The Vegetative Morphology of Pistia *and the Lemnaceæ.*

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Introduction.

The nature of the duckweed "frond" has presented a baffling problem to botanists since the early days of vegetable morphology. A detailed history of the views that have been held on the question need scarcely be attempted here, since the extreme reduction of the Lemnaceæ has offered scope for wild surmises of little scientific value.* The principal theories which have been put forward may, however, be summarised as follows:—

The "fronds" of the Lemnaceæ have been regarded as:—

(1) Entirely axial (Hegelmaier, F. (1868)).

(2) Entirely foliar (Goebel, K. (1891–3)).

(3) Foliar in the distal region and axial in the proximal region (Horen, F. van (1869), Engler, A. (1877), and Velenovský, J. (1907)).

The objections to (1) and (2) are obvious: these views can only be maintained if—in the first case—certain essentially foliar qualities be attributed to stem organs, and—in the second case—if leaves be assumed to possess some of the distinctive properties of stems. It is not inconceivable that such assumptions might find justification, but they should only be used as a last resort, in the case of no adequate explanation on normal lines being forthcoming.

The third view, first suggested by van Horen,† has been placed on a thoroughly sound basis by Engler's‡ exhaustive comparative study of the morphology of the more typical Araceæ and of their relation to *Pistia* and the Lemnaceæ. There is no doubt that the comparison of the river lettuce (*Pistia Stratiotes*, L.) and the duckweeds supplies the clue to the problem. Engler interprets the region of the frond of the Lemnaceæ above the basal "pockets" (Taschen) as of foliar nature, and he considers the buds developed in these pockets as the equivalents of the lateral shoots of *Pistia*, the main difference being that, in the river lettuce, only one bud is developed in connection with each leaf, while in the duckweeds there are two, one on each side. The position of the buds, which are lateral in relation to the leaf-limb, is the same in both. In the Lemnaceæ the axis of the vegetative plant is so

* See, for example, Dutailly, G. (1878).

† Horen, F. van (1869).

‡ Engler, A. (1877).

far reduced from the *Pistia* type as to bear only one leaf in a pseudo-terminal position, with two lateral buds; while in *Pistia* the stem bears a rosette of numerous closely-placed leaves accompanied by a series of lateral shoots.

The soundness of Engler's general position in regard to *Pistia* and the Lemnaceæ can scarcely be doubted by any botanist who studies his memoir on the Araceæ. There remain, however, two questions, to which he does not allude, but which seem to me to require answers. These questions are:—

(1) What region of the leaf do the "limb" of *Pistia* and the distal part of the "frond" of the Lemnaceæ represent?

(2) What is the exact morphological nature of the "pockets" of the Lemnaceæ, and what is their equivalent—if any—in the *Pistia* shoot?

The present paper is an attempt to find some solution of these two problems.

The Vegetative Morphology of Pistia Stratiotes, *L.*

The main part of the leaf of *Pistia* consists of a limb which is ob-cuneate or fan-shaped, with parallel veins, deeply grooved, and, especially in young stages, densely hairy. It is often much swollen—particularly in the median basal region—with air-containing tissue. A ligule, which is sheathing in its upper portion, occurs between the "limb" and the axis at the extreme base of the former.* This makes it obvious that the "limb" cannot be interpreted as of the nature of a leaf-sheath, and we are left with the alternatives that it may represent petiole, or lamina, or both. On the phyllode theory of the Monocotyledonous leaf, which I have advocated in a previous paper,† we should expect the lamina to be absent, while the limb would be of the nature of a flattened petiole—and there is nothing in its form and venation to make this view untenable. But for positive evidence we must look to the internal structure. Attention was drawn some years ago by a Japanese botanist‡ to certain features of the leaf anatomy, but the peculiar arrangement of the vascular bundles appears to have been hitherto overlooked. I have found, on cutting transverse sections, that, in addition to more than one row of normally orientated strands (*n.b.*, in figs. 1 and 2), there is, towards the upper surface of the leaf, a series of bundles with inverted orientation, *i. b.* In the paper already cited I have given reasons for regarding the presence in a leaf of such inverted bundles as an indication of petiolar origin. We may thus conclude that the relation of the leaf-limb of *Pistia Stratiotes* to its ligule, together with the evidence of its form, venation, and vascular anatomy, appear to

* Domin, K. (1911).
† Arber, A. (1918).
‡ Ito, T. (1899).

indicate that this organ is of the nature of a petiolar phyllode, flattened in the horizontal plane.

