On the Floating-Roots of Sesbania aculeata, Pers.

BY

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With Plate XVII.

SEVERAL aquatic members of the natural order Leguminosae are remarkable for a peculiar development of certain of their tissues, leading to the formation of a floating-apparatus, which serves to keep the stem or root, as the case may be, at the surface of the water. In the genera *Aeschynomene* and *Herminiera* it is the secondary wood of the stem which is adapted to this function[1]. In *Neptunia oleracea*, Lour., on the other hand, the floating-tissue owes its origin to the cortex of the stem. This case has been fully investigated by Rosanoff[2], who has shown that the floating-apparatus is here a form of periderm, though differing in almost every respect from ordinary cork. My own observations on this plant have fully confirmed those of Rosanoff. It will be worth while to give a short account of the phenomena in *Neptunia*, as they present many analogies with the case of *Sesbania*, which forms the special subject of this paper.

[1] See De Bary, Comparative Anatomy of the Phanerogams and Ferns, Eng. Ed. p. 500.

[2] Ueber den Bau der Schwimmorgane bei *Desmanthus natans*, Willd., in Bot. Zeitung, 1871. I am indebted to Mr J. G. Baker, F.R.S., of Kew, for information as to the synonyms of this plant. *Desmanthus natans*, Willdenow, is the *Neptunia leracea* of Loureiro, and was originally described by Roxburgh as *Mimosa natans*.

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The floating-tissue of the plant in question forms very conspicuous spongy masses on some of the internodes of the procumbent stem, which is thus enabled to maintain its position on the surface of the water. In Rosanoff's figure 1 (Plate X, l. c.) the tissue is shown at *c* and *d*. The drawing, however, gives but little idea of the very soft, loose texture of the swollen masses. The diameter of the whole body may be nearly an inch, while that of the unswollen parts of the stem is only about $\frac{1}{6}$ of an inch. The length of each mass may be as much as two inches. The external tissue is, in the mature condition, very loosely attached to the stem on which it grows. Humboldt[1] regarded it as extraneous to the plant, and indeed the impression it makes at first sight is quite that of the mycelium of some luxuriant parasitic fungus. The surface is very irregular, showing deep longitudinal furrows. Microscopic examination shows that the tissue consists of very loosely arranged cells, which are greatly elongated, and are sometimes branched. The intercellular spaces are very large, and it is in them only that air is contained. The cells themselves always possess a delicate primordial utricle, a nucleus, and starch-grains ; their cavity is at all stages filled with cell-sap, and never contains air. On the inside the floating-tissue passes gradually over into a dense periderm, with its cells in regular radial rows. This is continuous internally with the phellogen. Neither the cell-walls of the floating-tissue itself, nor those of the dense periderm, give the reactions of cork; they consist of unchanged cellulose. In moderately young stems it is easy to trace the remains of the epidermis and of the outermost layers of the primary cortex outside the floating-tissue. Sections through a young internode, when the formation of this tissue is beginning, show that the phellogen arises by division of the third or fourth layer below the epidermis. At first, ordinary periderm is produced all round the stem. The modification of the periderm into floating-tissue begins irregularly at various points of the circumference. At

[1] Cited by Rosanoff, l. c.

this stage the appearance presented is that of a young periderm during the development of the lenticels. In the regions where the production of floating-tissue is beginning, the phellogen is more active than elsewhere, producing more numerous tangential rows of cells towards the exterior. These cells next become rounded, while intercellular spaces appear between them. The cells then rapidly elongate, the epidermis and the two or three outermost layers of the primary cortex are forced outwards, and soon become broken through. The cells of the floating-tissue now successively assume their mature form, growing greatly in length and often branching. Only the ends of the cells and their branches remain in contact. All these changes, which, as we have seen, were at first limited to certain portions of the circumference of the stem, ultimately extend all round it; but in the later stages of growth the irregular furrowed surface of the floating-tissue still bears witness to its originally unequal development. Eventually, towards the end of the period of vegetation, the floating-tissue becomes detached, and the remaining denser part of the periderm acquires suberised walls. Thus a normal cork, of no great thickness, ultimately clothes the surface of those internodes which were before enveloped in the floating-tissue. Those parts of the stem from which this tissue is absent produce from the first an ordinary corky periderm.

