupted at several points by junctions between the outer and inner tracheides. The smallest xylem elements lie mostly at the periphery of the central core, but others are situated more interiorly.

From an examination of the angle which is cut at the highest level, it can be seen that from this peripheral zone pass out the xylem elements of the sarcotestal bundles. In this particular case, the portion has partially separated off from the central mass, and the corresponding bundle, owing to the double obliquity of the section, is again cut further

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[1] Loc. cit., Pl. XII, Fig. 11.

out in the sarcotesta. What was doubtless the second half of this strand is seen at the edge of the bundle cavity, and clearly shows that the course of the two halves was divergent.

In the next section, viz. S. 34, *b*, which is nearly parallel to the former, five sarcotestal bundles can be distinctly recognized, whilst the position of a sixth is marked by a lacuna.

Where the bundles are cut on the lower side of this section, the level is only about one-third of a millimetre above that at which the central bundle is cut in the previous slide, so that the distance is scarcely sufficient for other bundles to have been given off.

It would appear then, from these two preparations, that three bands of xylem in continuity with the peripheral part of the chalazal strand were given off simultaneously, each of which then almost immediately underwent bifurcation into two divergent halves.

The soft parenchymatous tissue which surrounded the bundle consisted of cells which, when cut transversely, appear more or less polygonal and isodiametric : where cut longitudinally they measure about 0·12 mm. × 0·022 mm., and are separated by slightly oblique transverse walls. This tissue may perhaps have served the purpose of phloem, though apparently quite undifferentiated ; that it had some definite function is supported by its sharp delimitation from the surrounding tissue, even where this too was parenchymatous in nature. A similar sheath accompanied each of the six sarcotestal strands in this, the basal region of the seed.

As seen in S. 34, *b* (Pl. V, Fig. 15) the central part of each bundle was occupied by a strand of elongated scalariform tracheides (*n.tr.*), and around this was a complete ring of much shorter and stouter spiral or slightly reticulate elements (*s.tr.*). Separating the outer zone from the central core, was a narrow space from which the bulk of the tissue has perished, but here and there can be seen patches of elongated parenchymatous elements similar to those forming the bundle-sheath, and no doubt they originally constituted a complete ring.

Each sarcotestal bundle was then essentially similar to that supplying the chalaza. An examination of the bundles of Dr. Scott's section 626 of *T. Parkinsoni* through the same region as S. 34, *b*, though exhibiting far less perfect preservation, seems to agree with the description here given.

Before leaving these sections it should be said that, though the type of preservation is the same as that of the bulk of the specimens of *T. Shorensis*, in none of the secretory elements present was I able to find the longitudinal striation characteristic of the wall in that species, though this feature is exhibited by well-preserved ducts in the stems of *Medullosa anglica*.

## V. THE NUCELLUS.

The total length of the free nucellus, from the point of junction with the testa to the base of the pollen chamber, was about 18 mm., and its diameter in the widest region about 11 mm. As the cavity in this part was some 15 mm. in width, there is left a space of 2 mm. all round for which to account. The question of an inner flesh has already been discussed, but in any case these dimensions for the nucellus are probably much too small, owing to post-mortem contraction.

The general outline of the nucellus conformed closely to that of the cavity within which it stood, following the same lines until near the base of the micropyle, where the nucellar tissue curved sharply inwards to the insertion of the pollen chamber.

Disregarding this latter structure, the conformation was that of a sharply pointed egg with its narrower end directed downwards and attached to the sclerotesta, whilst the blunt free end was surmounted by the pollen chamber.

The nucellar tissue is in most cases either lacking altogether or ill preserved, but fortunately, in the transverse series S. 33, *a* to S. 33, *d*, the structure is beautifully shown, though considerably contracted. In the uppermost of the series the nucellus occupies a one-sided position which is in part due to the slight obliquity, but no doubt in the main to displacement through asymmetrical shrinkage.

In the second of this series the nucellar tissue is seen surrounding the chalazal bundle. As already described, this consists of parenchymatous tissue, of which the cells are thin-walled and vary in size from about 0·01 to 0·050 mm., interspersed with secretory ducts, the largest of which are at the periphery and measure about 0·07 mm. in diameter. This ring of tissue is only 0·2 mm. in width, but from its ragged edge was evidently much more extensive in life.

Owing to the shrinkage of the soft underlying tissue, the much less contractable epidermis is thrown into numerous folds, but the projections thus formed do not, as in *Trigonocarpus Parkinsoni*, correspond to underlying vascular strands,[1] but to radial files of secretory elements (Pl. V, Fig. 20, *m.s.* and *n.r.*). Taking the distance from the edge of the megaspore cavity to the summit of these ridges as the basis of our estimate, the thickness of the nucellar tissue must have been, near the chalazal end of the seed, at least 0·3 mm., though above this level it diminished slightly and then remained of constant width up to the base of the pollen chamber. At the outside there was a very strongly defined epidermis, (S. 33, *c*, Pl. V, Fig. 20, *n.e.*), the cells of which (0·05 mm. radial × 0·03 mm. tangential) stand out all the more clearly since their contents are preserved as dark carbonaceous masses that have contracted away from the cell walls. Where, owing to the contortions

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[1] Scott and Maslen, loc. cit., p. 119.

of the surface, the longitudinal dimension can be estimated, it is about three times as great as the width (0·09 mm.). As seen in this view, the cells are more or less oblong in shape, whilst cut transversely they appear distinctly convex on the external face, a feature which seems to point to the absence of close contact with an inner flesh.

Under the best conditions of preservation, the epidermal cells resemble very closely the secretory sacs and, like them, have the appearance of possessing a thickened wall. In several places the outer layer of the exterior walls, together with part of the middle lamellae from between each pair of the component cells, has split away, so that in transverse section it appears as a thin membrane with pegs projecting inwards. Evidently this outer layer was of a durable character, as it can occasionally be recognized even where the interior tissue has decayed away, and is much less subject to contraction, suggesting that it may probably have been a cuticularized layer such as we find with similar pegs amongst modern plants.

Such a specialized epidermis we should hardly expect to find in a completely enclosed structure like the nucellus, if it were in close contact with a soft inner flesh.

Between the epidermis and the tracheal sheath there intervened a zone of soft parenchymatous elements in which numerous secretory cells were present. The ground-tissue was without intercellular spaces and formed of polygonal cells with very thin walls (0·03 mm. to 0·08 mm. x 0·15 mm.), The secretory cells were embedded in this ground-tissue, and where they did not occur singly, formed radial plates of varying extent and usually consisting of a single row of secretory elements, though more rarely at the base of the seed of two such rows. The greatest number of secretory cells which were present in any one radial plane appears to have been five. The proximity of the radial plates and the number of elements in each decreased as the apex of the seed was approached, so that some two-thirds from the base of the pollen chamber the plates were about a third of a millimetre apart and reduced to one, two, or at the most three elements. The secretory sacs themselves (0·06–0·09 mm.) exhibit much the same structure as those of the sarcotesta, but with thinner walls. In the longitudinal direction the carbonized contents show segmentation into short lengths, but the septation thus produced probably bore no relation to transverse walls.

In two of the seeds (viz. S. 31, U. C. Coll., and Man. R. 1161), besides the longitudinal ridges' already referred to, others more pronounced are present, occupying positions opposite to the commissural ribs, and bear no relation to contained radial files of secretory elements. In the series S. 33, U. C. Coll., with its excellently preserved nucellus, no such ridges are however to be seen, which may be correlated with the fact that this seed was probably in an immature condition, judging from its relatively small size, the thinness of the testa, and the slight development of the ribs. In S. 31, *g*, such ridges, corresponding to both the major ribs preserved, can be distinguished. Such commissural ridges,[1] of which an example is figured in Pl. V, Fig. 13, *n.f.*, from section S. 31, *e*, furnish the strongest evidence that the nucellar surface was in the mature condition in close contact with the sclerotic testa, a point which the well-developed cuticle further emphasizes.

## VI. THE POLLEN CHAMBER.

Our information respecting the structure of the pollen chamber is extremely meagre, as only two sections furnish data of any importance. The general form of the pollen chamber, as seen in S. 32, *c*, is rectangular, with longer sides forming the roof and floor (3 mm. wide × 1·26 mm. high). As will be seen from the diagram, the direction of the section passes tangentially through the pollen chamber in a plane slightly oblique to that of a minor rib.

The central part of the roof in this section shows a triangular, blunt-ended, upward projection of the epidermis, which may be the base of the micropylar tube.

The epidermis of the pollen chamber is continuous with that of the nucellus, and the component cells up to about half its height are of the same form in both. Beyond this point they become much larger (0·066 mm. radial by 0·04 to 0·08 mm. vertical), with thinner walls, and do not possess the black carbonaceous contents present in the lower part. The increased size is especially noticeable where the sides curve inwards to form the roof; these shoulders project somewhat laterally, partly owing to the larger size of the epidermal cells and partly to the slightly greater internal diameter (Pl. V, Fig. 11). The blunt apex of the angular projection is formed of cells which are much narrower in the tangential direction, 0·005 mm. Interiorly, the sides of the pollen chamber were occupied by a soft parenchymatous tissue, consisting of elongated cells with tapering ends. This is most pronounced in the shoulders, and the appearance presented very closely resembles that described and figured for other seeds of this affinity, as for example *T. Parkinsoni*,[2] *T. pusillus*,[3] *Aethiotesta*,[4] and *Stephanospermum*.[5]

In S. 32, *h*, the pollen chamber exhibits a prominent angle corresponding in position to a major rib, and also in Section I of Dr. Scott's series the shoulders appear double-angled, the lower of the four angles being the true

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[1] Cf. Renault: Angling of Nucellus in *Trigonocarpus pusillus*. Flore fossile d'Autun et d'Épinac, pt. 2, p. 398.

[2] Scott and Maslen, loc. cit., p. 121.

[3] Oliver: New Phyt., vol. iii, 1904, Pl. II, Fig. 3.

[4] Renault: Mém. Soc. d. Sci. Nat. de Saône-et-Loire, 1887, Pl. XVI, Fig. 3.

[5] Oliver: Trans. Roy. Soc. Lond., p. 370, Pl. XLII, Figs. 11 and 18.

shoulders, and the upper again coinciding with the positions of major ribs. There seems little doubt, then, that the pollen chamber was three-angled in correspondence with the projections of the nucellus lower down.

## VII. COMPARISON WITH OTHER TYPES.

### 1. *Trigonocarpus Parkinsoni*, Brongniart.

It is hardly necessary to recapitulate in detail the many points of general resemblance which *Trigonocarpus Parkinsoni* and *Trigonocarpus Shorensis* have in common. The main structural plan in both seeds is essentially the same, but this only serves to throw into greater prominence the many differences of their more minute structure.

We note the entire absence in *Trigonocarpus Shorensis* of tertiary ribs subtending the vascular bundles, and though the behaviour of the primary sutured ribs is alike in each, the beak into which they pass is short in *T. Shorensis* and long in *T. Parkinsoni.*

The secondary ribs of the latter seed are subject to considerable variation, sometimes being almost absent; but usually they persist to near the apex, where they die out before the micropylar beak is reached, an earlier disappearance of the secondary ridges which is still more pronounced in *T. Shorensis.* Scott and Maslen give the thickness of the stony layer in *T. Parkinsoni* as from 1 to 1·5 mm. (loc. cit., p. 106), which is two to three times the corresponding dimension for our seed. Probably this added thickness and the increased number of ribs are to be correlated with the small extent of the sarcotesta, as compared with that of *T. Shorensis*, necessitating greater mechanical strength in the layer beneath; or perhaps, put more correctly, the broad sarcotesta in the latter species, with its peripheral sclerotic system, had not involved the necessity for development of such mechanical strength in the sclerotesta.

The most interesting comparison between these two seeds is afforded by the sarcotestal structure. This tissue was in *T. Parkinsoni* bordered at the exterior by a narrow epidermis, followed by a thickened palisade-like hypodermis (Scott and Maslen, loc. cit., p. 102). As we have seen, the limiting layers in the present seed were much more complex, and formed a, probably anastomosing, complex of radial plates, accompanied by numerous secretory elements present also further in, which, though represented, were extremely few in *T. Parkinsoni.* Now the occurrence of radial sclerotic plates at the periphery, and of secretory elements both within these and interiorly, are characteristic features of the vegetative organs of Medulloseae, and especially of their petiolar structure,[1] so that *T. Shorensis* in this respect would appear to be far more primitive than its congener. The absence of the prolonged

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[1] Scott, D. H.: On *Medullosa anglica.* Phil. Trans., B, vol. cxci, p. 101, and Pl. VIII, Fig. 18, 1899.

sclerotic beak and secondary ridges opposite the bundles also point to a lesser degree of specialization.

A further striking difference is the tapering insertion of the seed of *T. Shorensis* as compared with its abrupt insertion in *T. Parkinsoni*; the former is probably a relatively older type than the latter, just as the horizontal departure of the leaf-trace characterizes the modern plant, in contradistinction to the oblique insertion, as found in the more ancient.

Analogy with *Physostoma elegans*[1] would seem to suggest that the presence of a secretory system in the nucellar tissue is a more primitive feature than its absence. If this has any significance, and the close relationship between the Trigonocarpeae and Lagenostomales supports such an assumption, then in this respect *T. Shorensis* stands in the same relation to *T. Parkinsoni* as does *Physostoma* to the other known members of the latter group.

We have shown good reason for believing that *T. Shorensis* was without a definite inner flesh, except in so far as we can apply that term to the lining of the micropylar canal. Such a tissue would, however, appear to have been present in *T. Parkinsoni.* Perhaps at first sight this might seem to be a pronounced distinction between the two, but the extreme peripheral situation of the sclerized layer in *Pachytesta,* surrounding an extensive inner flesh, coupled with the undoubtedly close relationship of the two genera, indicate that the position taken up by the region of sclerization was subject to considerable fluctuation in the group as a whole, and therefore of no great significance when exhibited in a smaller degree by members of the same genus.

The well-defined nucellar epidermis, even more pronounced than that of *T. Parkinsoni,* indicates a stage less far removed from the condition in which the nucellus was a naked sporangium unprotected by a surrounding integument; and probably the production of an inner flesh is likewise correlated with a phylogenetically more prolonged contact between the two surfaces, which functionally have become internal.

As previously indicated, the vascular organization of the two seeds was essentially similar, perhaps the most outstanding distinction between them being the much more peripheral position occupied by the sarcotestal strands in *Trigonocarpus Shorensis.* On the whole, the internal vascular system of our seed probably shows a somewhat more pronounced tracheal investment at the base of the nucellus, whilst the separate strands into which this passed were broader, though this may well be an outcome of the larger nucellus they supplied. If, as may have been the case, the Trigonocarpeae were derived from fern-like plants having sporangia with a complete internal tracheal investment, then it would appear from Scott and Maslen's description that in this respect *Trigonocarpus Parkinsoni* was more primitive than

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[1] Oliver: Ann. Bot., vol. xxiii, p. 73.

*T. Shorensis*, for in the latter anastomoses, if they existed, were probably of infrequent occurrence.

### 2. *Trigonocarpus Oliveri; its systematic position.*

This seed was described and figured by Scott and Maslen in 1907,[1] from a series of four sections through a single seed, and the diagnosis there given is as follows:

> 'Length nearly 2 cm., diameter about 0·9 cm., characteristically coffin-shaped in vertical sections. Base flattened. Sclerotesta produced around the base of the seed in the form of a circular ridge enclosing the stalk of the seed. Longitudinal ridges of the sclerotesta acute-angled, not rounded as in *Trigonocarpus Parkinsoni*.'

The number of longitudinal ridges which the seed bore is not explicitly stated, but, presumably from the description given, was assumed to have been six.

The writer has carefully examined the preparations and employed for their interpretation the methods recently described.[2] The conclusions arrived at differ essentially from those of Scott and Maslen, who evidently did not fully recognize the marked effects of obliquity in this seed, which are so clearly brought out by the modelling method.

As can be seen, the first section (S. 28, *d*)[3] is tangential to the surface of the seed and passes at unequal depths through two ribs, the divergent axes of which, towards the upper part, indicate that the plane was below the middle region, sloping away from the chalaza. The next section (S. 28, *c*) shows the more deeply cut of these ribs sectioned nearer the axis, and consequently represented by two angular projections, one at the apex and the other at the base. This section cuts the seed so far in that two lateral ribs, one on either side, are also encountered; where these are cut near the apex they appear as angular projections, whilst near the base they exhibit a curious truncated outline, but are unequal in size, owing to the obliquity which was also manifested in the previous section. It is these two lateral ridges at the base which have been interpreted as a circular ridge, though the true character where sectioned near the apex was recognized. In order to explain the peculiar form of the lower projections, the assumption was made that they were incomplete. The objections against such an interpretation furnished by this section alone are, that if a chalazal ring were present, it is highly improbable that the central rib would extend below it and the lateral ribs be in no way represented; whilst this difficulty cannot be overcome, since the interpretation of the median ridge as a part of the stalk is inadmissible, owing to the plane of section.

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[1] The Structure of the Palaeozoic Seeds *Trigonocarpus Parkinsoni* and *Trigonocarpus Oliveri*. Ann. Bot., vol. xxi, No. lxxxi, 1907.

[2] Salisbury: Methods of Palaeobotanical Reconstruction. Ann. Bot., April, 1913.

[3] Loc. cit., Pl. XIII.

On the interpretation here put forward no difficulties are involved, since converging ribs cut in a plane at a narrow angle with that which they themselves follow would necessarily acquire in section the square-ended form which they actually present.

In the section just described, one notes that the region of attachment of the nucellus is cut through, so that since in the next preparation the nucellus shows as a complete oval membrane it is clear that this section passes right across the axis of the seed, cutting through a rib on either side almost vertically, and it is the slight angling of the cavity corresponding to these which, as in similar sections of *Conostoma oblongum*, results in the coffin-shaped appearance.

At the apex of S. 28, *b*, we see the three ribs represented in S. 28, *c*, and at the lower end three other ribs sectioned almost transverse to their direction, so that the triangular form is preserved. If, on the other hand, they were really a chalazal ring, a section in this plane should render them convergent, not divergent, and furthermore, their size on that view is incompatible with the projections in the previous section, especially if the latter are to be regarded as incomplete.

*T. Oliveri* was then an eight-angled seed, and, until further specimens are obtained with better-preserved internal tissues, its systematic position, except for inclusion in the vague group of the Radiospermeae, must for the present remain uncertain. The removal of this seed from the genus *Trigonocarpus* makes it therefore unnecessary to institute any comparison between it and *Trigonocarpus Shorensis*.

### 3. Fructifications of *Neuropteris heterophylla* and *Neuropteris obliqua*.

Attention has already been called to the tapering and the abrupt insertion found within the genus *Trigonocarpus*, both of which are represented in the fructifications found attached to Neuropteridian foliage. Three specimens of *Neuropteris heterophylla* have been described by Dr. Kidston with attached seeds,[1] in which the abrupt insertion of the *Parkinsoni* type is clearly exhibited. More recently, Kidston and Jongmans[2] have described fructifications attached to the fronds of *Neuropteris obliqua*, in which the seed tapers towards its insertion on a bifurcated axis, thus conforming to the second type as represented by *T. Shorensis*. Owing to the incomplete preservation of the latter at the apex, its longitudinal extent cannot be exactly estimated, but nevertheless the comparison of the approximate dimensions of the two types of impressions and petrifactions given below shows that broadly the resemblances of insertion are accompanied by an approximately similar ratio in size.

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[1] Phil. Trans. Roy. Soc., ser. B, vol. cxcvii, 1904, p. 1.

[2] Archives néerlandaises d. sci. exactes et nat., sér. iii, B, tome i, 1911, p. 25.

| *Species.* | *Length.* | *Breadth.* |
|---|---|---|
| *T. Parkinsoni* | 4-5 cm. | 2 cm. |
| *N. heterophylla* | 3 cm. | 1·1–1·4 cm. |
| *T. Shorensis* | Over 4 cm. | 2·4 cm. |
| *N. obliqua* | About 6 cm. | 2·25 cm. |

A further feature that the fructifications of *N. obliqua* and *T. Shorensis* have in common is found in the marked striation exhibited by the surface of the former, and attributed by the authors cited above to the presence of a large number of sclerenchymatous strands of tissue near the surface of the seed. These are no doubt identical with the numerous radial sclerotic plates which we have described as a prominent feature in the peripheral layers of the sarcotesta in *T. Shorensis.*

In view of the occurrence of the seeds of *N. obliqua* in pairs on a bifurcated axis, it may be of some significance that in one of our series a portion of a second seed is present, having approximately the same orientation as the more complete specimen close to which it lies.

These considerations render it likely that our seed was itself borne on a plant possessing foliage of the *Neuropteris* type, and almost certainly belonged to the same subsection of the genus as Kidston and Jongman's specimens.

### 4. *Trigonocarpus corrugatus.*

Amongst the casts of Trigonocarpean seeds, none approach so closely to *Trigonocarpus Shorensis* as that described by Renault under the name *Trigonocarpus corrugatus.* The following is the diagnosis given by that author:

'Graines trigones, dilatées un peu au-dessus du milieu de leur hauteur, longues de 22 millimètres et larges dans la partie renflée de 12 millimètres, marquées de trois côtes saillantes qui vont jusqu'au sommet de la graine sans produire de point. Entre ces trois côtes on remarque trois plissements en relief qui s'étendent à peu près jusqu'à mi-hauteur.'[1]

From the above we see that the dimensions of the seed, though smaller than those of our own species, bear very nearly the same ratio for the corresponding parts of the sclerotesta.

| *Species* | *Width (max.)* | *Length.* | *Ratio Length, Width.* |
|---|---|---|---|
| *T. corrugatus* | 12 mm. | 22 mm. | 1·83 |
| *T. Shorensis* | 15 mm. | 28 mm. | 1·86 |

The presence of the three secondary ribs extending for only a part of the total length of the hard shell, though persisting for a greater distance than in *T. Shorensis*, also the absence of a beak (a description that might easily in this type of preservation be consistent with the presence of a very short structure of such a character), and the tapering base, still further strengthen the resemblance between the two seeds.

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[1] B. Renault, Bassin houiller et permien d'Autun et d'Épinac, p. 399.

### 5. Comparison with Cycads.

Recent work on the Cycadean ovule,[1] and the additional facts regarding the structure of *Trigonocarpus* here brought forward, serve to emphasize the unmistakable relationship between the two groups. In the organization of the integument, differentiated into three layers, the agreement is extremely close, even as regards the broad structure of the stony layer which in Cycads as well as in *Trigonocarpus* is formed of longitudinally directed fibres on the inside, which at the outside become interwoven with horizontally directed elements.[2] Also, in the vascular organization and the structure of the pollen chamber[3] the resemblances are particularly evident.

The chief interest of the present work in this connexion results from the recognition of the short Cycadean type of sclerotic beak within the genus *Trigonocarpus*, and the presence of secretory elements situated in the sarcotesta of the latter, and resembling very closely the mucilage sacs of the modern group.

The tendency for the non-vascular ribs to die out, of which an early stage is shown by *T. Shorensis*, reaches its culmination in the Cycadean family, where, too, the development of ribs in relation to the sarcotestal bundles, as found in *T. Parkinsoni*, likewise constitutes a prominent feature of certain genera.

The absence of a nucellar system in the Lagenostomales is probably correlated with the fusion between testa and nucellus. How, then, are we to account for the retention of this same system under similar conditions in the Cycadean ovule? The explanation seems to be found in the isolation of the nucellar and integumental systems from one another by the intervening sclerotesta, which thus prevents the latter from performing the functions of both.

The suggestion advanced by Worsdell[4] that the fused integument and nucellus was brought about by a congenital fusion rather than that it arose as an intercalated zone of growth, as suggested by F. W. Oliver,[5] seems the more probable, both on the grounds there adduced and in view of the absence of any evidence in Cycads, comparable to that found in the Lagenostomales, of such having taken place.

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[1] Kershaw: Structure and Development of the Ovule of *Bowenia spectabilis*. Ann. Bot., vol. xxvi, No. 103, 1912.

[2] Stopes: On the Double Nature of the Cycadean Integument. Ann. Bot., vol. xix, 1905, p. 564; Chamberlain: The Ovule and Female Gametophyte of *Dioon*. Bot. Gaz., vol. xlii, 1906, p. 332.

[3] Kershaw, loc. cit., p. 643.

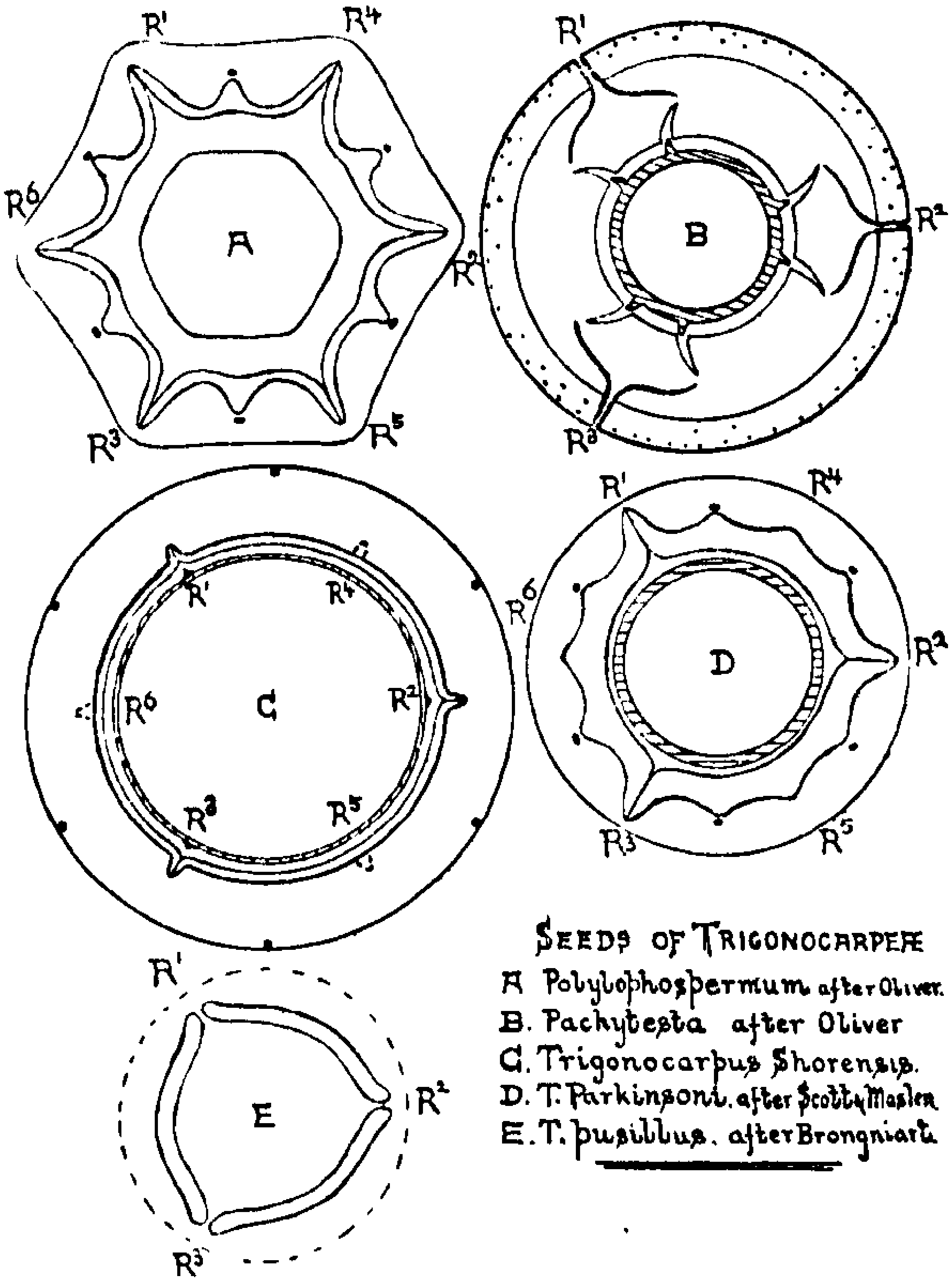
[4] Fasciation, its Meaning and Origin. New Phyt., vol. iv, 1905, p. 38.

[5] The Ovules of the Older Gymnosperms. Ann. Bot., vol. xvii, 1903.

## VIII. GENERAL DISCUSSION OF THE TESTA.

### 1. The Multiple Origin of the Integument in the Trigonocarpeae.

The general facts supporting the theory of a multiple origin for the integument of the Lagenostomales are well known,[1] and in the Trigonocarpean series the integument is also composed of several equivalent units, which may well have had a similar origin. We shall therefore briefly review the chief testal features which the members of this group exhibit.



TEXT-FIG. 8. Transverse sections of the seeds of various Trigonocarpeae. Corresponding ribs are in each case marked $R^1$, $R^2$, &c.

In the genus *Trigonocarpus* itself *T. Parkinsoni* had twelve ribs, three primary and fissured, three secondary and non-fissured, and six tertiary, opposite which the sarcotestal bundles were situated (Text-fig. 8, D).

In *T. corrugatus*[2] and *T. Shorensis* six ribs only were present, of which the three non-commissured died out, about half-way up in the former seed and one-third in the latter (Text-fig. 8, C).

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[1] Oliver and Salisbury: Palaeozoic Seeds of *Conostoma*. Ann. Bot., vol. xxv, 1911, p. 41.

[2] Renault, loc. cit.

In *T. pusillus*[1] the ribs had almost become obsolete and the sclerotesta was nearly circular in outline, with three commissured ribs only very slightly projecting (Text-fig. 8, E).

