DEVELOPMENTAL STUDIES.

A COMPARATIVE ACCOUNT OF THE ORIGIN, DEVELOPMENT AND MORPHOLOGY OF THE STIPULES OF *Artocarpus integrifolia* L., *Ficus religiosa* L. *and Ficus elastica* Roxb.

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(Communicated by Prof. G. P. Majumdar, Ph.D., F.N.I., F.A.Sc.)

(*Received June 24; read August 5, 1949.*)

Stipules in the family *Moraceae* have attracted the attention of botanists, particularly of the morphologists, since very early times. Trécul (1846) noted in the family *Artocarpae* (= *Moraceae*) all stages of stipules from single to a pair to each leaf, their axillary and free positions, their enormous development in some cases and their horizontal and oblique insertions on the axis. Hooker (1885) considered the huge stipules of *Ficus elastica* with their 'close parallel nervation (almost resembling that of Monocotyledons) as unmistakable diagnostic character of the species'. Porter (1891) noted the protective function of these structures in the species of *Artocarpus* in the temperate and tropical countries. In 1895, Lubbock published his classical work on the Stipules, their form and function. In 1897, Tyler published his dissertations on the nature and origin of stipules. In these two works all facts known till then have been incorporated. Tyler quotes a very interesting observation of Colomb (1886) who regards the sheathing stipules of *Ficus* and *Magnolia* as transitional stages between ochrea and stipules proper. In his later publication (1887) he regards them as axillary ligule.

Goebel (1905) distinguished the single stipule of *F. elastica* as an axillary stipular sheath, and those of *A. integrifolia* as a pair of free stipules. According to him the earlier the union by the transverse cushion (a new formation) takes place, the more the axillary stipules appear as a single structure, and if the stipules become united also upon the side opposite to the point of insertion of the leaf, a closed sheath must be formed. Besides noting the transverse cushions at the node, Goebel, it appears, has not studied the contributions of these structures to the development of stipules in these species.