The above description is chiefly founded on my own observations, which agree closely with those of Rosanoff. The conclusions which follow from the facts stated are, that the floating-tissue is here morphologically equivalent to the periderm of other Leguminosae, but that it differs from normal periderm in four respects:—(1) The cells do not lose their living contents; (2) their walls do not become suberised; (3) they have large intercellular spaces between them; and (4) it is in these spaces, and not in the cells themselves, that the air is contained.

As already pointed out, the resemblance of the floating-tissue, in its earlier stages, to the complementary tissue of a lenticel, is very striking. Possibly this may be more than a merely superficial likeness; but further comparative investigation will be necessary before this point can be decided.

Sesbania aculeata, Pers., is a very different plant from the *Mimosa*-like *Neptunia*. *Sesbania* belongs to the papilionaceous tribe Galegeae, and therefore has no near relationship with the plant already dealt with. In spite of this we shall find many points of agreement between them as regards the tissues under consideration.

Sesbania has a tall upright stem, rising high above the water; in this case the floating-tissue is developed in the aquatic roots. In external appearance the tissue much resembles that on the stem of *Neptunia*, forming soft spongy masses as described above. The roots are much branched, and it is only on the relatively main roots that the floating-tissue is formed, the finer lateral branches retaining their normal structure.

The general anatomy of the root is of the usual type; the vascular cylinder is tetrarch, pentarch or hexarch, each phloëm-group having a strand of bast-fibres on the outside, as is so common in the Leguminosae. The pericambium is at first one layer of cells only in thickness, but its cells undergo tangential divisions, beginning opposite the xylem-groups. In the oldest roots examined the pericambium was always three layers at least in thickness. This multiplication of the pericambial layers is a very common phenomenon[1], quite apart from any formation of internal phellogen, with which, as we shall see, the pericambium here has nothing to do. Opposite the xylem-groups the inmost layer of the pericambium is of course used up to complete the cambial ring. Secondary thickening takes place in these roots in the normal manner, as in *Phaseolus* or *Vicia*. The endodermis is distinctly marked, and shows the characteristic structure of its radial walls. The cell-walls of the endodermis ultimately become cuticularised throughout. The primary cortex consists of rounded cells, among which

[1] Cf. Olivier, Appareil tégumentaire des Racines, in Ann. des Sci. Nat. sér. VI, tom. XI.

are very large lacunae filled with air, the structure thus being of the usual aquatic type. It may be added that the larger roots have a persistent parenchymatous pith, while in the smaller lateral roots the groups of primary xylem meet in the middle of the vascular cylinder.

The mature floating-tissue is in most respects similar to that described in *Neptunia*. The cells are much elongated in the radial direction, but as a rule they remain unbranched (see Fig. 4). They are so arranged as to leave large intercellular spaces, containing air, between them. Each cell retains its protoplasm, nucleus, and cell-sap, throughout its existence, and air is never found inside the cells. The walls of the great majority of the cells give the reactions of unaltered cellulose. The tannin-sacs, which occur here, as well as in the primary cortex, form the only exception to this rule; their walls appear to be slightly cuticularised. These tannin-sacs also differ from the other cells of the floating-tissue in their form, which is almost spherical. Their number is insignificant compared to that of the elongated cells, and they may be left out of account in considering the general character of the tissue.

On a superficial examination, the idea suggests itself that the floating-tissue might be formed simply by the elongation of the cells of the primary cortex. Investigation of the development shows, however, that this is not the case. If transverse sections be made of a moderately young root, it is easy to find cases in which some layers of the long-celled floating-tissue are already well developed, while outside them the round-celled lacunar tissue of the primary cortex is still present, though somewhat torn by the extension of the internal structures (see Fig. 3).

The floating-tissue passes over on the inside into a zone of closely-packed cells arranged in regular radial rows, and these again fit accurately into a layer of thin-walled cells, showing recent tangential divisions, and having all the characters of an internal phellogen. Great as is the difference in form between the elongated cells of the mature floating-tissue and the flat cells of the phellogen, it is easy to find every intermediate stage. In the younger stages the radial rows can be traced outwards from the phellogen far into the floating-tissue ; in the mature state the regularity of the radial arrangement is of course less distinct, owing to the displacements which must necessarily be associated with the formation of the intercellular spaces (Fig. 4).