*Polylophospermum*[2] possessed twelve ribs, of which six were fissured, the alternating and non-fissured ribs corresponding to the radial planes of the six sarcotestal bundles (Text-fig. 8, A).

*Ptychotesta* and *Hexapterospermum*.[3] Six-angled seeds with very prominent ribs, all of which in the case of the former were fissured (perhaps also in the latter) and enlarged at the ends, owing to the separation of the two parts in that region.

*Polypterospermum*.[4] An hexagonal seed with six acute ribs at the angles of the testa, and alternating with them six others which were short and blunt.

*Pachytesta*.[5] A circular seed, but exhibiting, like *T. pusillus*, three commissures. The bundles had undergone considerable branching, so that not only are they numerous tangentially, but also form two concentric series, a complexity of vascular organization that goes hand in hand with an elaborate internal structure (Text-fig. 8, B).

*Stephanospermum*.[6] The two species were circular, and all vestiges of ribbing have disappeared. The sarcotesta is usually only represented by the tissue occupying the apical cup, so that its vascular structure is unknown.

The species of *Trigonocarpus*, we see, thus form a consecutive series involving the gradual elimination of the secondary ribs.

The production of ribs in relation to bundles is a phenomenon of widespread occurrence, met with elsewhere in the seeds of Dicotyledons, Gnetales, and Cycadales, as well as in the vegetative organs of many plants. They are probably an expression of mechanical utility, and, except from the taxonomic standpoint, the absence of such ribs from the seeds of *T. Shorensis* and *T. corrugatus* is a point of little importance.

Disregarding the vascular ribs, the general sclerotestal structure in *Trigonocarpus Shorensis* and *T. Parkinsoni* is identical. Scott and Maslen[7] remarked on the variability in development of the secondary ribs in the latter species, which always die out before the primary, and in some cases are so slightly developed as to be practically absent. The two species *T. corrugatus* and *T. Shorensis* constitute further stages in the reduction series, for in the former these ribs only extend for half the length of the seed, and in the latter are mere chalazal vestiges. In *T. Noeggerathi* only the primary ribs are present. And, finally, in species such as *T. pusillus* and *T. elongatus* all indication of the secondary ribs is lost, which applies almost equally to the primary ones also. It is evident that the secondary ridges in the genus *Trigonocarpus* were in an obsolescent condition, which would fully account for the absence of commissures if such did, as the writer believes, originally exist.

[1] F. W. Oliver, New Phyt., vol. iii, 1904, pp. 96–104.

[2] F. W. Oliver, Ann. Bot., vol. xxi, 1907, pp. 303–4.

[3] Brongniart, Comptes rendus, tome lxxviii, 1874, pp. 15a, 16.

[4] Brongniart, loc. cit., p. 16.

[5] F. W. Oliver, New Phyt., vol. i, No. 7, 1902.

[6] Oliver, Trans. Linn. Soc. Bot., vol. vi, 1904.

[7] Loc. cit., p. 107.

F. W. Oliver has called attention to the remarkable resemblance between the plans of *T. Parkinsoni* and *Polylophospermum*,[1] one which is rendered complete if we assume that the secondary ribs of the former were the representatives of originally commissured structures. The conclusion, then, seems warranted that the six ribs of *T. Shorensis* and the non-vascular ribs of *T. Parkinsoni* are homologous with the six commissured ribs of *Polylophospermum* (in other respects, of course, this seed is specialized). It is, moreover, probable that the sutures themselves represent the planes of lateral fusion between six originally free members—a view which is further supported by the recognition of six component units in the micropylar region of *T. Shorensis.*

Newberry[2] has figured a cast showing the apex of a *Trigonocarpus* with its sarcotesta preserved, and in which the micropylar canal is seen as a star-shaped opening surrounded *by six small but free sarcotestal lobes.*

We have noted how, in the genus *Trigonocarpus*, ribs have become completely eliminated and each pair of units fused laterally, so that three sutures only remain. This condition obtains in the genus *Pachytesta*, and further reduction might well result in the production of a non-commissured seed, as in *Stephanospermum.*

The remaining genera cited above are either six- or twelve-ribbed seeds, and in the latter case the additional members may well correspond to the six vascular ribs of *Polylophospermum.*

Other genera there are, belonging to the Radiospermeae, which nevertheless possess ribs that in number are some multiple of two, e.g. *Eriotesta, Codonospermum.* Our review has, however, shown that there existed a group of seeds agreeing in their internal structure and consistent with our hypothesis in their sclerotestal plan, moreover including all those forms in which an undoubtedly Trigonocarpean organization has been established.

The possible origin of dimerous from trimerous forms is considered in the sequel, but the Radiospermeae is doubtless an artificial aggregate of which the Trigonocarpeae is one of the included natural groups; a statement that is borne out by the constant association with these seeds of the Neuropteridian type of foliage.[3]

None of these genera militate, then, against the theory that the integument originated as a whorl of six free members, each with a single vascular bundle, which subsequently became laterally fused. Such an interpretation necessitates the recognition of the sarcotesta and sclerotesta as constituting a phylogenetically homogenous structure, and in the next section will be given data that amply warrant that conclusion.

A striking feature of the Trigonocarpeae is not only the occurrence

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[1] Ann. Bot., vol. xxi, 1907, pp. 303-4.

[2] Rep. Geol. Survey of Ohio, vol. i, Pt. 2, 1873, p. 336 and Pl. XLII, Fig. 5.

[3] See M. Grand' Eury, Comptes rendus, vol. cxxxix, 1904, p. 3.

throughout of the hexamerous type, but also the absence of variation in the individual species. This stereotyped character suggests analogy with present-day Monocotyledons, and is in marked contrast to the variability exhibited by the Lagenostomales, not only as between different genera and species, but also as between individuals. For example, in *Physostoma*[1] nearly 50 per cent. of the seeds had ten ribs, but the remainder exhibited from nine to twelve. In *Conostoma* the number was six or eight according to the species, with one recorded variant of *Conostoma oblongum* possessing seven.[2] In *Lagenostoma Lomaxi* the normal number was nine,[3] and for *L. ovoides* eight, with variation from six to nine.[4] Finally, in *Gnetopsis elliptica* the number of ribs was four, with perhaps two others vestigial.[5] In this series we see that there is almost every variation from four up to twelve, and whilst a multiple of three is by no means infrequent—a reminiscence perhaps of relationship to the Trigonocarpeae—the more normal feature is some multiple of two.

Our knowledge of the structure of *Conostoma* and *Gnetopsis* has shown how narrow is the dividing line between radiospermy and platyspermy.[5] Also the recent discoveries of *Aneimites fertilis*[6] and *Pecopteris Plukeneti*,[7] together with the obvious relationships between Pteridosperms and the Cordaiteae, render it necessary to consider the possibility of deriving bilateral forms from a trigonous group. The fact that the fructification *Pecopteris Plukeneti* was borne on a Medullosean type of foliage certainly indicates such a change, so that the analogy afforded by examples from the carpellary structures of the present-day Flora may not be without value. The *Carices* are represented in the British Flora by about fifty species, of which over thirty possess three stigmas associated with a triangular nutlet; the remaining species mostly have two stigmas, and the nut is either bilaterally symmetrical or plano-convex. In a few species with two stigmas the nut is slightly trigonous, and in *Carex paludosa*, Good., the stigmas vary from three to two, accompanying which the nut is either trigonous or lenticular.

As an example from the Dicotyledonous series, the Polygonaceae furnish us with a group in which triangular fruits are the rule. In part of the genus *Polygonum*, and in the genus *Rumex*, a triangular nut is associated with three stigmas. In the section *Persicaria* of the genus *Polygonum*, and in *Oxyria*, the fruit is lenticular and composed of only two carpels, as shown by the pair of stigmas.

To come much nearer, the fructifications of *Ginkgo biloba* have been

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[1] Oliver: Ann. Bot., 1909.

[2] Oliver and Salisbury: Ann. Bot., vol. xxv, 1911.

[3] Oliver and Scott: Phil. Trans. Roy. Soc., vol. v, 1903, p. 197.

[4] Prankerd, T. L.: Jour. Linn. Soc. Bot., vol. xl, No. 278, p. 463.

[5] Oliver and Salisbury, loc. cit.

[6] Dr. David White: The Seeds of *Aneimites*. Smithsonian Misc. Coll., vol. xlvii, pt. 3.

[7] M. Grand' Eury, Comptes rendus, vol. cxl, p. 920.

found with three ribs in place of two, a variation that may even be a reversion.

Such examples suffice to show that the assumption of an originally hexamerous integument (later becoming trimerous in some forms) for the Trigonocarpeae does not preclude the origin of closely allied genera possessing bilaterally symmetrical structures. (The position of the tetramerous Radiosperms awaits details of their internal structure.)

In view of the frequent association in the monocotyledonous series of trimerous flowers with a triangular stem structure, an expression probably of similar mechanical relations, it is of interest to note that the general outline of the stems both of *Medullosa anglica* and *Sutcliffia insignis* was broadly triangular,[1] though the character does not of course hold for other species of the former genus.

Before leaving this subject it is of interest to note that Drs. Stopes and Fuji regarded *Yezostrobus Oliveri* as more nearly approaching to *Trigonocarpus* than any other known fossil or recent group,[2] and therefore, on the foregoing hypothesis, the triangular outline which this seed exhibits in transverse section[3] may have a phylogenetic significance.

### 2. The Question of a homogeneous or dual Phylogeny.

The question at once arises in relation to the integument: was this structure of uniform origin or was it dual, as suggested by Stopes for Cycads?[4] The close agreement of the two groups makes the assumption of a double nature for the one almost necessitate its acceptance for the other. The main grounds on which this theory is based are, briefly, the presence of two series of bundles, both supposed to be integumental, and the resemblances that exist between *Lagenostoma* with its cupule on the one hand, and the Cycadean ovule with its sarcotesta on the other. The recent work of Miss Kershaw[5] on *Bowenia spectabilis* has shown that in this species at least the inner vascular system is nucellar. On the other hand, Dr. Stopes traced some members of the inner vascular system of Cycads into the integument beyond the free part of the nucellus, and unless future work should show that it is only the accessory branches from the integumental system that behave in this manner, the evidence as to the nature of the inner bundles must remain in its present contradictory state. But in view of the diverse data at present available, we are not warranted in attaching any great importance to the occurrence of two systems, even should they prove to be both integumental in certain cases. The branched

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[1] Scott, Phil. Trans. Roy. Soc., B, vol. cxci, 1899; and Scott: On *Sutcliffia insignis*. Trans. Linn. Soc. Bot., vol. iii, 1906, Pt. 4, ser. 2.

[2] Phil. Trans. Roy. Soc., ser. B, vol. cci, 1909. More recently, however, Prof. Fuji has come to regard the nearest living relatives of this plant as being the Araucarieae.

[3] Loc. cit., Fig. 14.

[4] On the Double Nature of the Cycadean Integument. Ann. Bot., 1905.

[5] Ann. Bot., vol. xxvi, No. 103, 1912, p. 636.

and double system of integumental strands in *Pachytesta* evinces a tendency that might well have subsequently developed, and its origin in consequence have gradually become obscured.

With regard to the second argument in relation to *Lagenostoma*, recent work has shown that, in spite of the free nucellus exhibited by the Trigonocarpeae, they agree both in the structure of their fructifications and stem anatomy much more closely with the modern group than do the Lagenostomales.[1]

When we turn to *Trigonocarpus Shorensis* we find that the evidence for a homogeneous origin for the whole integument is abundantly clear. Such inner flesh as is present is but the unsclerized internal lining of the hard shell, and this latter, though broadly composed of an outer and inner part, is formed from one and the same tissue by the different course which its elements pursue.

The sarcotesta on its inner periphery shows a complete transition from the outer sclerotestal cells, so there is no zone to which we can point as possibly representing the fusion plane of two morphological units. And if further evidence were necessary it is furnished by the course of the secretory elements which pass from sclerotesta to sarcotesta irrespective of the differences of texture which, in the mature fruit, these regions present.

## IX. THE ORIGIN OF THE INTEGUMENT IN THE TRIGONOCARPEAE AND THE LAGENOSTOMALES.

The addition of yet another Trigonocarpean seed, showing a well-defined nucellar epidermis, adds to the certainty that the group was characterized by the possession of an extensive free region of the nucellus, to which part the megaspore cavity was almost entirely confined. This would seem to be a fundamental difference separating them off from the other members of the Pteridospermeae.

The considerable resemblances which the Trigonocarpeae bear to the Lagenostomales, both as regards the general organization of their seeds and the broad features of anatomy, in the few stems which have been allocated to fructifications, indicate that the two must have had a closely allied ancestry, either in some semi-Pteridospermic group which possessed a generalized type of fructification, giving rise to the characters of both; or in two parallel developments arising independently from the Pteridophytic stock.

The theory of intercalated growth put forward by F. W. Oliver in a similar connexion[2] to homologize modern with fossil forms, applied in the manner indicated below, seems to offer the best explanation of both the resemblances and differences which these two groups exhibit.

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[1] Kershaw, loc. cit.; and de Fraine: On *Sutcliffia insignis*. Ann. Bot., vol. xxvi, 1912.

[2] The Ovules of the Older Gymnosperms. Ann. Bot., vol. xvii, 1903.

In *Physostoma*, the most archaic type of the Lagenostomales, the megaspore cavity projects into the free portion of the nucellus, the plinth being only slightly developed.

In the more advanced *Lagenostoma*, the plinth exhibits intercalary growth, so that there is a greater extent of free nucellus in the older than in the younger phase, whilst in *Conostoma* the plinth reaches its greatest extent.

These facts seem to indicate that the free apical portion of the nucellus was in this series a phylogenetically late development, resulting from a zone of intercalated growth.

On various grounds *Physostoma* is regarded as the most primitive seed yet known,[1] therefore it is of greater significance as being the only member of the Lagenostomales exhibiting a free apex of the nucellus into which the megaspore cavity projects. We may therefore suppose that the potentiality for the development of a free nucellus was possessed by the ancestors of *Physostoma*; but was only exhibited by the majority of the group in the intercalated growth of the region *above* the contained megaspore, resulting in the elaboration of the plinth.

Probably, then, the common ancestors which gave rise to the Lagenostomales on the one hand and the Trigonocarpeae on the other possessed a nucellus unenclosed at the apex, and round the base of which were fused a whorl of members with free apical portions, affording protection to the sporangium, in which the prothallus was now retained. With the inception of the seed habit came an increase in the size of the megaspore cavity, accompanying enlargement of the nutritive prothallus. Here is where the divergence in the two lines of descent arose. In the one case there was an upward extension of the megaspore cavity and the surrounding free pro-integumental lobes, resulting in the production of a free nucellus which may either have had its origin in an already vascularized sporangium,[2] or the nucellar system may have arisen in relation to the greater demands upon the water-supply now created.

Along the line of the Lagenostomales the increased dimensions were brought about by a similar phylogenetic intercalation of growth, which took place, however, in the lower part where the whorl of protective members constituting the pro-integument was laterally fused to form a ring around the base of the sporangium. The close proximity of the integumental bundles would account either for the suppression or non-development of a special nucellar system. Such a view would not only explain the intermediate characters exhibited by the archaic *Physostoma*, but it further accords with the broad features of the testa as seen in the two groups.

A marked characteristic throughout the Lagenostomales is that at the

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[1] Oliver: Ann. Bot., 1909.

[2] Oliver: A Vascular Sporangium. New Phytologist, vol. i, 1902, p. 60.

apex of the seed the multiple nature of the integument exhibits itself with almost sudden clearness after it becomes free from the nucellus. In the seeds of the Trigonocarpeae, on the other hand, the component units of the testa are in general equally distinct at the base as at the apex, or even throughout their length. These two conditions seem only explicable on the hypothesis that in the one group lateral fusion was simultaneous throughout, representing in fact the elongation of the free parts, and in the other took place in the 'canopy' and body of the seed at phylogenetically distinct periods.

Our investigation of the present seed has shown us that the external periphery of the integument was circular in outline throughout; in other words, the lobing is only shown superficially at the internal periphery, where it extends from near the base to the apex, though in the body of the seed the six lobes manifest near the chalaza, and reappearing at the micropyle, had become reduced to three.

What is true of this species was, judging from impressions with sarcotesta preserved, true also for its congeners, and may well have been a group character. The Trigonocarpeae were then characterized by an internal lobing almost to the base of the seed, whereas in the Lagenostomales such internal lobing is only to be found in the apical region, so that superficially as well as internally the major part of the integument in the one is to be homologized with the distal extremity in the other.

We have assumed that the ancestral fructification of the two groups possessed a whorl of surrounding members fused at the base between themselves. In both *Trigonocarpus Shorensis* and *Trigonocarpus Parkinsoni* the sutures of the primary ribs disappear a little before the floor of the seed cavity is reached.

The structural facts therefore justify the assumption that in both groups there was a phylogenetically earlier lateral fusion of the prointegumental members at the base, followed later by their fusion at the apex.

The congenital fusion of the integument with the contained nucellus was but a matter of time, naturally evinced first in the basal region or zone of earlier lateral fusion. This latter, in the Trigonocarpeae, is wellnigh vestigial, so that a free nucellus resulted, whilst in the Lagenostomales it represents the greater part of the seed body.

Later on in the history of the Trigonocarpeae and their descendants, congenital fusion followed in the upper part, giving us the condition in modern Cycads; though here, as in the more recent Lagenostomales, the apical region has remained permanently free in relation to its specialized structure and functions.

## X. RELATION TO VEGETATIVE ORGANS.

In two of our series of sections there occur, associated with the seed structures, Medullosean petioles of which portions of as many as three are present in one and the same preparation. This fact would, in the light of present knowledge,[1] appear of itself significant, and, added to this, numerous secretory elements are present in these petioles which agree in structure with those found in the sarcotestal tissue of *Trigonocarpus Shorensis*. Each is enclosed by a sheath-like layer of somewhat flattened cells, and the wall surrounding the dark carbonaceous mass in the centre exhibits externally the characteristic longitudinal striations. Both of these features are also exhibited in the stems and petioles of *Medullosa anglica*.

The individual bundles are collateral in structure, the phloem being represented by an empty space upon which the smallest protoxylem elements abut. The xylem is surrounded by a band of sclerotic fibres in close contact with the tracheides. The xylem exhibits no admixture of parenchymatous elements, so that in all respects the bundles are distinct from those of *Rachiopteris Williamsoni*,[2] but agree very closely with those of *Myeloxylon*.[3] If, then, the petioles above described really belonged to the plant which bore our seed, the petrifaction known as *Myeloxylon* probably represents an aggregate of petiolar structures corresponding to at least two species of Trigonocarpean fruits, and possibly in both cases having as their stem a structure of the *Medullosa anglica* type. In any case, the evidence at present available is against any suggestion that *Trigonocarpus Shorensis* was the fructification of *Sutcliffia insignis*, though the above association may be entirely without significance.

The presence of numerous secretory ducts is a feature shared by both the known British Medullosean stems. In the structure of the chalazal bundle, whilst the protoxylems of *Trigonocarpus Shorensis* appear to be grouped in pairs (a feature of *Sutcliffia insignis*), in the presence of internal parenchyma and a secretory duct within the xylem our sections of *Trigonocarpus Parkinsoni* show a closer agreement with that stem.

## XI. DIAGNOSIS.

*Trigonocarpus Shorensis*, sp. nov.

**Locality:** Shore Littleborough.
**Horizon:** Lower Coal Measures.

A radially symmetrical obovoid seed tapering to its insertion and circular in transverse section. Length over 4 cm., width 2·4 cm.

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[1] Scott, Progressus Rei Botanicae, vol. i, p. 206.

[2] Seward, Ann. Bot., vol. viii, No. 30, 1894, p. 208.

[3] Ibid., vol. vii, 1893, p. 1.

Testa differentiated into two parts:

(*a*) **Sclerotesta** (length 2·8 cm., width 1·5 cm.) produced at the apex into a short triangular beak and bearing six ribs, viz. three principal and commissured extending throughout, and three minor and non-sutured reaching to some 8 mm. from the base. (*b*) **Sarcotesta** about 4 mm. in thickness, lacunar in structure with numerous secretory sacs, and six peripherally situated vascular bundles alternating in position with the ribs. **Limiting layers** containing sclerotic strands. **Nucellus** free, containing vertically directed secretory sacs, and limited within by vascular tissue forming a continuous lining at the base but above passing into separate bundles.

## XII. SUMMARY.

In the foregoing pages a detailed description is given of the Palaeozoic seed *Trigonocarpus Shorensis*, of which the chief diagnostic features are summarized in the preceding section.

The sclerotesta differed principally from that of the well-known species in its obovoid form and tapering insertion, the absence of ridges in relation to the vascular bundles, and in the relatively short beak. In the early disappearance of the secondary ribs it resembled closely the external cast of *Trigonocarpus corrugatus*.

Both sarcotesta and sclerotesta showed considerable complexity, with nevertheless a well-marked transition, such as can only be reconciled with differentiation of the same organic unit. The sclerotesta was built up of fibrous elements longitudinally directed within and without, intertwined in a complex manner. The sarcotesta was unusually broad, lacunar in structure, and contained numerous secretory sacs comparable to those of Cycads.

The limiting layers were formed of a ground-tissue of parenchyma containing a system of probably anastomosing and tangentially flattened strands of fibres, with secretory sacs like those of the interior. The whole structure in this region approached much more nearly to that of the peripheral layers of a Medullosean petiole than in *Trigonocarpus Parkinsoni*.

The sarcotesta exhibited no flattening, but was circular in form throughout, whilst an inner flesh was probably only present as an inconspicuous layer within the micropyle.

The vascular system comprised two parts, viz. a sarcotestal and a nucellar.

The most notable feature of the former is the extreme peripheral position occupied by the six mesarch vascular bundles.

The single chalazal bundle had the protoxylem groups just within the periphery, and expanded at the base of the nucellus into a tracheal cup, which was probably formed of twelve laterally fused bands that gradually increased in number to form numerous mesarch lenticular bundles lining the inner limit of the nucellus.

The nucellus was attached at the base to a sclerotic papilla, but was otherwise free from the testa, and its outstanding features were—a well-developed and thick-walled epidermal layer; the occurrence of three longitudinal flanges, corresponding with the commissures; and the presence of numerous secretory sacs in the ground-tissue, arranged in radial files.

Two sections of *Trigonocarpus Parkinsoni* are described which indicate that the chalazal bundle gave off three branches simultaneously, which almost immediately bifurcated to form the six sarcotestal strands.

A comparison with Cycads and allied types leads to the conclusion that *Trigonocarpus Shorensis* is in several respects a relatively more primitive type than its congeners. In this connexion *Trigonocarpus Oliveri* is shown to have been an eight-angled seed, and is therefore probably to be excluded from the Trigonocarpeae.

In the general discussion on the testa, the evidence for its homogenous origin is set forth, and the theory is advanced that it had its inception in the lateral fusion of a whorl of six originally free members. The testal structure of the various genera is discussed in the light of this theory.

The resemblances and differences between the Trigonocarpeae and Lagenostomales are shown to be explicable on the hypothesis of intercalated growth, followed by subsequent congenital fusion between the nucellus and integument.

Medullosean petioles associated in the coal-balls with *Trigonocarpus Shorensis* are briefly described, and resemble *Myeloxylon*.

## EXPLANATION OF PLATES.

Illustrating Mr. Salisbury's paper on *Trigonocarpus Shorensis*.

R = Owens College, Manchester, Collection; S = University College Collection; D.H.S. = Dr. Scott's Collection.

### PLATE IV.

Figs. 1–10, photomicrographs.

Fig. 1. Nearly transverse section through the middle of the seed, showing the three commissural ridges ($\mathrm{R}^1$, $\mathrm{R}^2$, $\mathrm{R}^3$) and the extensive sarcotesta (*st.*). The nucellus is seen in part on the right with a ridge near the commissure slightly displaced (*n.f.*). The black dots in the sarcotesta are the carbonaceous contents of the mucilage sacs. R. 1161, *h*. × about 4.

Fig. 2. Slightly oblique section through the micropyle, showing sarcotesta with secretory sacs (*m.s.*). Within the triangular sclerotesta the inner flesh can be faintly seen. R. 1161, *k*. × 2·5.

Fig. 3. Tangential section through the outer sclerotesta. The band-like aggregates of fibrous cells are seen overlapping n a plait-like manner (*f.b.*) and passing in different directions. S. 32, *g.* × 60.

Fig. 4. Slightly oblique transverse section near base of seed; on one side a small projection is seen, representing the termination of a minor rib ($r^1$). Within is the contracted nucellus (*nu.*) with secretory sacs in radial files, over which the contracted epidermis has formed ridges. S. 33, *c.* × 2.

Fig. 5. A tangential section through the zone of transition between the sclerotesta (*scl.*) and the sarcotesta (*st. c.*). The slightly thickened walls, the elongated form, and the sinuous course of the inner sarcotestal cells are here seen. S. 32, *g.* × 90.

Fig. 6. An oblique section through the base of the micropyle, showing the extensive unflattened sarcotesta with limiting layers at *l.l.*, and secretory sacs in outer sclerotesta (*m.s.*). S. 31, *i.* × 5.

Fig. 7. Obliquely longitudinal section through chalazal end of the seed, showing vascular bundle (*v.b.*), chalazal papilla (*c.p.*), and the tapering base of seed. S. 32, *e.* × $2\frac{1}{2}$.

Fig. 8. Section through extreme apex of sclerotic beak. The sclerotesta is seen to be thinning out rapidly, and at the higher level on the right is only some three elements in width. The sides show a median constriction (*m.c.*) resulting in a six-lobed structure (*m.l.*). The inner flesh (*i.f.*) shows a gradual transition from the sclerotic tissue. R. 1161, *e.* × 28.

Fig. 9. Oblique section through the base of the seed, passing through all six ribs ($R^1$, $R^2$, $R^3$, and $r^1$, $r^2$, $r^3$). At *c.p.* the chalazal papilla is seen perforated by the single vascular bundle (*v.b.*). R. 1161, *b.* × 4.

Fig. 10. Tangential section through the periphery of the sarcotesta, showing the lacunae (*lac.*) separated in places by the superposed peg-like projections of the stellate cells (*p.*), and elsewhere by the cells proper. S. 32, *h.* × 90.

## PLATE V.

Figs. 11–20, photomicrographs.

Fig. 11. Vertical section through the pollen-chamber wall (*p.w.*), from which the cuticle has become separated (*cu.*). The shoulder is occupied by thin-walled parenchymatous tissue (*sh.*). The oval bodies are fungal spores (*sp.*). S. 32, *c.* × 50.

Fig. 12. Transverse section through the sarcotesta with two secretory elements, probably derived by branching, in close contact (*m.s.*). S. 31. × 60.

Fig. 13. A portion of a transverse section to show the nucellar flange, consisting of parenchymatous tissue (*n.f.*) and corresponding in position to a commissural rib (*com.*). A lenticular nucellar strand is seen on the left (*v.b.*). S. 31, *e.* × 30.

### *Trigonocarpus Parkinsoni.*

Fig. 14. Transverse section through the chalazal bundle of *Trigonocarpus Parkinsoni* at the level at which the sarcotestal strands (*v.b.*) are given off. At the top one of these has branched into two. The central xylem mass (*c. xy.*) is surrounded by a discontinuous sheath of parenchyma (*par.*), exterior to which more tracheides (*tr.*) are seen. A single secretory element (*m.s.*) occupies a position within the xylem mass. In the space between the bundle and the sclerotesta several more secretory elements are seen and remains of parenchymatous tissue. S. 34, *a.* × 90.

Fig. 15. A single sarcotestal bundle from near the base of *Trigonocarpus Parkinsoni*, showing the dual nature of the xylem. The centre of the strand is occupied by narrow tracheides (*n.tr.*) surrounded by a parenchyma sheath (*par.*), and this again is followed by a zone of short broad tracheides (*s.tr.*). S. 34, *b.* × 90.

