The Journal of the Indian Botanical Society.

(Formerly "The Journal of Indian Botany.")

VOL. VII. MARCH, 1928. No. 1.

ON THE SHOOT MORPHOLOGY OF *LIMNANTHEMUM*.

BY J. F. R. d'ALMEIDA, B.A., B.SC. (HONS).

St. Xavier's College, Bombay.

Goebel (3) was the first to elucidate the shoot morphology of *Limnanthemum*. He studied *L. indicum* and other species from this point of view. Besides this contribution and a general descriptive paper dealing with the development, branching, etc., of *L. nymphaeoides* Hoffm. and Link by Wagner (5), there seems to be comparatively very little work done on this most interesting aquatic genus. Only a very inadequate notion of the morphological nature of the parts can be gained from the Floras, as the subtler details of morphology are not discussed therein.

The following account of the two Indian species, *L. cristatum* Griseb. and *L. indicum* Thwaites, by adding further details, emphasises the interpretations of the parts given by Goebel (3) and attempts to throw light on points of morphological interest which have either not been satisfactorily explained by previous writers or have escaped their attention.

L. cristatum.

The rhizome of *L. cristatum* (Figs. 1 and 2, Rh) is erect or slightly oblique. It bears a number of leaves (Fig. 2, L), peticle-like branches which we propose to call stolons (St) and roots (Rt). In some plants (Fig. 1) the part of the rhizome formed during the previous season (Rh1)—now marked with the scars (Sc) of old stolons and bearing some old roots (Rt1)— may still be found attached to the base of the portion of the rhizome (Rh) formed during the current season. The leaves that appear first on the rhizome are of the ordinary floating type characteristic of Nymphaeas consisting of orbicular, deeply cordate blades borne peltately on petioles which vary in length

with the depth of the water (Fig. 2, L). The petiole is slightly compressed at the base, where it bears a pair of thin membranous, adnate stipules (S). As we proceed upwards on the rhizome these floating leaves show a gradual transition to membranous scales. The latter are derived from the former by a process of reduction in which the petiole becomes flattened out and the blade dwindles down in size and changes in shape, becoming spathulate (L1), lanceolate, and finally disappearing altogether leaving the flattened petiole and midrib in the form of a subulate membranous scale-leaf (L2). These leaves Goebel (3) calls *Niederblätter* (under-leaves). The long-petioled floating leaves of the rhizome bear no branches in their axils but the scale-leaves which later on appear instead of them higher up the rhizome have each in their axil a branch, the stolon, very much resembling the petiole of the floating leaf described above except for the absence of stipules. Each stolon bears at the surface of the water a short-petioled floating leaf (Figs. 1, 2 and 3, L3) and an inflorescence (Figs. 1, 2, and 3, If). Between these two is an abbreviated stem (Figs. 2 and 3 AS) which arises as a bud (vegetativer Spross.) This abbreviated stem resembles the parent rhizome and repeats the production of stolons (Fig. 3, St1) in the axils of scale-leaves (L4). From the abbreviated stem may hang down into the water a few stout roots (R) of a green colour which are usually branched. Each stolon borne on the abbreviated stem in turn bears a short-petioled floating leaf, an inflorescence, and an abbreviated stem like the parent-stolon and in this way the branching may go on indefinitely (Fig. 3).

It was at first supposed that the long stalk given off from the rhizome (which we have here called stolon), since it bore both lamina and flowers, was a petiole, and that the flowers were borne laterally from it. Such a view was entertained by Grisebach (4), Eichler (2) and others. Goebel (3) has shown this interpretation of the parts to be erroneous, that the leaf though occupying a terminal position is in reality a lateral organ, whilst the inflorescence is terminal and that in the course of development the leaf has pushed the growing point to one side and comes to occupy a terminal position. This being the case, the abbreviated stem which grows out of a bud between the leaf and the inflorescence is really an axillary branch and the branching of the plant is to be looked upon as a mixed cyme. The petiole (p) of the floating leaf which is only about ·5-3 cm. long has a sheathing base which together with its stipular appendages envelopes and protects the inflorescence when young and persists as a collar round its base after it has expanded. This collar is very conspicuous in *L. indicum* (Figs. 5 and 6 Sh). The inflorescence is not cymose as

has been described in the case of *L. nymphaeoides* by Wagner (5) and in the case of other species by Goebel (3). Neither in *L. cristatum* nor in *L. indicum* is there a terminal flower. The inflorescence in both these plants is of the racemose type and may be described as a corymb with a very short main axis. The individual flowers spring from the axils of small membranous scale-like bracts (Figs. 3 and 6 Br). They are borne on long pedicels and expand one at a time in acropetal succession.

