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THE EYE OF POLYCYSTIS GOETTEI (BRESSLAU)

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FIVE FIGURES (ONE PLATE)

The rhabdocoele on which this study was made has appeared from time to time during the cold months of the year in a pond near the University of Virginia. It is found in greatest abundance at a depth of about two feet when the water is at winter temperature. In the warm months of the year they must seek greater depths, for we have not encountered them in our summer collecting. Bresslau ('06), in describing the species, says: "Unmittelbar hinter der Russelbasis liegt das Gehirn, auf ihm jederseits am Vorderende ein Auge, dessen schwartzes Pigment von kugeligen Granulationen gebildet wird." (p. 417). In his figure 1 he indicates a posterior black portion and an anterior clear or colorless part in each eye. The posterior portion is evidently the pigmented part of the eye, while the clear region is comparable to what von Graff ('82) refers to in different rhabdocoeles' eyes as 'Lense.' We agree, however, with Böhmig ('87) when he says: "was von Graff als Linse bezeichnet, ist zweifellos der beim Conserviren geschrumpfte Inhalt des Pigmentbechers." (p. 487). So that the light anterior end of each eye in Bresslau's figures must be the projecting visual elements seen in profile along the margin of the mouth of the pigment cup.

Since Hesse's ('97) work, the histology of the eye of Turbellaria has been well understood. He showed that there are two sets of elements or cells entering the formation of the eye of the Turbellaria, namely, (a) pigment-cells, and (b) visual cells or retinulae.

In all cases the pigment cells form a pigmented cup about certain portions of the retinulae. These pigment cups may be unicellular or multicellular. So far as our knowledge goes

Böhmig was the first to describe what may be called a compound pigment cup in a Turbellarian eye. Of the eye of the rhabdocoele, Vorticeros auriculatum, he says:

> Der Pigmentbecher jedes Auges wird durch eine mittlere Pigmentscheidewand in eine vordern und hintern Kammer gelegt. Der Pigment besteht aus kleinen rotlichen Kornchen. Einen Plasmasaum mit Kernen den Pigmentbecher habe ich nicht auffinden können, doch soll damit nicht gesagt sein, das er in der That fehle. Durch die Pigmentscheidewand ist natürlich bedingt, dass der Pigmentbecher zwei Öffnungen besitz, von denen jede durch eine einige vor ihr liegende Zelle von linsenformigen Gesalt mit deutlichen Kern und Kernkörperchen geschlossen wird. (p. 486).

Thus it appears that there are two kinds of pigment cups associated with the visual elements of rhabdocoeles: (*a*) simple, in which there is but a single lumen and, (*b*) compound, in which the lumen of the cup is subdivided to give two secondary lumina.

In the eye of the flatworm there may be one or more visual elements which send part of their cell bodies into the lumen of the cups formed by the pigment cell or cells. In all cases the nuclei of the visual cells or retinulae lie outside of the lumen of the pigment cup. Dendy (see Benham '01) shows in his figure of the eye of Geoplana a single visual cell whose nucleus lies in the fundus of the pigment cup. This condition is so strikingly exceptional that we feel that Dendy may have mistaken another structure for the nucleus of the cell. There has recently been described a highly refractive body forming a part of the retinula of Prorhynchus applanatus Kennel (Kepner and Taliaferro, '16). The paper by Kepner and Taliaferro presents a description of the retinula of a rhabodocoele in which there is a refractive body within the cytoplasm, between the nucleus bearing portion of the cell and the end-organ or rhabdome of the cell. Kepner and Foshee ('17) showed that a striking comparison could be made between the visual element of Prorhynchus applanatus and the retinula of a vertebrate.