In the oldest roots examined the floating-tissue had become detached, leaving behind the densely-packed cells immediately outside the phellogen. The walls of these cells then become suberised, so that the old root has a corky periderm of the usual character.

The most interesting point which remains to be noticed is the place of origin of the phellogen. In a large proportion of roots with secondary thickening the pericambium, as is well known, is the layer from which the peridermal structures take their rise. To this rule, however, there are many exceptions, as has been especially shown by Olivier (l. c.), who has observed that in a large number of dicotyledonous roots the periderm is external, arising in the outermost living layer of the cortex. In *Sesbania* we have a case different from either of those I have referred to. Sections from the younger roots show clearly that the divisions to which the phellogen owes its origin begin immediately outside the endodermis, in the first or second layer of the primary cortex (Figs. 1 and 2). In some cases both these layers begin to divide (Fig. 1) ; from comparison with later stages it is probable that in this case the innermost layer alone continues its divisions for any length of time. Careful investigation of roots in every stage of development leaves no doubt that all the peridermal structures arise exclusively from this extra-endodermal phellogen ; the pericambium undergoes no further development, beyond the two or three tangential divisions above mentioned, and the endodermis is persistent throughout.

The results attained may be summed up as follows :—

1. The floating-tissue of the roots of *Sesbania* is a secondary cortical structure, arising from a phellogen.

2. This tissue, though thus falling under the definition of periderm, differs from cork in its permanently living cells, its non-suberised cell-walls, and its large intercellular spaces, in which alone air is contained. In all these respects it agrees with the floating-tissue of the stem of *Neptunia*.

3. The phellogen originates *immediately outside* the endodermis, thus differing from the phellogen of most roots with typical periderm.

It may be mentioned that the development of phelloderm, on the inner side of the phellogen, is quite insignificant in amount.

In the light of recent investigations on roots as organs of respiration[1] it seems not improbable that one function of the floating-tissue may be to facilitate the supply of oxygen to the organs on which it occurs. This tissue would then present an analogy with lenticels—a point not without interest, considering the similarity, above noticed, in the development of the two organs.

It has long been known that some species of the genus *Jussiaea* also possess modified roots, which serve as floats, and develop a special floating-tissue. The existing investigations tend to show that this tissue here forms part of the primary cortex, but a renewed investigation of these plants seems desirable[2].

I have to thank Mr. Thiselton Dyer, Director of the Royal Gardens, Kew, both for first calling my attention to the plants investigated, and also for the supply of material.

[1] Goebel, Uber die Luftwurzeln von Sonneratia, in Berichte d. Deutschen Bot. Gesellschaft, Bd. IV, Heft 6, July, 1886. Ludwig Jost, Ein Beitrag z. Kenntniss der Athmungsorgane der Pflanzen, in Bot. Zeitung, 1887, p. 601.

[2] Martins, Sur les racines aérifères des espèces aquatiques de Jussiaea, in Mém. Acad. de Montpellier, Tom. VI (1866).

EXPLANATION OF FIGURES IN PLATE XVII.

Illustrating Dr. D. H. Scott's and Mr. H. Wager's paper on the Floating-Roots of *Sesbania aculeata*, Pers.

Fig. 1. Portion of a transverse section of a young root, showing the first divisions of the inner cortical cells to form the phellogen. *l*, primary lacunar tissue of cortex. *ph*, phellogen. *e*, endodermis. *pc*, pericambium. *ph. f*, bast-fibres of a phloëm group. × 360. The shaded cells in the cortex are tannin-sacs.

Fig. 2. Similar section from a much older root. The phellogen is now in full activity. *fl*, youngest part of floating tissue. *t*, tannin-sac. Other letters as before. × 360.

Fig. 3. Transverse section of a young tetrarch root. One or two layers of the floating tissue have already been formed. The torn primary cortex is shown outside the floating tissue. Letters as before. × 120.

Fig. 4. Section of an old root, showing a portion of the floating tissue in position. Letters as before. × 200.

