THE ROOTS OF LYCOPODIUM PITHYOIDES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XCV

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(WITH PLATES V AND VI AND ONE FIGURE)

Lycopodium pithyoides Schlecht. & Chamisso is a subtropical form of rare occurrence, but, according to UNDERWOOD and LLOYD, of unexpectedly wide distribution. In spite of its striking and unmistakable appearance, it has been confused with other forms, such as *L. dichotomum*.

The material which formed the basis of this investigation was collected in September 1906 near Jalapa, Mexico, by Professor BARNES, Dr. CHAMBERLAIN, and Dr. LAND, of the University of Chicago. They found in that region only one specimen, which they secured and which is now growing in the greenhouse of the University. This plant, or rather clump of plants, was growing as an epiphyte on the trunk of a recently fallen tree.

This species of Lycopodium attains a size unusual in the genus. The stem is dichotomously branched, erect, and rigid, with a diameter of 6 to 10^{mm}; and the slender dark green leaves are 2.5 to 3.5^{cm} long. The fact that practically every leaf is a sporophyll indicates that this form is of relatively primitive character. The length of its leaves, the stoutness and rigidity of its stem, and its unusual size give it such a shrub-like aspect that SCHLECTENDAL and CHAMISSO (**10**) in the original description very aptly compared it to a young *Pinus silvestris*.

A cross-section of the stem, however, is much more striking than the general habit. The stele, which in structure and arrangement is similar to that of *L. lucidulum* or *L. Selago* is comparatively small, being about one-tenth the diameter of the stem. The conspicuous feature of the stem is not the central stele, but the numerous smaller heavily sheathed steles which surround it (*fig. 1*). These are the "inner roots" of STRASBURGER (**11**). The "inner root" is not an example of a particular type of root, but of a peculiar habit which

exists in certain species of Lycopodium. The roots arise in acropetal succession at any point of the stele of the stem. Instead of penetrating the cortex at once and emerging as aerial roots, they turn down in

FIG. 1.—Lycopodium pithyoides

the cortex, boring canals through long stretches of cortex, and emerge finally at or near the base. This habit is associated with erect forms of Lycopodium, both terrestrial and epiphytic. A similar habit is described in the Marattiaceae, SACHS (**9**) having given a brief description of its occurrence in *Angiopteris evecta*, in which the roots are said to bear a definite relation to the leaf bases.

The "inner roots" of Lycopodium were described by BRONGNIART (1), who stated that they were characteristic of erect dichotomous forms. STRASBURGER (11) described the more obvious features of the "inner roots" of *L. Selago*, and gave a list of about twenty species characterized by their presence. All the species noted are members of the Selago group except *L. Phlegmaria*. In none of the species described have the "inner roots" attained a development comparable to that in *L. pithyoides*. Few have been studied in sufficient detail to afford a basis for comparison. STRASBURGER records *L. Selago* as showing eight roots in a cross-section taken 5^{cm} above the base of the stem. BRONGNIART (2) figures *L. phlegmaria* and *L. verticillatum* with fifteen "inner roots." *Fig. 2* shows a cross-section of *L. pithyoides*, taken $10–12^{cm}$ above the base of the stem, in which fifty-two roots were found. The extraordinary development of these roots is no doubt an important factor in giving the stem its characteristic stoutness and rigidity.

The root primordia usually appear within $2–5^{mm}$ of the tip of the stem, but occasionally there will be none within $5–10^{cm}$ of the tip. The primordium shown in *fig. 3* and *fig. 4* was found about 2^{mm} from the apex of a stem which was about 25^{cm} high. The vascular cylinder of the stem was still in the promeristem stage.

The roots of *L. pithyoides* show four distinct initial regions for the plerome, periblem, dermatogen, and calyptrogen. The plerome arises from an initial region consisting probably of only one initial cell. It was impossible to determine with certainty the exact number of initials, but such preparations as that shown in *fig. 5* indicate a single initial; it is possible, however, that there are several, as in the forms studied by BRUCHMANN (3). The periblem initial region consists of several layers forming a well-defined although not sharply differentiated region. There is a well-defined one-layered dermatogen which gives rise to the epidermal cells and trichoblasts.