L. indicum.

L. indicum is a much larger plant, with larger leaves (up to 30 cm. or more in diameter) and stouter stolons. The rhizome is much thicker and the stolons spring in the axils of membranous scales as do those of *L. cristatum*. The roots borne by the abbreviated stems are not, however, green like those of the latter plant.

From the specimens examined the writer is unable to say whether there are any long-petioled floating leaves in *L. indicum* like those which first appear on the rhizome of *L. cristatum*. Goebel (3) has suspected the existence of such leaves in younger plants which he has not had the opportunity to investigate. The presumption, on the whole, seems to be in favour of their occurrence in younger plants, and this presumption is confirmed by the fact that the abbreviated stem (borne on the stolon) which is to be looked upon as the morphological equivalent of the rhizome has in addition to the ordinary subulate scale-leaves (L1) one or more scale-leaves (Figs. 5 and 6 L2) which possess a type of floating lamina (f) which is clearly an approach to the peltate floating lamina borne on a long petiole.

Goebel (3) considers that the peculiar habit of the plant, in having both the flowers and the foliage leaf on one and the same stalk, confers a definite biological advantage. In the first place the broad swimming leaf lying on the surface of the water gives the inflorescence the requisite support and enables it to raise its flowers well above the water-surface so as to attract insects. In addition to this the stolon forms a substitute for both the elongated petiole and peduncle of the water-lilies, so that the materials assimilated in the floating leaf-blade find their way by the shortest route to the ripening fruit instead of, an in *Nymphaea*, having to descend to the rhizome down the petiole and then to ascend again a similar distance up the peduncle. "But," as Goebel suggests, "such an arrangement as met with in *Limnanthemum* would have less value in the case of water-lilies, because the *Nymphaceae* store so much food in their rhizome that the ripening of the fruit is not dependent upon the

products of contemporaneous assimilation" (3). According to Arber (1) it would be "utterly unsafe to suppose that the morphological differences between the water-lilies and *Limnanthemum* are to be explained on such simple adaptational lines, though it is obvious, from the success which both families achieve that their respective types of construction must be well suited to aquatic life." To the present writer's mind the totally different structure of these two genera of water plants is to be attributed to their having sprung from phylogenetically distinct stocks whose original construction was so different from each other that, when they took to the water, each evolved along the lines laid down in its original structure and produced types which, though differing widely from each other, were equally suited to live in water, in other words to achieve the same object, in two different ways.

We have seen above that the floating leaves first borne by the rhizome have no stolons in their axils, but that the upper scale-leaves bear each in their axils a stolon from which springs laterally a large floating leaf. It appears that the occurrence of the latter renders the possession of laminae by the radical leaves which subtend the stolons superfluous. These leaves consequently undergo reduction to mere scales.

The most conspicuous feature of the two species of *Limnanthemum* just described is the repeated branching by means of vegetative buds which become abbreviated stems as seen in Figs. 3 and 5. This branching is carried on on all sides without stint. Thereby the plant is able to explore the surrounding expanse of water so as to cover the surface with a close mosaic of leaves which not only secures for the plant the best illumination but also effectually checks the growth of competitors. The development of adventitious roots in connection with each abbreviated stem provides an efficient means of vegetative multiplication, since by means of these roots each abbreviated stem is clearly able to feed itself and live an independent life in case it should become separated off from the rest of the plant (e.g. by the decay or breaking up of the connecting shoot or stolon). In this connection it may be mentioned that *Limnanthemum* is very tenacious of life. Pieces of the lamina of *L. cristatum* are capable of producing new plants (Fig. 4) and detached flowers of *L. indicum* may bear adventitious roots.

In conclusion it will not be out of place to observe that in *Limnanthemum* we have a type of water-plant which is intermediate in habit between the *Nymphaea* type which is rooted in the mud and the floating type whose roots do not penetrate the soil but hang freely in the water. The habit and mode of growth of *Limnanthemum*

suggest the lines along which floating plants have evolved from a type of plant originally rooted in the mud which like *Limnanthemum* were capable of producing, at the ends of branches that floated up to the surface of the water, plantlets which could live independently when detached.