### *Trigonocarpus Shorensis.*

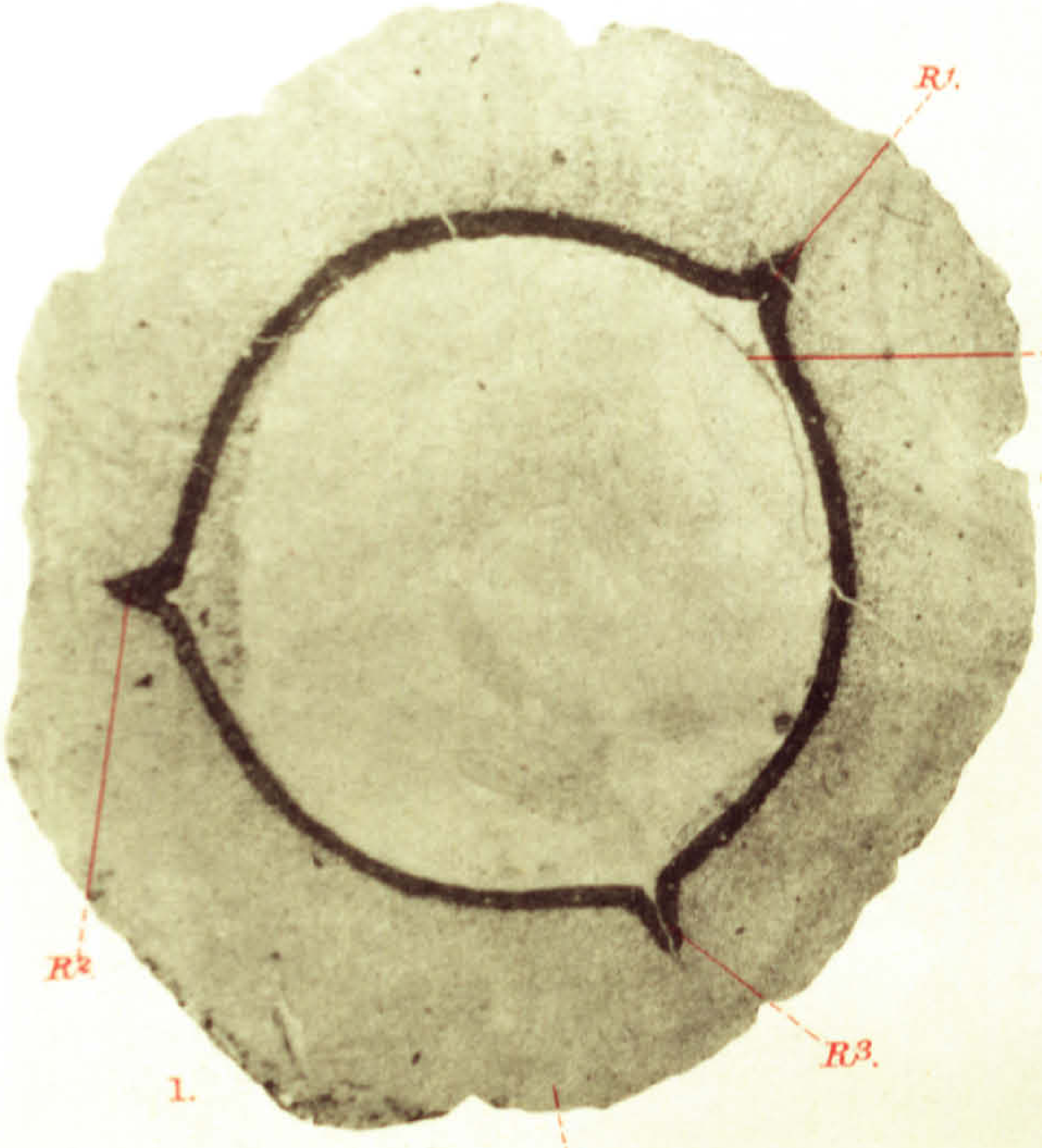
Fig. 16. Transverse section through the chalazal bundle of *T. Shorensis.* The parenchyma sheath (*p.s.*) around the bundle and the radially extended tracheides of the outer zone are clearly seen. The protoxylems are seen occupying a position just within these latter. *m.s.*, mucilage sacs. S. 33, *b.* × 100.

Fig. 17. Transverse section through a sarcotestal bundle, showing the thick-walled protoxylem elements (*pt.x.*), the small elements of the centrifugal xylem (*cf.x.*), and the large short tracheides comprising the centripetal (*cp.x.*). Touching the bundle on the right is a sclerotic strand of the limiting layers. *m.s.*, mucilage sac. S. 31, *i.* × 100.

Fig. 18. Oblique section through the chalazal bundle, from the same preparation as Fig. 7, showing the scalariform thickenings of the tracheides (*tr.*). *scl.*, sclerotesta. S. 32, *e.* × 80.

Fig. 19. Transverse section through the limiting layers of the sarcotesta, occupied by several radially extended sclerotic strands (*scl.p*) partially displaced by contraction. The sclerotic plate on the extreme left is interrupted by a medianly placed mucilage sac, and both here and in the other here present (*m.s.*) the thickened wall stands out clearly as a transparent zone around the dark contents. S. 31, *i.* × 100.

Fig. 20. Transverse section through the nucellus from the same preparation as Fig. 4. The radial files of mucilage sacs (*m.s.*) are clearly seen, causing corresponding ridges (*n.r.*) upon the surface of the contracted nucellar epidermis (*n.e.*). The ground-tissue is occupied by thin-walled parenchymatous tissue (*par.*), and the inner limit is marked by a zone of tracheides (*tr.*). S. 33, *c.* × 120.



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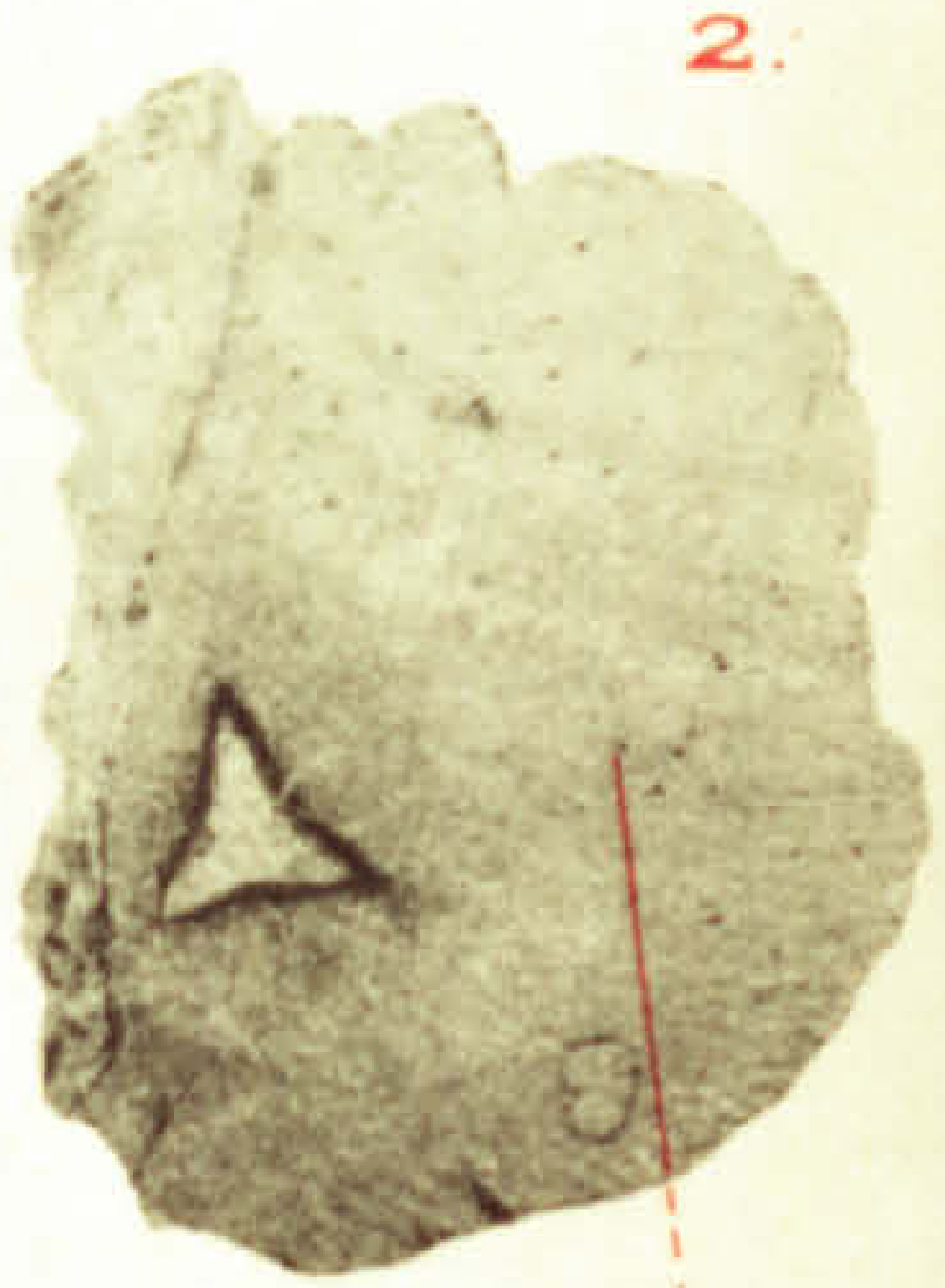

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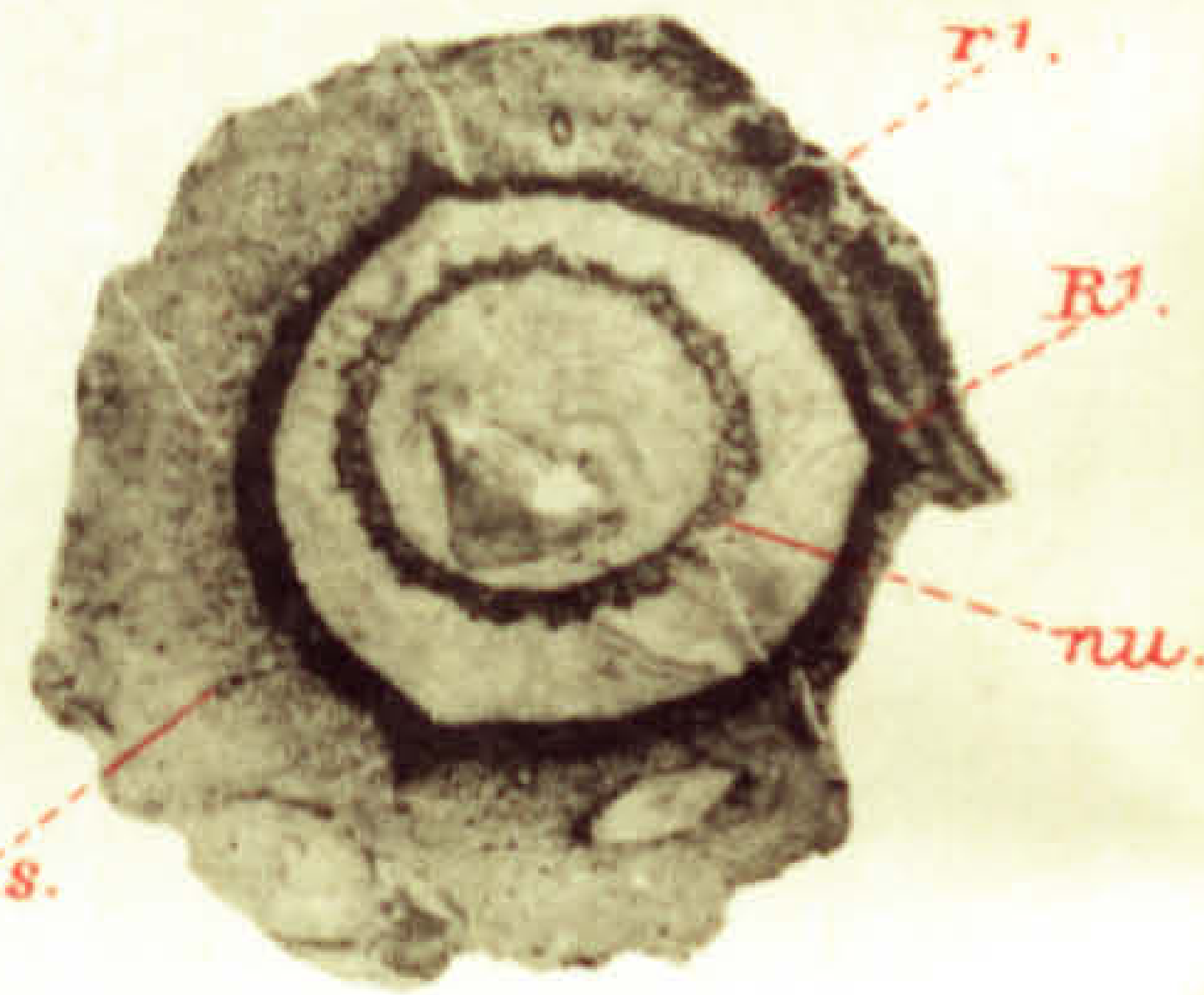

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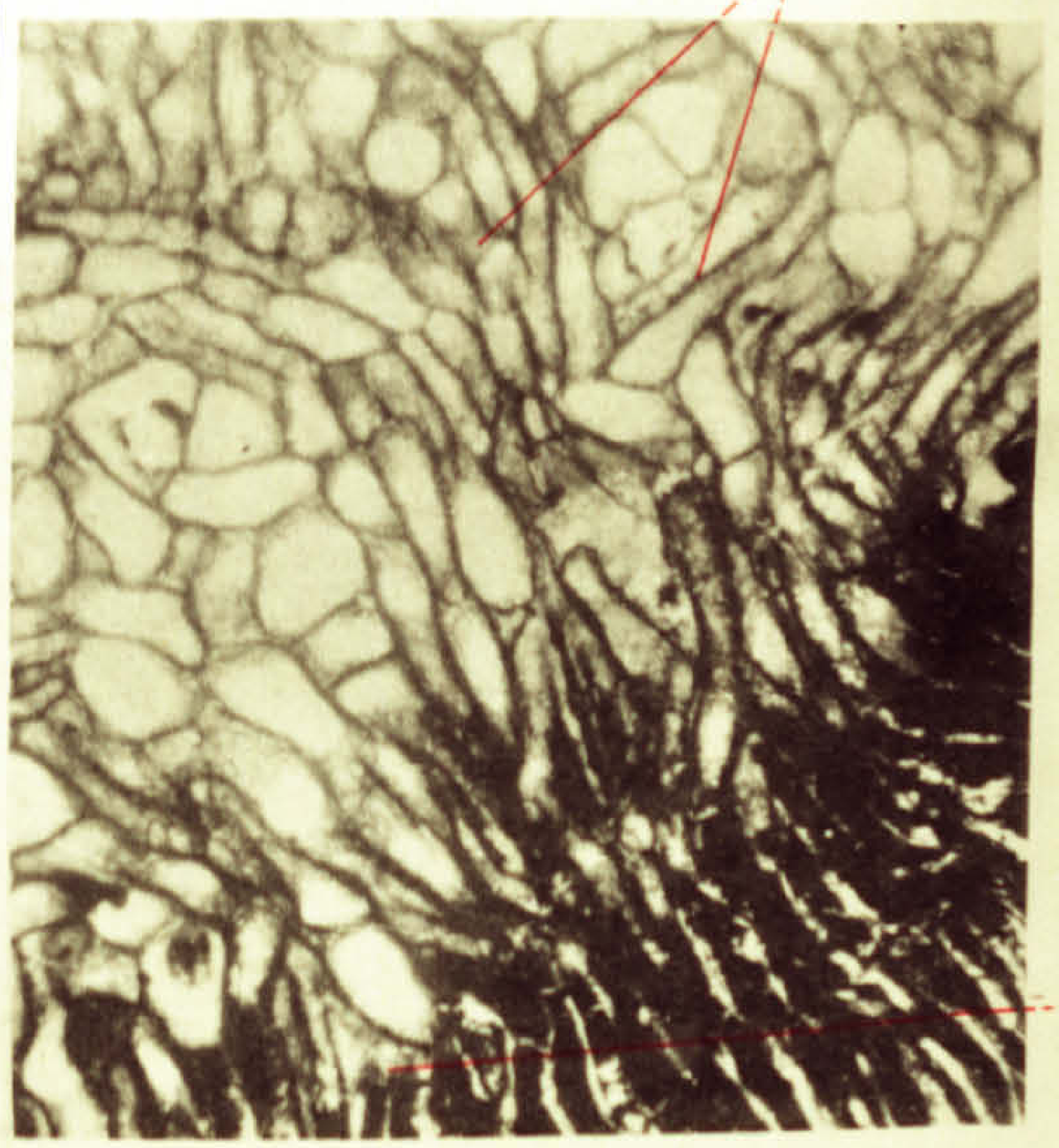

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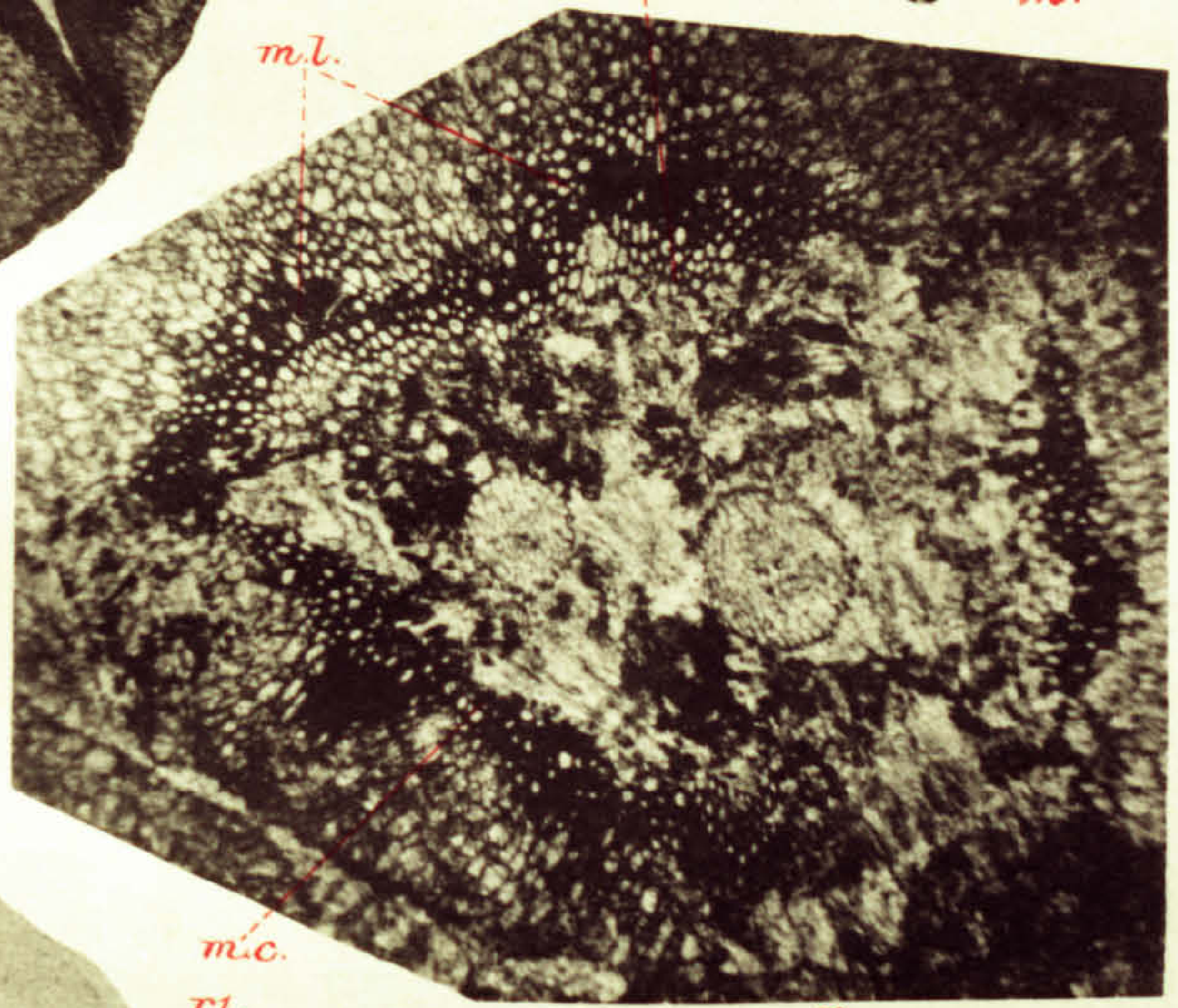

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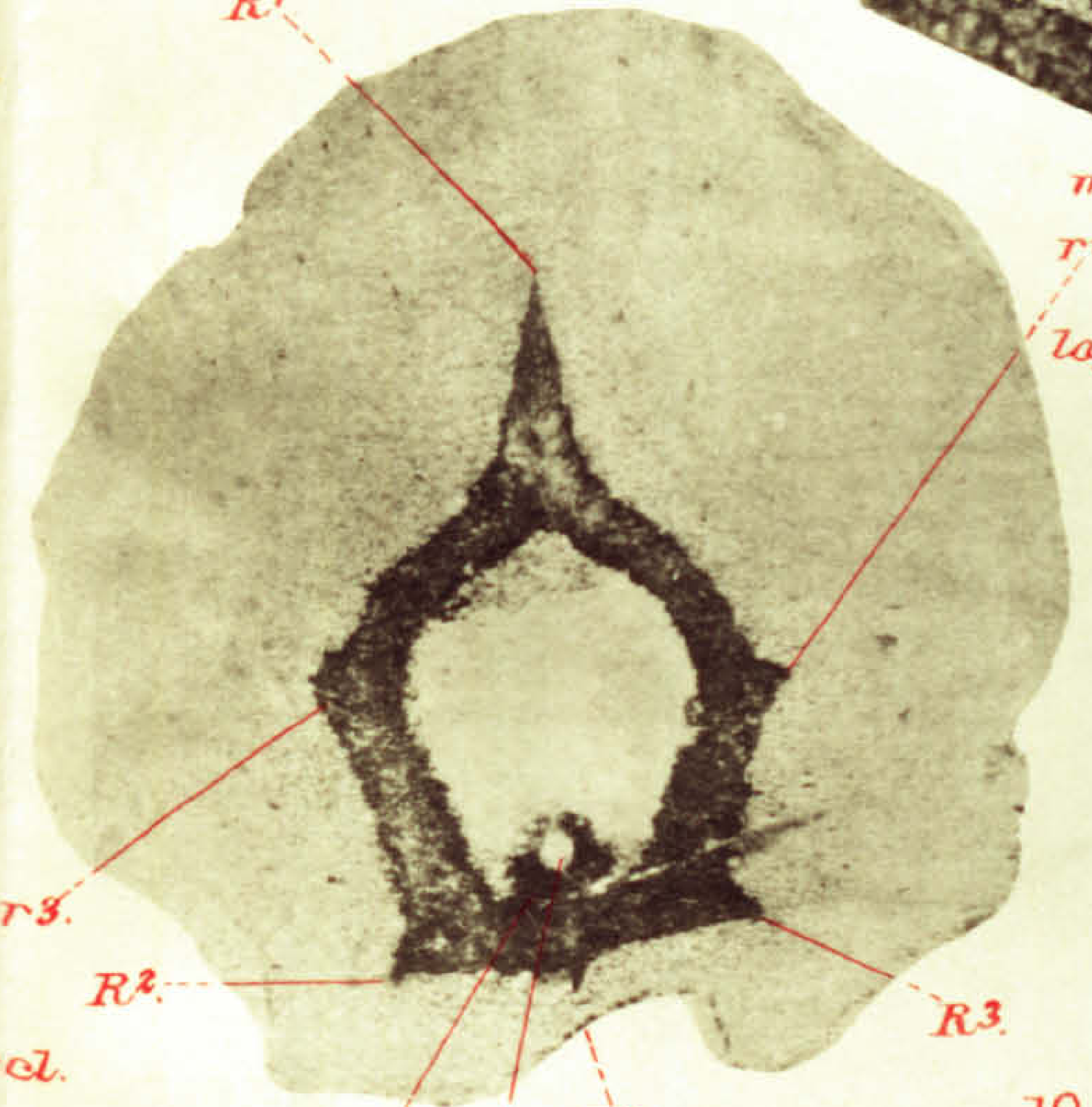

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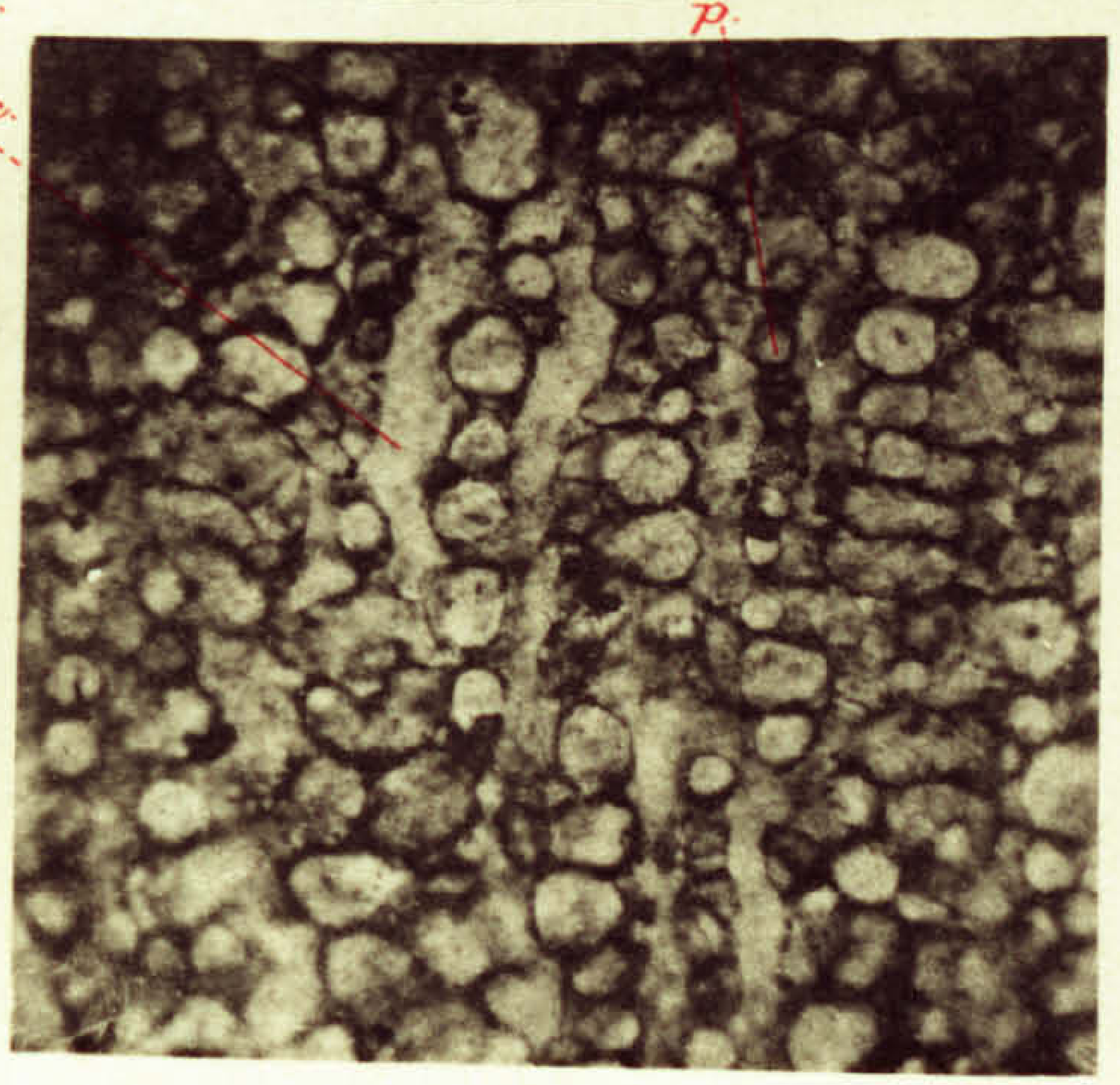

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SALISBURY—TRIGONOCARPUS SHORENSIS.