The trichomes arise from definite cells which are cut off by curved oblique walls from the original epidermal cells a short distance back of the apex of the root (*figs. 6, 7, 8*). With the growth of the epidermal cells and trichoblasts, the latter come to have the appearance of wedge-shaped cells. The outer wall rounds out and a papilla appears which rapidly elongates into a slender, rather thick-walled, persistent

trichome. The trichoblast usually divides once longitudinally, so that the trichomes are usually found in pairs (*fig. 9*). Since almost every epidermal cell gives rise to a trichoblast, the trichomes are abundant and very uniformly distributed. The trichoblastic cells are cut off as regularly in the "inner roots" as in the external, but of course produce trichomes only in aerial and soil roots. The formation of trichoblasts in Lycopodium was first described by NAEGELI and LEITGEB (**6**). LEAVITT (**5**) has described them in greater detail, giving *L. inundatum* as an example of the type in which the trichome is cut off by a straight anticlinal wall, and *L. lucidulum* as an example of the type with oblique walls. The development of the trichomes in *L. pithyoides* seems to be the same as that in *L. lucidulum*.

The root begins to grow downward immediately after leaving the stele (*fig. 10*), dissolving and crushing the cortex to make way for its rapid enlargement. The roots bend and curve, winding in and out around each other and around the leaf traces as they work their way down the stem. Several roots often run side by side for a considerable distance, so crowded together that the sheaths appear to fuse. PRITZEL (**7**) and STRASBURGER both describe branching as of frequent occurrence. It must be extremely rare in *L. pithyoides*, for no cross-sections have revealed the slightest trace of it, and an extensive dissection of the stem was equally unsuccessful. That it does occur is shown by a root-tip taken from an "inner root" which has the dichotomous forking so characteristic and abundant in external roots (*fig. 11*). It is possible that in such cases one branch may become abortive owing to the crowded condition under which the root is growing.

A typical "inner root" is shown in *fig. 12*. On the outside is a heavy sclerenchyma sheath, which in some roots attains a thickness two or three times as great. Within the sheath is a region of slightly thickened parenchyma which extends to the stele. The parenchyma region is the one which STRASBURGER erroneously called the outermost region of the root, because of the ease with which it is separated from the adjoining sclerenchyma. BRUCHMANN (**4**) in his discussion of *L. Selago* corrected this error. The tearing between the two regions is due not to a lack of organic connection, but to the weakness

of the middle lamella of the inner cells. It is so delicate that any pressure sufficient to section the sclerenchyma sheath is almost certain to cause a splitting of the middle lamella. Although the two regions are rather sharply defined, there are always a few cells in the transition stage. The thin-walled cortex is limited by the endodermis, which although not sharply differentiated can be easily recognized by its suberized walls.

In the genus Lycopodium there is great variation in the type of stele found in the root. Russow (**8**) has described that of *L. annotinum* and *L. complanatum* as being almost identical with that of the stem, but the stele of *L. Selago* and *L. inundatum* as being strikingly different. *L. pithyoides* is similar to *L. Selago*. The vascular strand is collateral, with a crescent-shaped xylem, the phloem lying between the horns of the crescent. The protoxylem is found regularly occupying the horns, but occasionally it spreads along the outer region of the metaxylem. There is no evident differentiation into protophloem and metaphloem either in root or stem. Russow in his discussion of *L. Selago* regards the parenchyma region outside the xylem as belonging to the phloem, and consequently classes the bundle as concentric. This indefinite region may be one or two cells thick or may be altogether lacking, and it seems better to regard it as pericycle rather than as phloem. It consists of small thin-walled parenchyma cells containing protoplasm and nuclei, with none of the wide-mouthed thick-walled cells which characterize the phloem region. The shape of the xylem strand varies somewhat in different parts of the root. The origin from the stele is seen in *figs. 13* and *14*. It is connected with two of the xylem strands and one of the phloem; this arrangement is shown in the primordium stage shown in *fig. 4*. As the root leaves the stele of the stem, the xylem strands move together, forming a U-shaped figure, with the closed end toward the center of the stem (*figs. 15* and *16*.) As the root passes down the stem, the xylem becomes massed together, so that when the root leaves the stem it has the form shown in *fig. 17*, which is the arrangement characteristic of external roots. The behavior of the xylem during forking of the root is shown in *figs. 18, 19, 20*. The xylem divides at the place where the two strands had previously united, and each strand rapidly assumes the characteristic crescent-shaped form.