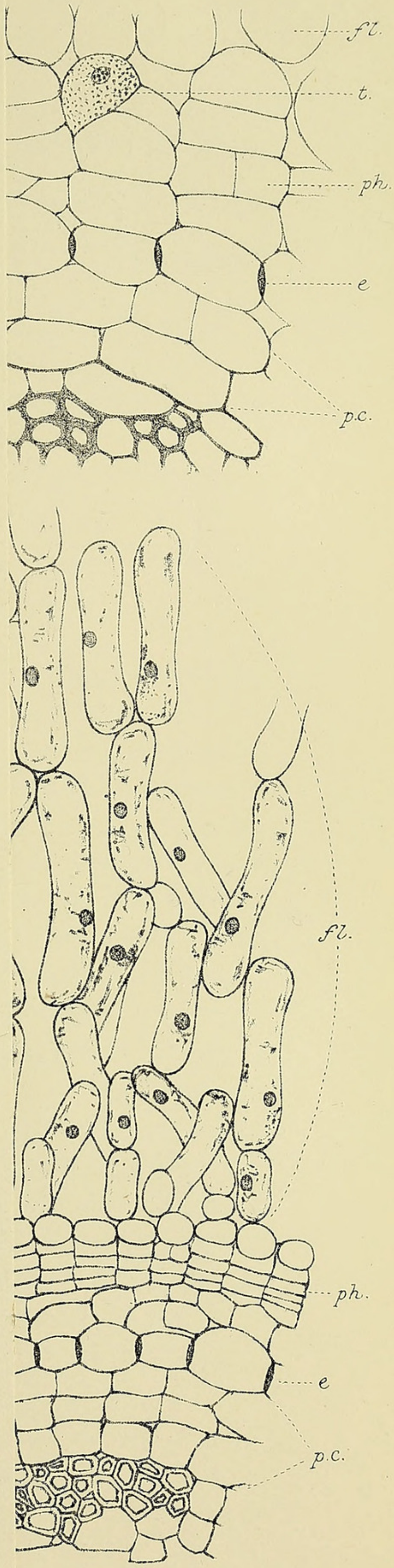

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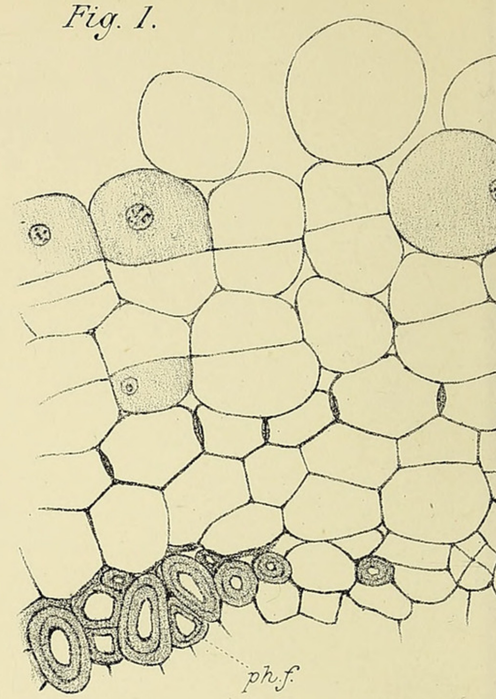
Fig. 1.



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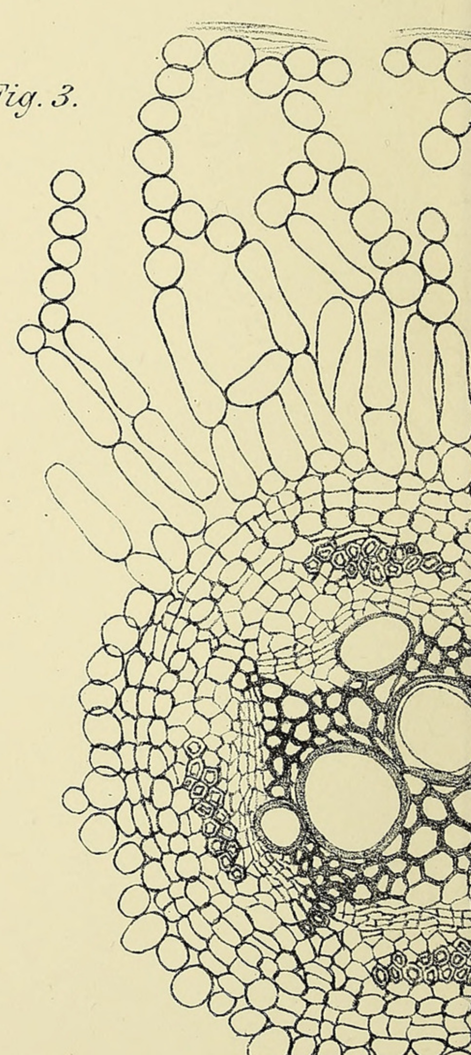