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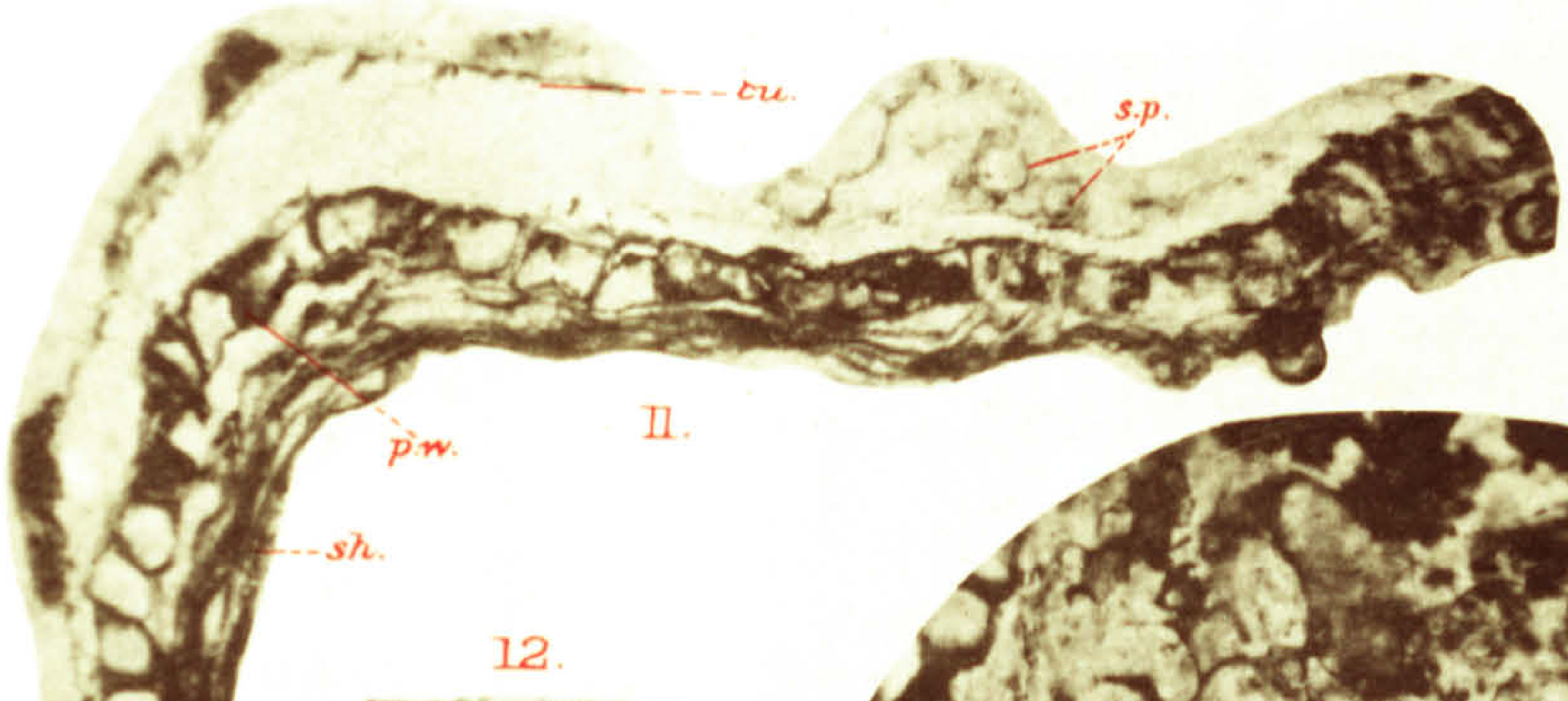

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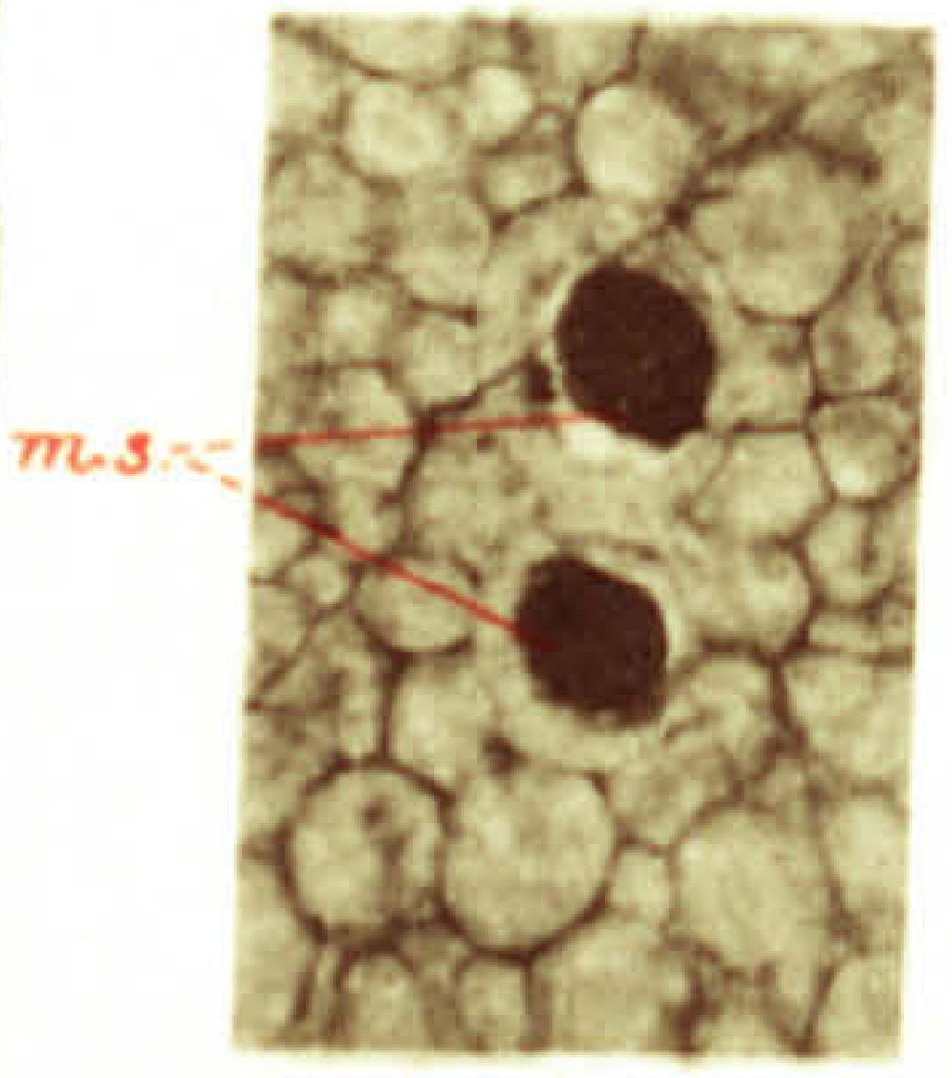

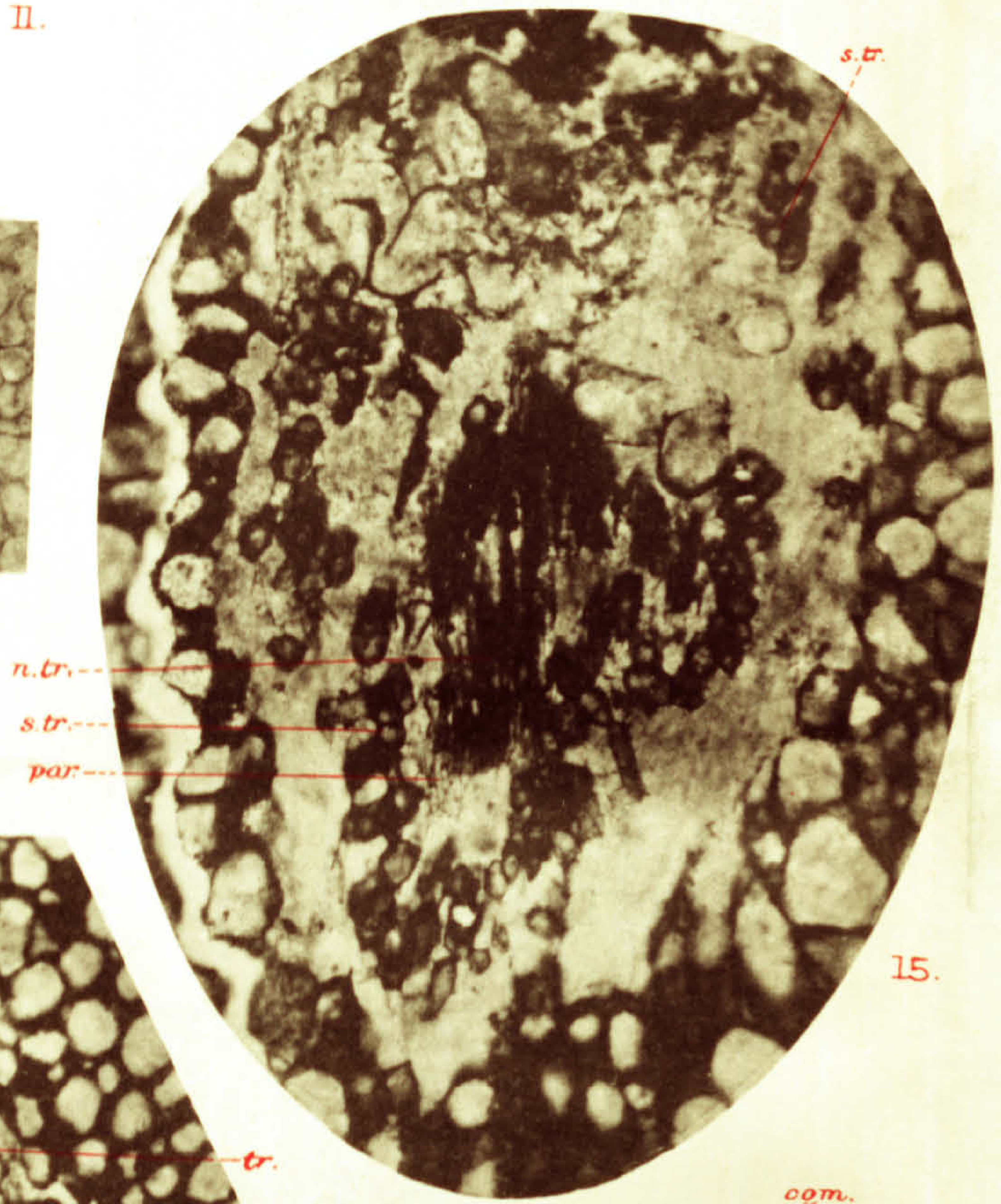

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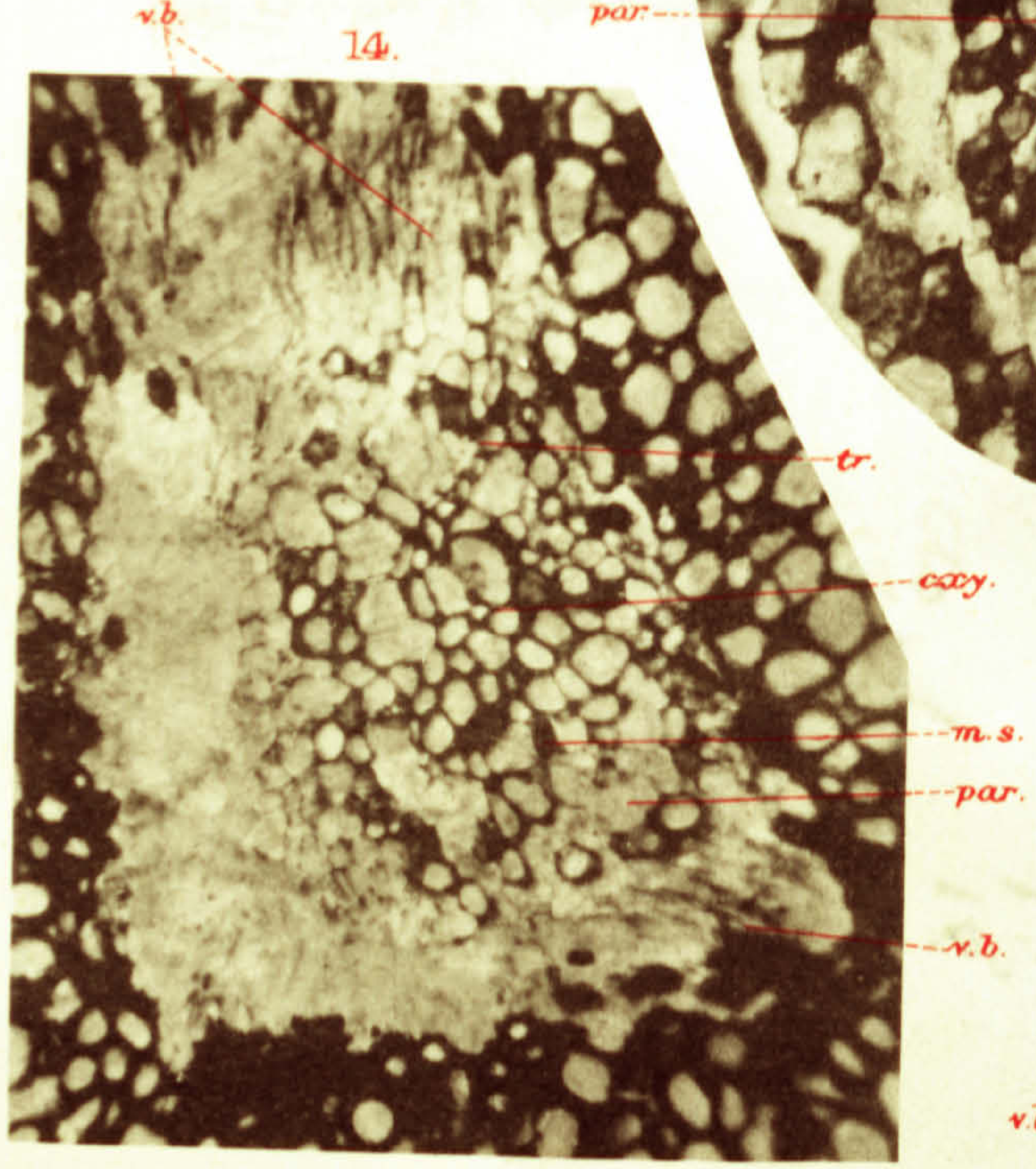

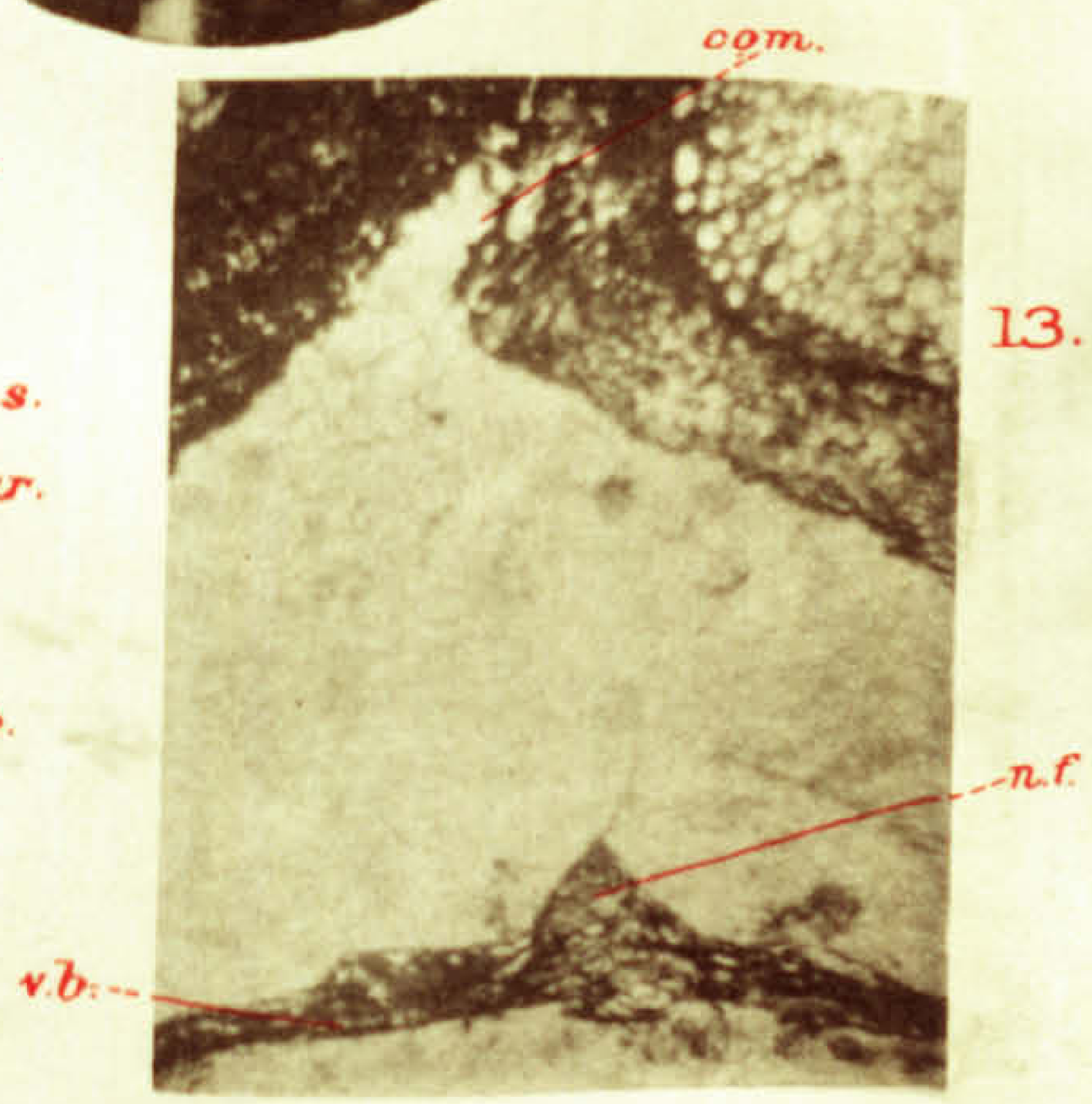

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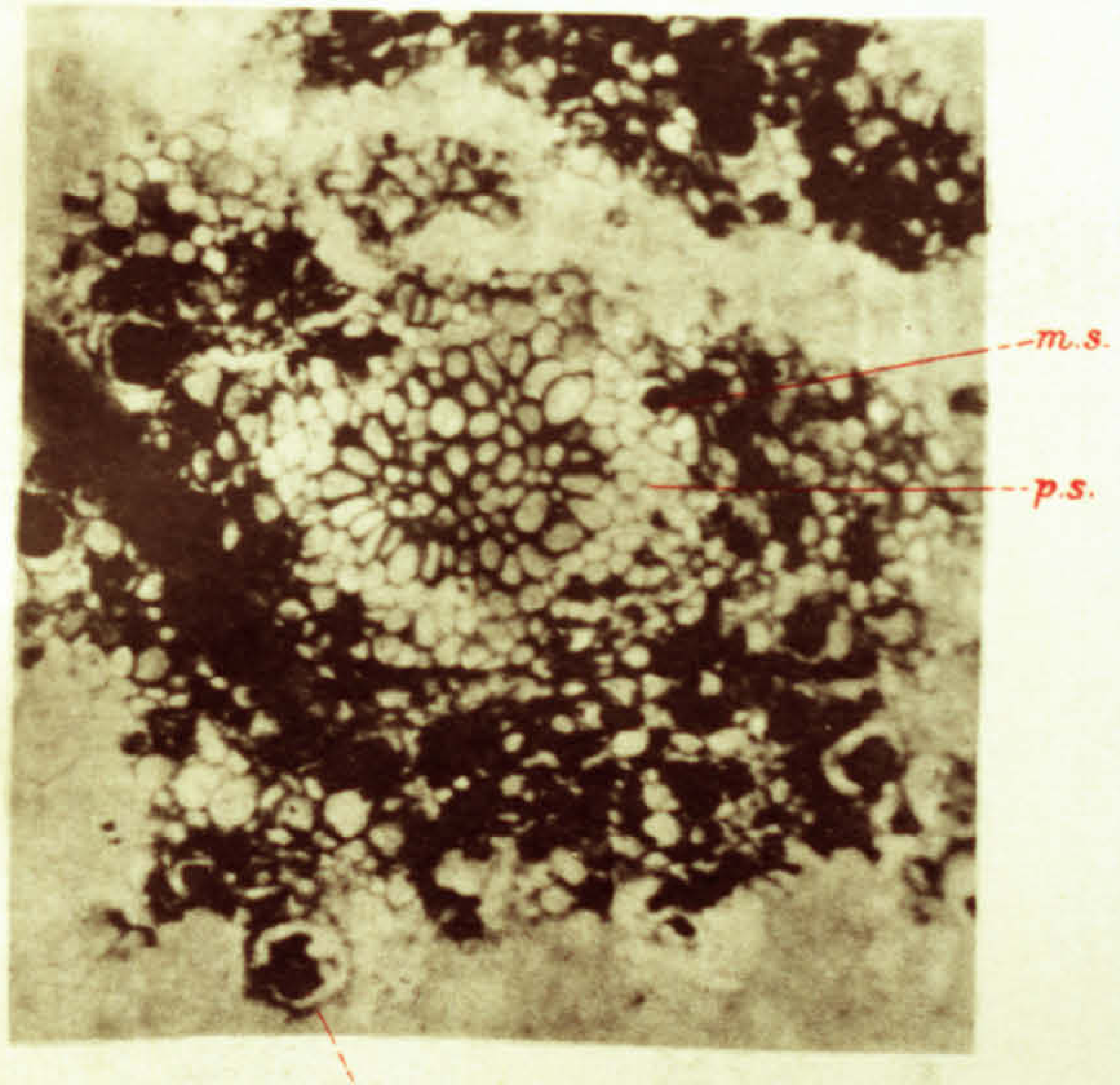

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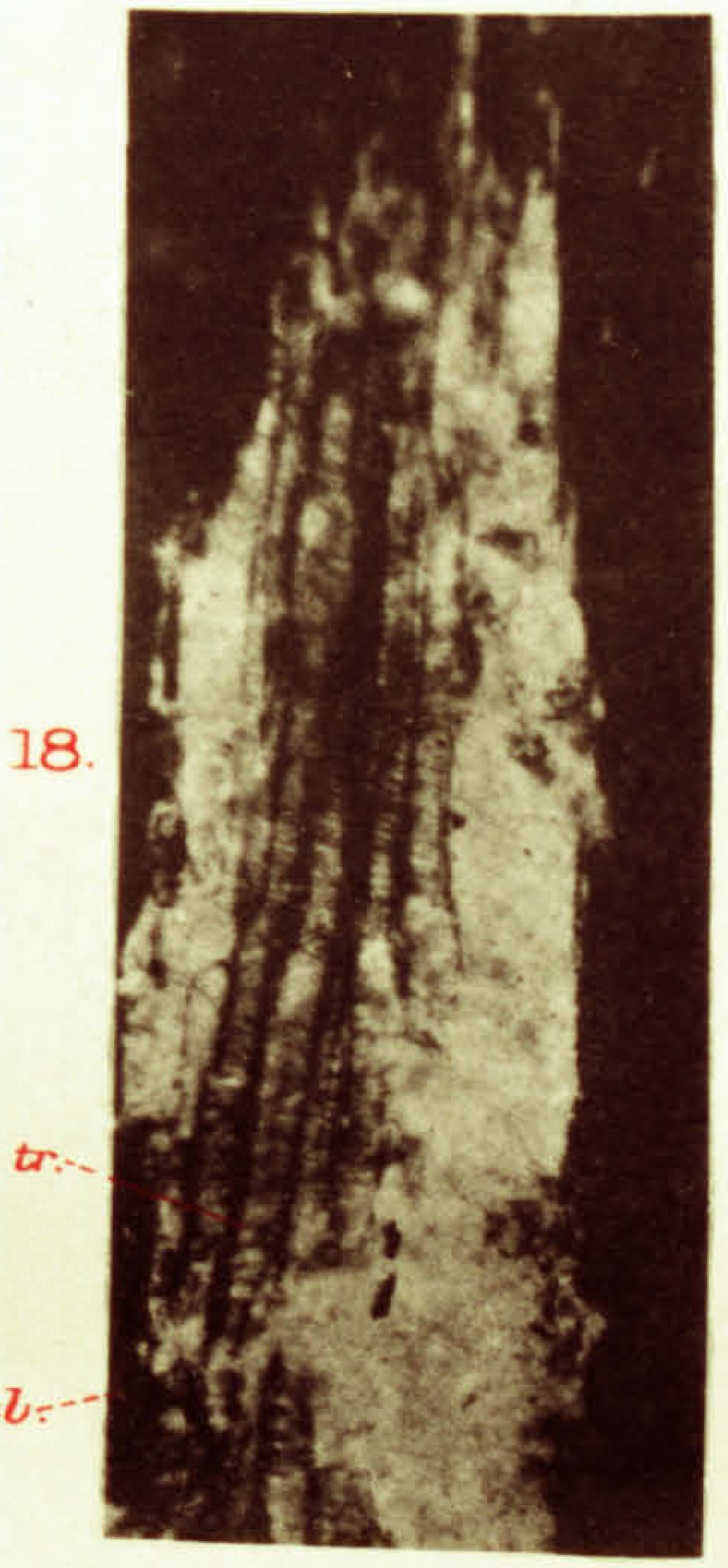

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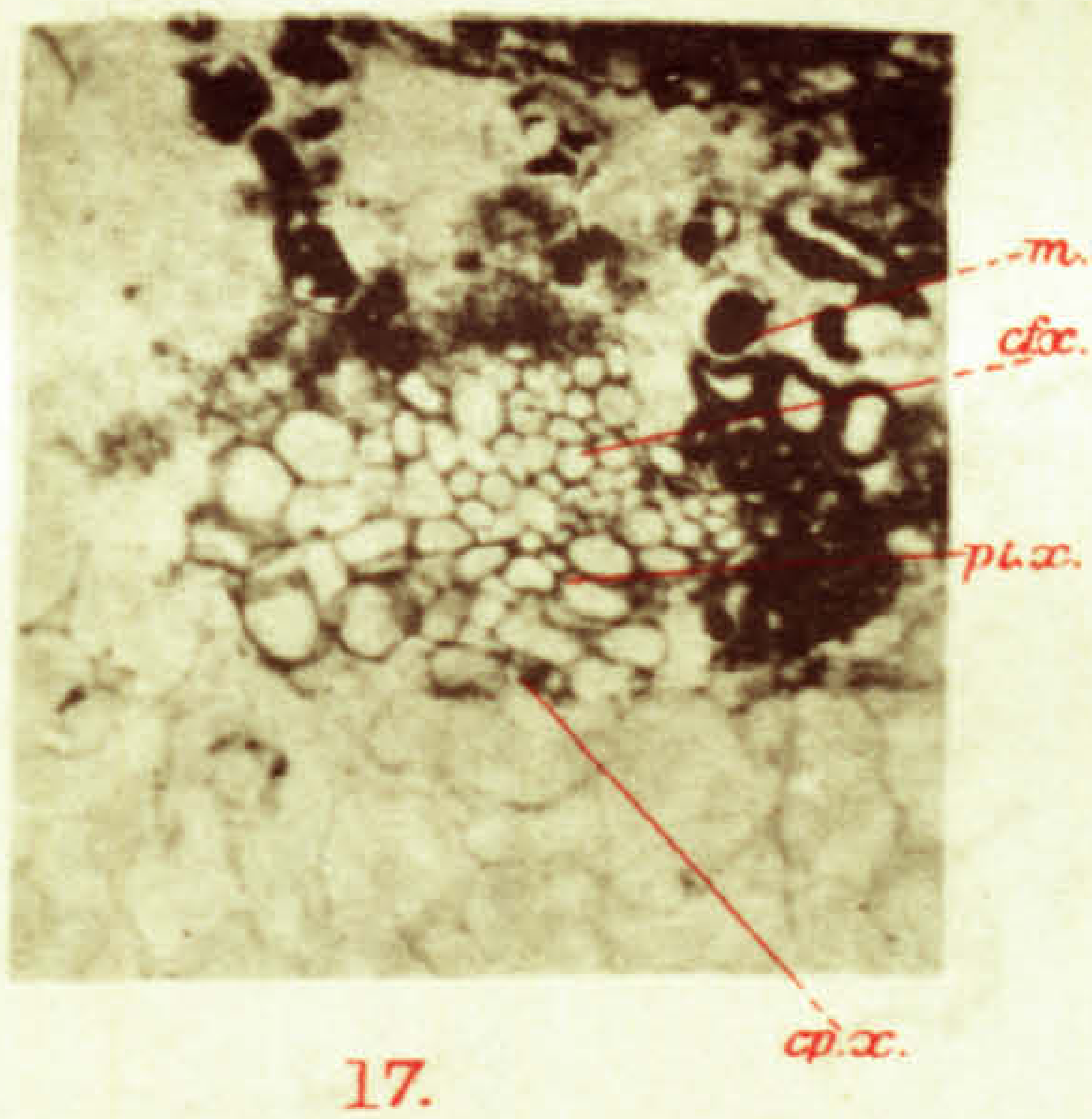

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SALISBURY — TRIGONOCARPUS SHORENSIS.

Huth coll.

The Flora of the St. Albans
District.
by E. J. Salisbury.
Trans. Herts. Nat. Hist. Soc.
Vol XIV. Pt III.

## VI. FLORA.

### 1. PHANEROGAMIA.

Although comprising some 58 square miles, the district dealt with in this brief review (viz., that within a five-mile radius of St. Albans Town Hall) is strikingly uniform as to the nature of its soil; this is, in the main, either gravel and sand or a stiff clay (brick-earth, clay-with-flints, or boulder-clay) overlying the Chalk, which, though not infrequently coming to the surface, never becomes exposed over any large area.

The amount of calcareous soil is therefore relatively small, and the chief contrast to the clay is afforded by the sands and gravels. These owe their origin either to streams existing at the present day or whose beds were long since dry; or, in the case of the plateau gravels, are glacial in origin and frequently covered by a degradation product of sandy loam or clay. Peaty soil is one of the rarest types in the district, occurring only in one or two very restricted areas such as Colney Heath and Bricket Wood.

Bearing in mind the limited area with which we have to deal, as we should expect, the climatic factor is not sufficiently variable to play any important part in determining the distribution of species. We must therefore turn our main attention to the edaphic, or soil conditions as being the main factors influencing the nature and constitution of our flora.

A considerable portion of the land is under cultivation, either as pasture or as arable, mostly the former.

Whilst the area of cultivation offers interesting problems both as regards the specific nature of its weeds and their distribution, yet the œcologist naturally finds his chief opportunities for study in the comparatively untouched woods and commons.

The woods, as we should expect to find from the nature of the soil, are of the oak-hazel type, and the species of oak, that usually associated with clayey soil, viz.: *Quercus robur* (= *Q. pedunculata*). The ground flora is chiefly comprised of such plants as the wood-anemone (*Anemone nemorosa*), enchantress's nightshade (*Circæa lutetiana*), lesser celandine (*Ranunculus ficaria*), yellow dead-nettle (*Galeobdolon luteum*), wild strawberry (*Fragaria vesca*), ground-ivy (*Nepeta glechoma*), wood-sorrel (*Oxalis acetosella*), wood-violet (*Viola riviniana*), and *Brachypodium sylvaticum*. Less frequently the buckwheat (*Melampyrum pratense*), wood-rush (*Luzula vernalis*), and primrose (*Primula acaulis*) are to be met with; whilst the teazle (*Dipsacus sylvestris*) and *Millium effusum* are distinctly local.

Abundant forms in the more loamy woods are the pearlwort (*Arenaria trinerva*), woodruff (*Asperula odorata*), and wood-sanicle (*Sanicula Europæa*), and more locally the wood-sage (*Teucrium scorodonia*) and foxglove (*Digitalis purpurea*). The largest wood in the district is that known as Symond's Hyde

Great Wood, which corresponds with a drift soil of sandy loam and gravel. Like the other woods around, it is of the oak–hazel type, but it is interesting to find that the change in soil has been accompanied by a change in the dominant species, which is here not *Quercus robur* but *Q. sessiliflora*, Salisb. (See Moss, 'Journ. Bot.,' Jan.–Feb., 1910.)