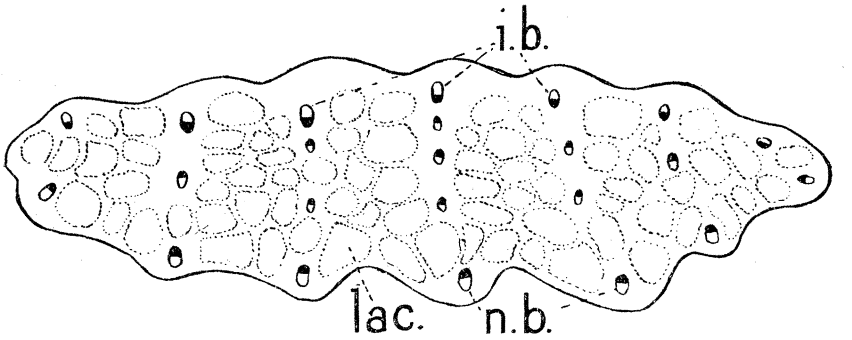


FIG. 1.

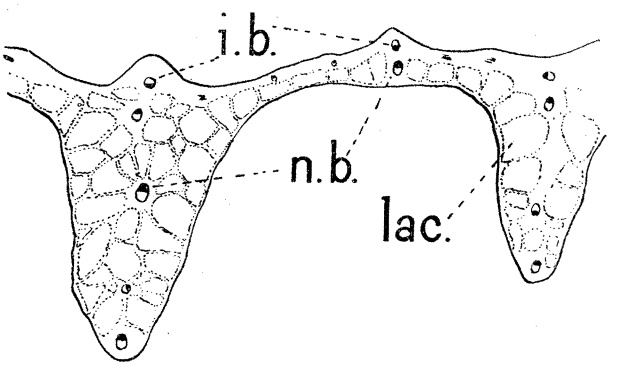


FIG. 2.

FIGS. 1 and 2.—*Pistia Stratiotes*, L. Transverse sections of leaf (×21). Fig. 1, complete section near base of leaf. Fig. 2, two of the ribs in the median region of the fan-shaped limb; *n.b.*, normally orientated vascular bundle; *i.b.*, inversely orientated bundle; *lac.*, lacuna.

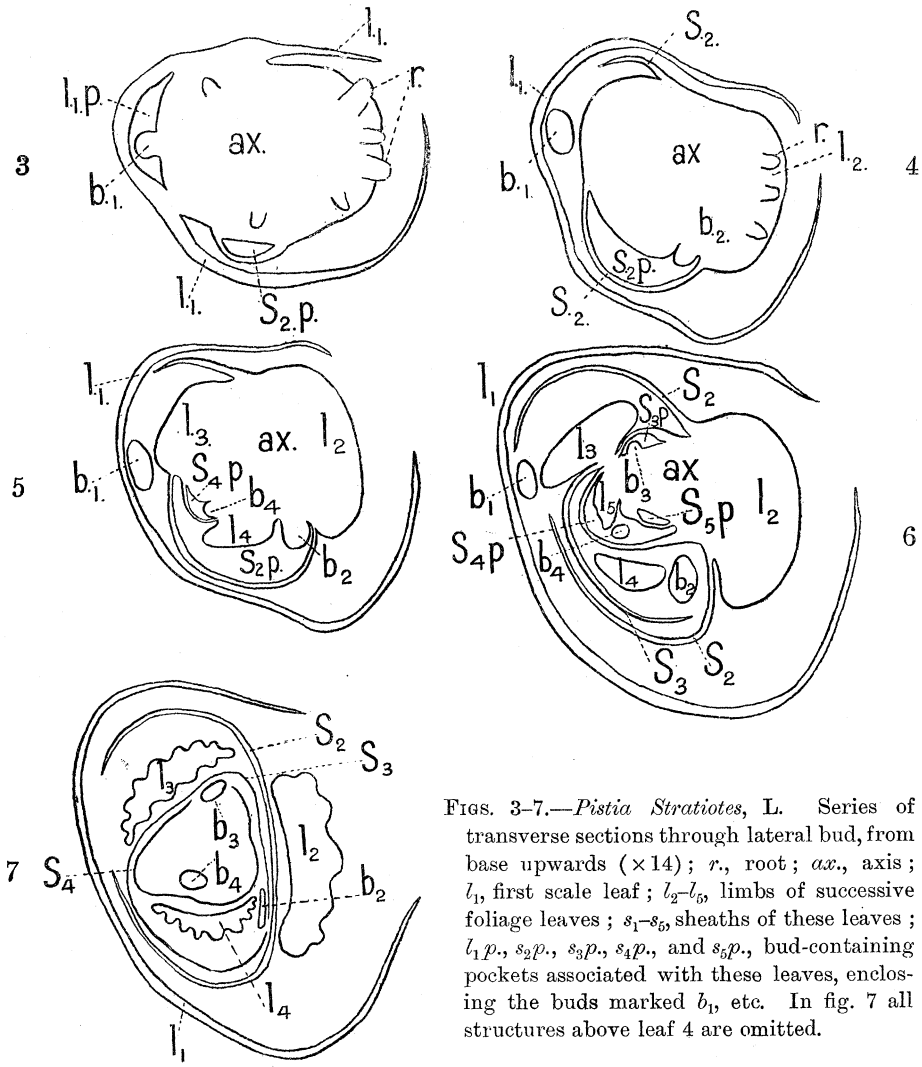
The distal region of the frond of *Spirodela polyrrhiza*, Schleid., the greater duckweed, bears a strong general resemblance to that of *Pistia*, both in form, venation, and development of air-tissue. The vascular system is, however, much simplified, and only one series of bundles remains. These are normally orientated, but in such a reduced type of leaf, in which, as compared with *Pistia*, several rows of bundles may be supposed to have been lost, it is not surprising that the inversely orientated series has failed to survive. There seems every reason to interpret the distal part of the frond of the Lemnaceæ as a petiolar phyllode—exactly equivalent to that of *Pistia*—especially if, as we hope to show, both sheath and ligule of the river lettuce are represented in the proximal region of the frond of the greater duckweed.

