THE STIPULES, PULVINUS AND STIPELS OF *DOLICHOS LABLAB* L. AND THEIR VASCULAR SUPPLY

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INTRODUCTION

Dolichos lablab is a herbaceous, prostrate or twining, plant cultivated in Bengal and elsewhere for its edible pods. Leaves are pinnately trifoliate; stipules are small, subpersistent, *cauline* (Parkin, 1948); stipels subulate, one to each of the lateral leaflets, but a pair to the terminal one; leaves and leaflets are provided with pulvini. The pulvinus of the leaf runs into the rachis which is long, grooved on the upper surface flanked by two prominent ridges which disappear at the divergence of the first pair of leaflets, but appear again on the other side and run up to the base of the terminal leaflet (Fig. 1).

VASCULAR SUPPLY TO THE STIPULES

Since the time of Colomb (1887) the origin and nature of vascular supply to the stipules has been thoroughly studied, and it is now accepted as a morphological dictum that the stipular traces are derived exclusively from the laterals of the trace of the leaf to which they belong (Sinnott and Bailey, 1914; Dormer, 1944; Mitra, 1945, 1948, 1949*a*, 1949*b*, 1950*a*, 1950*b*, 1950*c*). Mitra and Mitra and Majumdar (1952) have shown that all types of stipules (*cauline* and *adnate*, Parkin, 1948) are leaf-base outgrowths.

In *D. lablab* the node is pentalacunar and five bundles form the leaf trace, one median (M) and four laterals (L_1, L'_1, L_2, L'_2), two in each wing (Fig. 2). The laterals leave the axial cylinder before the median. On their way to join the median at the base of the pulvinus the laterals jointly give out branches in the foliar foundation (leaf-base) and each stipule receives about five feeble branches which form its trace (Fig. 3). The stipules do not develop to a great extent but they are wide at the base and subpersistent.

VASCULAR SUPPLY TO THE PULVINUS

The four lateral bundles (L_1, L'_1, L_2, L'_2) unite with one another and with the median to form a closed ring of vascular bundles in the pulvinus (Fig. 4). Sinnott and Bailey (1915) in tracing the factors involved in foliar evolution state that 'the primitive leaf with its three (or more) traces, widely separate in origin passing directly from node to lamina, was thus constricted at its base and its three (or more) bundles forced close together in the petiole' (pp. 13, 14). This feature of vascular system is characteristic of the petiole and not of the leaf-base. The pulvinus, therefore, on anatomical evidence cannot be regarded as the base of the leaf as has been suggested by Green (1897), Vines (1910), Lawson and Sahni (1949) and others.

Mitra (1950*c*) and Mitra and Majumdar (1952) have elaborated the above statement of Sinnott and Bailey (1915) and have shown that anatomically the

leaf-base and the petiole can be distinguished one from the other by the behaviour of the leaf trace bundles while passing through them to the lamina. In the *leaf-base* the laterals of the trilacunar and multilacunar nodes after leaving the axial ring run parallel for some distance and then bend horizontally or obliquely towards the median and *they unite* to form a closed ring, or an open arc, or a ring of vascular bundles *at the base of the petiole and remain so up to its top.* In *D. lablab* after a short parallel course they run horizontally in the leaf-base and unite with the median to form a closed ring in the pulvinus (Figs. 3 and 4).

Rachis is the 'back-bone' of the leaf and is defined 'as the prolongation of the petiole in a pinnate leaf forming the principal axis from which leaflets are given off' (Heinig, 1899). In *D. lablab* the pulvinus prolongs into the rachis. If the pulvinus is the leaf-base as held by the European authors, then the leaf of this plant has no petiole which seems untenable on the evidence presented here.

Stipels.—Stipels are defined as the 'stipules of a leaflet', but with a difference. Asa Gray (1879) describes stipels as 'small and slender and unlike stipules they are single to each leaflet except to the terminal one which has a pair' (p. 106; cf. also Heinig, 1899; Green, 1897; Vines, 1910; Lawrence, 1951 and others). None of them, however, appears to have studied the true morphology of the stipel except Goebel (1905).

Goebel (II, pp. 379–381) distinguished two different types of stipels: one is independent in origin, whereas the other type is a reduced pinnule. The first type is exemplified in a few species of Thalictrum (his Fig. 254). Such stipels occur in pairs to each leaflet, and they are comparable to a pair of stipules at the base of a stipulate leaf.