Amongst the rarer woodland species may be noticed the saw-wort (*Serratula tinctoria*), bird's-nest orchid (*Neottia nidus-avis*), roast-beef plant (*Iris fœtidissima*), and spurge-laurel (*Daphne laureola*); the last two named are associated with chalk near to the surface. Wherever this denudation of the clay has taken place the change is usually marked by the presence, in the ground flora, of chalk plants such as the hairy violet (*Viola hirta*) and hairy St. John's wort (*Hypericum hirsutum*), though these are absent from the woods around.

The common weeds of the arable land are mostly typical clay plants; less frequent, though far from rare, are *Papaver argemone*, fool's parsley (*Æthusa cynapium*), *Valerianella dentata*, white forget-me-not (*Lithospermum arvense*), field-mint (*Mentha arvensis*), *Galium tricorne*, corn-cockle (*Githago segetum*), and Venus looking-glass (*Specularia hybrida*). Associated with the more gravelly soils are the knawelwort (*Scleranthus annuus*), field-madder (*Sherardia arvensis*), and *Sysymbrium thalianum*. *Mercurialis annua* only occurs at Harpenden and in one other locality in the county.

By far the greatest interest, both for the systematist and the œcologist alike, attaches itself to the commons; of these our area boasts four of some considerable size, viz., Bricket Wood Common, Colney Heath, Harpenden Common, and No-Man's Land.

The first of these is mostly covered with scrub, so that it is rather of the nature of a wood than a heath. A marked feature here is *Rhamnus frangula*, a rare plant in the county, though the other species, *R. catharticus*, is frequent in hedges on the Chalk outcrops. Other plants uncommon elsewhere are *Serratula tinctoria*, *Lysimachia nemorum*, and *Achillea ptarmica*.

Colney Heath is perhaps the most interesting spot botanically within walking distance of St. Albans; for not only are many plants met with here which are seldom to be found elsewhere in the county, but also several which may be ranked amongst our British rarities. This heath was formerly the home of that rare denizen of inundated spots *Lythrum hyssopifolia*; of recent years, however, diligent search has failed to discover it. A similar fate has probably befallen *Ranunculus parviflorus*, but *Teesdalia nudicaulis* is still there, though it would take but the plucking of a single vandal to render it extinct.

The heath is traversed by a small stream which, owing to the absence of any banks on the south side, forms there a considerable area of marshy ground. Here we can observe the zonation so frequently met with by sluggish streams and around the larger ponds (Smith, "Notes on the Vegetation of Ponds," 'Naturalist,' Oct. 1903). At the margin of the marshy ground and above the water-level stands the zone of rushes which forms a sharp boundary between the marsh-association below and the furze-heath above. This is followed by a broad zone of swampy turf which, though rarely, if ever, covered by the water, is completely saturated. The chief of the plants comprising this zone are the marsh-stitchwort (*Stellaria uliginosa*), milkmaid (*Cardamine pratensis*), marsh-marigold (*Caltha palustris*), strawberry clover (*Trifolium fragiferum*), *Triglochin palustre, Eleocharis palustris,* and *Alopecurus geniculatus*; more rarely the sneezewort (*Achillea ptarmica*) and waterblinks (*Montia fontana*). Next follows a zone of varying width, but usually narrow and constituted by plants rooted in very shallow water; here in varying frequency are to be found the water-dropwort (*Œnanthe fistulosa*), water-horsetail (*Equisetum limosum*), bur-reed (*Sparganium ramosum*), water-celery (*Sium nodiflorum*), yellow flag (*Iris pseudacorus*), flowering rush (*Butomus umbellatus*), and bog-bean (*Menyanthes trifoliata*). Owing to the shallowness of the stream at some points this zone may extend to the further bank, but here and there the water becomes sufficiently deep to mark a fourth zone comprised by such species as are more or less entirely submerged; of these the commonest are pondweed (*Potamogeton natans*), water-starwort (*Callitriche verna*), Canadian water-weed (*Elodea canadense*), *Glyceria fluitans,* and *Chara hispida.* The last named forms the home of numerous snails and leeches.

To the action of this stream, when vastly more considerable, was no doubt due the formation of the sand and gravel which characterize the major portion of the heath. With the presence of these are associated such plants as allseed (*Radiola millegrana*), dwarf furze (*Ulex nanus*), wood cudweed (*Gnaphalium sylvaticum*), chamomile (*Anthemis nobilis*), and the bird's-foot (*Ornithopus purpusillus*).

The south end of the heath differs greatly from the portion traversed by the stream, for here the soil contains a large amount of humus, and the occurrence of a new association of plants is at once apparent. Small patches of needle-furze (*Genista anglica*) alternate with clumps of dwarf furze; scattered amongst these are the upright tufts of the moor-grass and bog-rush (*Nardus stricta* and *Juncus squarrosus*), whilst red-rattle (*Pedicularis sylvatica*) and dog-violets (*V. canina*) furnish bright patches of colour. The two ponds in this part of the heath are also of interest, not only for the zonation they exhibit, but also for the richness of their algal flora.

No-Man's Land and Harpenden Common are linked together by the fact that both are traversed by the same dry river-bed with extensive deposits of valley-gravel. Both show signs of having become drier in recent years, a feature the more marked at Harpenden, where such plants as heather, red-rattle, rushes, and ferns have either disappeared or are rapidly doing so. On the more peaty common of No-Man's Land the dwarf furze, needle-furze, and red-rattle occur in some quantity, but are absent at Harpenden, the last-named species having died out there some 15 years ago.

Of the less common plants met with here *Potentilla argentea*, cat-mint (*Nepeta cataria*), and *Filago minima* do not occur at Harpenden, whilst common to both are *Moenchia erecta*, bird's-foot (*Ornithopus purpusillus*), *Trifolium filiforme*, chamomile, and other plants characteristic of gravelly soils.

Among the grasses it is of interest to note the rapid spread during recent years on both commons of *Koeleria cristata* and *Triodia decumbens*.

A striking object-lesson for the œcologist is furnished both at Harpenden and No-Man's Land, where in each common there is a small area from which clay was at one time dug, thus exposing the chalk below. These "dells," as they are popularly termed, have now been left for many years undisturbed. We thus find in each of these two commons an isolated patch of calcareous soil surrounded on all sides by clay and gravel. In both cases a characteristic chalk association has sprung up, the most conspicuous members of which are salad burnet (*Poterium sanguisorba*), purge-flax (*Linum catharticum*), autumn gentian (*Gentiana amarella*), flea-bane (*Erigeron acre*), and the carline thistle (*Carlina vulgaris*). The total absence of these species from the surrounding common renders the contrast striking.

The chief feature of interest at Harpenden, and one possibly associated with the lowering of the water-level, is the struggle still in progress between the furze and the bracken. Little more than ten years ago the greater part was a furze heath with a small amount of bracken, chiefly at the higher southern end; this latter has gradually spread downwards and northwards, till now, when seen in summer, the major part exhibits large areas where isolated and dishevelled furze-bushes, like almost submerged islands in a sea of green, alone remain to tell of what was once a dense stretch of gorse, relieved in the more open parts by the stately tussocks of *Aira cæspitosa.* Bernard's Heath, where the soil is a gravelly loam, is mainly covered by brambles, gorse, and wood-sage; and, perhaps in part owing to its nearness to the city, has a comparatively poor flora.

The alien phanerogams of the district are chiefly of interest by reason of the rapid spread of several species. Coleman in his manuscript Flora (1839) refers to *Veronica buxbaumii* as rare; at the present day it forms one of the commonest of our weeds on arable land. The recently introduced *Matricaria suaveolens* affords an example of a species which is spreading at the present time. This portion of Hertfordshire in no way escaped the sudden invasion of its streams by *Elodea canadensis* subsequent to its introduction into England about 1841; and the monkey-flower (*Mimulus luteus*) bids fair to become equally ubiquitous.

## 2. Filices, Musci, Hepaticæ, and Algæ.

Little can be said respecting the œcology of the Cryptogamia of our area, for with the exception of the Filices and Algæ practically no work has been done, from this standpoint, on the various groups. We are greatly in need of workers to undertake this aspect of Cryptogamic research. Records of the rarer forms alone are comparatively useless; the need is for complete lists from as many localities as possible, with data as to the soil and environmental conditions of each species together with details of association both with regard to the other Cryptogams and also to the Phanerogamic Flora.

Filices.—The ferns of the district, though never common (with the exception of the bracken, which is increasing rapidly), are becoming rarer every year, no doubt due in the main to the lowering of the water-level and to the rapid increase of population. The most frequent of the ferns are *Aspidium filix-mas*, *A. angulare*, *Polypodium vulgare*, and *Asplenium adiantum-nigrum*. *Blechnum spicant*, *Asplenium trichomanes*, *A. ruta-muraria*, and *Ophioglossum vulgatum* are now distinctly rare, and *Ceterach officinarum*, which formerly occurred at Harpenden, is extinct.

Musci.—About eighty species of mosses have been recorded from the district, but the paucity of workers in this field has doubtless left many lacunæ.

The Sphagnaceæ are, like their habitat, rare in our area. *Sphagnum subsecundum* is found at Colney Heath and at Bricket Wood, in which latter locality the two varieties, var. *contortum* and var. *obesum*, and also *S. intermedium* occur. Other water-loving mosses found in the district are *Philonotis fontana*, *Webbera carnea*, *W. albicans*, and *Fissidens adiantoides*. Besides supplying our wettest forms, Bricket Wood and Colney Heath are the only localities for *Leucobryum glaucum*.

Quite a moss flora is to be found on the old walls of Verulam, including, besides the more common species, *Barbula unguiculata*, *B. revoluta*, *Encalypta vulgaris*, *Bartramia pomiformis*, *Eurhynchium crassinervum*, and *Rhynchostegium confertum*. The walls at Gorhambury also yield some interesting species such as *Barbula vinealis* and *Eurhynchium pumilum*; here also on the banks and fields may be found *Pottia starkeana*, *Didymodon rubellus*, and *Hypnum chrysophyllum*. Most of the records for the district are to be found in Mr. A. E. Gibbs' paper in our 'Transactions' (Vol. III, pp. 67–81).

Hepaticæ.—The number of Hepaticæ recorded is small. The complete list is given in the hope that it will stimulate new workers to add to their number. *Marchantia polymorpha*, *Asterella hemispherica*, *Frullania dilatata*, *F. tamarisci*, *Radula complanata*, *Porella platyphylla*, *Odontoschisma sphagni*, *Cephalozoa zyssacea*, *C. bicuspidata*, *Lophocolea bidentata*, *L. heterophylla*, *Chiloscyphus polyanthus*, *Scapania nemorosa*, *Diplophyllum albicans, Jungermannia crenulata, J. incisa, Nardia scalaris*, and *Fossombronia pusilla.*

ALGÆ.—In spite of the paucity of our information as to the Algal Flora there is sufficient to show that it compares favourably with that of other counties.

The following list of genera and species from a pond in the district will sufficiently illustrate the character of the Algal Flora in the stiff clay:—*Spirogyra catæniformis, S. Hassallii, S. quadrata, S. tenuissima, S. varians, Eudorina elegans, Pandorina morum, Chætophora elegans, Œdogonium* sp., *Tribonema, Ophiocytium, Zygnema, Microspora, Cosmarium* spp., *Closterium lunulatum, C. kutzingii, C. acerosum, Ulothrix zonata, Microthamnion, Mougeotia, Ankistrodesmus, Sphærella, Chlamydomonas, Gleocystis, Sphærocystis characium, Clathrocystis, Anabæna*, and *Oscillaria*, with numerous diatoms.

In the more peaty soils such as one finds at Colney Heath and Bricket Wood, desmids are a prominent feature; among the more interesting Algæ found in such habitats may be mentioned *Closterium cornu, C. incurvum, Nephrocytium lunatum, Chroococcus turgidus, Bulbochæte varians, Aphanochæte*, and *Palmodactylon varians.*

The Algal periodicity recently investigated by Fritsch & Rich ('Ann. Bot.,' vol. xxi, July, 1907, and 'Proc. Bristol Nat. Soc.,' vol. ii, pt. 2, 1909) is seen to advantage in the district. The spring phase is characterized by the abundance of such genera as *Spirogyra, Zygnema*, and *Microspora*, all three frequently forming almost pure cultures; in the summer these give place to *Œdogonium* spp., *Cladophora*, and epiphytic diatoms; and the autumn phase is marked by the almost entire absence of all forms except Diatomaceæ.

Only two species of *Chara* have been recorded for the district, viz. *Chara vulgaris* and *C. hispida.*

## 3. LICHENES, FUNGI, AND MYCETOZOA.

LICHENES.—The published records of the lichens observed in our district are but few, being limited to three brief lists in the reports of our field meetings ('Trans.,' Vols. III and V), one for St. Peter's, containing 7 species, and the others for Bricket Wood, in which (excluding duplicate records) 16 are enumerated. Two are common to both localities, so that the total number is 21.

So far as can be judged from this small number of records the most frequent species is *Parmelia caperata*, that being the only one which is common to the three lists. The rarest species are *Calicium melanophæum* and *Pertusaria globulifera*, both detected by Mr. E. M. Holmes at our fungus foray in Bricket Wood in 1885.

FUNGI.—The records of the larger fungi are based almost entirely upon the results of fungus forays of the Herts Natural History Society, particulars of which are given in Vols. III, V, VI, and IX of the Society's 'Transactions.' The localities visited

Subsidiary Papers.

SALISBURY

# EXTRA-FLORAL NECTARIES OF POLYGONUM

# The Extra-floral Nectaries of the Genus Polygonum.

BY

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**With Plate XVI, and six Figures in the Text.**

THE present research was undertaken with a view to ascertaining the function of the glands which occur on the underside of the leaf-cushion in various species of Polygonum. The following species have been under observation, viz. :—

*Polygonum baldschuanicum*, *P. cilinodum*, *P. compactum*, *P. Convolvulus*, *P. cuspidatum*, *P. multiflorum*, *P. sachalinense*, and *P. scandens*.

All the above agree in possessing leaves which are variations upon the cordate-saggitate type and are either herbaceous or annual.

The only woody species is *P. baldschuanicum*, which produces climbing shoots that die back in the winter. *Polygonum cilinodum*, *P. Convolvulus*, and *P. scandens* are also of climbing habit.

The extra-floral nectaries of *P. cuspidatum* have been described by Delpino (5) ; those of *P. baldschuanicum*, *P. Convolvulus*, and *P. multiflorum* by Schwendt (15), and those of *P. sachalinense* by Ono (12). The two latter papers were published during the course of the present research. Detailed descriptions of the above species need not therefore be included.

For convenience, the paper is divided into the following sections, viz. I, General ; II, Special ; III, Microchemical ; IV, Physiological ; V, Summary and General Conclusions.

## I. GENERAL.

The extra-floral nectaries are oval, triangular, or circular depressions. In all except the circular nectary of *P. cilinodum* the depressions are boat-shaped. The nectaries lie in the plane of symmetry of the leaf and are situated upon the underside of the base of the petiole just below the abscission layer which is differentiated at an early stage (Pl. XVI, Fig. 4). *Polygonum cilinodum* is, however, an exception to this rule, for in this species where, though the glands were fully developed, no abscission layer could be recognized. Like most nectaries these stand in close relation

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to the vascular system. The vascular supply of the petiole is therefore of some interest and attains greater significance when viewed in the light of the physiological experiments to be described later on. In general, the petiole of the Polygonums is convex or angled upon its lower surface and concave or grooved upon its upper.

The bundles form a dorsal arc which is closed by a bundle or bundles placed ventrally and which of course have the xylem directed inwards. (The terms dorsal and ventral are applied to the lower and upper surface of the leaf, respectively.)

In the simpler types of petiole the bundles are six in number, so that the ventral and one of the five dorsal bundles lie in the median plane, and the other four are arranged symmetrically with regard to these. (The pair of bundles which occupy the upper angles of the petiole are frequently reduced.)

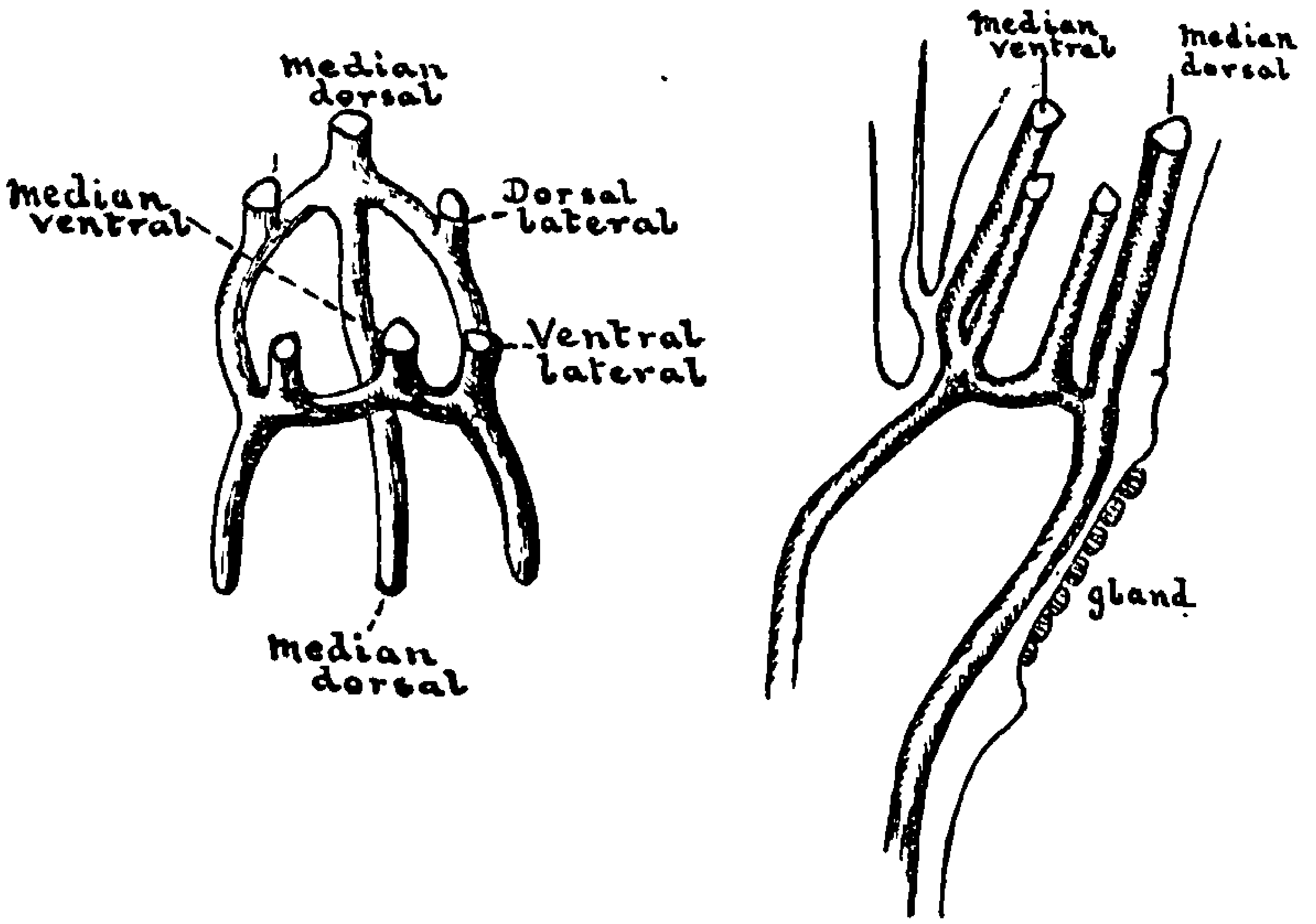

FIG. 1. Vascular supply of petiole in *Polygonum multiflorum*. The bundles passing to the ochrea have been omitted.

In the more complex forms the arrangement is the same, but owing to subdivision the bundles are more numerous.

It is opposite the dorsal median bundle that the nectary is situated (Text-fig. 1).

Around the nectary the tissue is somewhat raised, and may even slightly overhang, especially at the upper edge. For convenience of description this will be termed the lip.

The nectaries are fully developed and function before the leaf unfolds: large drops of secretion were observed upon nectaries of *P. cuspidatum* when the lamina was not quite 2 mm. in length.

Winter buds upon their emergence in the spring have actively secreting nectaries upon bud-scales which possess no lamina.

In only one species, viz. *P. Convolvulus* were seedlings obtained; and these showed variations in the occurrence of the nectaries.

In no case were they present upon the cotyledons, but whilst they appear to be normally present on the petiole of the first leaf, occasional specimens had no nectary till the second or third leaf was reached. The depressions forming the nectaries are lined with secretory trichomes which form a closely packed layer over the whole surface. The trichomes or unit structures of the nectary consist of three parts.

The lowest or basal portion consists of large sac-like thin-walled cells, which with their neighbours form an almost continuous layer one cell deep, and for each gland number four or more in a single story (Text-fig. 2, *b*, on left).

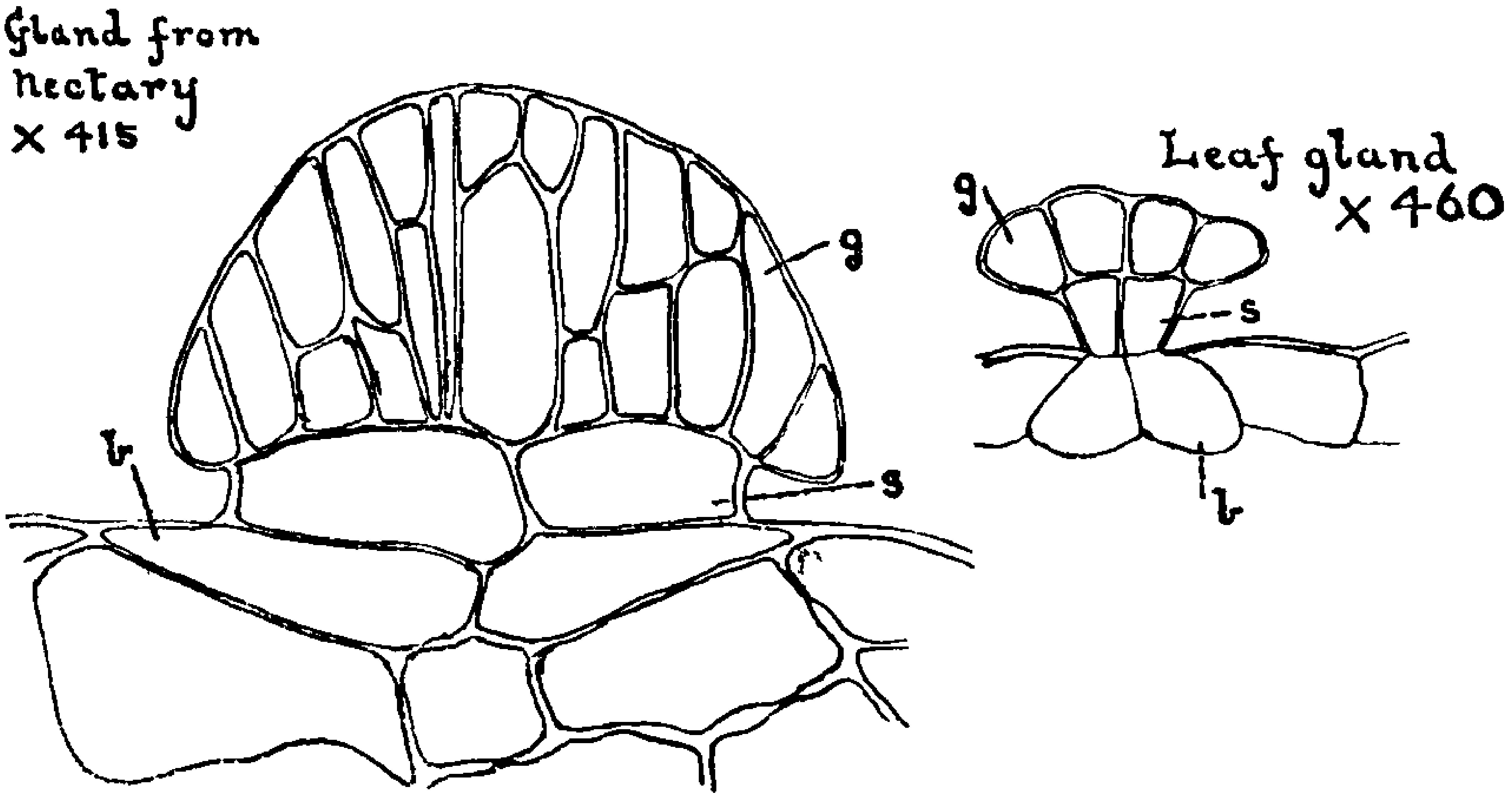

FIG. 2. Nectary- and leaf-glands of *Polygonum compactum*. *g*. gland cells; *s*. stalk cells; *b*. basal cells.

The middle layer is also one cell deep, and consists of flattened cells whose vertical walls are thickened, the horizontal walls—separating them on the one hand from the basal cells, and on the other from the gland cells—remain thin (Text-fig. 2, *s*).

The gland cells forming the third portion are usually not more than one cell deep, but may become subdivided by transverse walls; they form an enlarged head of numerous cells elongated in the vertical direction and with comparatively thin walls (Text-fig. 2, *g*). This type of structure is frequent in secreting trichomes, and also finds its parallel in the hydathodes of Piperaceae, Bignoniaceae, and species of *Artocarpus* as was shown by Haberlandt (8, p. 420).

As regards the cytological details, they are those characteristic for secretory cells in general; the gland cells when young are completely filled with a dense granular and highly refractive cytoplasm and possess large nuclei. At maturity they become markedly vacuolate. This vacuolation was observed by Gardiner (7) in the gland cells of *Dionaea*, and more recently, Miss Huie has shown that the gland cells of *Drosera* exhibit vacuolation, which is most marked at the period of secretion (9). See also Saunders (13).

The development of the nectaries was studied in *P. cuspidatum*, and agrees with that described by Schwendt (15, p. 250) for *Muehlenbeckia sagittifolia.*

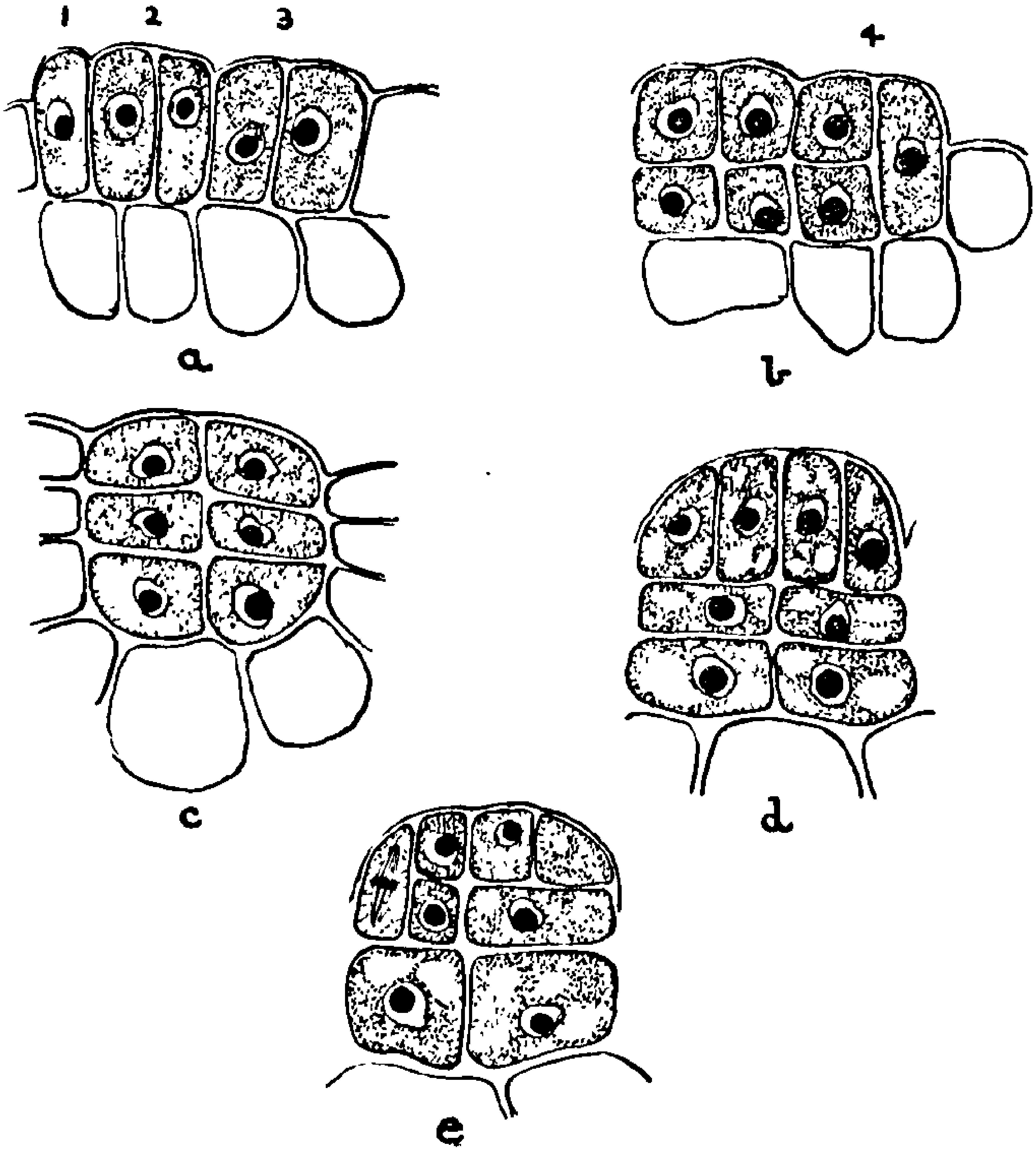

FIG. 3. Development of nectary glands in *Polygonum cuspidatum*, shown in vertical section. The successive stages are seen in *a*, *b*, *c*, *d*. In *c*, the longitudinal division of the glandular portion has taken place before the completion of the last horizontal division. The figures 1–4 denote successive stages in development. × 460.