The region of exit of the roots extends from the base of the stem to about 1 cm above. BRUCHMANN (3) found that in *L. Selago*, when the stem was closely appressed to the ground, an earlier exit was favored. The root may bend abruptly and leave the stem at a right angle, or it may run around the stem for a short distance not far below the epidermis, leaving the stem at a tangent; but it is more usual for the root to turn gradually toward the outside of the stem and leave it obliquely. The root hairs which in the "inner roots" develop no further than the trichoblast stage, develop extensively and form a dense mat around the external root (*fig. 21*). The epidermis, which soon disappears in the "inner root," is persistent in the external. In an old stem in which the departing roots are numerous and thickly crowded, the cortical tissue of the stem becomes torn and fragmentary. Most of it disappears, leaving a brush-like mass of roots with very little cortex between them.

This investigation was conducted at the University of Chicago under the direction of Professor JOHN M. COULTER and Dr. W. J. G. LAND, and arose incidentally in connection with an investigation of the development of the stele of Lycopodium.

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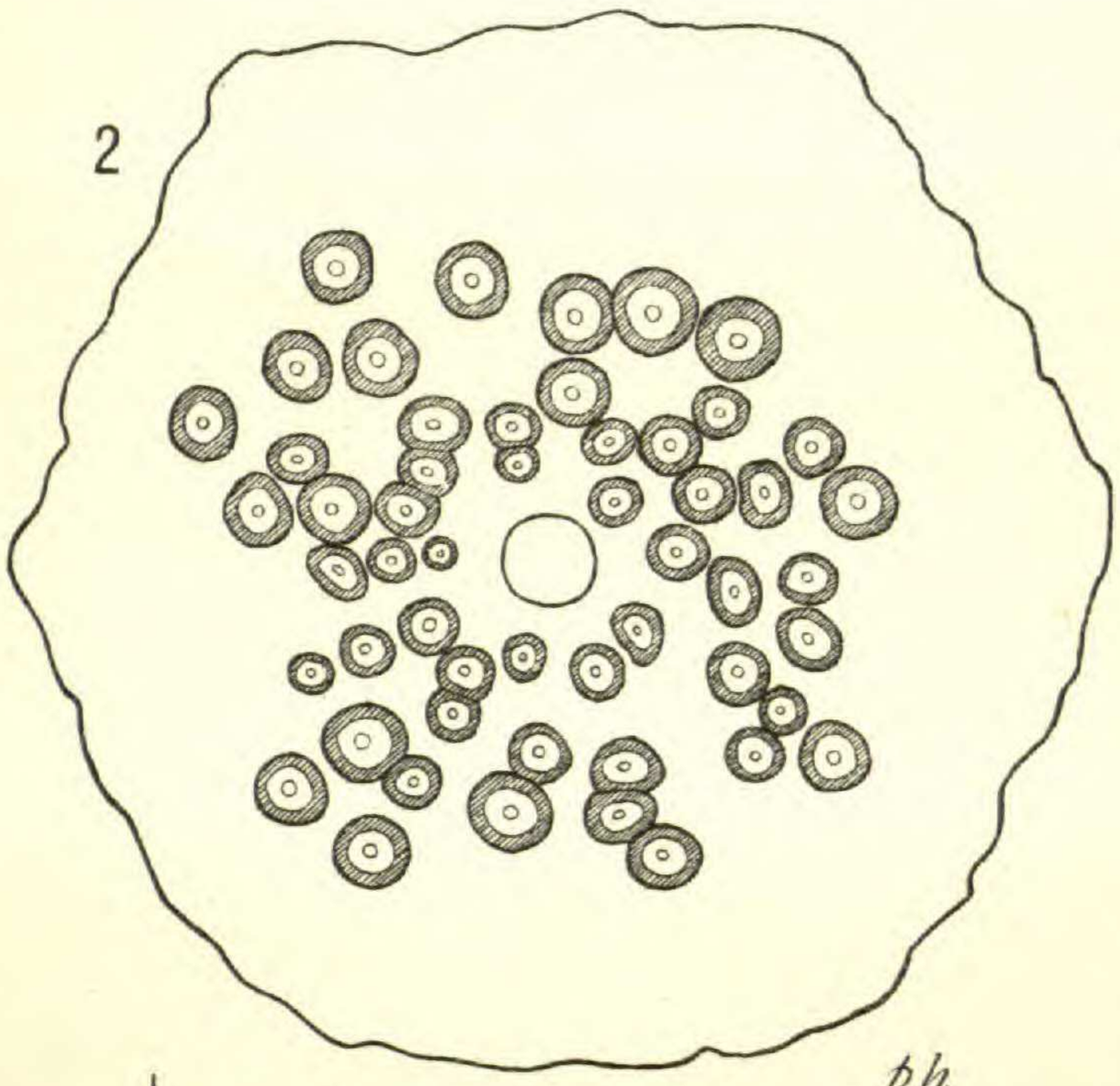