The pigment cup, when seen in the living specimen, is spheroidal in contour and intensely black both by reflected and transmitted light. The average diameter of the cup is twenty-five

microns or less. Beyond this no further details of the pigmented part of the eye could be recognized in the living condition nor in sections that were too thick. In series of sections cut five microns the cytology of the pigment cup could be worked out fairly well. These sections show that the pigment mass of the eye is unicellular. The nucleus of the pigment cell is oval and has a large nucleolus. These two characteristics mark it off distinctly from the nuclei of adjacent cells, such as nerve and mesenchymal cells (fig. 1, *P-N*). A bit of the cytoplasm is shown about the nucleus in figure 1; but, for the most part the cytoplasm is completely obscured by the presence of many black spheroidal pigment bodies (fig. 1, *P*, fig. 2, *P*). The cell body of the pigment cell forms the wall of the pigment cup of the eye, but a very striking feature of this cell body is that it forms a conspicuous partition of pigmented cytoplasm, which, standing up from the floor of the pigment cup, divides its lumen into two secondary lumina. The accessory portion of this eye, therefore, is a divided cup and presents two mouths or openings instead of one. Thus in this eye there are two principal axes instead of one as is usually the case. In short, here we have a compound eye similar to the one described by Böhmig ('87). Ordinarily one mouth of this compound cup is directed anteriorly, while the other is directed posteriorly. These mouths open dorsally as a rule. However, in our fixed material we have seen specimens in which one opening of the pigment cup was ventral to the other and the axis of each lumen was directed anteriorly. Again, we have fixed material in which the mouths lie one behind the other and the axes of the lumina are directed laterally. This shifting of the axes of the lumina of the pigment cup in fixed material is not to be considered as being due to torsion resulting from fixing; but we believe that the animal has the power to move its eye through a fairly wide range as it lies in the parenchyma. This is perhaps due to the play of the adjacent muscles of the proboscis.

A single retinula which fills the lumen of each half of the pigment cup, lies quite close to the dorsal ganglia so that it appears to arise out of the mass of cephalic nerve cells. The

shape of the retinula is that of a bent spindle. The proximal third of the cell is bent almost at right angles to the distal two-thirds. This proximal third of the cell is that part of the cell-body which projects beyond the contour of the pigment cup. The parts of the two retinulae that do not lie within the cup leave the pigment cup in opposite directions (fig. 3). This proximal third of the retinula represents one of the three regions which can be recognized in this cell. The nucleus lies within this region. The cytoplasm of this nuclear-bearing portion of the retinula shows no striation (fig. 1, *M*). The part of the retinula, enclosed by the pigment cup, presents two other regions. The distal of these is closely applied to the inner surface of the surrounding pigment cell. The cytoplasm of this region displays a homogeneous, or better, a uniformly finely granular texture. It is only on the slides that show the best general fixation[1] of tissues that we find the uniform texture of this part of the cytoplasm. In slides that show a little, but no great shrinkage it is suggested that there may be lines of less density present in this region of cytoplasm. These lines, due to slight shrinkage in some fixing, break, and a striated condition of part or all of this part of the cell results. That this variation, due to the method of fixing, expresses some specific condition of the rhabdome is indicated by the fact that the striae are always directed from the inner surface of the surrounding pigment cell towards the middle region (ellipsoid) of the retinula (fig. 1, *R*). In this distal part of the retinula we have the end organ of the visual cell—the rhabdome (figs. 1, 2, 3, *R*). Striated rhabdomes have been described for Turbellaria. There is, however, a third region in the retinula of this rhabdocoele, which is well differentiated by Mallory's connective tissue stain, by which the basal portion of the cytoplasm and the rhabdome take a blue color, while the third region of the visual cell has an affinity

[1] We have used Carnoy's fluid, chrom-aceto formalin, aceto-sublimate, and Flemming's stronger solutions. These are given in the order in which we found them yielding results—the poorest fixing resulting from Carnoy's and the best from Flemming's stronger mixture. All staining was with Mallory's connective tissue stain. The sectioning was done at five microns and serially.

for the red stain. This is especially the case with material fixed in chrom-aceto-formalin. This region, which we take to be homologous with the 'refractive body' which Kepner and Teliaferro ('16) described for the eye of Prorhynchus applanatus, is wedge-shaped. This region has been recorded for a triclad rhabdome, and a function suggested for it by Taliaferro ('17) who says,

> The rhabdome itself shows an optically denser region in its outer end as described in Prorhynchus applanatus by Kepner and Taliaferro ('16). This region because of its shape and density, must have some effect upon the rays of light if they pass through the long longitudinal axis, which it cannot have if they pass through in any other direction.