When we turn to Engler's figures and description of the *Pistia* shoot, we find no indication of anything corresponding to the "pockets" of the Lemnaceæ, while the buds are represented as situated *between* the ligule and the limb of the leaf. No drawings are given showing the actual origin of the buds from the axis, the diagrammatic transverse sections of shoots being all taken above the level of the apex of the axis. Engler's paper was published in the seventies of the last century, that is to say before the microtome had become one of the recognised instruments of botanical research. Now it happens that the extreme abbreviation of the axis in *Pistia* makes it almost impossible to follow the detailed relations of the parts of the shoot without the help of serial sections; this difficulty is enhanced by the fact that the levels at which the leaves become free from the axis are not consistent with their actual order of development (*cf.* figs. 3–7). It is probably for these reasons that my re-examination of *Pistia* has led to somewhat different results from those of Engler—results which serve, however, to corroborate and extend his general view regarding the relation of *Pistia* to the Lemnaceæ.

It is not easy in this country to obtain supplies of *Pistia* plants with actively growing axillary shoots suitable for microtoming, and the present account is based upon material in which only two buds proved perfectly adapted for the purpose. Fortunately one of these, which was entirely vegetative, displayed the general structure with great clearness. I am indebted to the Director of the Royal Botanic Gardens, Kew, for living plants, and to Prof. A. C. Seward, F.R.S., for herbarium material.

The axis of the developing bud of *Pistia*, which is illustrated by the transverse sections shown in figs. 3–7, bore, firstly, a zone of adventitious roots, r, in fig. 3, immediately followed by a sheathing scale-leaf, l_1. This was not attached to the axis in the median line, but considerably to one side, thus showing an asymmetry which was also displayed by the sheathing region of the normal leaves. The broader free segment was again fused with the axis at a second point of the circumference, thus forming a small pocket ($l_1p.$). Within this pocket a bud, b_1, was developed from the axis. The second leaf, l_2, which was a normal foliage leaf, behaved in an essentially similar manner, with certain modifications due to the possession of a differentiated limb. Below the level at which the limb became free from the axis, there was a distinct sheath forming a free flap, s_2, on one side, while on the other side it was free for a short distance laterally and then again attached to the axis, thus forming a pocket ($s_2p.$) containing a bud, b_2. Higher up, the margin of the pocket became free like the opposite sheath-wing (*cf.* figs. 5 and 6), and, higher still, this sheath detached itself entirely from the limb, and the two wings fused into a free axillary ligule (fig. 7).

The bud permanently occupies a position at the side of the limb, and lies between the sheath of the leaf to which it belongs and the axis. It is not necessary to follow the history of the succeeding leaves, l_3, l_4, etc., which form bud-pockets in a precisely similar way. The peculiar lateral position



FIGS. 3–7.—*Pistia Stratiotes*, L. Series of transverse sections through lateral bud, from base upwards (×14); *r.*, root; *ax.*, axis; l_1, first scale leaf; l_2–l_5, limbs of successive foliage leaves; s_1–s_5, sheaths of these leaves; $l_1p.$, $s_2p.$, $s_3p.$, $s_4p.$, and $s_5p.$, bud-containing pockets associated with these leaves, enclosing the buds marked b_1, etc. In fig. 7 all structures above leaf 4 are omitted.

of the buds may perhaps be interpreted as due to the congenital fusion of the base of the limb with the axis; this fusion obliterates the space which would normally be occupied by the bud.

It will be recognised, from the description just given and from the accom-

panying figures, that my observations conflict with those of Engler, who regards the bud as occupying an anomalous position *outside the sheath.* I am also unable to confirm Velenovskýs* statement that the buds are originally median, but are forced by pressure to occupy a lateral position; they are undoubtedly, from the first, completely lateral to the limb, though lying inside the sheath.

The Comparison of Pistia *and* Spirodela.