Explanation of Figures.

Fig. 1. *Limnanthemum cristatum* Griseo. Plant with rhizome, stolons and roots. *Rh*, rhizome of the present season; *Rh1*, rhizome of the previous season; *St*, stolon; *Sc*, scars on the portion of the rhizome formed during the previous season; *Rt*, roots borne on the part of the rhizome of the present season; *RtI*, roots of the portion of the rhizome of the previous season, *If*, inflorescence; *L3*, blade of the short-petioled leaf; *p*, petiole.

Fig. 2. A plant of *L. cristatum* Griseb. showing the transition from long-petioled floating leaves (*L*) to scale-leaves (*L2*) in the axils of which the stolons (*St*) arise. *S*, stipule of the long-petioled leaf; *Sh*, stipule of the short-petioled floating leaf (*L3*) forming a collar round the inflorescence (*If*); P. petiole of short-petioled floating leaf; *AS*, abbreviated stem which arises as an axillary bud between the inflorescence and the leaf.

Fig. 3. Upper portion of the shoot of *L. cristatum* Griseb. to show the branching. *St*, stolon borne on the rhizome; *If*, inflorescence; *br*, bract; *L3*, short-petioled floating leaf; *P*, its petiole; *L4*, scale leaves on the abbreviated stem (*AS*) in the axils of which stolons (*St1*) arise; *R*, roots borne on the abbreviated stem.

Fig. 4. Fragment of the leaf-blade of *L. cristatum* Griseb. which has produced a new plant. 1, 2, 3, 4 are the leaves in order of succession; *R*, roots.

Fig. 5. Upper portion of the shoot of *Limnanthemum indicum* Thwaites to show the branching. *St*, *St1*, *St2*, stolons borne respectively on the rhizome and the successive abbreviated stems; *L*, leaf-blade of the short-petioled leaf, *P*, its petiole; *If*, *If1*, *If2*; Inflorescences on the successive; stolons; *R*, roots coming off from the abbreviated stem; *L1*, Scale-leaf (subulate) on the abbreviated stem; *L2*, leaves on the abbreviated stem with floating laminae (*f*).

Fig. 6. Portion of the shoot of *L. indicum* Thwaites at the level of the inflorescence borne on the stolon springing from the rhizome. *St*, stolon; *If*, inflorescence; *Br*, bracts; *P*,

petiole of the short-petioled floating leaves; *Sh*, collar round the inflorescence formed by the sheathing base and stipular appendages of the short-petioled floating leaf. *R*, roots coming off from the base of the abbreviated stem; *L1* and *L2*, subulate scale-leaves and leaf with floating lamina (*f*) borne on the abbreviated stem; *St1*, stolon borne on the abbreviated stem.

References to Literature.

1. Arber, A. (1920) Water Plants, pp. 39–40.
2. Eichler, A. W. (1875) Blütendiagramme I, p. 246.
3. Goebel, K. (1891) Morphologische und biologische Studien. VI Limnanthemum pp. 120–126. *Annales du Jardin Botanique de Buitenzorg*, Vol. IX.
4. Grisebach, A. H. R. (1845) In Decandolle Prodromus IX, p. 139.
5. Wagner, R. (1895) Die Morphologie des Limnanthemum nymphaeoides (L) Lk. *Bot. Zeit.* Jahrg. 53, Abt. I. pp. 183–205.