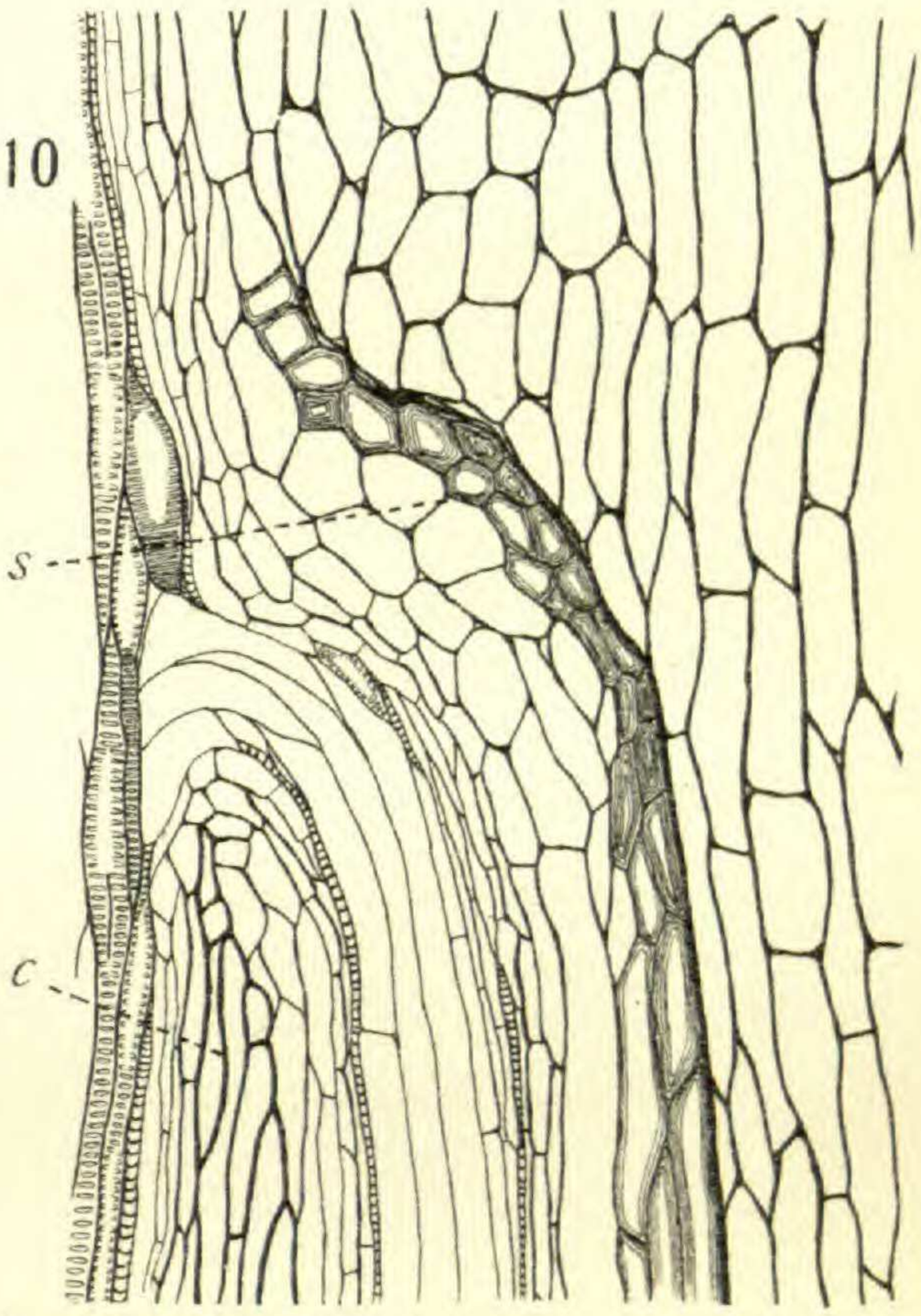

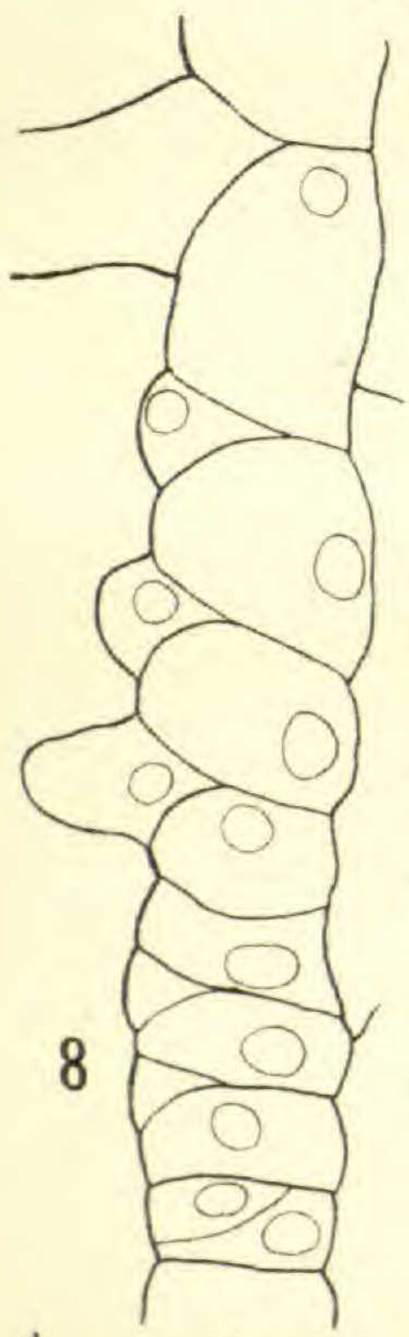

