STIPULES, STIPELS, LIGULES AND LEAF-SHEATH*

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Introduction

Stipule, stipel, ligule and leaf-sheath are structures closely associated with the foliage leaf. The first three are regarded as outgrowths of the leaf-base, and the last as "a primary element" of the leaf (Arber, 1925; Majumdar, 1955). The *stipule*† is defined as "an appendage at junction of a leaf, one on each side of the insertion" (Asa Gray, 1879); "an outgrowth of the base of the leaf" (Willis, 1951). The *stipel* when present is described as "the stipule of a leaflet usually one at the base of each in a compound leaf with two at the base of the terminal leaflet" (A, B). The *ligule* is "an outgrowth from the leaf-sheath or petiole of the Grasses where it joins the blade" (A); "a scale at the upper end of the leafsheath" (B). The *leaf-sheath* is "a close fitting tubular or enrolled case as that formed by the stem-clasping petioles (*i.e.*, lower portion of the leaf)" (A); "leaf-base forming a tube round the stem" in Grasses (B).

Thus the stipules may be an adjunct or an appendage of a leaf (A), or an outgrowth of the base (leaf-base)‡ of the leaf (B); stipels are secondary stipules associated with leaflets of a compound leaf (A, B); the ligule is an outgrowth of the leaf-sheath (A) or of the sheathing base of the leaf (B), and the leaf-sheath is the dilated base of the leaf or the petiole (A), or the sheathing leaf-base (B).

We propose to examine them individually with a view to determine their true morphology on the results of modern researches including those of our own.

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* The following are the outstanding contributors on stipules, ligules and leaf-sheath: Clos (1879), Colomb (1887), Tyler (1897), Lubbock (1899), Glück (1901), Goebel (1905), Domin (1911), Sinnott and Bailey (1914), Arber (1925), Philipson (1935), Parkin (1948), Mitra (1945, 1948, 1949 *a-b*, 1950 *a-c*).

† Abbreviations used in this paper: A and B represent American and British botanists respectively. Median and lateral for the median and lateral bundles of the leaf-trace. Two definitions, one American and one British, of each structure are given.

‡ *Leaf-base* and *base of the leaf* should be distinguished: Leaf-base is 'a primary element of the leaf' (B), whereas the base of the leat is the lower portion of the leaf, *i.e.*, the base of the petiole (A).

THEIR MORPHOLOGICAL STATUS

Stipule.— American botanists regard stipules as one of the three parts of a complete leaf; they do not recognize the presence of the leaf-base as a separate entity. The German and British botanists on the other hand, regard the leaf-base as an integral part of a complete leaf, and the stipules when present they regard as outgrowths of the leaf-base (Majumdar, 1955 *b*). It is quite natural, therefore, for Eames and MacDaniel (1925) to state that "the morphological nature of stipules has been much in dispute".

Researches of Colomb, Sinnott and Bailey, Dormer (1944), Mitra and Sharma (1955) have now definitely settled the question of the morphology of this organ. *It is an outgrowth of the leaf-base caused by the stimulating influence of a branch or branches sent out by the laterals* while on their way to the median with which they unite to form the petiolar trace. Mitra has further shown that whatever be the type of the stipule—free lateral, adnate, interpetiolar, intrapetiolar, foliaceous, bud-scale or ocreate*—the development of each one of them is correlated with the lateral trace bundles of the leaf with which they are associated. In the majority of cases, the trace of a stipulate leaf consists of three bundles—the median and two laterals, but in some special plants it may consist of many bundles (node-multilacunar).

Stipel.—They are secondary stipules associated with the leaflets of a compound leaf. We have already mentioned that the lateral leaflets have one stipel each, and the terminal one has a pair. Kar (1955) has worked out the origin and vascularization of the stipels of *Dolichos lablab* L. He has shown that the stipel of a lateral leaflet receives branches from the same lateral which goes to form the vascular system of the leaflet with which it is related. *This supports their stipular nature.*

The presence of a single stipel to each lateral leaflet and a pair to the terminal one has also been explained by Kar on the evidence of their vascularization (see Kar, 1955).

Ligule.—Ligules like stipules are outgrowths of the leaf-base. Stipulate leaves are more common in dicotyledons and ligulate leaves in monocotyledons, particularly, in the Grasses and the Zingiberaceæ. They are generally associated with the sheathing base of the leaf arising "from the junction of the leaf-blade and leaf-sheath". Under ligule we shall consider here only the ligule of Grasses.