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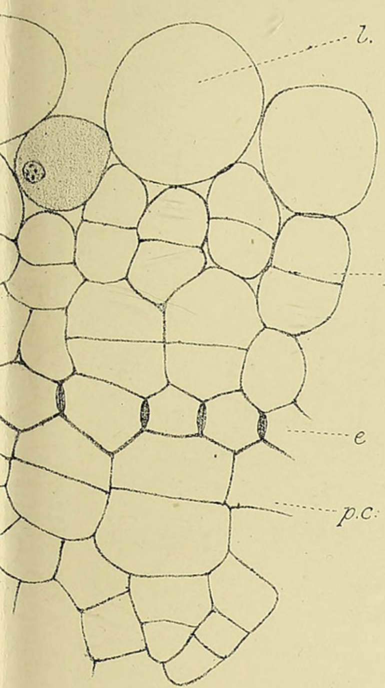

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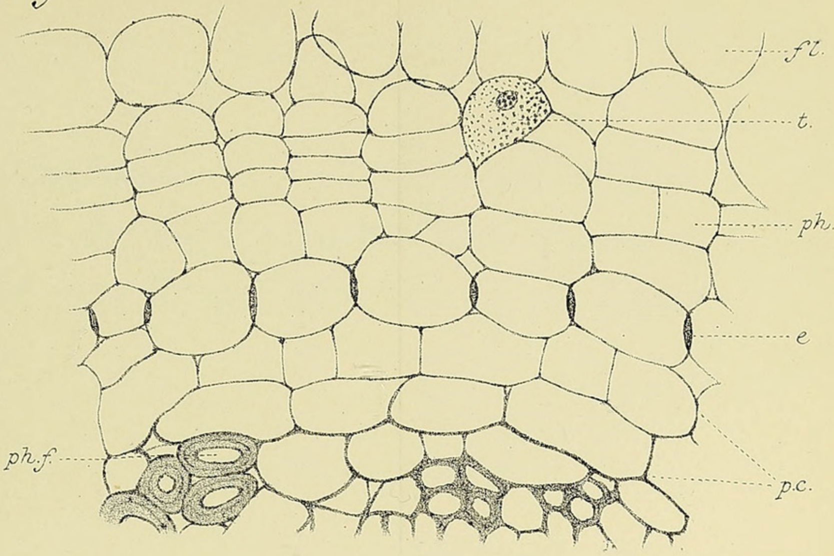