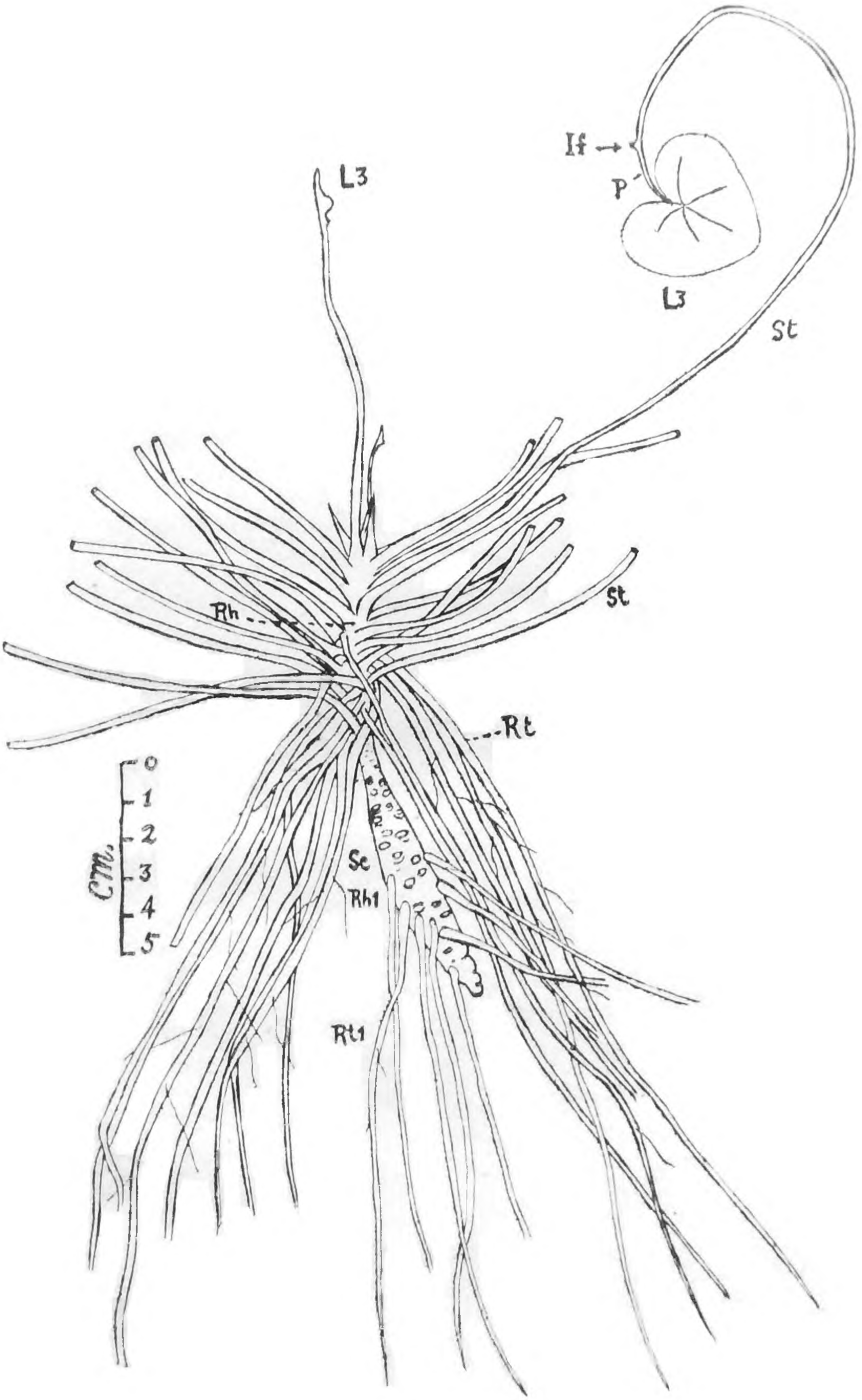

Fig. 1.

