THE COMPLETE FOLIAGE LEAF

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(With 8 Text-Figures)

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Generally speaking the foliage leaf is described in text-books by the shape, outline and other features of its lamina, such as, simple leaf, compound leaf, palmate and pinnate leaf and so on. But all these descriptive terms do not connote the idea of a complete leaf as understood by specialists in plant morphology.

A foliage leaf is an appendage of the axis on which it is borne. It is organically united with the stem by a *base*, its *blade* or lamina must be adjusted to sunlight and wind for which a flexible *stalk* or *petiole* is necessary. The leaf must also afford protection to its close associate, the axillary bud, in its early stages of development and rest. This it normally does by the development of a *pair of stipules* at its base. And yet the American and the European Schools of plant morphologists differ in their idea and description of a complete leaf.

The American School beginning with Asa Gray (1879) down to the modern text-book writers maintain that a typical leaf consists of three parts, namely, the *lamina*, the *petiole* and *a pair of stipules* or appendages at the base of the petiole (Eyster, 1932; Swingle, 1934; Sinnott, 1935; Hill and Popp, 1936; Lawrence, 1951, to name only a few). According to this School, therefore, *a complete leaf is without a base.*

The European School (Continental and British) on the other hand, hold that a complete leaf is made up of the *lamina*, the *petiole* and the *leaf-base*, the stipules when present are outgrowths of the latter (Bower, 1884; Green, 1897; Vines, 1910; Strasburger, 1930; Lawson and Sahni, 1949; Willis, 1951, and others). Eichler says that " stipules arise without exception as a product of the leaf-base of the primordial leaf " (Sinnott and Bailey, 1914). Goebel (1905) writes " As stipules, however, we can only designate appendages of the leaf-base." McLean and Ivimey-Cook (1951) also categorically state that " the name (stipules) should be limited to paired lateral outgrowths of the leaf-base".

There thus exists a fundamental difference between the two schools with regard to the conception of the constituent parts of a complete leaf:

in one case the leaf-base is replaced by a pair of stipules, whereas in the other case the stipules are replaced by the leaf-base, the former if present are being held as outgrowths, and therefore, a part of the latter. Even the European botanists are not very sure, so it seems, about the nature and extent of the leaf-base as they define the same as " the region by means of which the leaf is attached to the stem which bears it," though the sheathing base and the pulvinus are held by them as examples of modified leaf-bases (Green, Vines, Goebel, Lawson and Sahni). The blade may be absent, so may be the petiole, but it is nowhere indicated in their writings that the base is wanting in a complete leaf (the *hypopodium*, Green, p. 54).