* Stipular tendrils of Smilax has not been considered here. Chakravarti and Mitra (1948) have shown that these tendrils "originate, as pointed out by Arber in 1920, by chorisis or splitting of the petiole after it has separated from the sheathing base during the development and differentiation of the leaf primordium" (p. 27).

We have stated under the Section Stipule that the stipular traces are always derived from the branches of the laterals of a three and sometimes many-bundled leaf trace. Colomb applied this dictum to the ligules of *Arundinaria japonica* and *Oryza sativa* and found that the ligules of these plants are dual in structural organization: its two margins are prolongations of the margins of the leaf-sheath and the central portion is the " upgrowth of the adaxial (ventral) surface of the sheath joining these, *i.e.*, stipular " (Philipson, 1935) as it receives only the branches of the laterals. Philipson and Saha (1952) supported Colomb while interpreting respectively the ligules of *Phyllostachys aurea* and of Rice plant. *The ligule of Grasses therefore is a composite structure made up of the margins of the leaf-sheath and its stipule.*

Leaf-sheath.—The majority of American botanists consider the leaf-sheath to be the product of the base of the leaf or the petiole which becomes " much dilated and membraneous at base " (Asa Gray, p. 104). But Sinnott and Bailey (1914) think that the leaf-sheath is formed by the fusion of rows of adjacent stipules (one opposite each lateral in a multilacunar node) (p. 448).

The European botanists on the other hand regard the leaf-sheaths as modified leaf-bases as in the Umbellifers and Monocotyledons. Curiously enough Parkin (1948) supports the stipular origin of the leaf-sheath (p. 70).

I have discussed the morphological nature of the leaf-sheath in my paper on " The Complete Foliage Leaf " (1955 *b*). In that paper I have shown that even when the lamina and the petiole are absent, either simultaneously or one at a time, the leaf-base, as a primary element, is always present. A leaf without a base cannot thus be conceived.

The leaf-base may remain included entirely in the axis as its outer component or the mantle, or a part of it may develop free from the axis as the *leaf-sheath.* The development of the leaf-sheath is closely associated with the trilacunar, as in Rose, but mainly with the multilacunar conditions of the node, as in Heracleum, Polygonum and Centella.

Whether the leaf-base 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 long distance through the axial component and then gradually or abruptly shift towards the median. The laterals and the median come together and unite at the base of the petiole and then enter the same as its trace. In the petiole they do not ordinarily branch nor separate from one another (pp. 68–69; *cf.* Sinnott and Bailey, 1915; Swamy, 1949).

During its ontogeny the leaf primordium starts as *soubassements foliares* (Gregoire, 1935; Louis, 1935) with one provascular strand, the median. It then extends laterally around the free apex when more bundles come from the axial cylinder in twos, one on each side of the median. The node becomes tri- or multi-lacunar depending on the extent of the wings around the apical dome (for details see Majumdar, 1955 *b*).

Modern researches, therefore, conclusively prove the existence of the leaf-base even where it is apparently absent, as in China Rose and *Morus alba*. The *leaf-sheath* is the extended portion of the leaf-base free from the axis, formation of which is determined by the behaviour of the laterals in it (Majumdar, 1955 *b*).

PHYLOGENETIC CONSIDERATION AND CONCLUSIONS

Only the stipule, ligule and the leaf-sheath will be considered here. The question is: Are these structures independent morphological entities or they are derived one from the other and phylogenetically connected ? Verdicts of four plant morphologists are examined below. They are Sinnott and Bailey, Arber and Parkin: the former two are American and the latter two are British eminent and foremost botanists. *They are all living.*

Sinnott (1914) worked on the anatomy of the node as an aid in the classification of angiosperms. He studied and analyzed 400 genera and came to the conclusion that the trilacunar condition of the node is the primitive form from which the unilacunar condition has been derived either by the suppression of the laterals or by their approximation and juxtaposition with the median, and the multilacunar condition, by the amplification, *i.e.*, by an increase in the number of laterals of the trace of a leaf.

In the same year Sinnott and Bailey in their paper on the nodal anatomy and the morphology of the stipules came to the following conclusions:

(i) Stipules are associated with the trilacunar condition of the nodes; unilacunar nodes normally bear exstipulate leaves, and sheathing bases are connected with the multilacunar condition;

(ii) in the formation of the stipules branches are sent out from the lateral trace bundles which stimulate their origin and growth and form their vascular system. In this conclusion they supported the findings of Colomb (1887); and

(iii) the leaf-sheath is formed by the fusion of rows of adjacent stipules on the two sides of the petiole, each stipule of a row is being stimulated to growth by a branch of the lateral of the multibundle leaf trace.