The wider faces of the denser wedge-shaped region of the rhabdome of Polycystis goettei are parallel to the partition of the pigment cup (fig. 5, *E*) and their apices are directed towards the fundus of the lumina of the cup (fig. 2, *E* and fig. 3). In brief, we may say that there are three regions clearly differentiated in the retinula of this rhabdocoele: (a) a proximal region that bears the nucleus; (b) a distal region, which is the end organ or rhabdome; and (c) a middle region arising from the distal end of the basal part of the cell and extending into the cone-shaped rhabdome.

This three-fold differentiation of the retinula of Polycystis goettei is homologous with the retinula of Prorhynchus applanatus where there is a basal region which bears the nucleus and is homologous with a similar region in the retinula of this rhabdocoele (fig. 4, *A* and *A′*). The second region of this cell of Prorhynchus applanatus has been seen in fresh material compressed between cover-glass and slide to be highly refractive. In the retinula of Polycystis goettei (Bresslau) we have a region homologous with this refractive region (fig. 4, *B* and *B′*). Finally the end organs in the two retinulae of the two rhabdocoeles are homologous (fig. 4, *C* and *C′*).

Thus we have homologous regions in the eyes of the two rhabdocoeles, which are strikingly analogous to, if not homologous with, the three regions that have been described in the

retinulae of the vertebrate eye. Prorhynchus has, as the analogue of the cylindrical or conical end organ, a solid low rhabdome, while in Polycystis there is a hollow, rather high conical rhabdome (fig. 4, *C*, *C′* and *C″*). Comparable with or analogous to the ellipsoid of the vertebrate, Prorhynchus applanatus has a concava-convex lens-shaped refractive body; in Polycystis goettei, a wedge-shaped body (fig. 4, *B*, *B′*, and *B″*). Finally, analogous to the nuclear-bearing region of the vertebrate visual cell there is the nucleated region of the retinulae of both Prorhynchus and Polycystis (fig. 4, *A*, *A′*, *A″*).

SUMMARY

1. There are two visual cells and one accessory, pigmented cell entering the formation of the eye of Polycystis goettei.

2. The pigment cell is spheroidal with two lumina within it.

3. Into each lumen of the pigment cell there enters a retinula.

4. The retinula resembles the visual cell of Prorhynchus applanatus in that it has a third region homologous with that animal's 'refractive lens-shaped body.'

5. This homologue of the refractive lens-shaped body of Prorhynchus is conspicuously analogous, if not homologous with, the ellipsoid of the vertebrate retinula.

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PLATE 1

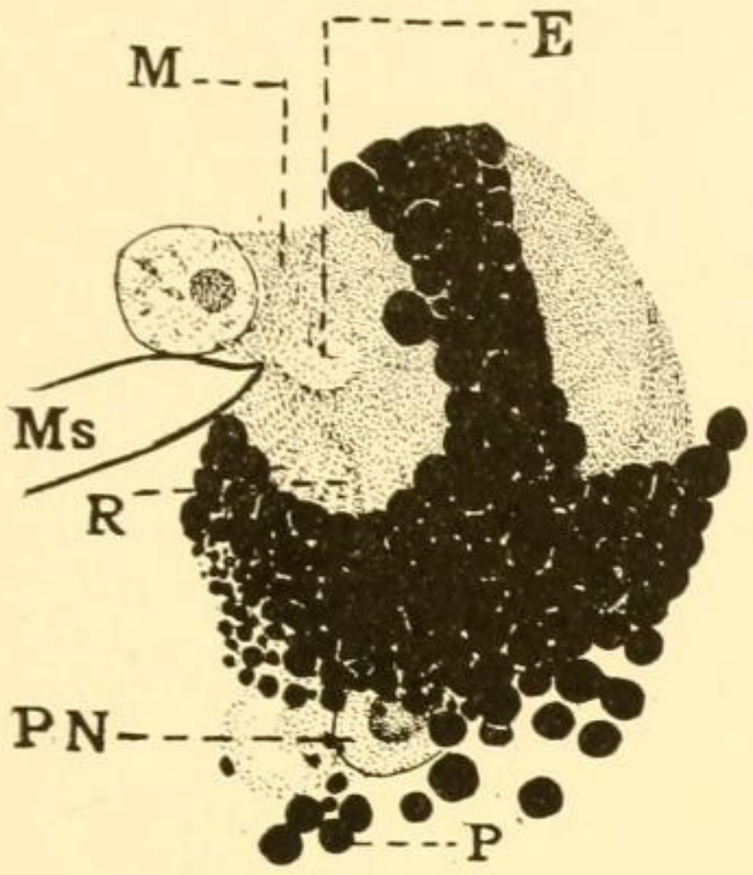
1 Section involving the pigment-cell and the two retinulae of the eye. *M*, myoid or proximal portion of the retinula, which bears the nucleus; *E*, base of the wedge-shaped region of the retinula cut obliquely; *R*, rhabdome, showing striae; *P.N*, nucleus of pigment-cell; *P*, pigment granule; *Ms*, muscle of proboscis, which passes by the eye. The plane of section is indicated by line *1* in figure 3. × 1500.