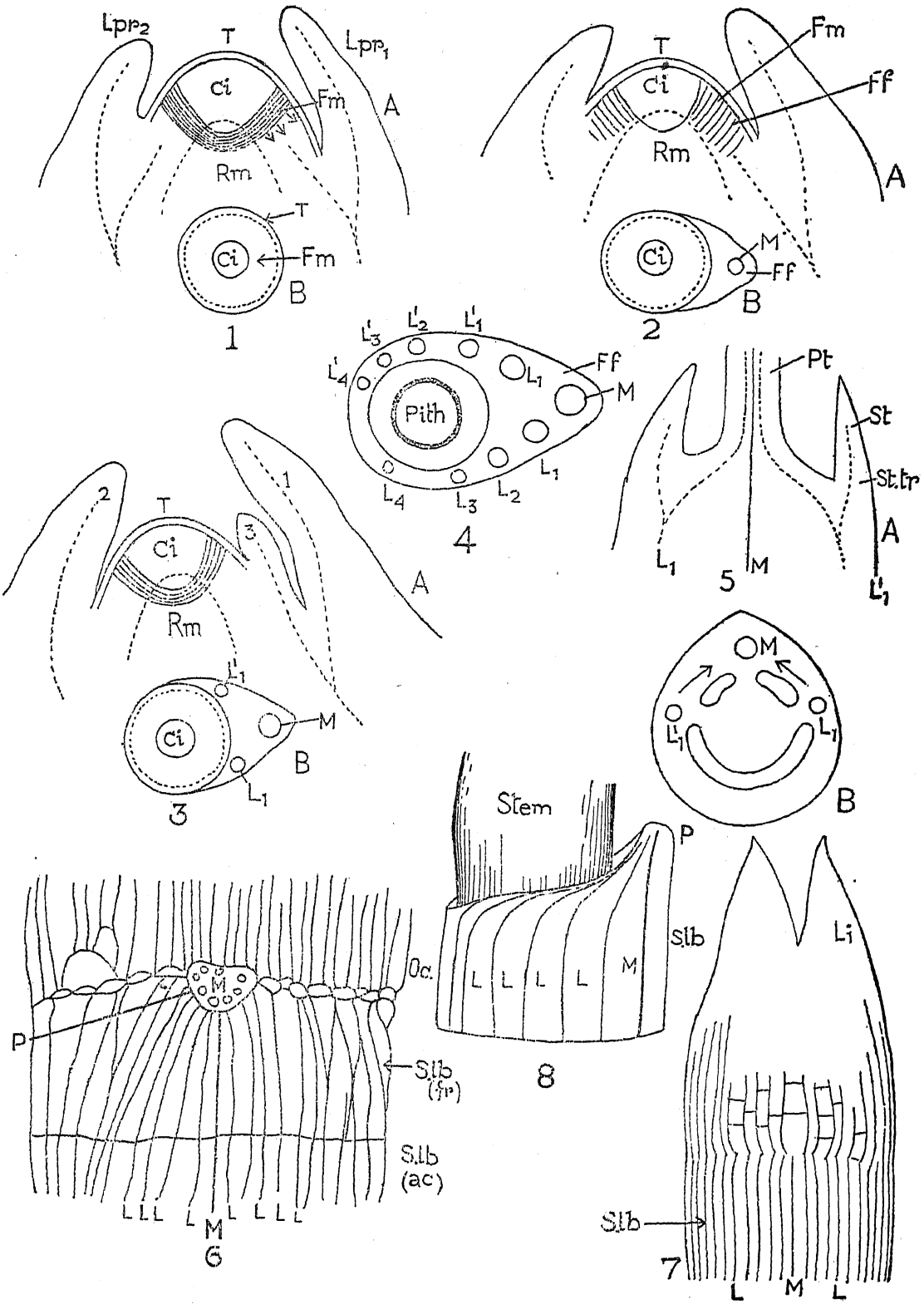
I am not aware of any attempt being made to critically examine the above two views on the results of modern researches. This is my justification for this short paper.

The question before us is to decide: (i) whether a complete leaf has a base of its own; if so what is the nature and extent of the leaf-base, and if the stipules are its outgrowths, and (ii) whether the stipules are appendages (of the leaf) at the base of the petiole, and as such, are parts of a complete leaf and the leaf-base is non-existent. I propose to deal with the questions separately.

Developmental studies show that whenever a leaf primordium (*primordialblatt* of Eichler) on its subsequent behaviour can be distinguished into an upper (*oberblatt*) and a lower region (*unterblatt*) the upper develops into the blade and the lower into the base of the leaf. The petiole, if it develops, is added later by its intercalation between the blade and the base (Strasburger, 1930). According to Sinnott and Bailey (1915) the petiole is the last part to appear in ontogeny, more recent in evolutionary ontogeny than the rest (p. 13). If that is so we have to concede that the primitive angiosperm foliage leaf consisted of a blade and a base, the petiole and the stipules came later as efficient adjuncts.

THE BASE OF THE LEAF

I now propose to discuss the issue of the presence or absence of a base in a complete leaf on the evidence provided by the morphogenetic studies at the vegetative shoot apex. Gregoire (1935) and his pupil, Louis (1935) showed that at the initiation of a leaf at the vegetative shoot apex a *soubassement foliare* is laid down first and later the free limb of the leaf is erected on it (Figs. 1–3). Foster (1935) translated these two terms as " foliar buttress," but I consider that " foliar foundation " is a better rendering of the same. As the foundation is an important integral part of a building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8
Oc.
P
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FIGS. 1–8

FIGS. 1–8. All figures are diagrammatic.