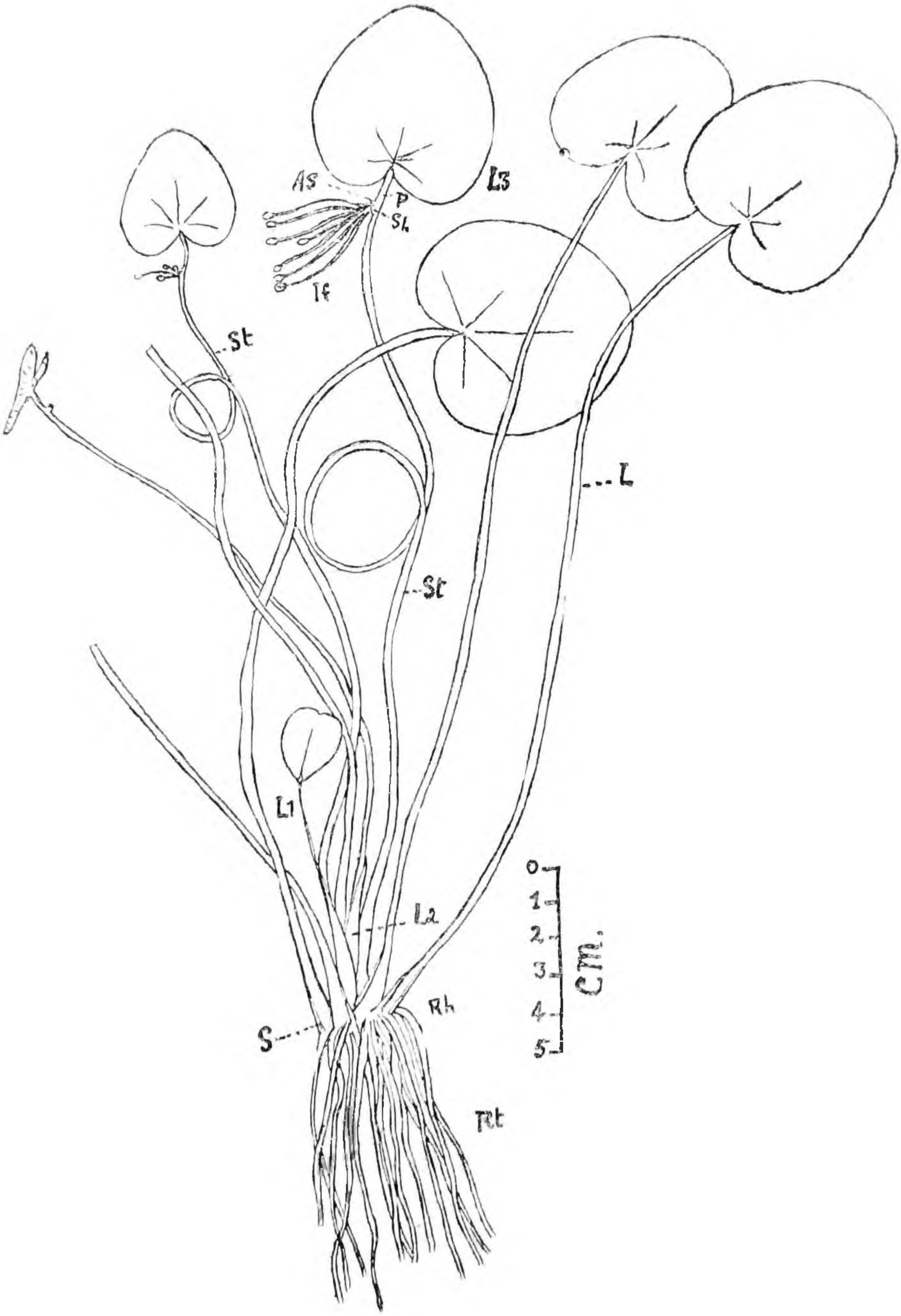

Fig. 2.