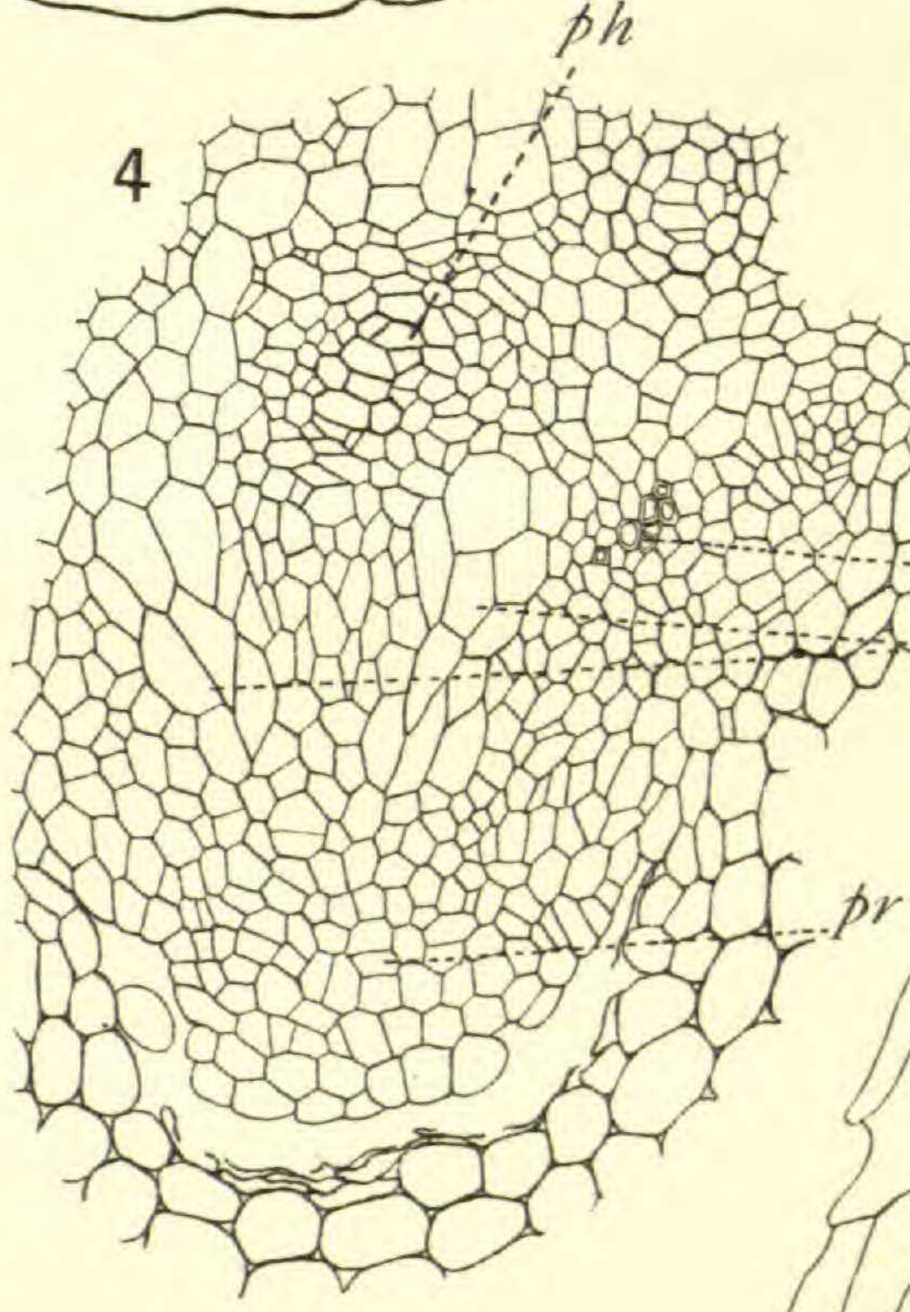