2 Section of eye, parallel to the partition of pigment-cell and to the wedge-shaped region of the two retinulae. The left side of the drawing is ventral, the right dorsal. *R*, rhabdome: *E*, wedge-shaped body (ellipsoid): *P*, pigment granules. × 1500.

3 Diagram of a meridional section of eye. *P.C*, pigment-cell with its nucleus: *R*, rhabdome: *E*, wedge-shaped region (ellipsoid) of retinula: *M*, proximal part of visual cell (myoid): *1*, plane of section of figure 1; *2*, plane of section of fig. 5.

4 Diagram of retinula of: *I*, Prorhynchus applanatus. *II*, Polycystis goettei; and: *III* vertebrate. *III* is based upon Arey's figures. Line *A-A'* connects the rhabdomes; line *B-B'*, the refractive bodies (ellipsoids): line *C-C'*, the nuclear bearing regions (myoids) of the retinulae.

5 Transverse section of a retinula involving the rhabdome, *R*: the wedge-shaped body (ellipsoid), *E*: and a part of the pigment-cell. The plane of the section is shown by broken line *2* in figure 3. × 1500.



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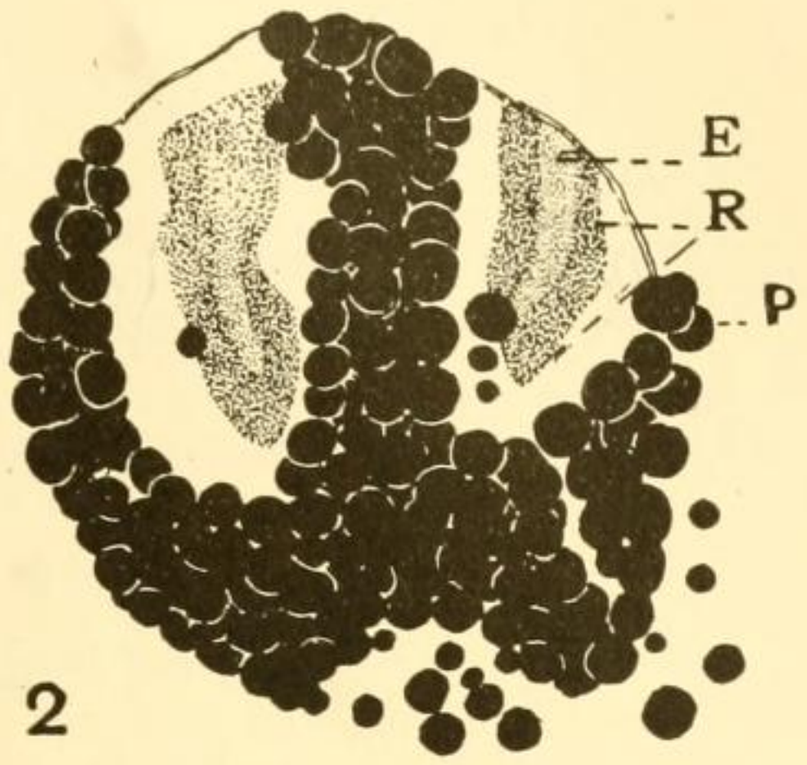