Arber (1925, refer to her Figs. 74 A–H, p. 97) discussed the leaf-sheath, stipule and ligule somewhat in detail in her classical work, Monocotyledons. She considers the simple leaf-sheath as the fundamental type (A) " from which stipules and ligules are developed by a secondary process of winging " (p. 97). Then she describes the steps in their evolutions: " By a simple upward extension of the leaf-sheath, where it abuts on the petiole a ligulate type (B) is easily derivable from A. The upper lateral margins of the leaf-sheath may on the other hand grow out into two wings (C), which by reduction of the basal part of the sheath may come to form stipules of the free lateral type (D). As a further modification the wings of the leaf-sheath may fuse with greater or less completeness in front of the petiole base (E, H), and from such types an ' axillary ' stipule or ligule (G, H) may be developed by reduction of the rest of the leaf base. H may, alternately, be derived by the same process from such a form as B". "In the case where the position is axillary stipules and ligules are synonymous, the former distinguished from the latter by the bifurcation at the tip (G, H), the bifurcation indicating the double nature of the pair of stipules." According to Arber the ligule of Grasses is an axillary stipule.

Parkin (1948) has considered the stipule phylogenetically. He divided different kinds of stipules into two broad categories: Cauline (free) and petiolar (adnate) (p. 65). He concluded that " a pair of free stipules is an original accompaniment of the angiospermous leaf " (p. 79). This conception is based on Sinnott and Bailey's (1915) conclusion that the primitive angiospermous leaf was trilobed from which Parkin speculated that the two lateral lobes became " modified as stipules for protective purposes and that the middle lobe became transformed into the simple oval leaf (1953, p. 85). He thus regarded the free cauline stipules as earlier forms from which all other kinds of stipular outgrowths could be theoretically derived; adnate stipules are the result of the fusion of the pair of free lateral (cauline) stipules with the petiole, and he believed that the sheath and the ligule are of stipular origin rather than as peculiar outgrowths of the leaf base. He doubted " the leaf-base as a morphological element of the foliage on a par with lamina and petiole" (p. 80). In this respect he thus holds the same view with Sinnott and Bailey. Finally as a corollary of his above view he believed that the leaf-sheath had been derived from the adnate stipules.

These conflicting views held by eminent plant morphologists on the true morphology and phylogeny of the stipule, ligule and leaf-sheath appear to me to be due to the want of a clear and proper realization of the presence, nature and extent of the leaf-base as a morphological element of the foliage leaf.

In 1851 Hofmeister propounded his Berindung Theory which postulated the existence of an outer mantle formed from the leaf-bases enveloping a core in the make-up of the axis (in Saunders, p. 145). Nobody apparently took notice of this theory. In 1922 Saunders revived this theory in a modified form and postulated her Leaf-Skin Theory. She firmly established the fact that the outer skin of the axis (internode) is made up of the bases of the leaves (leaf-bases). Arber (1925) considered this theory of Saunders somewhat in detail and without any commitment she wrote: " if we accept the Leaf-Skin Theory we cannot escape the conclusion that the leaf plays a much more important rôle in the organization of the shoot than has hitherto been generally held " (p. 93). She compares the leaf of the text-book with the visible part of an iceberg and the leaf-base forming the outer layers of the axis, to the portion below the sea-level. In 1952 Mitra and Majumdar re-examined both the theories of Hofmeister and Saunders in the light of modern researches and established the correctness of the Leaf-Skin Theory but supported Hofmeister in so far as the radial depth of the leaf-skin is concerned. Sharman (1942) has also shown that in maize stem each internode is made up of the lower half of the leaf cushion. *The existence of the leaf-base as an element of the leaf can therefore no longer be doubted.*

I now propose to examine the view-points of Sinnott and Bailey and Arber and Parkin on the morphology and phylogeny of the stipule, ligule and leaf-sheath on the basis that the leaf-base exists as a ' primary element ' of the foliage leaf. I even go so far as to state that even where the lamina and/or the petiole is absent its base is present as the outer component of the axis (leaf-skin) and as the bud-scale in some cases (Majumdar, 1955 *b*).