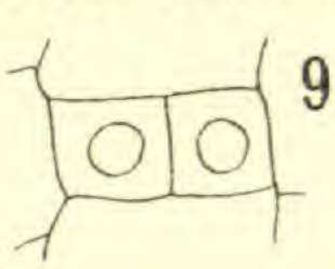

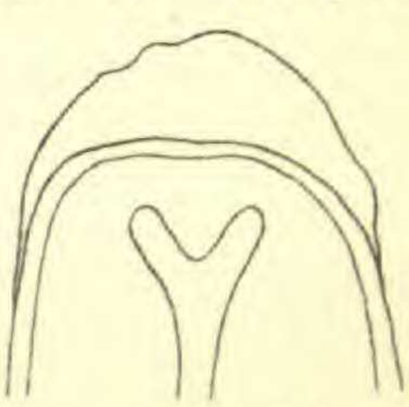

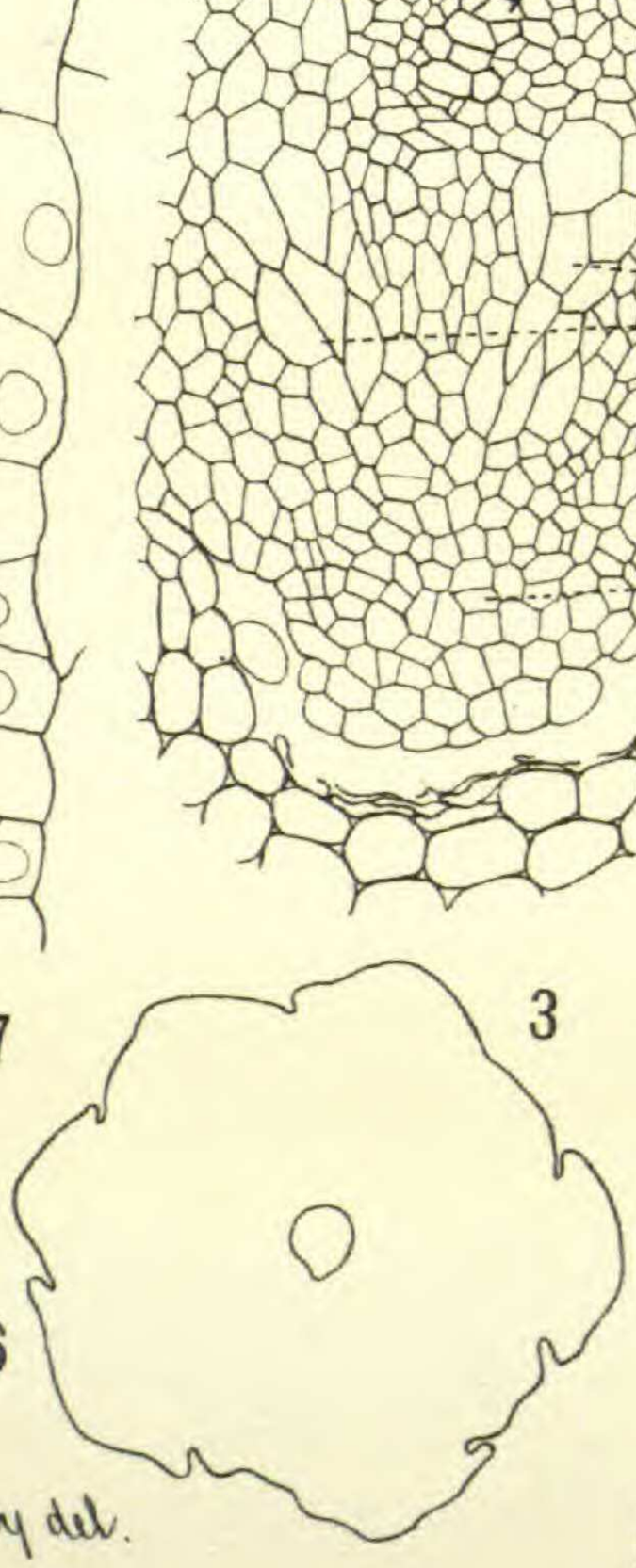

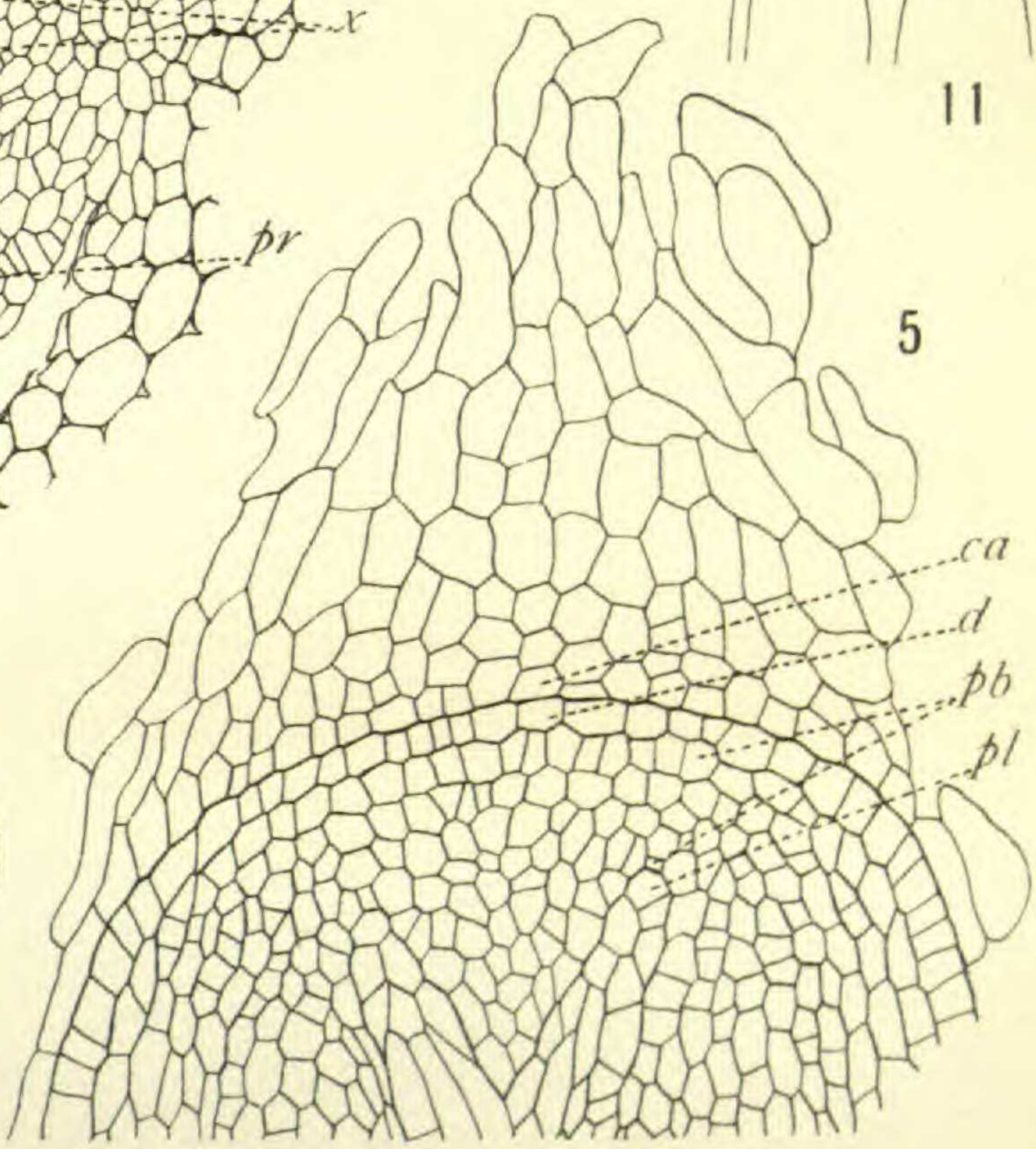

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