Fig. 1 *a*, *b*. L.S. and T.S. of the vegetative shoot apex of a dicotyledon. The apical meristem has just started laying down the foliar foundation of primoridum 3, and the shoot apex has become asymmetrical (exaggerated). Fig. 2 *a*, *b*. L.S. and T.S. of the same through Ff of Lpr 3; the median trace bundle has just reached the base of Ff. Fig. 3 *a*, *b*. L.S. and T.S. through the same showing erection of the free limb of Lpr 3 on Ff with the median and two laterals as its trace. Ff has extended tangentially around the apex. Fig. 4. Ff of a sheathing base (axial component) with many laterals. Fig. 5 *a*, *b*. L.S. and T.S. of nodal region at the base of the petiole. Fig. 5 *a*. Laterals branch to give rise to the stipule and stipular trace while moving towards the median at the base of the petiole. Fig. 5 *b*. Trilacunar node and three bundled leaf trace (5 *a*—after Mitra). Fig. 6. Sheathing base—free and as axial component, split open and spread; the two are shown separated from each other by a transverse line; laterals branch on their way to the median;—origin of ocrea in *Polygonum orientale* (after Mitra). Fig. 7. Sheathing base and ligule of Rice leaf split and spread open; origin of ligule and its nature (after Saha). Fig. 8. Behaviour of the laterals in a sheathing base without stipules. Absence of branching of the laterals is correlated with absence of stipules.

Legend.—*T*, tunica; *Ci*, central initial zone; *Fm*, flank meristem; *Rm*, rib meristem; *Ff*, foliar foundation; *Lpr*, 1, 2, 3-leaf primordia; *P*, petiole; *St.*, stipule; *M*, L_1, L_2, etc., median and laterals of the leaf trace; *Sttr*, stipule trace; *Li*, ligule; *Slb*, (*fi*)—free sheathing leaf-base; *Slb* (*ac*), sheathing base as axial component; *Oc*, ocrea.

which is erected on it, so I hold that the foliar foundation is an integral part of the leaf, and *its real base*. This foliar foundation may be wholly included in the axis when we should call it *axial component*, or a part of it may develop free from the axis when we call this portion *sheathing leaf-base* (see below). Sharman (1942), Majumdar (1949), and Mitra and Majumdar (1952) have shown that this foliar foundation is really the base of the leaf which singly or with bases of other leaves form the *mantle* of the axis (*cf.* the Mantle-core theory of Hofmeister, 1851; Saunders, 1922; Mitra and Majumdar, 1952).

When the foliar foundation of a leaf is laid down at the shoot apex it occupies only a small sector of the apical dome with only the median bundle as its trace (Fig. 2 *b*). This portion of the foliar foundation becomes continuous with the petiolar and the midrib region of the adult leaf. The foliar foundation then gradually extends tangentially along the two sides of the shoot apex when more bundles, the laterals of the leaf trace, enter its two extending wings (Figs. 3 *b*, 4). Ultimately the wings may meet on the opposite side of the apex and fuse or overlap to give rise to the sheathing base. In this case a part of it becomes always free, as in Polygonum, Centella, etc. The number of laterals in each wing varies with its extent around the free apex.

Whether the foliar foundation will develop into a free base or not is determined by the behaviour of the laterals during their courses through it towards the base of the petiole. The laterals after their departure from the axial cylinder run parallel for a short or a long distance through the axial

component and then gradually shift towards the median which, however, follows an undeviated course from the base to the extreme tip of the leaf. The laterals and the median come together and unite at the base of the petiole either to form a closed ring or an open arc (open on the ventral surface), or divide to form a ring of vascular bundles, particularly when the petiole is cylindrical. In the petiole they do not normally branch, nor separate from one another (*cf.* Sinnott and Bailey, 1915). During their oblique or horizontal course through the foliar foundation the laterals may or may not branch. If they branch they give rise to the stipules (see under Stipules).