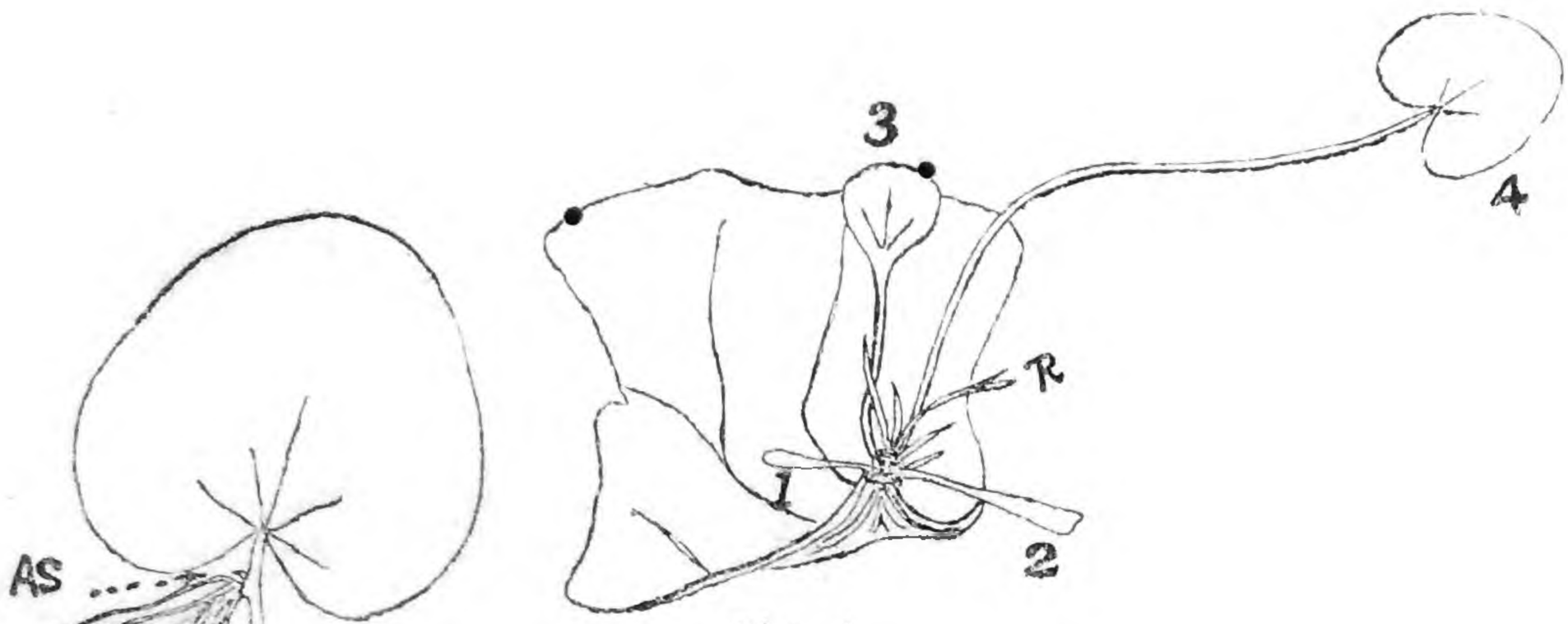

Fig. 4.