The interest of the points in which my results conflict with those of Engler and Velenovský, lies in the fact that, in every case in which I differ from these two writers, my results point to an even closer morphological relation between *Pistia* and the Lemnaceæ than has been hitherto claimed. It seems clear that the lateral bud-containing pockets formed by the sheath of *Pistia* are exactly equivalent to the pockets of the Lemnaceæ. The sketch of a *Spirodela* plant seen from below (fig. 8) will perhaps help to explain this

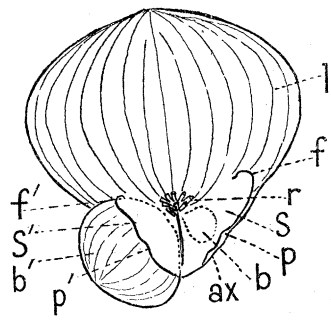


FIG. 8.—*Spirodela polyrrhiza*, Schleid. A plant viewed from the underside (enlarged); *l.*, limb of leaf belonging to main axis, *ax.*; *r.*, roots (cut short); *p.* and *p′.*, pockets between wings of sheath (*s.* and *s′.*) and axis, enclosing buds, *b.* and *b′.*; *f.* and *f′.*, ligular flaps of sheath.

relation. The petiolar phyllode, *l*, passes at its base into the reduced and flattened axis, *ax.*, of which it forms the apparent continuation, exactly as the spathe of *Acorus* continues down into the scape, but with the difference that in *Spirodela* the growing point of the axis completely aborts, whereas in the fertile shoot of *Acorus* it forms the spadix. Just where the limb of the duckweed frond fuses with the axis, a group of roots, *r.*, takes its origin. We find an analogy to this in *Pistia*, where fig. 4 shows roots arising from the base of the limb of leaf 2, at the level of its junction with the axis. The two wings of the sheath of *Spirodela*, *s* and *s′*, are developed, just as in *Pistia*, below the attachment of the limb to the axis. They do not meet and fuse into a

* Velenovský, J. (1907).

conspicuous axillary structure, as in *Pistia*, but the two small free flaps, *f* and *f'*, may be interpreted as reduced ligules. The basal regions of the two sheath-wings each form a bud-containing pocket, *p* and *p'*, equivalent to the one sheath-pocket accompanying each leaf in *Pistia*. These pockets are ultimately open in *Spirodela*, but in younger stages they are closed in the basal region as in *Pistia*. The development of the buds in pockets between the sheath and axis, below the limb and occupying a lateral position with regard to it, is thus identical in *Pistia* and the Lemnaceæ.

Summary.

Anatomical examination of the "limb" of the leaf of *Pistia Stratiotes*, L., the river lettuce, shows that, in addition to normally orientated vascular bundles, there is a series of inverted bundles towards the upper surface. This fact is regarded as indicating that the leaf is of the nature of a petiolar phyllode. This interpretation is extended to the distal part of the frond of the Lemnaceæ (duckweeds).

The general view, put forward by Engler 40 years ago, as to the morphological relation of the Araceæ—through *Pistia*—to the Lemnaceæ, is accepted in the present paper, and it is shown that more detailed investigation by modern methods makes it possible to carry the comparison considerably further. Serial sections through a developing shoot of *Pistia* reveal the presence of a "pocket" in connection with each leaf, occurring below the level of the free part of the limb; this pocket is formed on one side by the leaf-sheath, and on the other side by the axis, and encloses a bud occupying a lateral position in relation to the limb of the leaf. It is shown that these pockets are exactly equivalent to the pockets at the base of the frond in the Lemnaceæ, which, in the case of *Spirodela*, are easily seen to be formed, on the lower side, by the wings of the leaf-sheath, terminating in two minute ligular flaps, and, on the upper side, by the axis.

Acknowledgments.

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The Genesis of Œdema in Beriberi.

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In a previous communication (1) it was shown: (1) that in avian beriberi (polyneuritis gallinarum) œdema was constantly (100 per cent.) associated with massive enlargement of the adrenal glands; (2) that 82.2 per cent. of cases having such enlargement of the adrenal glands presented evidences of œdema in some form; (3) that the enlargement of the adrenals was associated with a corresponding increase in the adrenalin-content, as determined by physiological means. Additional evidence confirmatory of these findings is recorded in the present paper.

Avian beriberi was produced experimentally in a fourth series of 22 young pigeons by means of a dietary of autoclaved milled rice (2 and 3). Detailed *post-mortem* examinations were made in all cases. The heart's blood was examined by aërobic cultural methods for bacterial organisms. Ten of the 22 cases presented evidences of œdema (Tables II and III).

The adrenal glands were removed, weighed, and the adrenalin-content immediately estimated by the method of Folin, Cannon, and Dennis (4). Similar estimations were made of the adrenalin-content of the adrenals in