If the laterals finish their course, both parallel and oblique or horizontal, within the axial component, as in China Rose, Calotropis, Jasminum, etc., no free base is formed and the petiole appears to sit directly on the axis. If, however, they run parallel beyond the axial component before they bend to meet the median at the base of the petiole a free base is formed as in Centella, Polygonum, Heracleum, etc. (Figs. 6, 8). For detailed information on the subject the reader is referred to the papers of Mitra and Mitra and Majumdar.

A foliage leaf, complete or otherwise, has therefore a base, whether it is manifested or not. It will be incorrect to say that a leaf has no leaf-base, or if it is present it is the region of its attachment to the axis which bears it, as if the leaf is an extraneous organ or a fixture.

The sheathing base and the pulvinus have however been described by these authors as modified leaf-bases. We have seen above that the sheathing base is only a part of the leaf-base the other part is included in the axis as its axial component. The pulvinus however, is the petiole of the leaf in which it occurs. One of my pupils in a paper on the leaves of *Dolichos lablab*, has shown its petiolar nature on anatomical evidence (in the press).

The Stipules (Fig. 5 *a*, *b*)

Are the stipules outgrowths of the leaf-base or free appendages at the base of the petiole? This time the answer was provided by Colomb (1897). He showed on the results of extensive studies of this organ that its vascular supplies come from the laterals of the trace of the leaf to which it belongs. Sinnott and Bailey (1914) put Colomb's statement to an elaborate and severe test and found it strictly correct. Dormer (1944) provided additional corroborative evidence from a study of the vascular supply to the single-stipuled leaves of *Lotononis corymbosa* and *Azara microphylla*, both with three-bundle trace. Sharma (1955) has produced further evidence from *Muntingia Calabura*, leaves of which have single stipule each.

Mitra in the dicotyledons (1945, 1948; 1949 *a*, 1949 *b*, 1950 *a*, *b*, *c*) and Saha (1952) in Rice plant have shown that in all the different types of stipules and ligule studied by them the above findings of Colomb, Sinnott and Bailey and others hold rigidly good. Mitra has shown further that the laterals send out branches to form the stipules and their traces either at the top of the axial component or of the free sheathing base (ocrea) on their way to meet the median at the base of the petiole. Want of a proper realization of the nature and extent of the leaf-base as made out in this short paper, made Parkin (1948) to describe the free lateral stipule as *cauline*, and Cross (1937) to describe them as originating from a *leaf-stem transition region* in *Morus alba*.

CONCLUSION

We are now in a position to describe the parts of a complete leaf, which consists of:—

(*a*) *The lamina or the blade.*—This most important part of the leaf may be absent or modified when its principal function is taken over either by the petiole (phyllode), or by the stem (phylloclade, cladode), or to some extent by the leaf-base (bud scales of Horse Chestnut, Ash, Sycamore, etc., see Priestley and Scott, 1938; Goebel, 1905).

(*b*) *The petiole or the leaf-stalk.*—This part of the leaf is absent in the sessile types and in leaves with sheathing bases of monocotyledons. According to Sinnott and Bailey (1915) the petiole is the last part to appear in ontogeny, and more recent in evolutionary ontogeny than the rest.

(*c*) *The leaf-base.*—Even when the other two parts are absent, either simultaneously or one at a time, the leaf-base as we have seen, is always present. A leaf without a base cannot therefore, be conceived. Strasburger (1930) categorically states that " the petiole is never inserted directly on the stem " (p. 104). In the majority of plants it is included in the axis as its outer covering (mantle) but in some cases it may partly grow as a free base (Figs. 6, 7, 8).

(*d*) *A pair of stipules.*—Though they are outgrowths of the leaf-base they are regarded as " original accompaniment of the angiosperm leaf " (Parkin, p. 79, 1948). Both Lubbock (1899) and Sinnott and Bailey (1914, p. 451) came almost to the same conclusion when they stated respectively that stipules are integral part of the leaf, and integral portions of the leaf-base.

Therefore, the *complete leaf* consists of *four parts*, namely, the *blade*, the *petiole*, the *leaf-base* and *a pair of stipules*. Lubbock came precisely

to the same conclusion in his pioneer work on Buds and Stipules (p. 222, 1899).

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