Stipels, which Goebel regarded as reduced pinnules, occur in Phaseolus, Robinia, Desmodium and other Leguminosae (*D. lablab* is one of them) and are found at the base of their leaflets. He writes: 'They appear usually in the form of small teeth and occasionally they are developed as leaves, e.g. upon sucker shoots in Robinia.' But Goebel himself was not very sure of his interpretation. From their position on the rachis just below the pair of lateral and the terminal leaflets, the stipels may very easily be mistaken for a pair of reduced pinnules (Fig. 1).

In *D. lablab* stipels occur, as I have already pointed out, on the ventral surface of the rachis, one to each of the first pair of leaflets, and a pair at the base of the terminal leaflet. How are we to explain this difference in the distribution of the stipels in two positions on the rachis? Vascular supply to these organs give the clue for an answer.

Vascular Supply to the Stipels of the Lateral Pair of Leaflets

Fig. 4 shows the nature of the leaf trace bundles immediately below the subapical region of the pulvinus. Just at the top of it where the pulvinus prolongs into the rachis the closed ring of bundles opens a little on its ventral side and an open arc is formed (Fig. 5). From each of the two ends of this open arc, i.e. from the distal ends of L_2, L'_2, a branch (*rb*, *rb'*) is sent out to stimulate the growth and formation of the two ridges (pulvinus is cylindrical) in which they enter and a groove is formed between them (Figs. 6 and 7). In the rachis the five trace bundles become prominent again with small branches interconnecting them (Fig. 7). This arrangement continues up to the point of the divergence of the stipels at the base of the lateral pair of leaflets. Stipels appear directly on the rachis slightly below the articulation of the leaflets to which they belong (Fig. 1).

Branches from the laterals, L_2 and L'_2, and from the ridge bundles (*rb* and *rb'*) on the two sides of the rachis are sent respectively to the two stipels to form their traces (Fig. 8). Each stipel of a leaflet thus receives, like the stipule at the base of a leaf, its vascular supply from the branches of the lateral L_2 or L'_2, and the leaflet

to which each stipel belongs, gets either L_2 or L'_2 but not both (see below), whereas the leaf with a pair of stipules receives both or all the laterals.

The stipels are, therefore, stipules to the leaflets and their position on the rachis and vascular supply explain the presence of only one stipel to each leaflet.

Vascular Supply to the Pair of Leaflets

A little higher up the rachis the first pair of leaflets diverge. The laterals L_2 or L'_2, the ridge bundles *rb* or *rb'* and a branch from L_1 or L'_1 enter the base of each leaflet on the corresponding side of the rachis, leaving only the median (*M*) and the laterals (L_1 and L'_1) to form the rachis bundle (Fig. 9).

Behaviour of the Rachis Bundle beyond the Pair of Leaflets

The rachis bundle, now constituted of only three original leaf trace bundles, proceeds to the terminal leaflet. Soon after passing the bases of the lateral leaflets L_1 and L'_1 send out a branch each to reconstitute the ridges and their bundles (Figs. 10 and 11). At the base of the terminal leaflet they (L_1 and L'_1) give out branches again, and each branch with the corresponding ridge bundle goes to constitute the vascular system of the stipels, now a pair at the base of the terminal leaflet (Fig. 12). In the pulvinus they unite with the median to form a closed ring of bundles, the characteristic feature of the petiole (Fig. 13). On entering the base of the terminal leaflet they resolve into five main branches which form the five ribs of the palmiveined leaflet (Fig. 14).

Discussion

The leaf and the leaflets: lateral and terminal.—Two or three very interesting features come out of these observations: Vascular supply to the leaf and the leaflets —lateral and terminal—does not follow the same pattern. The main leaf gets from the axial cylinder five bundles, one median and four laterals. Each lateral leaflet receives only one of these laterals (L_2 or L'_2), the ridge bundle (*rb* or *rb'*, which is also a branch of the lateral L_2 or L'_2) and a branch of the lateral L_1 or L'_1. Altogether each leaflet receives three bundles with L_2 or L'_2 forming the median. On entering the blade they resolve into five main nerves of the palmiveined blade. The terminal leaflet also receives three trace bundles, *M*, L_1 and L'_1, which on entering the blade resolve into the five main veins of the palmate leaflet, the median forming the mid-vein. On the basis of the vascular supply, therefore, the lateral leaflets cannot be regarded as equivalent to a simple leaf, but it should be regarded as equivalent to its lobe or a tooth which is equally fed by a lateral trace bundle or its branch.