We have already indicated before that in the angiospermous leaves the leaf-base exists in two forms: In the majority of cases where the petiole appears directly seated on the axis it exists fully incorporated into the axis as its outer mantle (skin), so that to the uninitiated the leaf appears without a leaf-base. This led the American botanists to deny the existence of the leaf-base in foliage leaves, and as a corollary they consider the leaf-sheath as the dilated base of the leaf or the petiole. Accepting this position Parkin described the stipules as arising directly from the axis (his cauline stipules) and Cross (1937) described the stipules of *Morus alba* as originating from the leaf-stem transition region (see Majumdar and Mitra, 1948).

Hofmeister's Berindung and Saunders' Leaf-Skin Theories apparently had no influence on the attitude of these botanists. Curiously enough Sinnott and Bailey (1914) who established firmly the fact of the correlation of the stipule development with the laterals of the leaf trace with a conclusion that

the " lateral trace exerts a stimulating influence which results in the formation of the stipule " are silent as to the morphology of the region of which they are the outgrowths.

The other form in which the leaf-base exists is a more common form among monocotyledons and in a few herbaceous dicotyledons. It exists partly incorporated into the axis and partly as the free leaf-sheath, *e.g.*, in Heracleum, Polygonum, Centella and Rose.

In all cases, without any exception, the stipules are leaf-base outgrowths correlated with the laterals of the trace of the leaf with which they are associated (Mitra, 1945–50).

In the so-called adnate stipules of Roses, the central radially thickened portion is regarded as the petiole and the two wings as the pair of stipules adnate to it. In 1949 Mitra published his paper "On the Origin, Development and Morphology of Adnate Stipules in *Rosa centifolia* L.". On morphogenetic and anatomical evidence he showed that the ' sub-petiolar ' region of the adult leaf of Roses is the sheathing leaf-base, only the two distal free lobes of this sheath at the sides of the petiole and whose traces are derived from the branches of the laterals represent the pair of free stipules. Thus he supported the morphological interpretation of the stipules of Roses given by Gœbel (1908) and Vines (1910) (for details see Mitra, 1949).

Arber (1925) suggested that " there is no hard and fast line between the anatomical characters of petioles and leaf-sheaths " (p. 112). We have seen above that modern researches do not support this statement of Arber. Mitra and Majumdar (1952) showed that anatomically the three regions of a typical leaf, namely, the base, the petiole and the upper leaf, could be distinguished. In the *base* the laterals remain separate, laterally spread and unbranched or branched in connection with stipule formation; in the *petiole* they unite with the median to form a cylinder or an arc or branch and arrange themselves in a ring without branching and in the *upper leaf* they again branch in connection with leaflet or lamina development (p. 365; *cf.* Sinnott and Bailey, 1915; Swamy, 1949 and Majumdar, 1955 *b*). Subsequent investigations have supported the correctness of the above observations of Mitra and Majumdar.

The ligule of Grasses is a stipule *plus* the vertically extended margins of the sheathing leaf-base. We have already discussed its morphology. Arber (1925) from its bi-fid nature regarded ligule as an axillary stipule, but Saha's (1952) developmental studies of the ligule of Rice plant have shown that the bi-fid nature of the ligule is the result of differential growth of the margins of the sheathing base and of the stipule.

Morphogenetic studies at the growing apex show that the leaf-sheath is the upward extension of the leaf-base free from the axis. Mitra and Majumdar (1952) have shown that the number and behaviour of the laterals through the axial component (leaf-base) determine the nature of the leaf-base. Only when the laterals run parallel to one another beyond the upper end of the axial component before they bend towards the median the base has a free growth, as in Heracleum, Polygonum and Centella and the sheathing base of the monocotyledons. Therefore our studies do not support Sinnott and Bailey and Parkin when they state that the sheath is formed by the fusion of the rows of adjacent stipules. Stipules themselves are leaf-base outgrowths, and ocrea and ligule are stipules outgrown from the sheathing bases of Polygonum and Grasses and Zingibers. Therefore to consider the leaf-sheath as formed from the stipules is like putting the cart before the horse.

Arber's idea that the sheathing base is the primitive type from which stipules and ligules have been derived may be partially true so far as the ocrea and ligules are concerned as they are the outgrowths of the sheathing base. But to derive the so-called cauline stipules from the sheathing leaf-base is rather difficult to accept with our present state of knowledge of the ontogeny of these structures.

If ontogeny of an organ is the recapitulation of its phylogeny then the unilacunar condition of the node should be regarded as the earliest from which tri- and multi-lacunar conditions came to be evolved. If that is so the sheathing base should come last in the phylogeny of the leaf-base. This goes counter to the findings of Sinnott (1914).