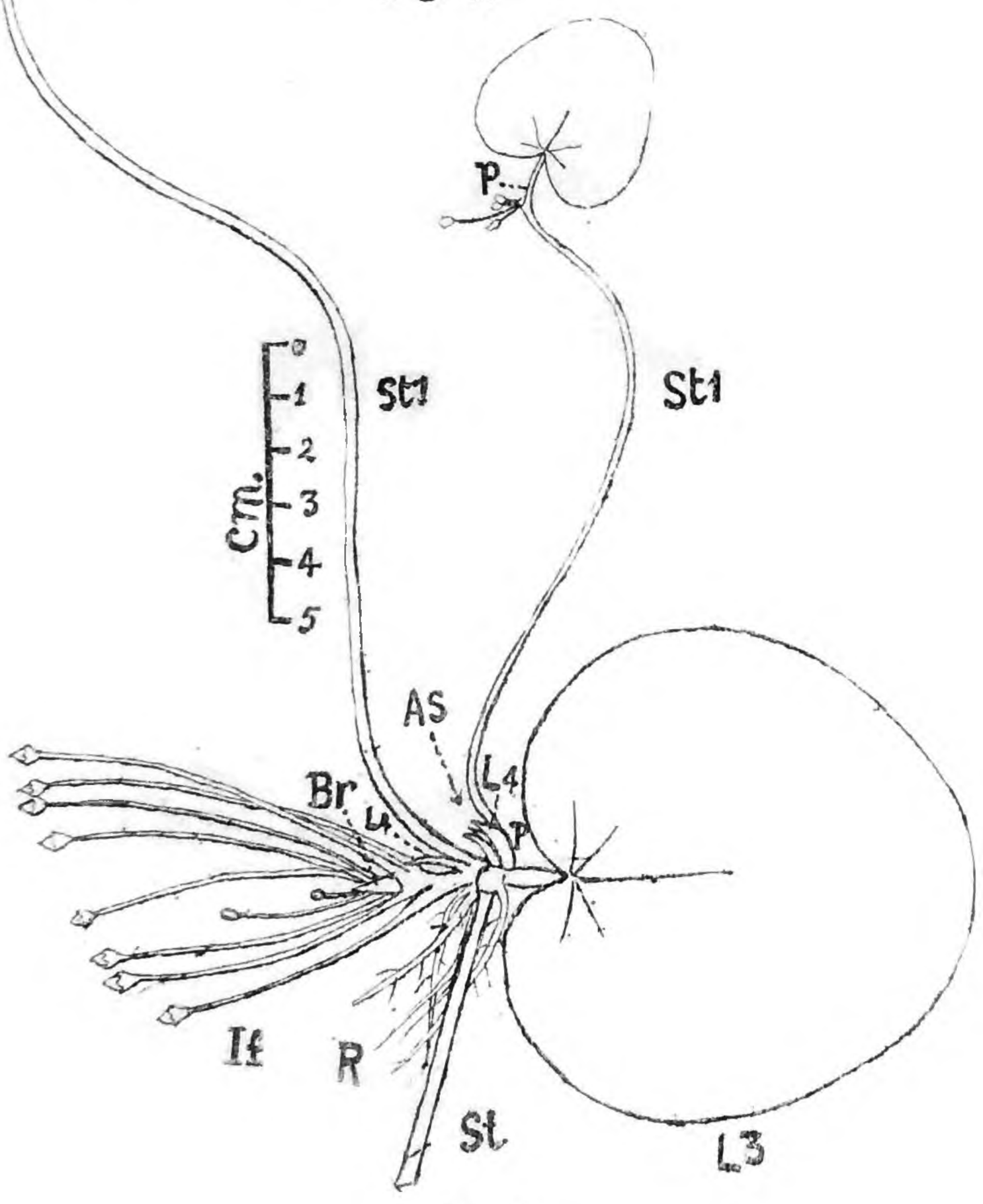

Fig. 3.

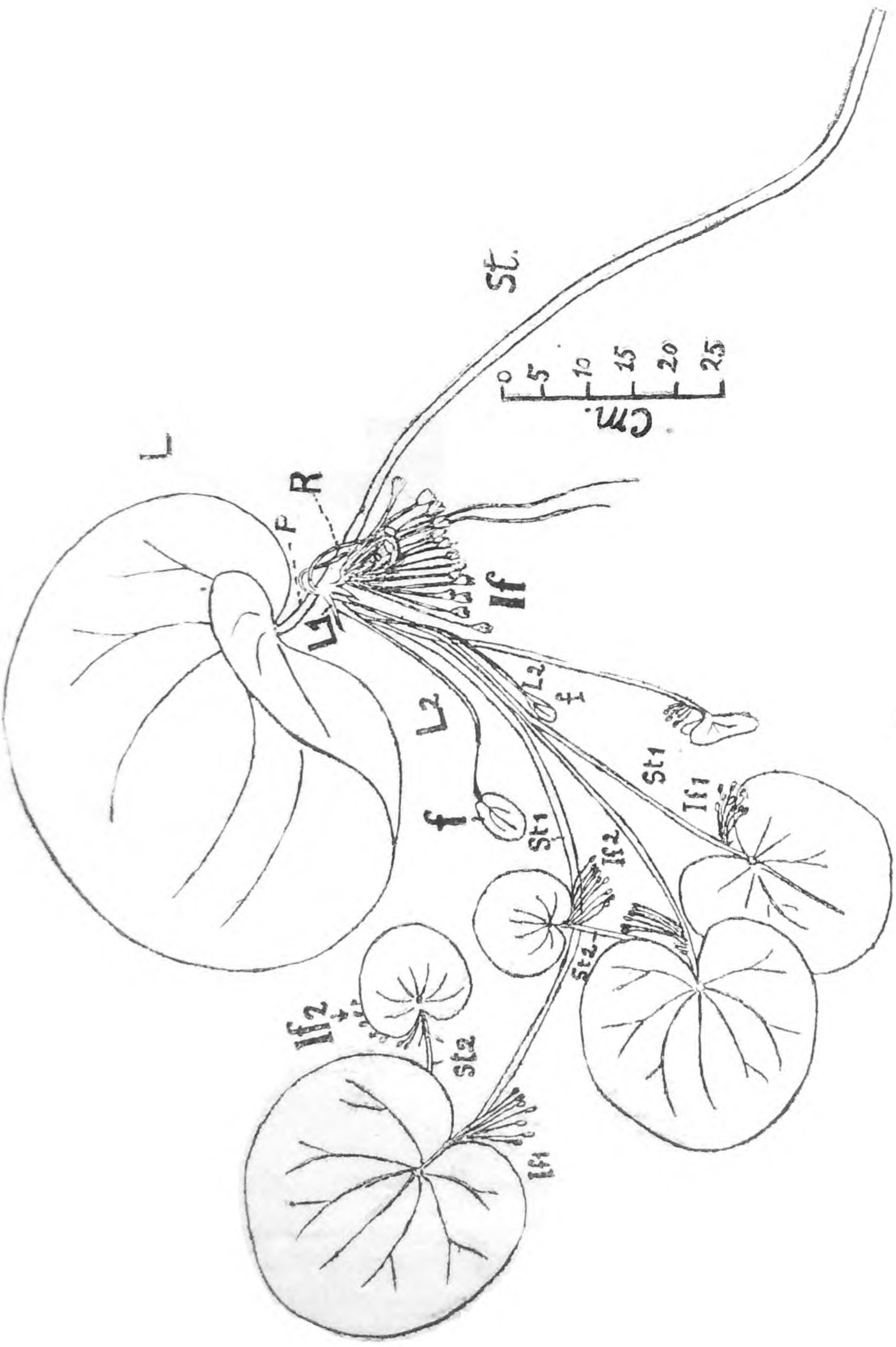

Fig. 5.