The development of the trichomes starts from the centre of the nectary and passes to the periphery. It begins with the radial division of the gland mother-cells in two planes at right angles to one another. Division parallel to the surface of the nectary then takes place, and we thus have formed an upper and a lower story, each of four cells. The cells of the upper group again divide horizontally, and we thus have formed the three series representing the basal, stalk, and gland cells. This sequence may, however, be subject to slight variation (Text-fig. 3, *c*).

Further subdivision generally takes place in the glandular portion as this reaches maturity; the walls are usually vertical but sometimes horizontal or inclined. Further subdivision of the stalk and basal cells is not infrequent, but does not take place to the same extent as in the secretory region.

In all the species enumerated, and in others not bearing extra-floral nectaries, isolated glands which secrete gum occur upon the ochrea, petioles, stems, and leaf-blades (Pl. XVI, Fig. 5, *g*).

The structure of these glands is in all essentials identical with that of the nectary-units just described (see Text-fig. 2).

They arise as epidermal papillae, and follow the same course of development as those of the nectary; subdivision is however much less, and practically confined to the secretory portion.

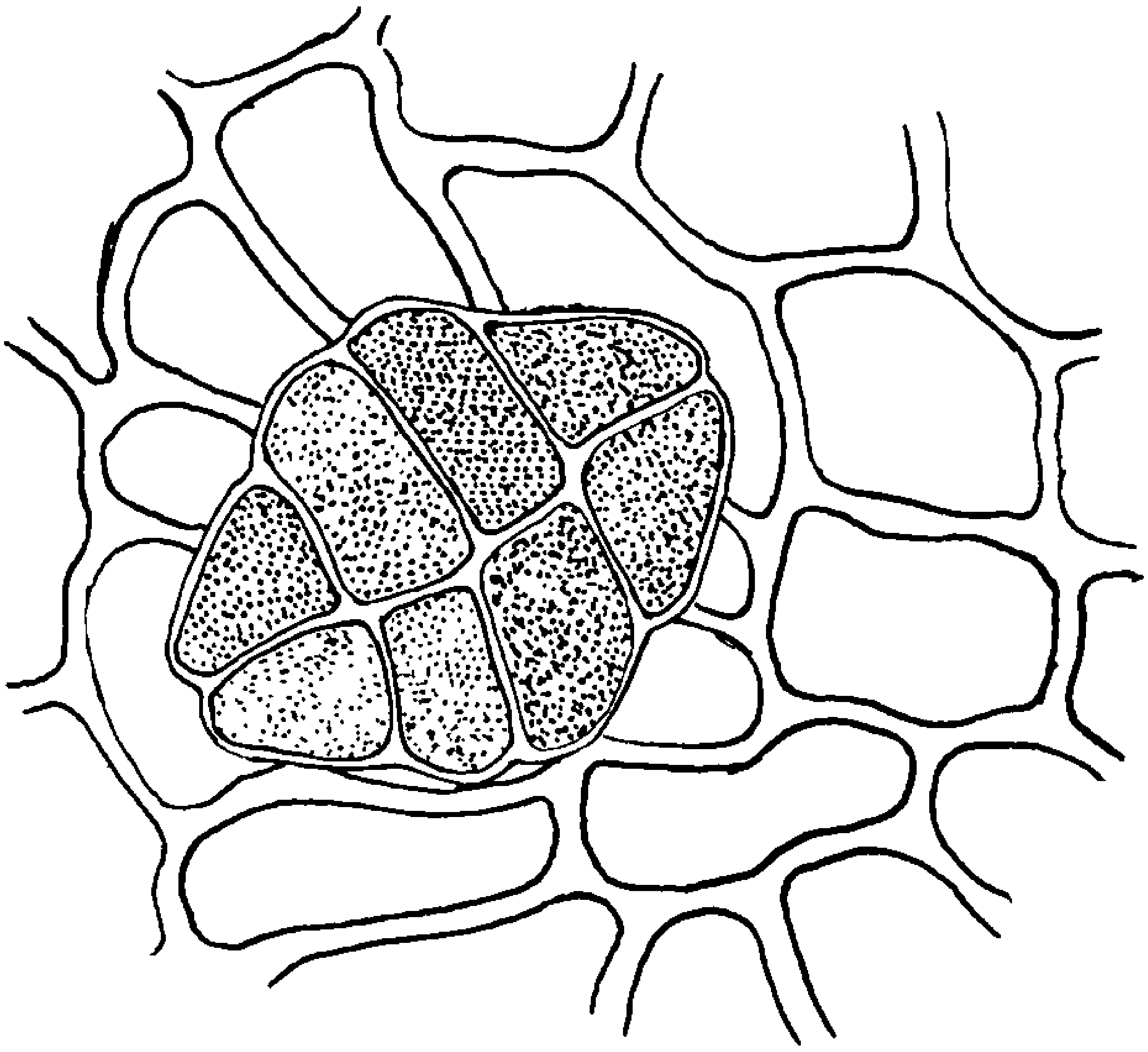

FIG. 4. Gland from ochrea of *Polygonum sachalinense*. × 580.

These, like the foregoing, function long before the leaf unrolls, and mostly fall off before the organs reach maturity.

It is interesting to note in this connexion that similar glands secreting a mucilagenous substance and probably functioning as hydathodes have been described by Areschoug (1) on leaves of various species of Mangroves.

## II. SPECIAL.

### *Polygonum cilinodum* (Pl. XVI, Fig. 1).

The nectaries in this species are circular in outline with a diameter of about 0·63 mm. They are saucer-shaped depressions surrounded by a well-marked lip, which slightly overhangs the concavity.

The lip consists of slightly thickened cells covered by an epidermis of radially elongated elements and strongly thickened external walls, whilst near the nectary its cells are sometimes divided tangentially. The median dorsal leaf-trace accompanied by a sclerenchyma sheath, which is a continuation of that which surrounds the stele of the stem, passes close beneath the nectary.

Opposite the nectary the sclerenchyma sheath is pierced, and through this opening there passes from the bundle to the nectary a band of small-celled tissue with dense contents, large nuclei, and strongly thickened walls, which latter are deeply pitted (Pl. XVI, Fig. 2, *s p*).

This, which we may term the epithem tissue, broadens out as the nectary is approached, and on reaching the latter forms an almost continuous layer beneath the basal cells. Around this epithem strand is large-celled parenchyma which in a transverse section appears as two groups to right and left of the small-celled tissue (Pl. XVI, Fig. 2, *l p*).

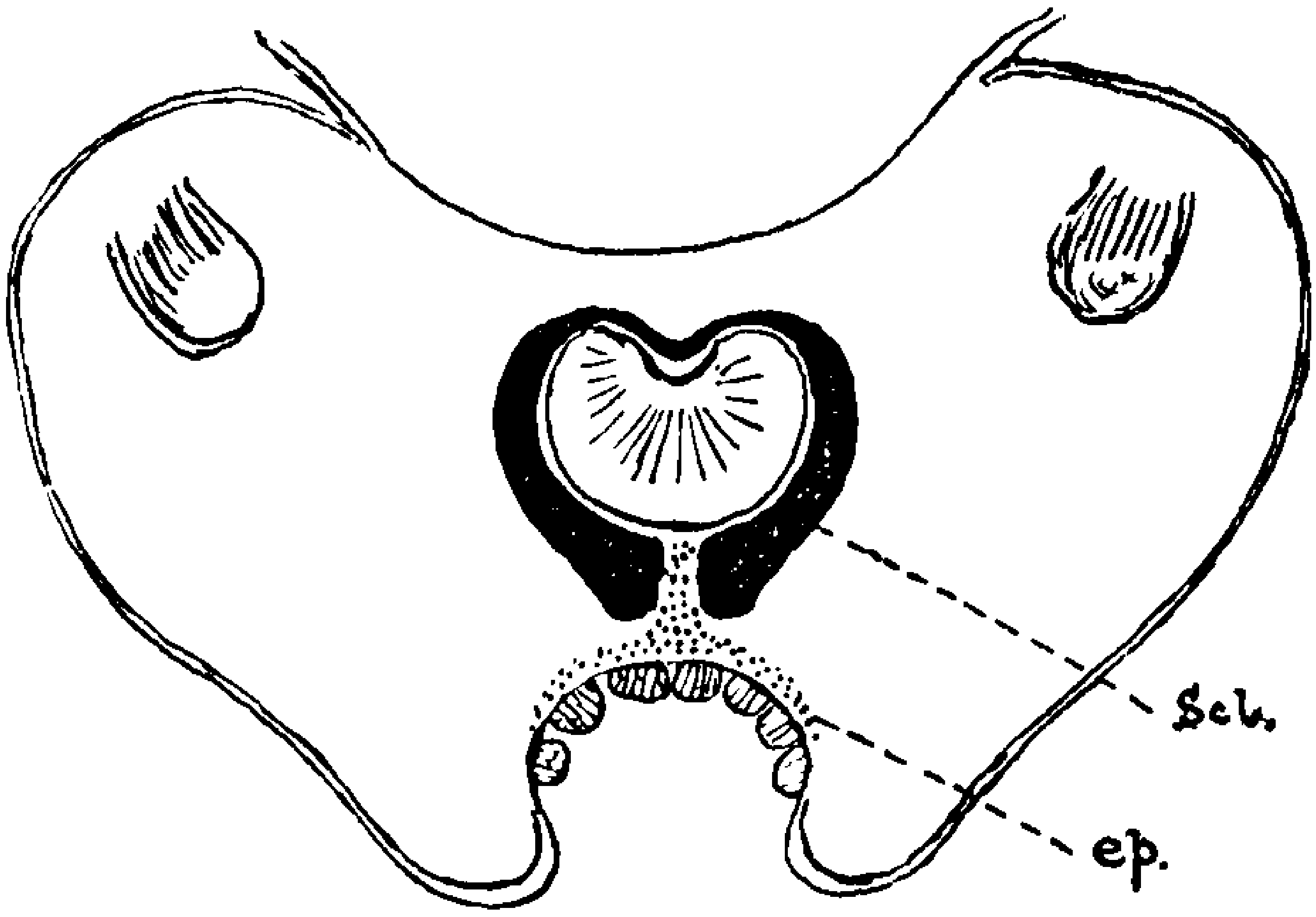

FIG. 5. Diagram of gland of *Polygonum cilinodum*. *Scl.* sclerotic tissue; *ep.* small-celled epithem.

The secretory trichomes themselves are in this species much more complex than in any of the others examined; this is due to increased division, and applies not only to the secretory but also to the stalk and basal regions.

The glandular head shows both radial and transverse division, the latter may take place in some or all of its cells.

The petiole of this species is rounded in transverse section with a slight concavity above (Pl. XVI, Fig. 9). It contains six bundles, the five forming the dorsal arc are of nearly equal size, whilst the ventral bundle is larger. A noticeable feature in this species is its fringed ochrea. The hairs which arise from the base of the latter are directed downwards and might perhaps prevent any small insect that had been attracted by the nectar from climbing the stem further.

Sphaerocrystals of calcium oxalate are generally distributed throughout the plant, and are always relatively crowded in the young organs and beneath the nectaries.

The blades, besides possessing mucilage-secreting glands, have cells which appear to contain mucilage scattered at intervals in the epidermis.

### *Polygonum compactum.*

In this species the nectary is an oblong, almost rectangular, shallow, flattened depression. It measures about 1 × 0·75 mm. (Pl. XVI, Fig. 11).

The glandular heads of the trichomes show both radial and tangential subdivision, and the stalk cells also divide. The basal cells seldom appear to do so, and exhibit a tangentially extended appearance.

In this species the sclerotic sheath around the stele of the stem is discontinuous; it only accompanies the median dorsal bundle of the petiole as slight sclerotic strands on either flank, the epithem tissue therefore abuts direct upon the phloem.

It consists of 2–3 layers of cells with dense contents and sclerized walls which are pitted. The lip does not overhang but has a well-developed and strongly thickened epidermis of radially elongated cells.

The petiole is roughly rectangular with rounded corners and with three ridges on the upper surface (Pl. XVI, Fig. 7). Its vascular supply is somewhat more complex than in the previous species. It consists of twelve bundles—two of which, situated in the lateral ridges, are small, and two other small ones occur one on either side of the median dorsal strand. Here again, calcium oxalate crystals are numerous beneath the nectary.

### *Polygonum sachalinense.*

This species, which is by far the largest of those investigated, has a much more complex petiole structure (Pl. XVI, Fig. 6).

In transverse section as many as nineteen or twenty bundles may be present. Associated with this large size and consequent increase of vascular supply we find an augmented system of extra-floral nectaries; a large one about 2 × 1 mm. upon the abaxial face of the leaf-cushion, and from 2–4 paired nectaries of ellipsoid form situated above the main lateral veins of the leaf-base, at the points where they emerge from the stem. All these glands are present on the youngest leaves. The accessory glands measure about 0·25 × 0·75 mm., and except in point of size their structure agrees with the main nectary. The latter is sunk about a millimetre below the surface, and is an almost flat depression (Pl. XVI, Fig. 4). The basal cells are separated from the phloem of the underlying bundles by from 3–4 layers of cells which are strongly sclerized and deeply pitted (Text-fig. 6).

These cells appear to be of two kinds, some show a deeply stained protoplasm, the rest stain but faintly and contain large nuclei. The staining reagents used being Methyl blue and Kleinenberg's hematoxylin and safranin.

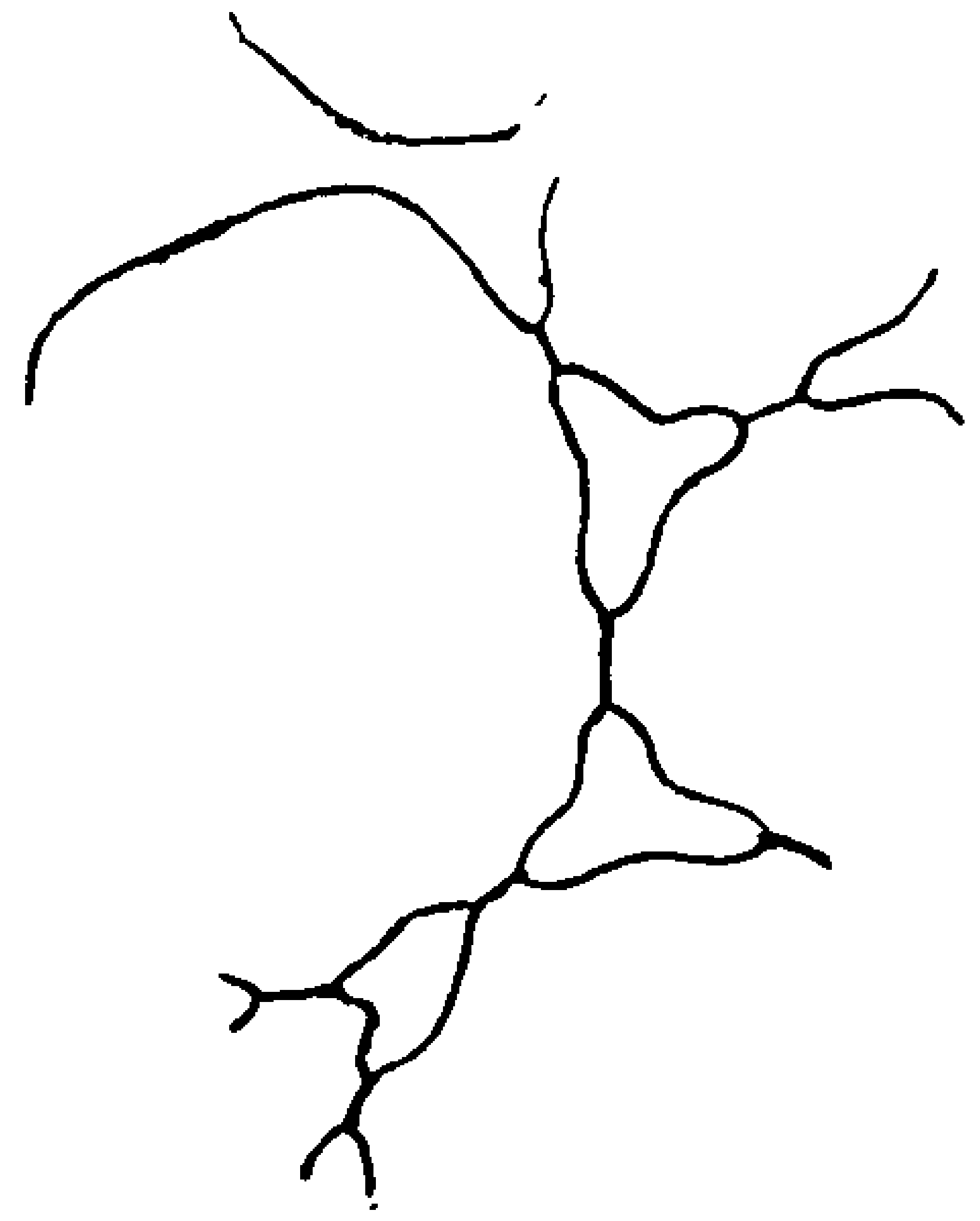

FIG. 6. Pitted epithem of *Polygonum sachalinense*.

### *Polygonum multiflorum.*

The nectary here is triangular in form; only slightly depressed, and with poorly differentiated lips. Immediately beneath the nectary are from 2–3 layers of sclerized and pitted cells, between these and the bundle are parenchymatous cells interspersed with sclerenchymatous groups. The median petiolar bundle has a sclerotic sheath which is perforated opposite the nectary (Pl. XVI, Fig. 8). Calcium oxalate sphaerocrystals occur around the gland and mucilage cells are present in the leaf-epidermis. The petiole is of a rounded pentagonal form; the bundles of the upper angles are somewhat reduced.

### *Polygonum scandens.*

The nectary is slit-like, measuring about 0·8 × 0·75 mm. Immediately beneath are two layers of sclerized and pitted cells, and between these and the bundle 3–4 layers of cells (Pl. XVI, Fig. 3).

The chief interest of this species lies in the fact that it possesses at once the smallest nectary and most reduced petiolar structure of all the species examined. The petiole, which has a deep groove on the upper surface, has six bundles; but two of these, situated in the wings bordering the groove, are extremely reduced (Pl. XVI, Fig. 12). What appear to be wax glands occur on the leaf-blade.

### *Polygonum baldschuanicum.*

The nectary here is not well developed, and the lip is poorly differentiated; the underlying tissue is sclerized and pitted, and between this and the bundle is parenchymatous tissue. The petiole is rounded—pentagonal in outline; it contains six bundles, the upper two being small. An interesting feature of this species, which is a woody climber, is that nectaries are absent from the rosette of leaves at the base of the annual shoots; in some cases it was not till the eighth leaf that the nectary was present.

### *Polygonum Convolvulus.*

This species has a somewhat small elongated nectary of triangular form about 0·9 mm. long by 0·5 mm. as its greatest breadth. The lips are well developed. Below the glands the tissue is strongly sclerized and pitted. The petiole is pentagonal in outline, the upper side being the longest; the bundles at the upper angles are somewhat smaller than the other four (Pl. XVI, Fig. 10).

### *Polygonum cuspidatum.*

The nectary is oval in form and slightly concave transversely. The tissue beneath is strongly thickened and deeply pitted. The petiole is of oval-rectangular form with prominent ridges on either side of the upper surface. It contains from 8–9 bundles.

## III. MICROCHEMICAL.

In all the investigated species it was found that the tissue below the gland was rich in a substance which gave a blue reaction with hydrochloric and osmic acids. This was especially marked in the stalk cells, whilst the gland cells remained unchanged (Pl. XVI, Fig. 11).

Heating sections with Fehling's solution gave a red precipitate in the gland cells only. But previous heating with $H_2SO_4$ and neutralization resulted in an instant reduction of the copper, which formed a copious precipitate in the epithem tissue between the nectary and the vascular bundle. Older non-secreting nectaries showed hardly any precipitate in the epithem. Ferric chloride gave a bluish precipitate in the epithem, but in the basal cells this was so marked as to render them almost black. Fehling's solution reduces the secretion itself without any previous treatment with acid.

The above results suggest the presence of a glucoside in the epithem tissue which by its breakdown supplies the glucose secreted from the nectary.

Concentrated sulphuric acid completely dissolves the sections placed in it except the cuticle, the gland cells, and the stalk cells. Sulphuric and iodine causes a brown coloration which is darkest for the stalk cells.

Concentrated caustic potash colours the stalk cells yellow, the tint becoming brighter on heating; the gland cells appear unchanged. Thus it would appear that the gland cells are cuticularized and the radial walls of the stalk cells are strongly suberized.

## IV. PHYSIOLOGICAL.

Most of the following experiments were performed upon plants in pots under glass. The experiments with saturated air were conducted on all species except *P. scandens*. The other experiments were chiefly carried out on *P. cuspidatum* and *P. compactum*.

Washing out young nectaries with water showed that these have the power of repeated excretion of fresh sugar, but after a while this ceases.

If, however, fresh secretion from another nectary be placed upon the glands they function again.

Washing nectaries with 0·1 per cent. corrosive sublimate solution killed the gland cells, and no further secretion took place.

The same result obtained when the nectary was washed and the gland cells carefully scraped off with a scalpel.

The root pressure was determined for an actively secreting plant of *P. cuspidatum*, and was found to be equivalent to 13·1 cm. of mercury. Water injected at a higher pressure only produced an increased secretion or rather bleeding from the lowest nectary of the shoot employed.

Secretion was equally active where the shoots were removed and placed with their cut ends in water.

Placing plants in saturated or nearly saturated air caused marked increase of secretion—this latter appearing as large drops clinging to the nectaries. The control plants showed no such increase. It was found that where the plants which were placed in saturated air possessed few shoots, and therefore few nectaries, the whole of the nectaries showed an increased activity.

But where large plants were used which bore numerous nectaries, only a few showed increased secretion.

One plant which bore fifty-two glands was placed in damp air. When examined after three hours only two nectaries were actively secreting.

The removal of eight leaves was followed after twelve hours by an increase in the number of actively secreting nectaries to six.

The result may have been due to an increase in the saturation, but a plant with a large number of nectaries, of which only three were secreting vigorously, showed an increase to only five after a lapse of sixty hours.

Where in the case of plants bearing numerous shoots one or two of these were enclosed in saturated air, whilst the remainder were in comparatively dry air, no increase of secretion was observed on the nectaries of the enclosed shoots.

Plants, which, in saturated air, had drops of secretion hanging to the nectaries, rapidly lost their drops on removal to dry air. In order to determine whether the loss of the drops was due to evaporation or absorption by the glands, control-drops of water of similar dimensions were placed on the axes and petioles. It was found that the drops of secretion were the first to disappear, notwithstanding their slower rate of evaporation in consequence of the dissolved sugar. We appear then to have glands here which, like those described by Kerner (10), are at once secretory and absorptive.

Experiments in saturated air were also performed upon the gum-secreting leaf-glands, and these too (particularly those of the ochrea) prove to be more active under that condition.

This was most marked in *P. sachalinense* where the nodes of one young shoot were bathed in the gummy secretion which hung down in sticky threads.

With a view to finding if there were any relation between vascular supply and secretory area, the following table was constructed. Where the cross-sectional area of the xylem in the petiole of each species has been estimated, and the area of the corresponding nectary, it will be seen that the value obtained by dividing the one area by the other approaches a constant.

| *Species.* | *Approx. area of nectary* ($n$). | *Approx. area of xylem in petiole* ($x$). | *Value* $\frac{n}{x}$ |
|---|---|---|---|
| *P. baldschuanicum* | 0·23 sq. mm. | 0·031 sq. mm. | 7·42 |
| *P. cilinodum* | 0·30 ,, ,, | 0·030 ,, ,, | 10·00 |
| *P. compactum* | 0·75 ,, ,, | 0·076 ,, ,, | 9·87 |
| *P. Convolvulus* | 0·22 ,, ,, | 0·025 ,, ,, | 8·80 |
| *P. cuspidatum* | 0·57 ,, ,, | 0·068 ,, ,, | 8·51 |
| *P. multiflorum* | 0·26 ,, ,, | 0·028 ,, ,, | 9·29 |
| *P. sachalinense* | 2·25 ,, ,, | 0·247 ,, ,, | 9·11 |
| *P. scandens* | 0·16 ,, ,, | 0·019 ,, ,, | 8·42 |

## V. Summary and General Conclusions.

The petiolar nectaries are in all cases surrounded by a lip which is raised and covered by thickened epidermal cells.

This lip, which projects most at the upper edge (Pl. XVI, Fig. 1, *l*), may serve to protect the gland cells and to prevent the washing out of the nectary by rainwater. It may possibly further serve as a protection for the cells beneath against the plasmolyzing action of the osmotically powerful secretion contained in the nectary.

For it is these thick-walled lip cells with which the secretion is in contact. The tangential division of the epidermis of the lip which was observed in *P. cilinodum* still further supports this view. And in this connexion we may refer to the well-developed lip-structure described by Miss Ewart (6) in *Ipomoea paniculata*, as here, too, the lip exhibits a tangential division which may have the same significance.

A like function may be served by the suberization of the stalk cells, for the secretion has access to these notwithstanding the close packing of the glandular heads.

The high osmotic pressures involved may further account for the sclerization of the epithem cells, as the deep pittings, which are fairly numerous upon their surfaces, allow of sufficient facility for translocation. It is worthy of note that a similar pitted tissue has been observed below the gland cells of *Ipomoca paniculata* (6) which, as we have seen, closely resemble the glands of *Polygonum* in other respects. M. Vuillemin (16) has also called attention to the pitted tissue beneath the glands of the Tamariscineae, Plumbagineae, and Frankeniaceae, all of which secrete osmotically active substances.

The secretory activity of the nectaries appears to be due to osmotic action, largely independent of root pressure. The thin-walled character of the basal cells may be associated not only with the need for ready permeability, but also with communication of the turgor pressure of the surrounding tissue.

The experiments seem to show that the plant can accommodate itself to local inequalities of transpiration, and that these nectaries are, from the physiological point of view, water-secreting organs whose action is dependent upon osmosis.

To summarize the reasons for this view:

(1) The structure of the glandular trichomes agrees with that of the leaf-glands.

(2) The nectaries function at an early stage in the development of the organs upon which they are borne, and therefore at a period when excess of turgidity would be most injurious.

(3) There is a marked increase of secreted fluid accompanying an increase of humidity.

(4) The nectaries stand in close relation to the vascular bundles, and there is an increase in their number and extent accompanying an increase in complexity of the vascular supply. In those species which have a reduced petiolar vascular supply a reduced or simplified nectary is present.

(5) In no case were glands observed to be visited by ants, either in the exotic species at Kew, or in *P. Convolvulus* in its native haunts. In this latter some dozens of plants in various situations were kept under observation, and in no instance were they found to be visited by insects.

That some physiological purpose was served by extra-floral nectaries was suggested by Schimper (14). That this was, in the case of floral nectaries, of a hydathodal nature was advocated by Burck (4), and the same view in respect to floral nectaries has been put forward by Renner (12) and Schwendt (15, p. 42). The ant protection theory, whilst it is undoubtedly applicable in certain instances, has only been proved for a few. Aufrecht (2) and others have remarked on the absence of insects during their observations. Such protection must be regarded as an altogether secondary adaptation.

An admirable historical summary of the views regarding the function of extra-floral nectaries is given by Niewenhuis-Uxküll (11).

Bonnier (3) showed for floral nectaries that the maximum secretion took place when the soil and air were saturated.

Ono (12), who worked on numerous extra-floral nectaries including those of *P. sachalinense* and *P. cuspidatum*, summarized his results as follows. 'Among different external circumstances, moisture seems to be of the greatest importance' (p. 18).

Burck (4) showed that the floral nectaries in many instances act as hydathodes, causing dehiscence of the anthers even in saturated air.

The frequent occurrence of extra-floral nectaries in tropical plants, where very sudden changes of humidity are often daily phenomena, cannot be without significance.

There does not, therefore, seem any difficulty, so far as known facts are concerned, in deriving all nectaries originally from osmotic hydathodes, subserving a physiological function, which have in certain cases secondarily acquired biological importance.

In conclusion, I should like to take this opportunity of recording my thanks to Professor F. W. Oliver, at whose suggestion and under whose direction the present work was undertaken.

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## EXPLANATION OF PLATE XVI.

Illustrating Mr. Salisbury's paper on the Nectaries of *Polygonum.*

Fig. 1. *Polygonum cilinodum.* Median longitudinal section through node. *a.s.* axillary shoot; *l.* lip of nectary; *och.* ochrea; *pet.* petiole; *scl.* sclerenchyma; *t.* trichomes; *v.t.* vascular tissue. × 15.

Fig. 2. *P. cilinodum.* Transverse section through nectary. *s.c.* stalk cells; *scl.* sclerenchyma; *s.p.* small-celled epithem; *l.p.* large-celled parenchyma. × 178.

Fig. 3. *P. scandens.* Transverse section of nectary. *cr.* crystals of calcium oxalate; *l.* lip; *t.* trichomes; *v.b.* vascular bundle. × 35.

Fig. 4. *P. sachalinense.* Longitudinal section of nectary. *a.l.* abscission layer; *ep.* epithem tissue; *t.* trichomes; *v.b.* vascular bundle. × 39.

Fig. 5. *P. scandens.* Transverse section of young leaf. *g.* gum secreting gland. × 35.