Sinnott and Bailey (1915) from their elaborate and exhaustive studies of vascular plants came to the conclusion that the primitive angiospermous leaf was palmately lobed with three major veins, one to each lobe. From this Parkin speculated that the two basal lobes of this primitive leaf became modified into a pair of free lateral stipules (see also Arber, 1950, regarding origin of axillary bud; Majumdar, 1955 *a*).

We have stated before that stipules and ligules are inseparably associated with the branching and branches of, and not directly with, the laterals of the leaf trace. The two lateral lobes of the primitive angiospermous leaf received lateral bundles and not their branches. Therefore they can be modified for any purpose other than to give origin to the pair of stipules as suggested by Parkin.

Stipules, stipels, ligules and the leaf-sheaths are primarily protective in their function. It is possible, therefore, that their origin took place in response to that function.

In the early stage of its origin the angiospermous leaf consisted of the eaf-base and the lamina, the former entirely incorporated into the axis as its outer mantle, and the latter with a broad base seated directly on the axis. The node was perhaps unilacunar. Thus the broad sessile base of the lamina, at this stage, gave all the necessary protection to its axillary bud. There was no petiole at this initial stage of leaf origin.

According to Sinnott and Bailey (1915) " the ever-increasing broad base of the lamina was in need of a greater flexibility " for proper exposure to sunlight, against wind, etc. Therefore a petiole was next added between the base and the lamina. The lateral bundles (two or many) which were more or less widely separated from each other at their departure from the axial cylinder were forced to come closer in the petiole. Morphogenetic studies at the shoot apex also show that the petiole is the last part to appear in the ontogeny of a leaf primordium, and is " more recent in evolutionary ontogeny than the other two parts of the leaf" (Sinnott and Bailey, 1915; Majumdar, 1955 *b*).

The broad base of the lamina was now separated from the leaf-base (axial component) by the petiole whose base was too narrow to give adequate protection to the axillary or the terminal bud. The demand for additional protection was met by the development of a pair of stipules from the leaf-base on the two sides of the petiole. The three together formed an effective protective structure. There are many instances where the petiole development is soon arrested and the pair of stipules grow much quicker and bigger to cover not only the axillary bud but the growing point as well. The condition of the node was perhaps trilacunar in most of the cases.

The origin of the stipule may thus be taken as a consequence of the addition of the petiole to the leaf.

Meanwhile the *soubassements foliares* started extending around the apical dome until it completely embraced the same. With this extension more bundles from the axial cylinder entered the wings of the axial component as its laterals and the node became multilacunar.

When the node became multilacunar, the leaf alternate and the axial component completely surrounded the axis the petiole with the two small stipules at its base was not enough to ensure protection to the axillary and terminal buds. This vulnerable situation was met by the leaf-base (axial component) in two ways:

In plants like Magnolia, Michelia, *Ficus elastica*, *F. religiosa* and *Artocarpus integrifolia* the leaf-base remained as axial component but produced stipules which either singly or in pairs completely ensheathed the apical or

axillary bud as bud-scales, the petiole seldom taking any part in the protective function. The vascular supply as usual came from the branches of the laterals.

In Monocotyledons, such as the Grasses and the Zingiberaceæ, and in some herbaceous dicotyledons, such as the Umbellifers and Polygonums, where the internodes become very long during the unfolding of the buds, the laterals do not change their courses at top of the axial component but pursue their vertical course beyond the latter thereby causing its upward extension free from the axis *to form the leaf-sheath.*

The leaf-sheath itself affords protection to the axillary bud but it does not as adequately protect the vegetative bud and its delicate growing tip particularly when the environment is inclement. In such cases an additional stipule, ocrea or a ligule, is formed.

Summary of the stages through which the leaf-base is supposed to have passed during its phylogeny

Forms of the leaf-base	Nodal condition	Leaf : sessile or petiolate	Exstipulate, stipulate or sheathing leaf-base	Protection : how effected ?
A Leaf-base entirely incorporated into the axis as axial component; no free leaf-base	1 Unilacunar or trilacunar ?	Sessile	Exstipulate	*By the broad base of the lamina
	2 Trilacunar	Petiolate	Stipulate	By the petiole *plus* the pair of stipules
	3 Multilacunar	Petiolate	Stipules forming sheathing bud-scales	By the stipules forming a complete sheath covering the bud
B. Leaf-base partly incorporated into the axis and partly as the free leaf-sheath	1 Trilacunar	Petiolate	Leaf-sheath	Sheathing base, *e.g.*, Roses
	2 Multilacunar	Petiolate	Exstipulate	By sheathing leaf-base : leaf-sheath, *e.g.*, Centella
	3 Multilacunar	Petiolate	Sheathing	Leaf-sheath *plus* ocrea or ligule

* Primitive leaf.