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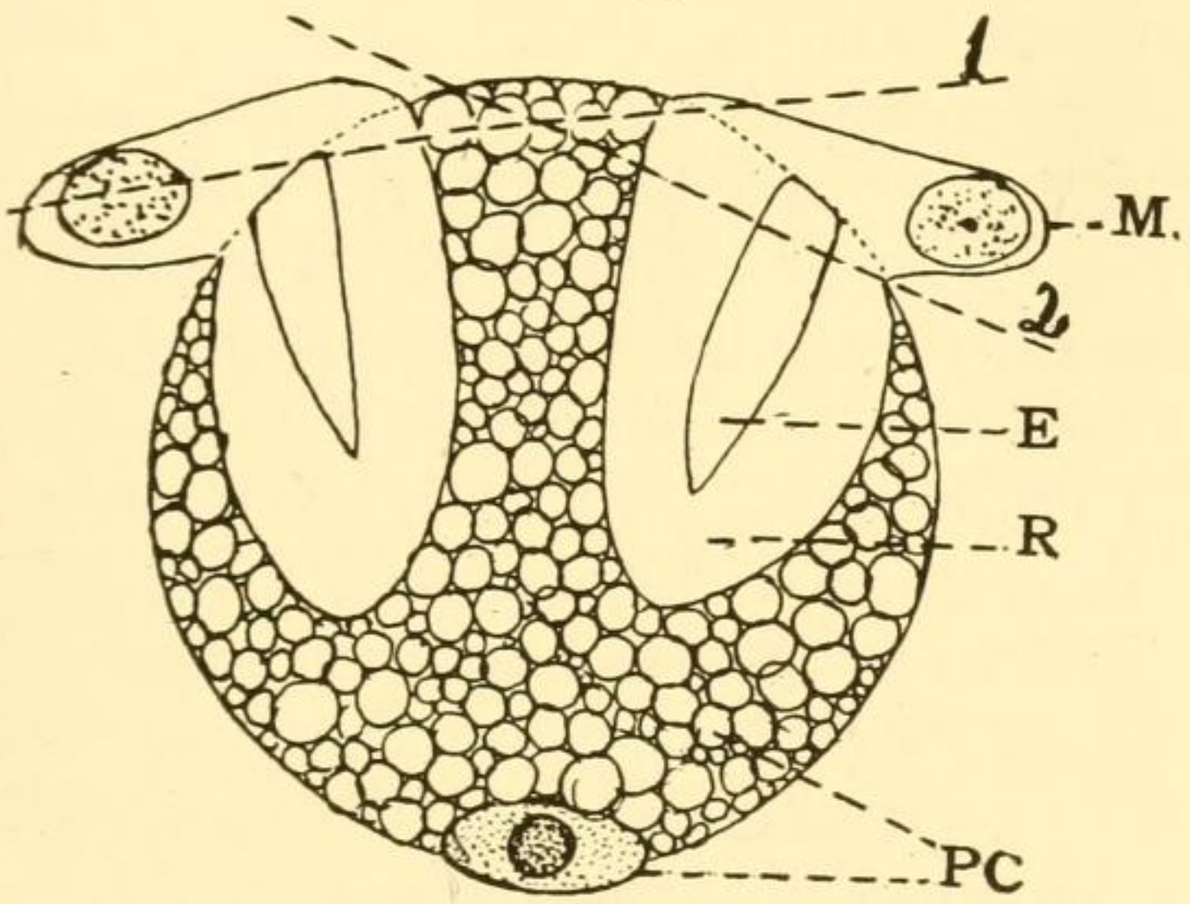

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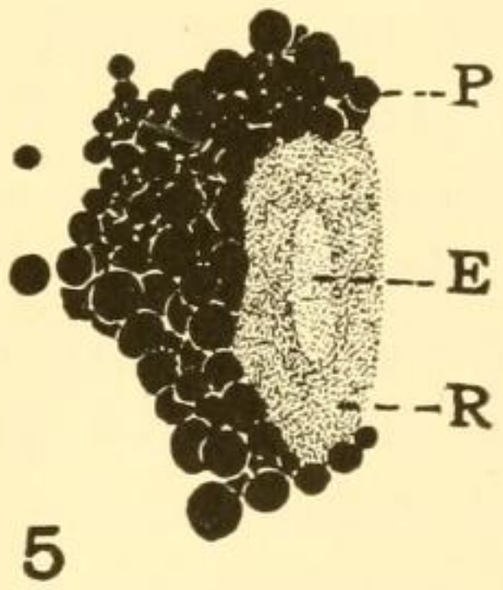