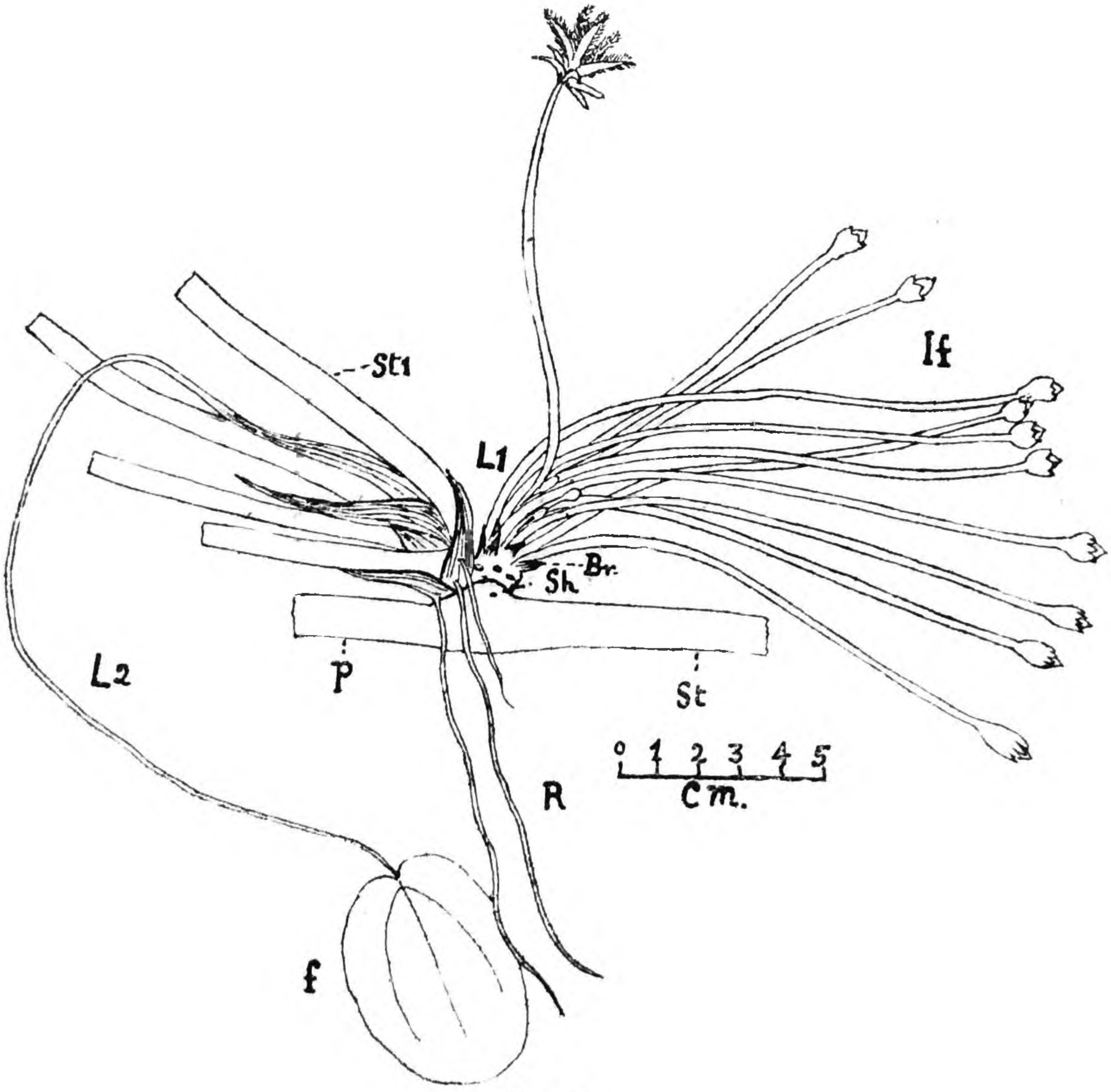

Fig. 6.