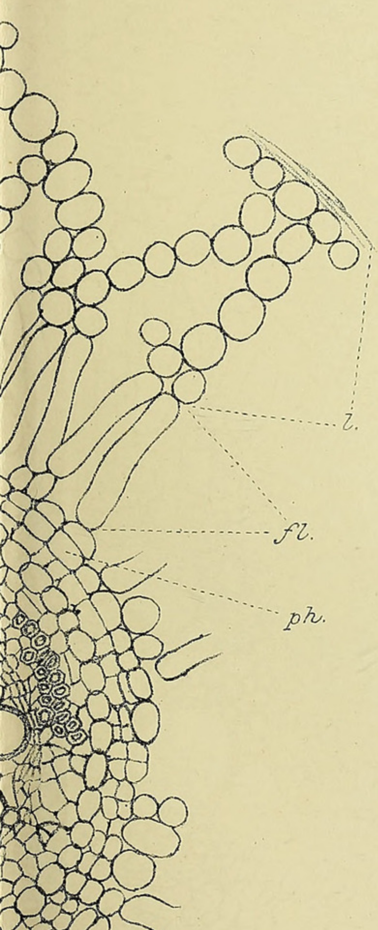

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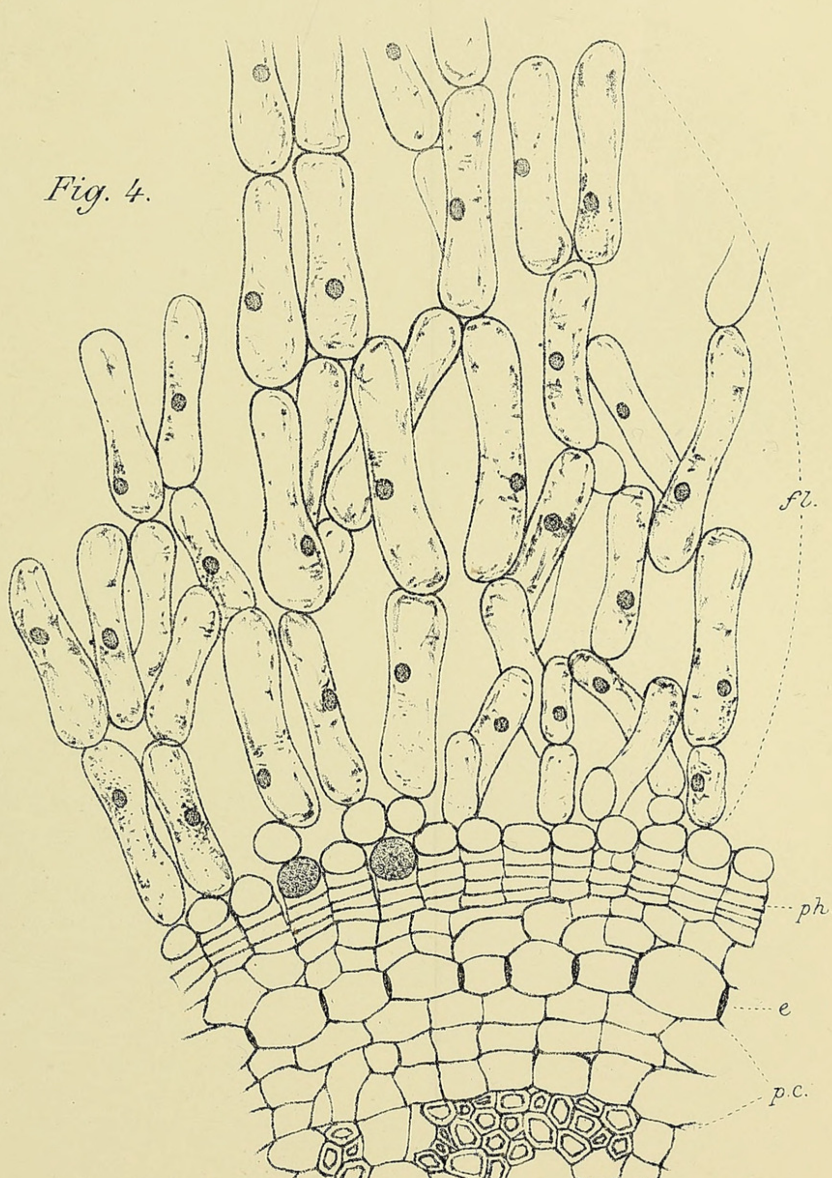

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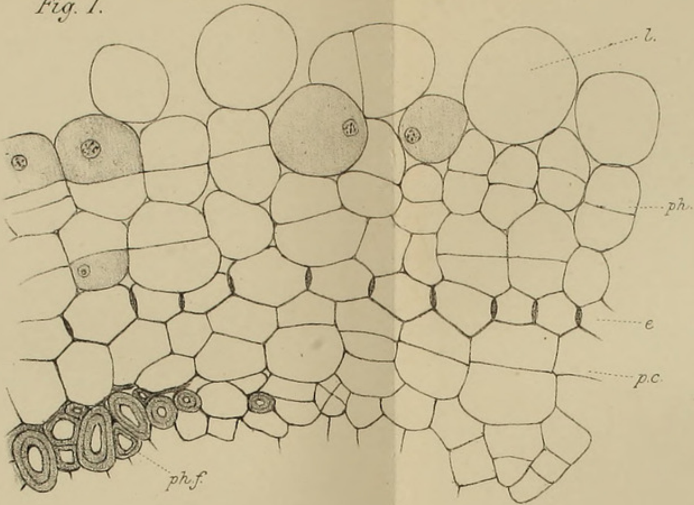
FLOATING-ROOTS IN SESBANIA.