Fig. 6. *P. sachalinense.* Transverse section of petiole. × 12.

Fig. 7. *P. compactum.* Transverse section of petiole. × 12.

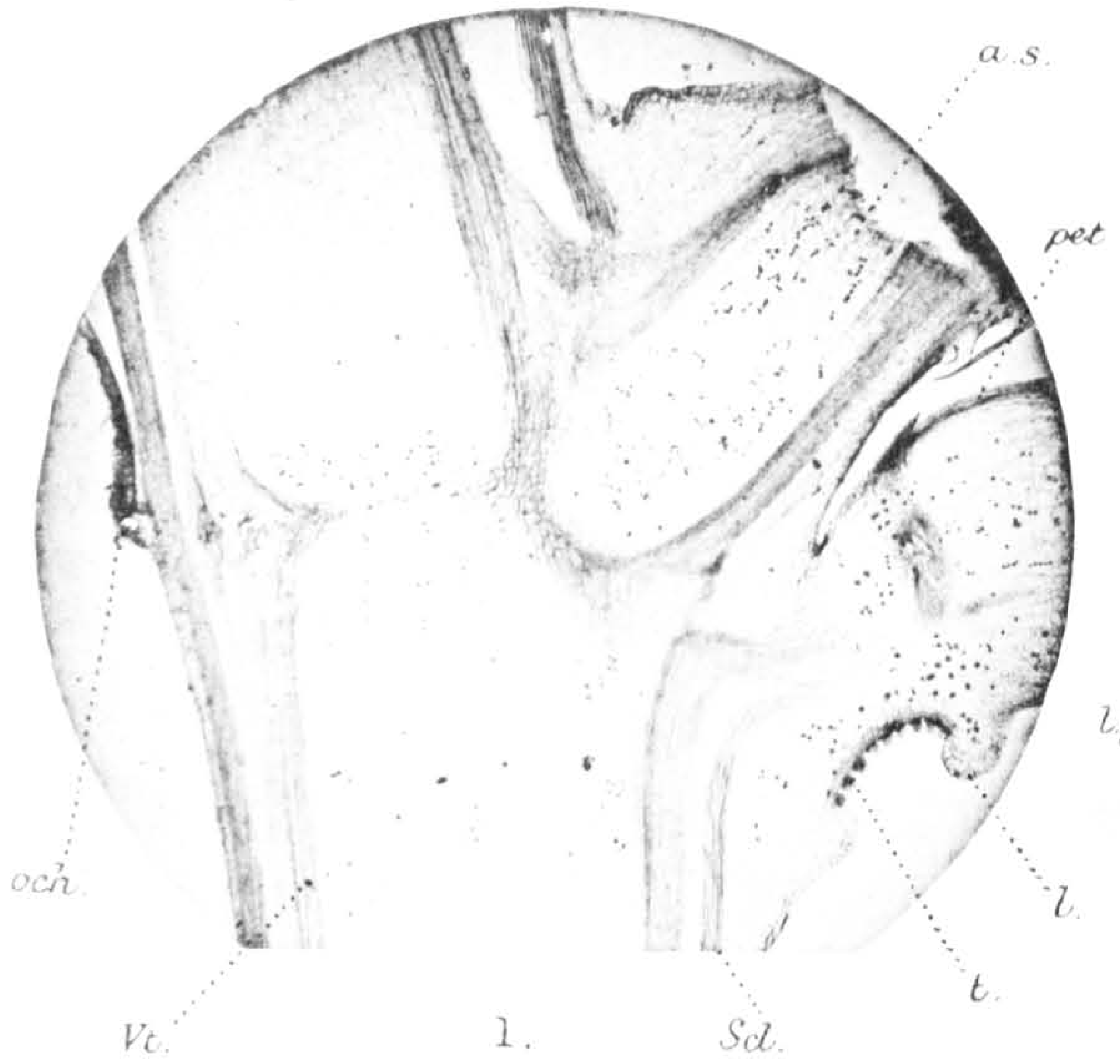
Fig. 8. *P. multiflorum.* Transverse section of nectary at upper end passing through the glandular area twice. *scle.* sclerized cell groups; *t.* trichomes; *v.b.* vascular bundle. × 35.

Fig. 9. *P. cilinodum.* Transverse section of petiole. × 12.

Fig. 10. *P. Convolvulus.* Transverse section of petiole. × 12.

Fig. 11. *P. compactum.* Transverse section of nectary taken after treatment with hydrochloric and osmic acids. *ep.* epithem; *l.* lip; *t.* trichome; *v.b.* vascular bundle. × 27.

Fig. 12. *P. scandens.* Transverse section of petiole. *ch.* ventral channel; *p.b.* phloem bundle. × 31.



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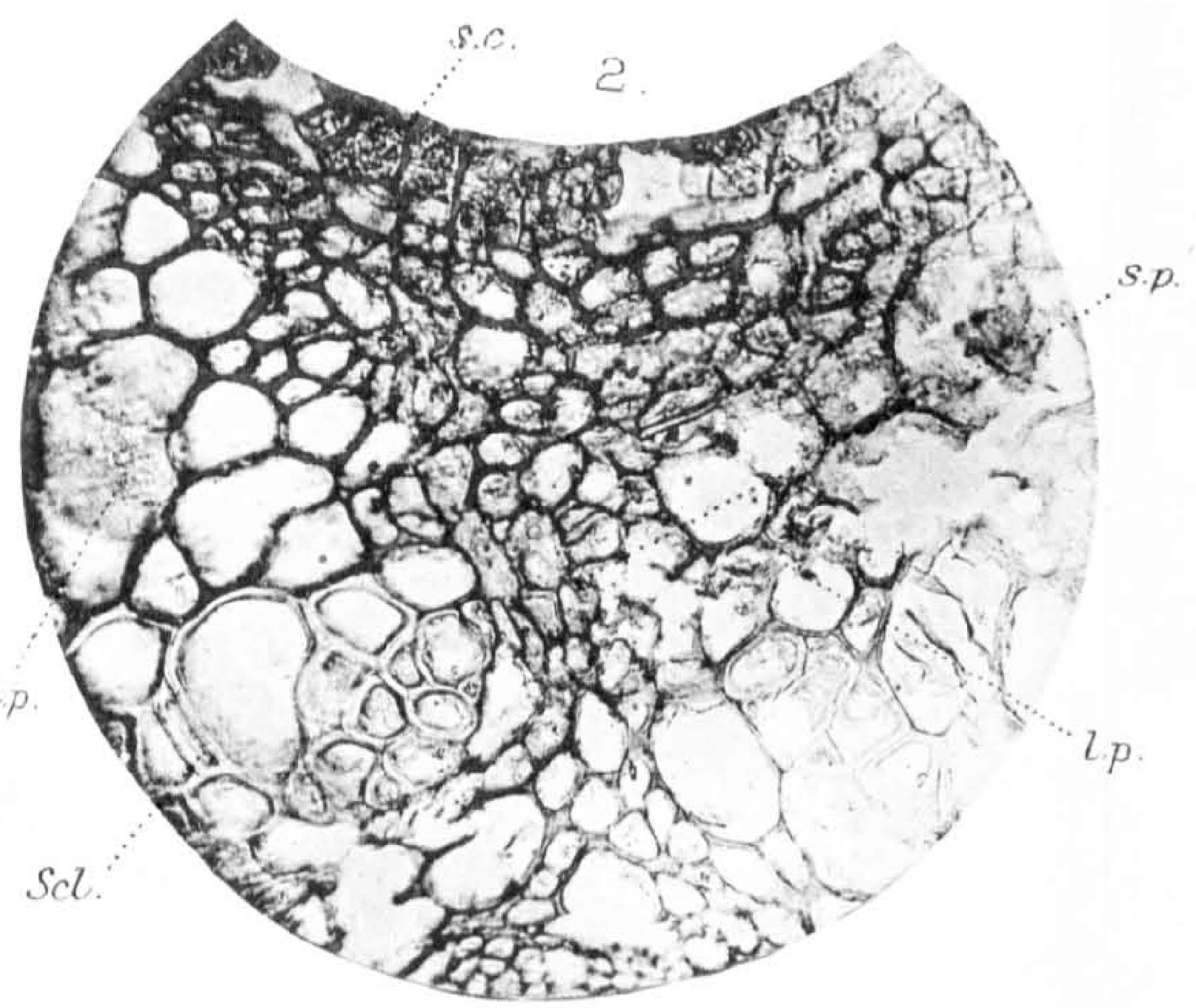

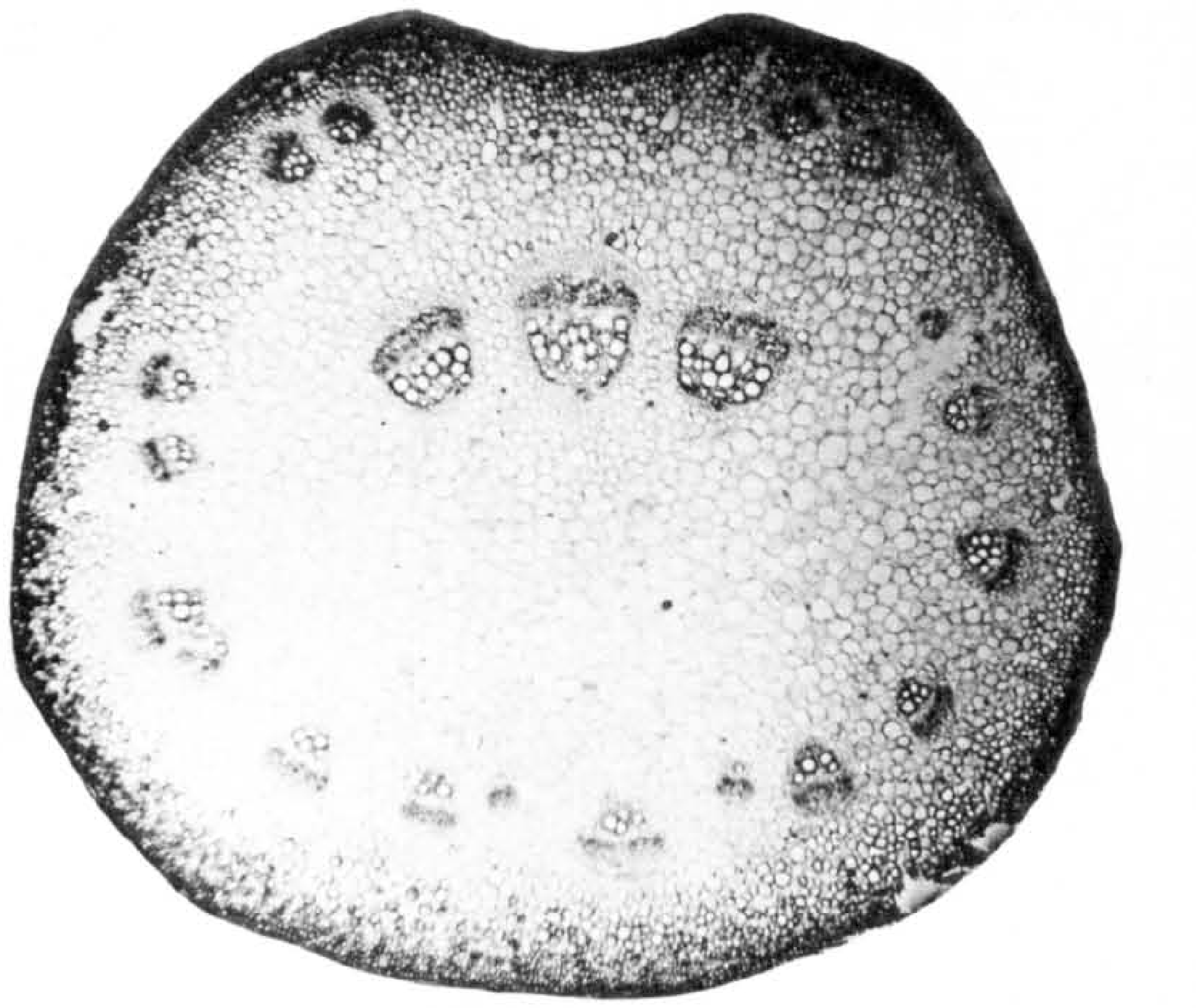

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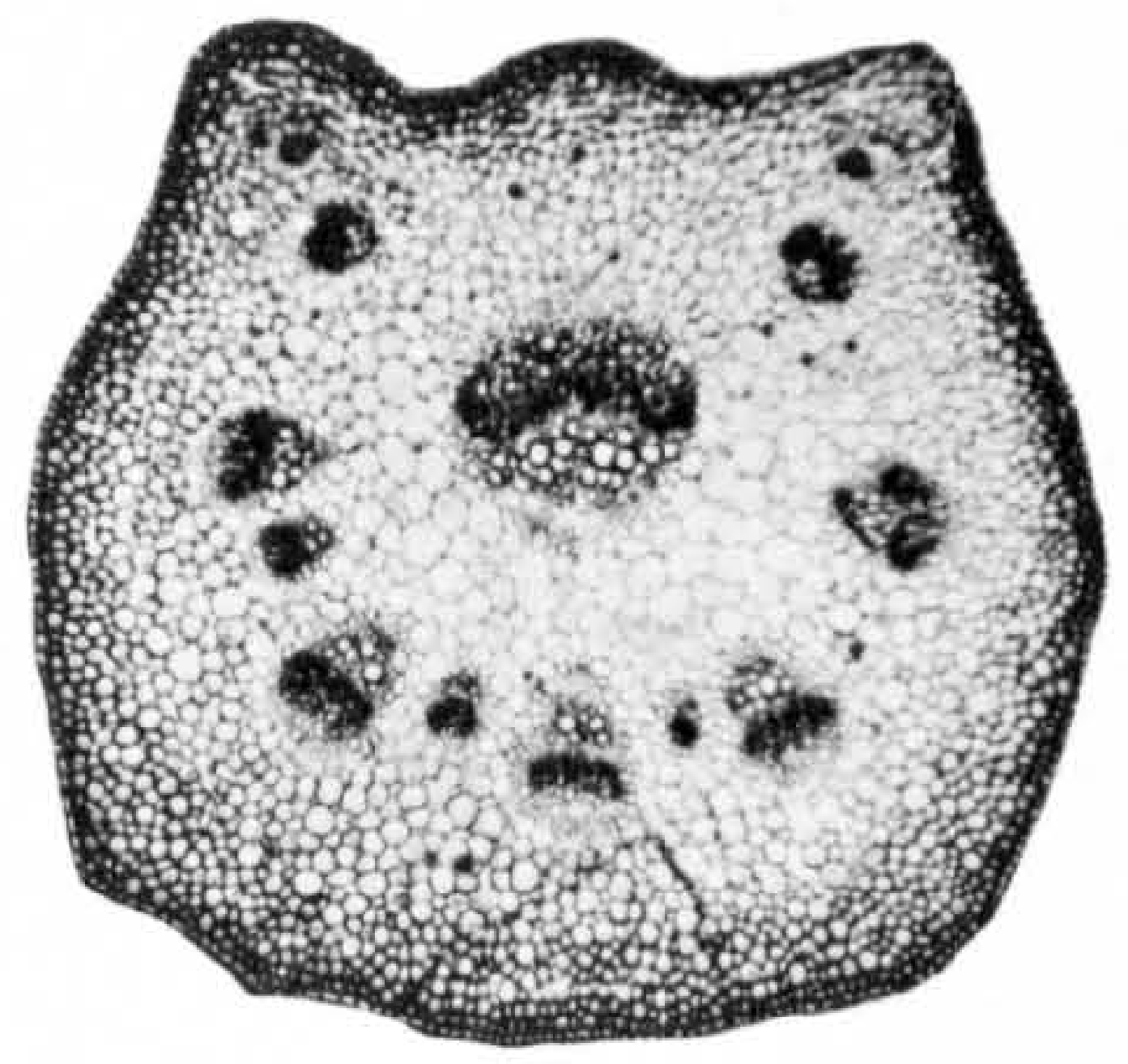

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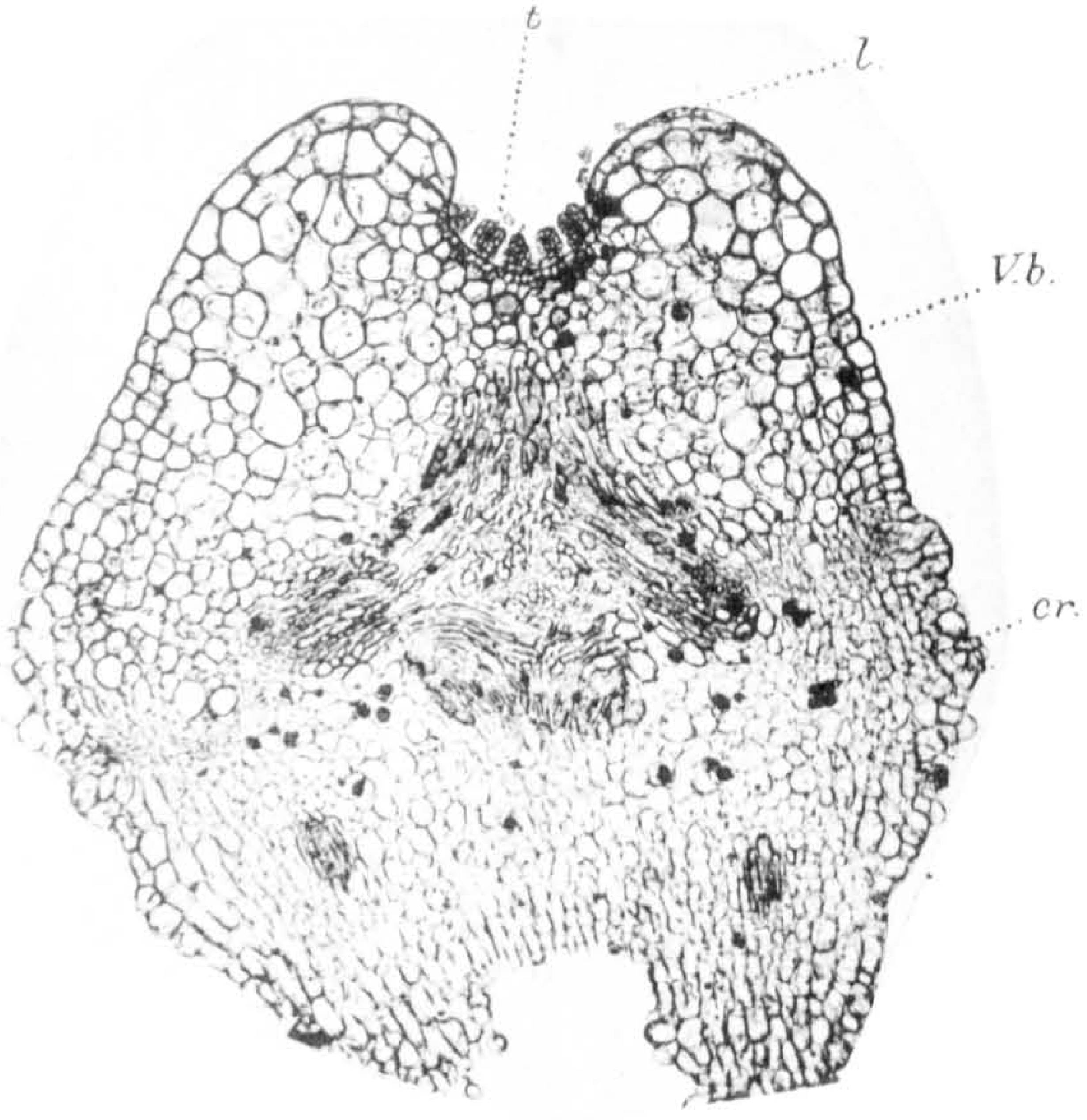

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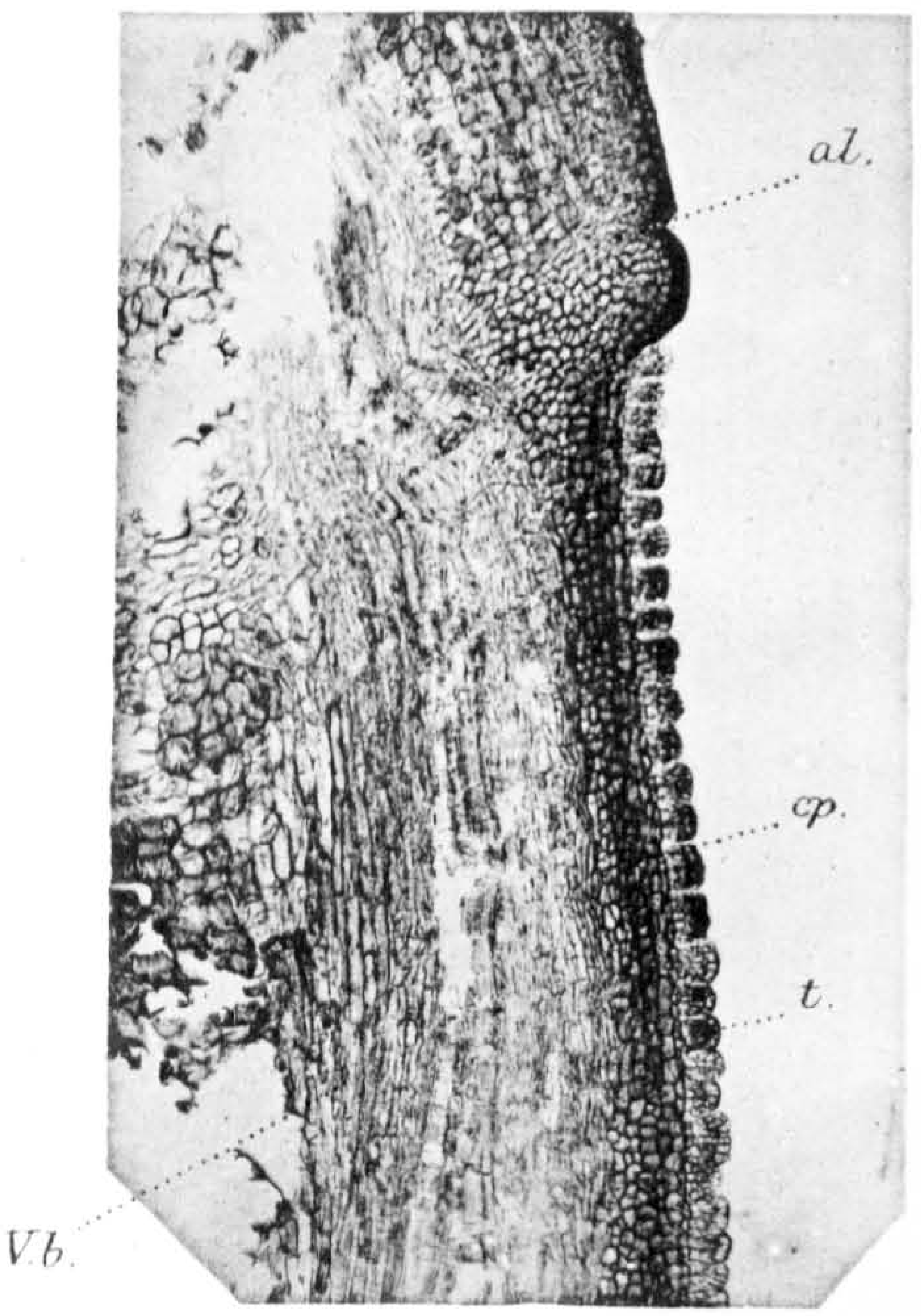

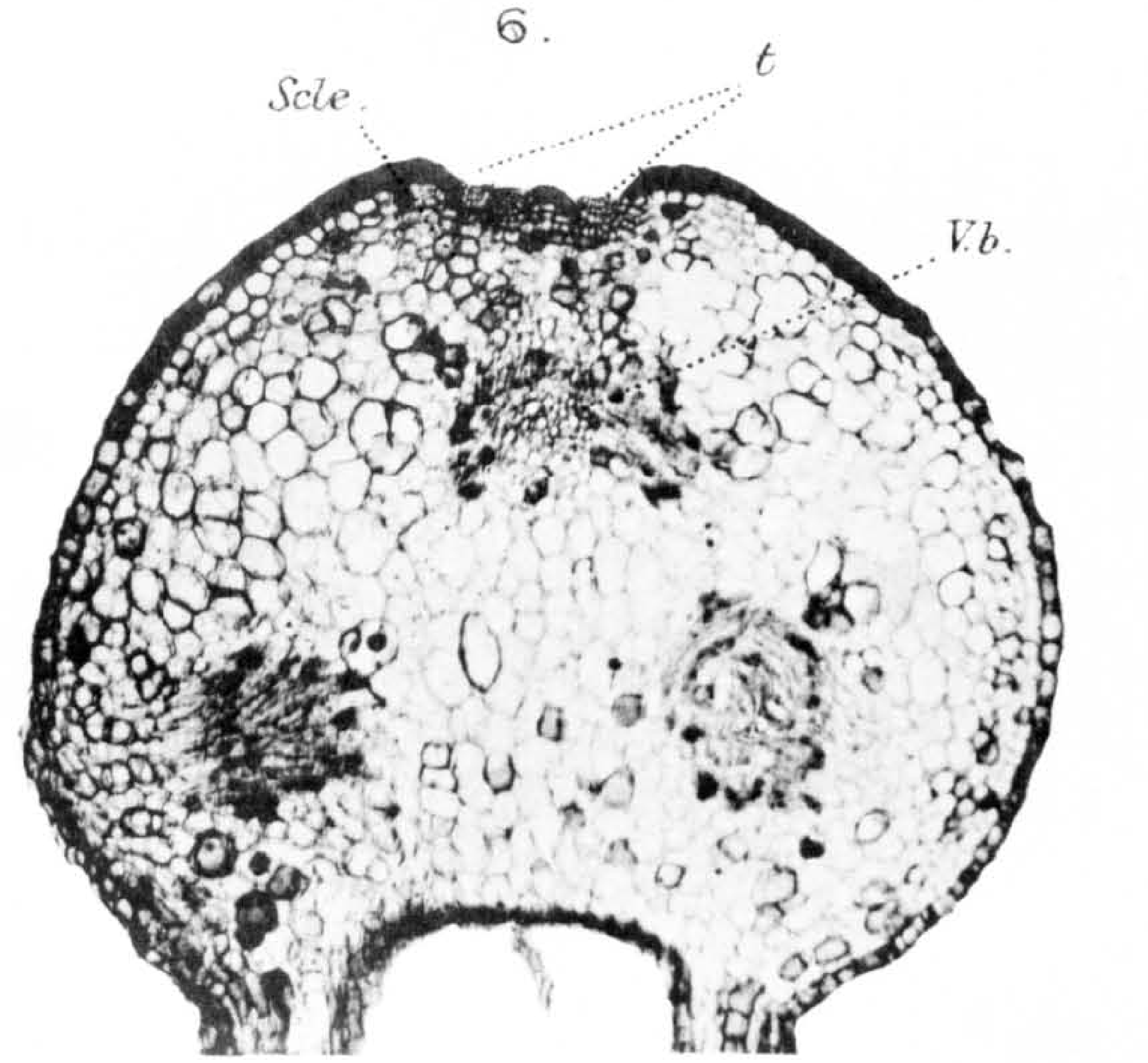

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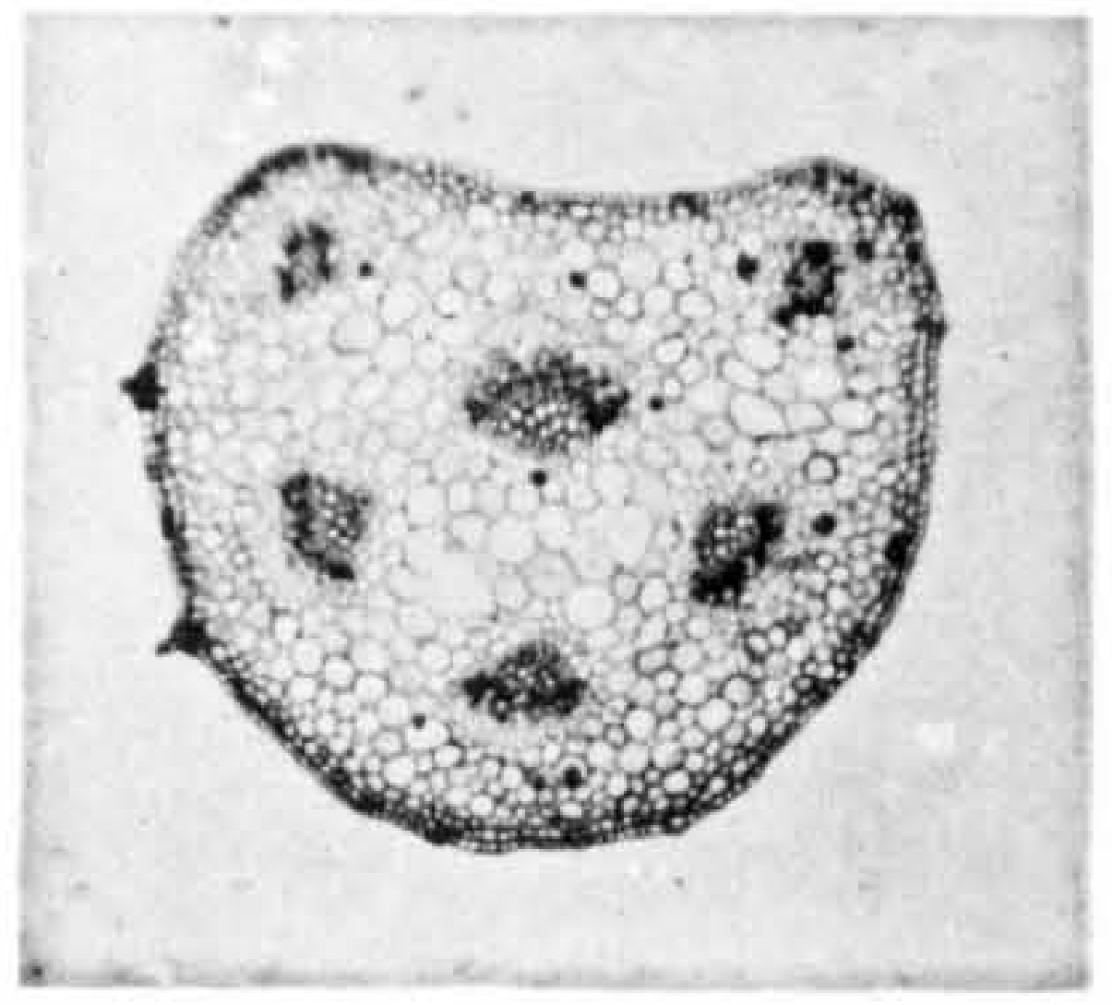