The stipules and the stipel.—The stipules as usual occur in pairs at the base of the leaf. Each stipule gets its vascular supplies from the laterals of the leaf trace while on their way to the base of the petiole (pulvinus). This supports the findings of Colomb and later authors. The stipel to the lateral leaflet is one. Like a stipule it gets its vascular supplies from the second lateral on the corresponding side of the rachis, the same lateral which goes to supply the leaflet to which the stipel belongs. The absence of the other stipel to this leaflet (on the analogy of stipules at the base of a leaf, there should have been two) is easily explained because the other lateral is on the opposite side of the rachis and it forms the trace of the leaflet on this side. But in the case of the terminal leaflet, both the laterals before entering the base of the leaflet give out branches to the two stipels just like what happens in the case of a stipulate leaf with a three-bundle trace. The *rachis* is the midrib which is a continuation of the petiolar region of the leaf. The *pulvini* of the main leaf and of the leaflets on anatomical evidence are really the petiole and petiolules and not the leaf-base modified as held by the European authors.

The morphological status of the lateral leaflets.—Are they equivalent to simple leaves? Their vascular supplies do not support their simple leaf nature. The leaf of *D. lablab* receives five bundles from the nodal ring, i.e. they cause five gaps in the axial cylinder. Each leaflet, on the other hand, receives the distal lateral bundle and a branch from the first lateral. The leaflet, therefore, cannot be regarded as equivalent to a simple leaf, but is homologous with a lobe or a tooth of the same.

Summary

1. The node is pentalacunar. Two laterals from each side and the median leave for the leaf, causing as many gaps in the nodal ring.

2. Stipules are leaf-base outgrowths, and each of them receives branches from both the laterals on each side of the median.

3. Pulvinus is the petiole, and not the leaf-base modified to aid movement of the leaf.

4. Stipels are stipules of the leaflets as they receive branches from the same laterals which form their traces.

5. The presence of a single stipel to each lateral leaflet and a pair to the terminal leaflet is explained on anatomical evidence.

6. The lateral leaflets on anatomical grounds should be regarded as parts of the blade equivalent to its lobes or teeth fed equally by laterals or their branches.