Fig. 1.



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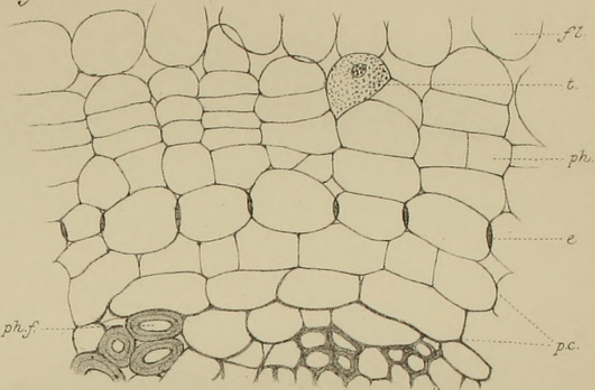

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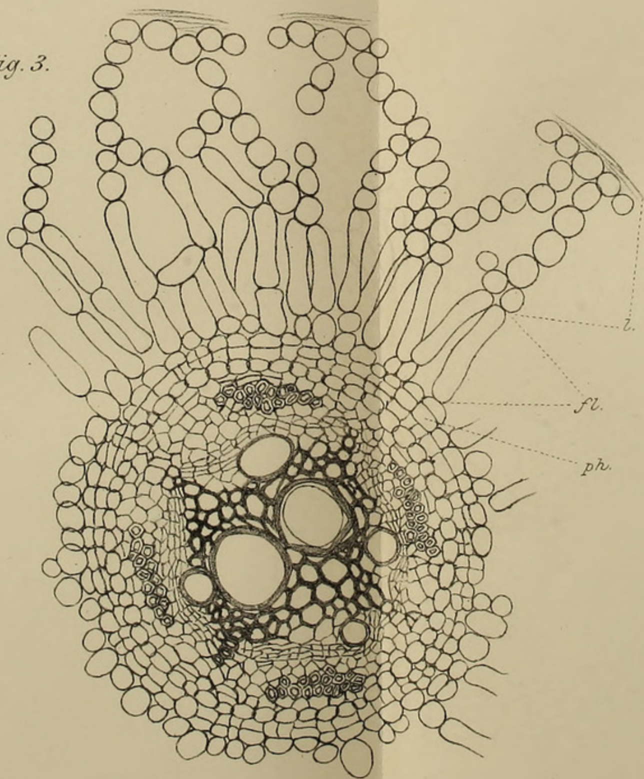

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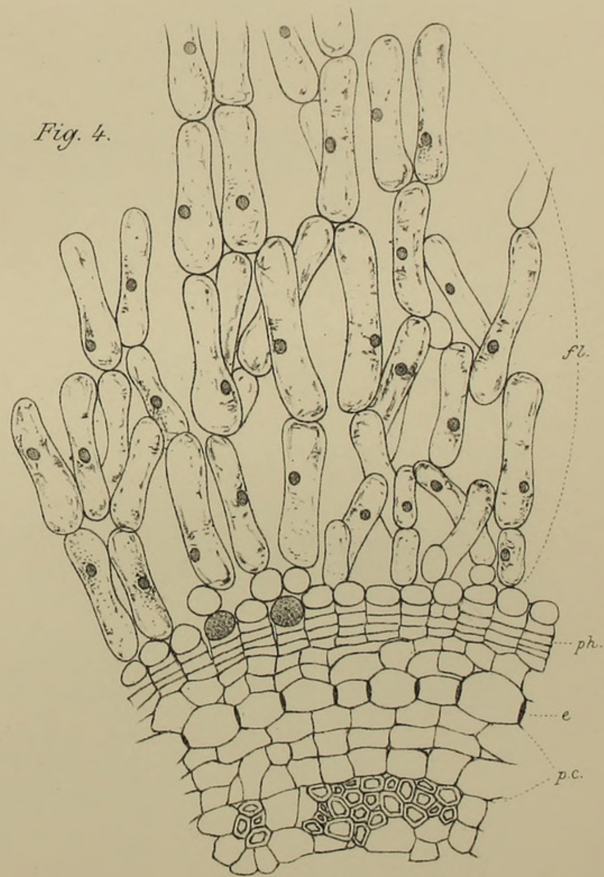

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