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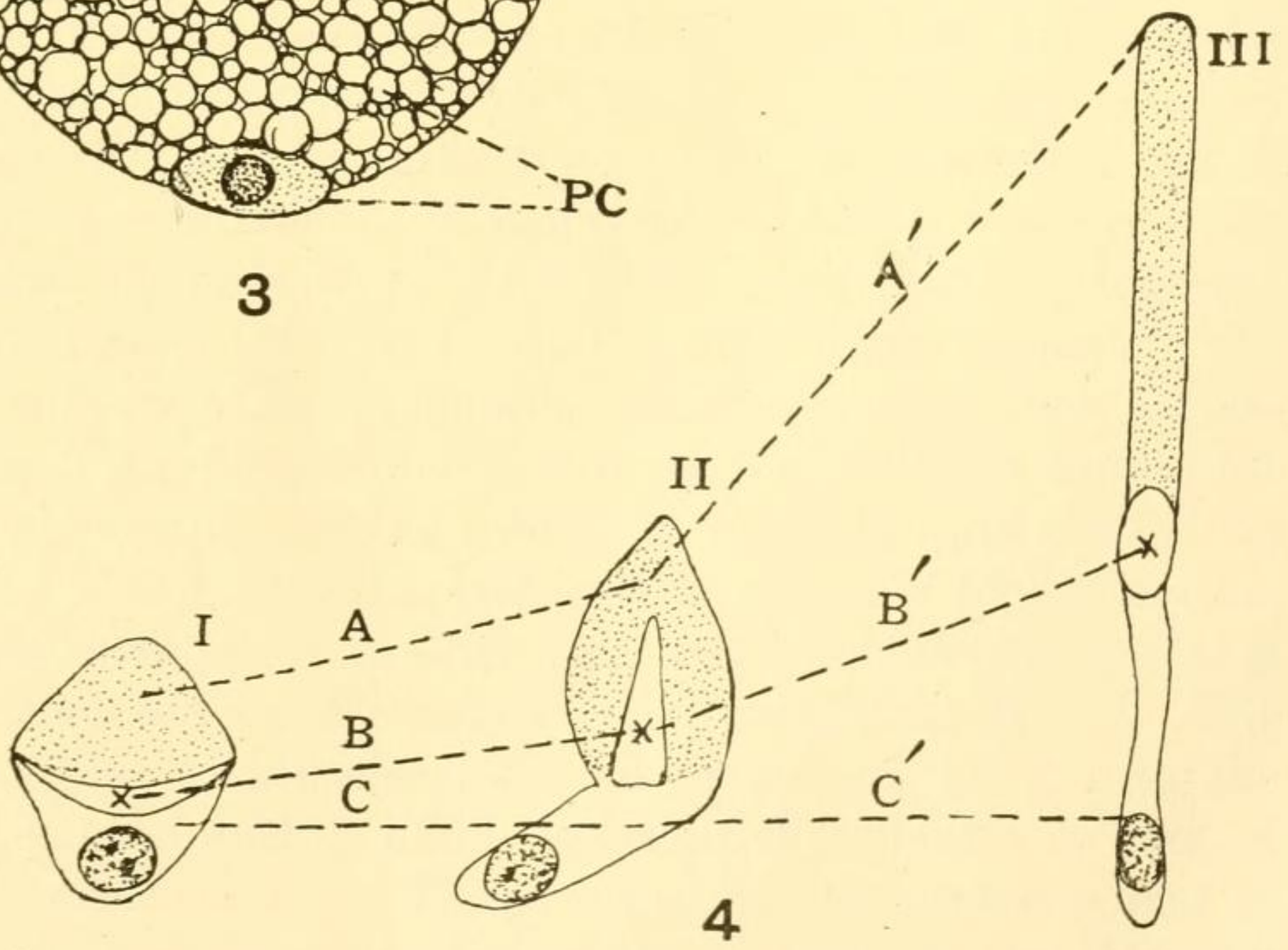

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