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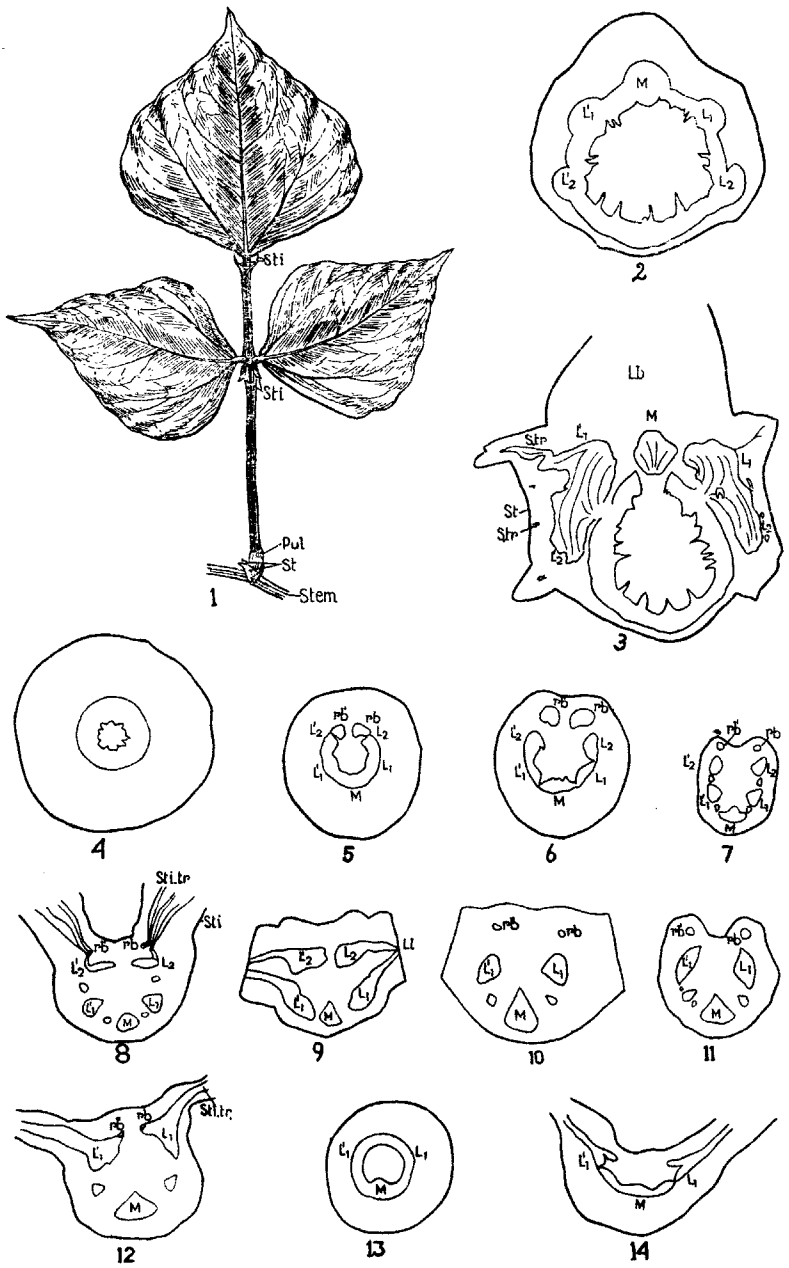
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EXPLANATION OF TEXT-FIGS. 1–14

All figures drawn under a projection apparatus under magnification noted against each figure

FIG. 1. A leaf of *D. lablab* showing the distribution of the stipules, stipels and leaflets. $\times \frac{1}{2}$.

„ 2. T.S. through the base of the node showing five leaf trace bundles prior to their departure for the leaf. $\times 8{\cdot}5$.

„ 3. T.S. through the level of insertion of the leaf showing the union of the laterals and their movement towards the median, and the origin of the stipular traces from them. $\times 8{\cdot}5$.

„ 4. T.S. of the pulvinus showing the union of the median and the laterals to form a closed ring of bundles. The median and the laterals have lost their identity in forming the ring. $\times 8{\cdot}5$.

„ 5. T.S. through the junction of the pulvinus and the rachis. The closed ring has opened on the ventral side and two ridge bundles are cut off from the distal ends of L_2 and L'_2. $\times 6$.

„ 6. T.S. through the base of the rachis showing movement of the ridge bundles and the formation of the ridges. The median and the laterals can now be distinguished. $\times 6$.

„ 7. T.S. of the rachis showing the ridges and the groove on its ventral surface and the five leaf trace bundles with their branches. $\times 6{\cdot}5$.

„ 8. T.S. through the bases of the stipels showing their vascular supplies from the laterals and the ridge bundles. $\times 6{\cdot}5$.

„ 9. T.S. through the base of the pair of leaflets showing their vascular supplies from the laterals, the median not taking part. $\times 6{\cdot}5$.

FIGS. 10 and 11. T.S. of the rachis beyond the pair of leaflets showing the beginning and reappearance of the ridges and their bundles. $\times 6{\cdot}5$.

FIG. 12. T.S. through the bases of the stipels of the terminal leaflet showing their vascular supplies. $\times 6{\cdot}5$.

„ 13. T.S. of the pulvinus of the terminal leaflet showing the ring of vascular bundles formed by the union of M, L_1, L'_1. $\times 6{\cdot}5$.

„ 14. T.S. through the base of the blade of the terminal leaflet showing the midrib region and the distribution of the first pair of veins. $\times 6{\cdot}5$.

Legend:—*Lb*—Leaf-base; *St*—Stipules; *Pul*—Pulvinus; *Sti*—Stipel; *Ll*—Leaflet; *S.tr*—Stipule trace; *Sti.tr*—Stipel trace; M—Median, and L_1, L'_1, L_2, L'_2—Laterals of the leaf trace; *rb* and *rb'*—ridge bundles.

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