We may now conclude: The primitive angiospermous leaf consisted of the *leaf-base* wholly incorporated in the axis as the axial component, and the *lamina* with a broad base directly inserted on the axis. The node was perhaps unilacunar. With the addition of the *petiole* to the leaf *a pair of stipules* came into being (cauline of Parkin). The node was trilacunar at this stage. The axial component meanwhile extended laterally around the apical dome and finally completely enclosed the latter and the node became multilacunar. It then produced the *sheathing stipules* of the type of bud-scales. In the next

stage the axial component extended vertically under the influence of its own laterals to produce the *leaf-sheath*. But this was found to be inadequate to afford complete protection to the apical bud in certain types of plants. Therefore stipules of the types *ocrea* and *ligules* were added.

The stipules, stipels and ligules are homologous structures, for without exception all of them are outgrowths of the leaf-base correlated with the branches of the laterals. The leaf-sheath as extension of the axial component developed later as it is usually found in herbaceous plants.

The phylogenetic history of development of the leaf-base through ages has been written above on two basic inferences, *viz.*, (1) that there exists the leaf-base as "a primary element" of *all* leaves, and (2) that the primary functions of the leaf-base and its outgrowths are protective and to some extent mechanical.

Summary

1. Stipules, stipels, ligules and leaf-sheaths have been discussed ontogenetically and phylogenetically with a view to examine their true morphology.

2. In this connection conflicting verdicts of Sinnott and Bailey and Arber and Parkin have been critically examined. It is felt that in arriving at their conclusions they failed to take into their account the presence, nature and extent of the *leaf-base* as a morphological unit constituting the foliage leaf.

3. Modern researches have proved beyond doubt that the leaf-base exists as "a primary element" of leaves of every kind.

4. The leaf-base exists in two forms: (1) totally incorporated into the axis as its outer mantle (Hofmeister, Saunders) described in this paper as the axial component, and (2) partly as the axial component and partly as the leaf-sheath which is the vertical extension of the former free from the axis.

5. Stipules, stipels and ligules are without exception outgrowths of the leaf-base formed only under the influence of branches of the laterals of the leaf trace.

6. Where the leaf-base exists only as the axial component the leaf is apparently without a base, and the casual observer is led to believe in such cases the origin of stipules as cauline (*cf.* Parkin).

7. As stipules are outgrowths of the leaf-base they cannot by their fusion give rise to the leaf-sheath (*cf.* Sinnott and Bailey, Parkin).

8. In Roses the subpetiolar region is the leaf-sheath (leaf-base) and its two distal free lobes on the two sides of the petiole represent the stipules (adnate of Parkin and others).

9. In ocrea only the upper portion fed by the branches of the laterals is to be regarded as the stipule and the lower portion in which the laterals run separate, almost parallel, courses is the leaf-sheath (leaf-base).

10. Ligules of Grasses are composite structures (stipule *plus* margins of the leaf-sheath) (Colomb, Philipson, Saha).

11. The leaf-base, petiole and the lamina of a leaf can be distinguished, one from the other on anatomical evidence (*cf.* Arber).

12. Derivation of the stipules and ligules from the leaf-sheath as suggested by Arber, is not supported.

13. If ontogeny of an organ is the recapitulation of its phylogeny then the unilacunar condition of the node is the primitive from which the trilacunar and then the multilacunar conditions must have evolved.

14. There is no direct evidence from which it can be definitely concluded that the two basal lobes of the primitive angiospermous leaves (Sinnott and Bailey) with three main bundles became modified into the pair of stipules at the base of the petiole (*cf.* Parkin).

15. Sheathing leaf-base (leaf-sheath) is the result of multilacunar condition of the node *plus* the behaviour of the laterals in the axial component. Leaf-sheath and sheathing stipules are morphologically different and distinct structures.

16. Stipules, ligules and leaf-sheaths are structures primarily meant for affording adequate protection to the axillary and terminal buds and their constituent parts. It is probable that the necessity of a pair of stipules, free or sheathing, and the leaf-sheath with ocrea and ligule arose after the addition of the petiole to the leaf.

17. Stipules, stipels and ligules are homologous structures. A tentative scheme of phylogeny of the stipules, ligules and leaf-sheaths has been suggested.

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