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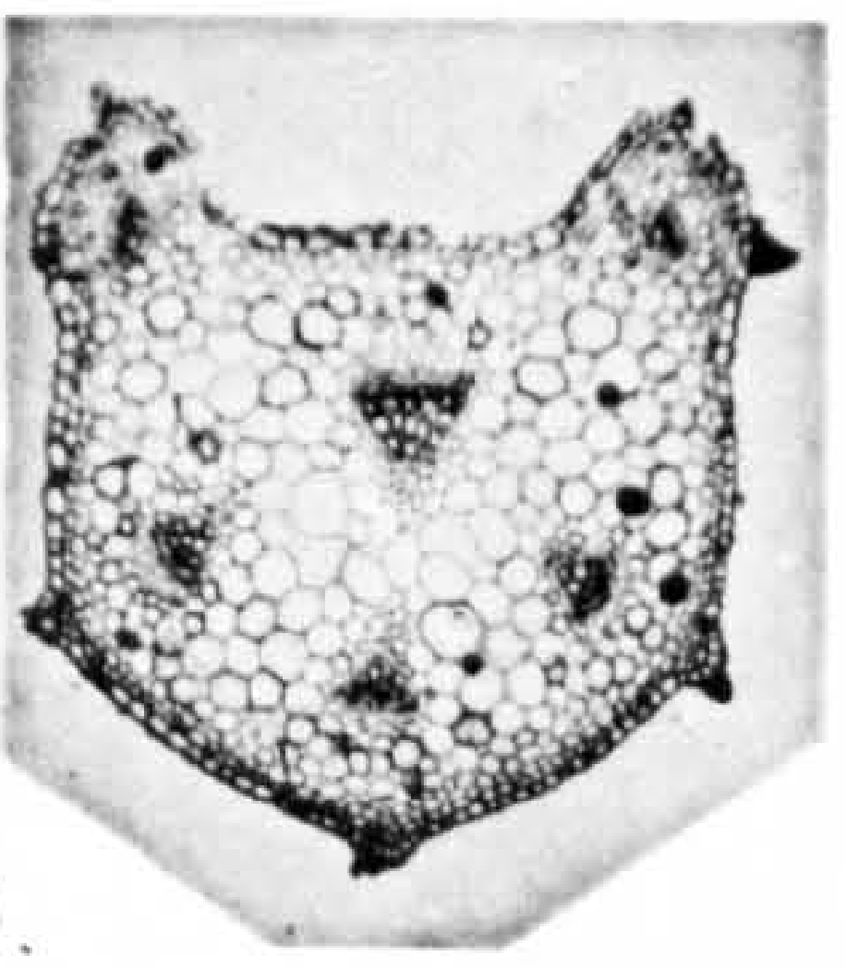

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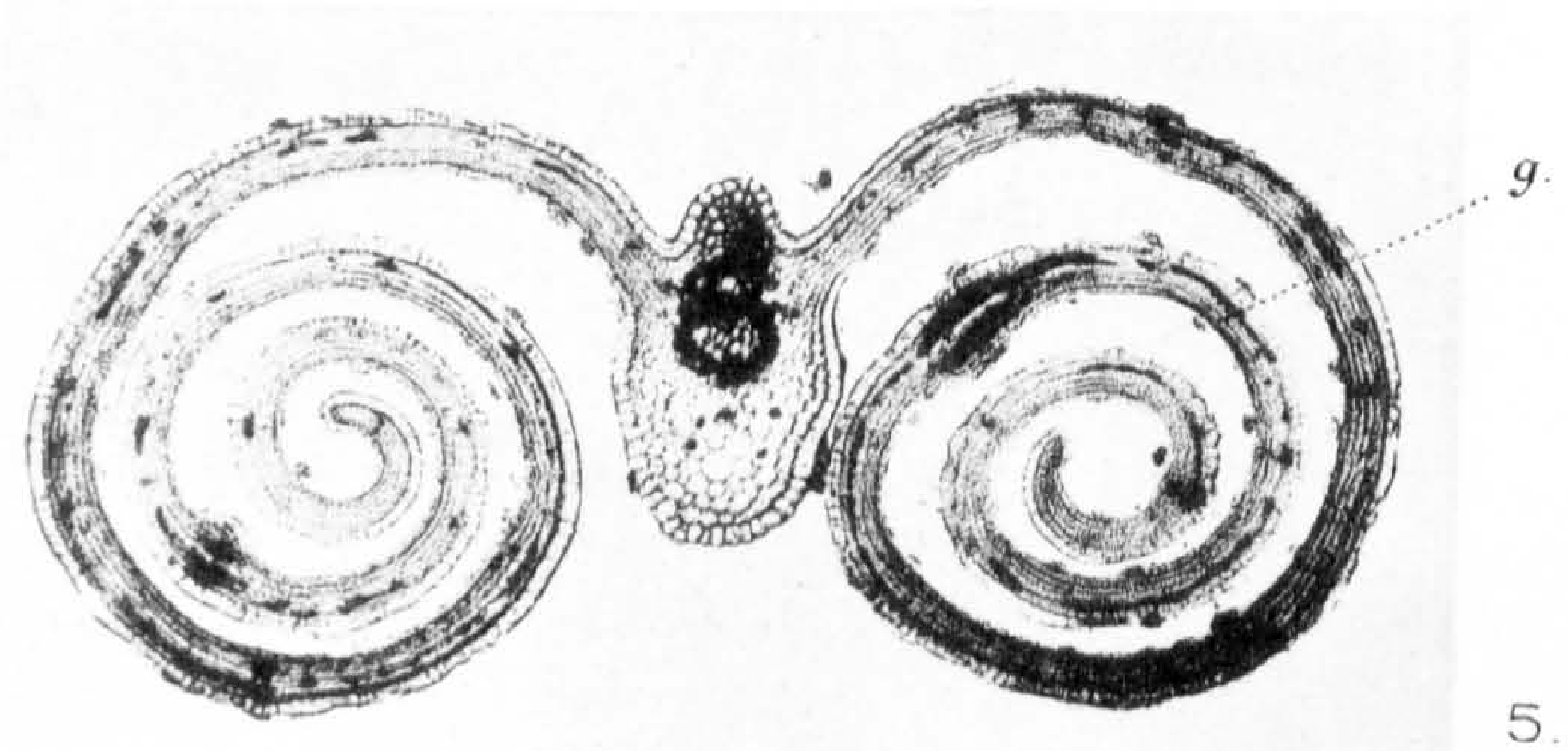

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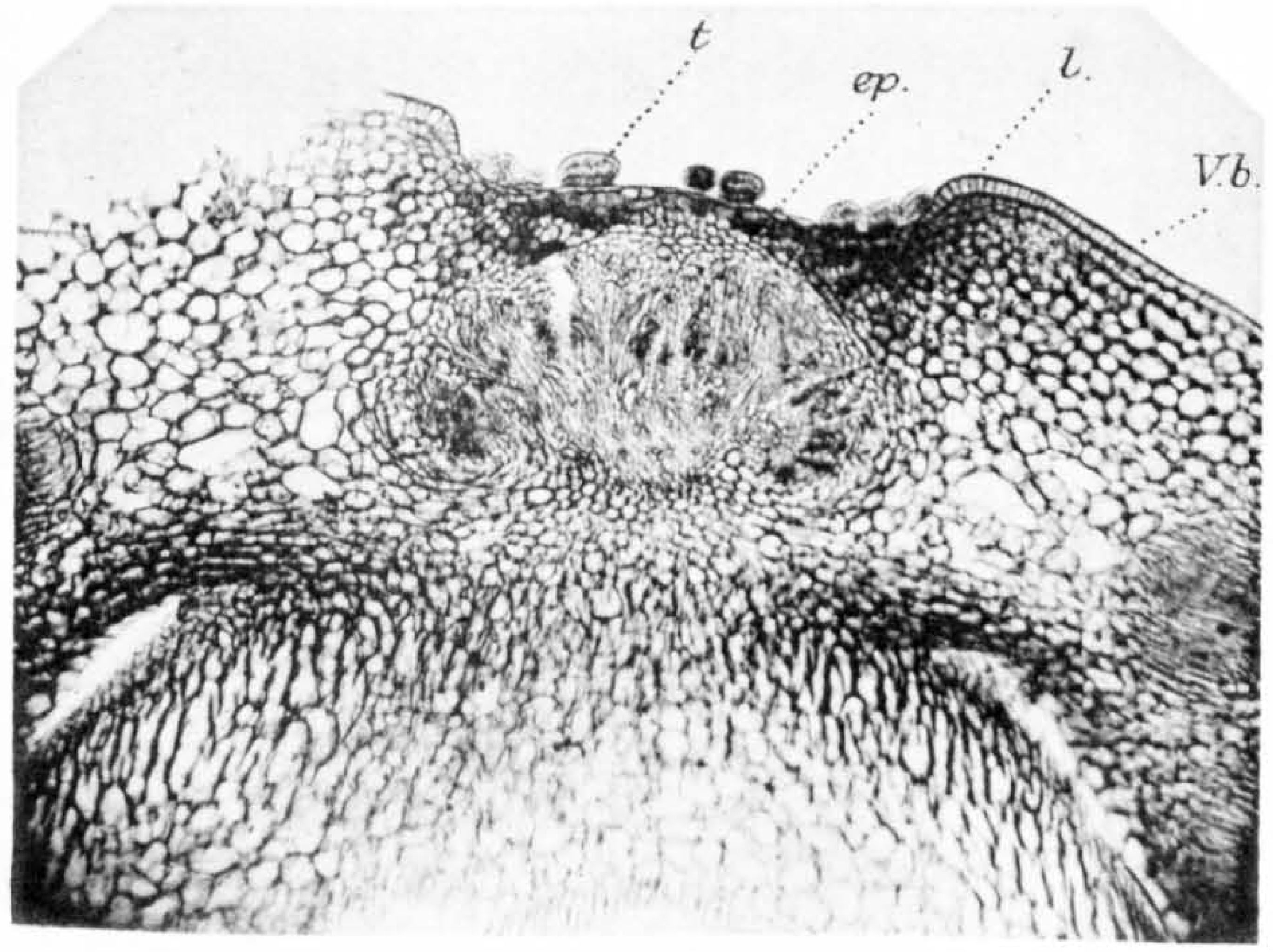

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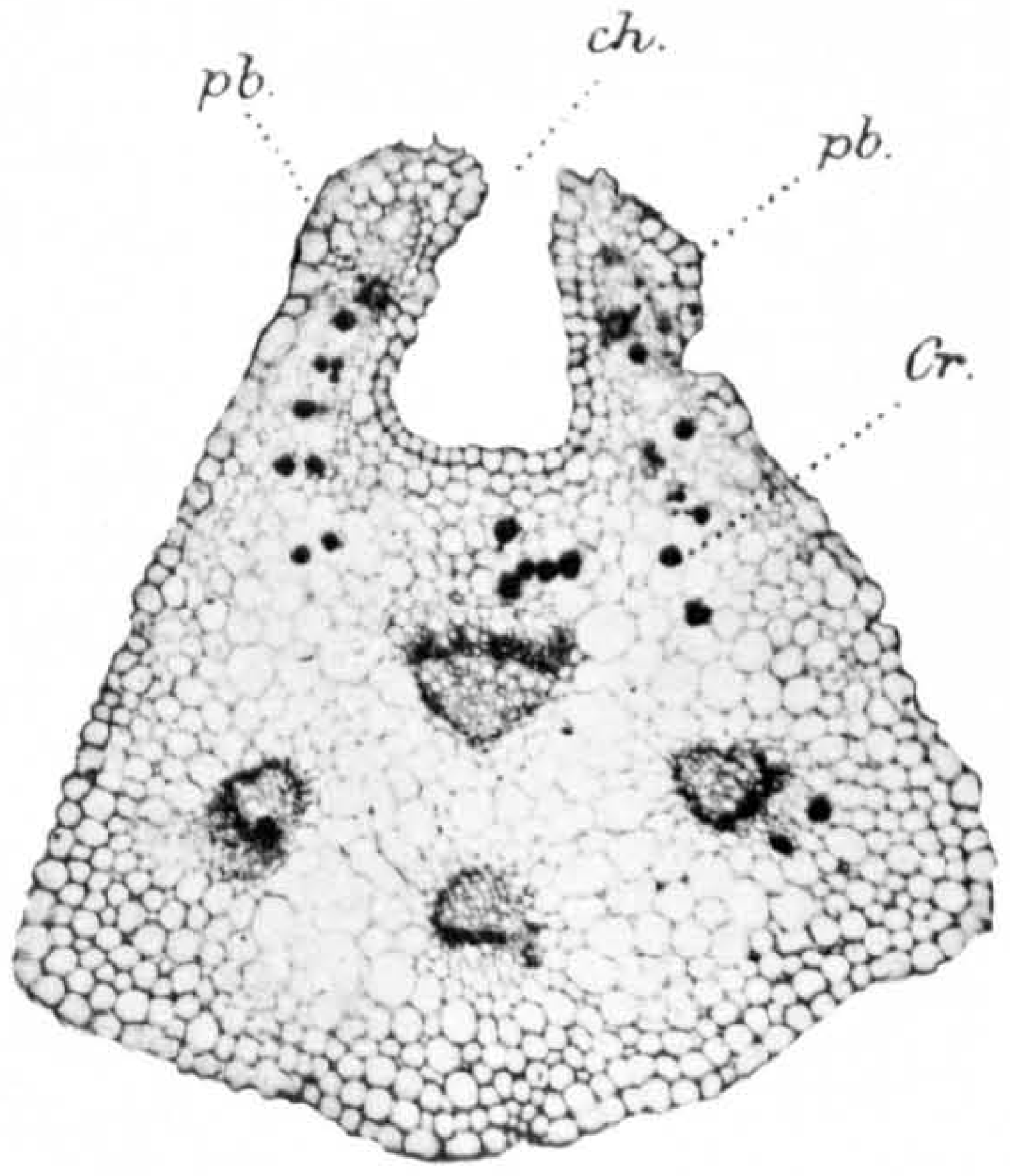

12.

SALISBURY — EXTRA FLORAL NECTARIES OF POLYGONUM.

Huth, coll.

# SALISBURY

# METHODS OF PALAEOBOTANICAL RECONSTRUCTION

[Annals of Botany, Vol. XXVII. No. CVI. April, 1913.]

# Methods of Palaeobotanical Reconstruction.

BY

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**With one Figure in the Text.**

THE rapid advances which our knowledge of Palaeobotany has made during the past few years have naturally resulted in a more detailed study and an increased accuracy of method in the reconstruction of fossil plants from petrified material.

Certainly one of the most important preliminaries to the investigation of any petrified structure consists in an accurate determination of the directions in which the sections have been cut.

Every one who works in this field is familiar with the fact that sections which approximate closely to the longitudinal or transverse planes are of very rare occurrence, so that not only are the vast majority of these oblique with regard to the main axis, but doubly oblique sections, not symmetrical about any plane, are also extremely common.

In the case of complex structures it is wellnigh impossible, and in some cases completely so, to think out unaided the distortions consequent upon such obliquities, and the difficulties of the problem are still further enhanced where serial sections are not available.

It is the object of the present paper to bring together the various methods which have been previously adopted for the reconstruction of petrified material, together with others which the writer has himself found useful in such investigations. These can be all regarded as belonging broadly to one of two classes according as they are applicable to the study of serial or non-serial sections.

## I. METHODS OF RECONSTRUCTION FOR SERIAL SECTIONS.

### (*a*) The wax sheet method.

In this method, which is that commonly employed by zoologists, the sections of the series are represented by sheets of wax, out of which are cut the structure as seen in each on an enlarged scale. For this purpose each section has to be drawn to the magnification of the required model, which can be done either by means of a camera lucida or by projection. If the

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former be employed great care must be exercised to ensure that there is no distortion, and that all the drawings are perfectly comparable; the other alternative is to project an image of each section on to the plate-glass screen of a photo-micrographic apparatus over which has been stretched a sheet of tracing paper, the section is then drawn and a fresh piece of tracing paper substituted. By the latter method all distortion is avoided and the same magnification can be always obtained without difficulty.

By means of the drawings each section is then cut out of a wax sheet, connexions being left where isolated portions occur. The wax sections thus formed are placed in order and joined together, either by pricking with a hot needle and applying pressure, or by running melted wax around the edges.[1] It is obvious that the thickness of the wax sheets must have the same relation to the actual interval between the successive sections as the magnified representations bear to the real sections, and the accuracy of the model depends upon the assumption that the sections are equidistant and parallel.

The method is particularly useful in the reconstruction of the stems or other structures with an elongated axis; its chief defects, however, come from the fact that the successive sections of a series are frequently far from parallel, and the interval between them not a constant one. Where, as in stems, roots, and petioles, there is seldom any very rapid change in direction of either the structure as a whole or of its internal organization, and the series is, moreover, usually a long one, these objections are not of great importance. But in seeds and similar structures where rapid changes occur such considerations necessarily render it useless to the palaeobotanist.

If permanent models are required which shall be unsusceptible to extremes of temperature, the sheets out of which the sections were cut can themselves be built up and employed as a mould from which a plaster of Paris model can be made.

Professor and Miss Sollas[2] used this method with considerable success. They found that the plaster of Paris adhered readily to that which had freshly set, and by taking advantage of this fact they were able to add the sections one by one, so that all projections could be filled in with the plaster, and by means of a special apparatus each was planed down before adding the next in order.

### (*b*) The cardboard method.

A method which has been adopted by the present writer, and which, though similar to the above, offers considerable advantages, is to paste drawings of the sections obtained by projection on to pieces of cardboard, which are then cut out and fixed in their appropriate positions by means

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[1] See W. J. Sollas, Phil. Trans. Roy. Soc., Ser. B, vol. cxcvi, pp. 259–65.

[2] Phil. Trans. Roy. Soc., Ser. B, vol. ccii, pp. 231–2.

of wires. The intervals between the sections are thus represented by spaces, so that the alterations both in these intervals and in the planes of section can be allowed for. Further, the magnification of the model is in no way limited either by the size or thickness of the wax sheets or other material used.

### (*c*) The glass method.

The most useful, and at the same time the most ingenious, of all the methods of this class is that invented by Professor Graham Kerr,[1] which, though primarily intended for the study of microtome sections, is, with certain modifications, of extreme value to the palaeobotanist. Here ground-glass sheets are employed; the successive sections are drawn upon them in pencil and the various structures differentiated by means of water-colour paints. A few drops of clove oil are placed upon each sheet and the next then added, so that the whole block thus formed appears transparent, whilst the structure itself stands out as if reconstructed. Graham Kerr's method is similar to that formerly employed by Vosmaer, but differs in the use of ground glass and an interposed fluid.

For the purpose of the palaeobotanist the sheets of glass should be attached by clips to three upright supports arranged in a triangular manner and permitting of movement in the vertical direction. In this way the variation in the interspaces can be allowed for and differences of angle obtained.

## II. RECONSTRUCTION OF NON-SERIAL SECTIONS.

Where serial sections are not available, or the structures under investigation are so short as to preclude series of more than 3 or 4 sections, the methods described above are of very little value. In all such cases it is necessary to assume, unless of course there be good evidence to the contrary, that all the sections at one's disposal have been cut from structures of approximately equal relative dimensions; and in the case of seeds where this method has been utilized such an assumption does not appear to have been unwarranted.[2]

At the outset a primary examination of all the sections is made in order to obtain all the dimensional data possible.

In any oblique section there is one plane in which the dimensions of the structure are not exaggerated by the direction in which it has been cut. By noticing these true values in all the sections at one's disposal, the real dimensions of several structures, such as the thickness of a testa or the width of a seed, are obtained.

The angle of obliquity of some of the remaining sections can then be

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[1] Q. J. M. S., No. 177, p. 1, 1902.

[2] Oliver and Salisbury, Ann. Bot., vol. xxv, 1911, p. 4.

deduced from these known values, and since the calculation of these angles involves considerable time it is usually much simpler to obtain them graphically. For example, the thickness of a testa is represented on the magnified scale by a horizontal line, and from one end of this a second line is drawn vertically upwards. Using the other end of the first line as a centre, an arc is then described having as a radius the magnified dimension of the testa in the oblique section. On joining up the centre to the point of intersection with the vertical, the angle of obliquity is obtained and can be read off by means of a protractor.

In this way from known values the plane of several of the sections can be determined, and by reversing the above graphical method the dimensions of other structures to those already known can be deduced from their oblique values, the latter being plotted at the known angles of section and projected on to the horizontal.

It will be seen that in this way quite a considerable number of dimensional values can be arrived at, and on the basis of these a preliminary ideal section of the structure as a whole can be drawn.

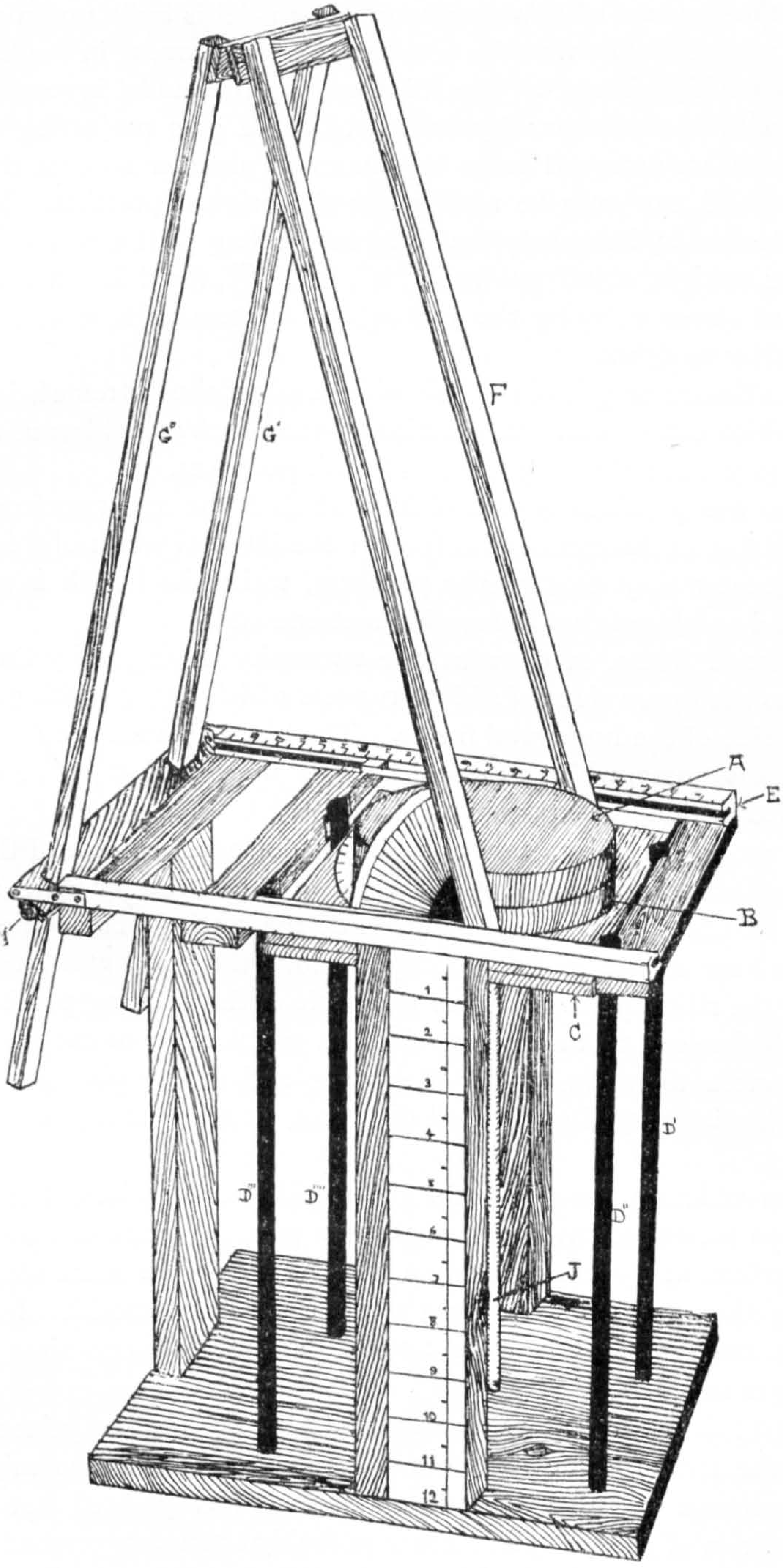
Each section is then measured along the line corresponding to the plane of intersection with the ideal section already constructed. The relative positions of the various parts and the boundaries of tissues along this imaginary line are plotted off along the edge of a strip of paper, so that for each section we have in convenient form the relative positions of its parts as they will appear when appropriately plotted.

If the original ideal section be approximately correct we should be able to fit in these lineal representations, so that the limits coincide at the angles which have already been determined.

In actual practice we shall find that our ideal section will undergo considerable modifications, after which we can proceed to reproduce it in the form of a model, using for the purpose some plastic and easily cut material such as plasticine.

It is obvious that for all the foregoing methods, and especially the last described, where the absence of serial sections greatly enhances the possibility of error, some means of checking the results must be adopted, and such a proof of one's results can be obtained by cutting the model at the angles and in the planes indicated by the plottings. If the model be a correct reconstruction the results will be magnified representations of the corresponding sections. Failure to obtain this will necessitate a revision of the model until any section can be reproduced upon it.

Adequately to cut such models in a perfectly flat plane necessitates the use of special apparatus, and a mechanism designed for this purpose will now be described by means of which the planes of obliquity of other sections, which do not admit of interpretation by the ordinary methods, can usually be elucidated (see Figure).



Apparatus for the cutting of models reconstructed from sections. A, removable platform for model; B, rotating platform; C, rising and falling platform carrying B; D′–D″″, guides for the platform C; E, grooved sides of frame carrying runners which bear the cutting face F; G and G″, supports to the cutting face F; H, screw clamp for fixing the position of G″. The clamp for fixing the rod J carrying the platform C is not seen.

For the purpose of this apparatus the model is built up on a circular disc of wood A, of the same size as a rotating platform, B, in the instrument itself, upon which it rests. The disc bearing the model is removable and engages with the platform by means of three pins projecting from this latter, which are arranged in an asymmetrical manner so that the model, when removed, can only be replaced in the original position. The lower disc is attached by its axis to the rising and falling platform C, which moves along four upright metal guides, D′, D″, D‴, D⁗, fixed below into a base-board, and above carrying the rectangular framework E, which is further supported by uprights.

The effective length of the guides determines the extreme height of the models which can be cut. In practice a twelve-inch model has usually been found to give sufficient magnification for all purposes.

When the platform is at the highest limit the upper surface must be just above that of the rectangular frame; the internal width of this latter is slightly greater than that of the platform, whilst its length is more than double and so placed that the model is at one end.

A second frame, F, open at one extremity is hinged by the two free ends on to the upper sides of sliding runners which engage with grooves on the inner side of the horizontal frame. The hinges permit the former to be placed at any angle, whilst supports from its upper end, G′, G″, enable it to be clamped in the desired position.

The model is cut by a taut wire drawn down the surface of the hinged frame, and scales appropriately placed give the necessary data as to the direction of the section, viz. the angle of the cutting plane; the position which the base of the frame F occupies along the horizontal grooves; the height of the rising platform; and the angle of the rotating platform.

It will be seen that such a mechanism enables one to cut the model in every possible direction, whilst the rising and falling platform can also, by clamping it at equal or unequal distances, be used for reproducing serial sections.

When utilizing the above for the elucidation by trial of the direction of a section which we have been unable to plot, the plane can be approximately arrived at by constructing a wire frame of the same shape as the outline of the section and placing this on the uncut model. In this way numerous trial sections can be avoided and thus much time spent in modelling is saved.

Whilst this instrument was constructed for the purpose of palaeobotanical research the use of some such check on one's observations might be of great advantage in other branches. Lawson has pointed out that the lateral position of the synaptic knot is probably often exaggerated owing to the obliquity of section.[1] And it may be that the effect of this on the form

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[1] Trans. Roy. Soc., Edinburgh, 1911.

of the structures investigated is not sufficiently taken into account in other fields beside Cytology. However justified this suggestion, there is always a satisfaction and advantage in possessing some means by which a check approaching the nature of a proof can be applied to one's conclusions, and this is especially the case with histological detail such as the true form and arrangement of cells, which, as was found in the testa of *Conostoma oblongum*, might readily yield totally wrong interpretations.