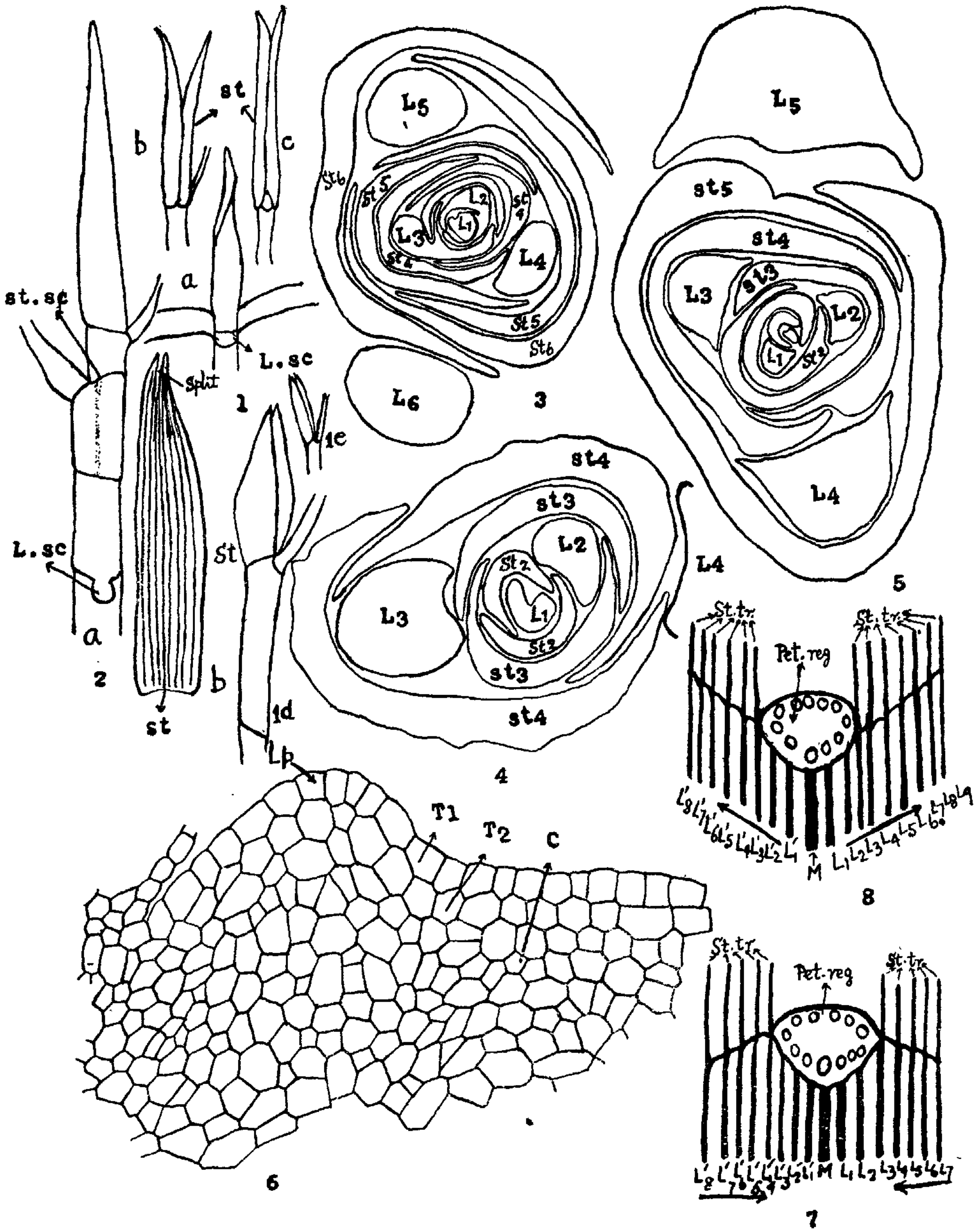
The stipules of *A. integrifolia, F. religiosa* and *F. elastica* have been described as bud scales or tegmenta in our general botanical text-books and manuals (Asa Gray, 1879; Green, 1897; Vines, 1910; Strasburger, 1930; Priestley and Scott, 1938 ; and others). Bud scales are scale-like foliar organs which invest the resting bud (Foster, 1929, pp. 126) and almost any part of a leaf may develop into a bud scale (Priestley and Scott, 1938).

With the exception of Goebel who has mentioned about the early or late fusion by the transverse cushion as determining the nature of the stipules in these plants, the author is not aware of any literature dealing with a detailed ontogeny and development of these structures, and the present communication records the result of such studies so that their morphological nature may be best understood.

Methods of studies have been the same as in previous communications (Mitra, 1945, 1948, 1949). All outline drawings and cellular details have been drawn under a camera lucida with magnifications noted against each figure.

External Morphology.

Leaves of *A. integrifolia* and *F. religiosa* possess *a pair* of stipules each. The position, attachment and the scars of the stipules on the axis are similar in both the species (Figs. 1*a–e*). They fall off very soon with the unfolding of the leaves and a circular but downwardly oblique scar is left at the node. The stipular scar appears



Text-figs. 1 to 8.

(See foot of p. 159 for Explanation.)

cauline and is not continuous with the leaf scar (cf. *Morus*, Cross, 1937). Figures 3 and 4 show arrangements of stipules and leaf primordia in a cross-section of a terminal bud in each case. A pair of stipules overlap each other by both their margins and enclose within them successive younger leaves and their stipules.

Leaves of *F. elastica*, on the other hand, possess *a single* stipule each (Figs. 2, *a* and *b*). Each stipule has a short, longitudinal split at its apex along the line of fusion of the anterior edges and is much bigger and robust in size and texture than the stipules of the other two species. Figure 5 shows arrangement of stipules and leaf primordia in a cross-section of a terminal bud. The stipular scar is formed around the axis and is obliquely extended into the upper internode, much above the insertion of the petiole of the leaf to which the stipules belong. The leaf-bases in all the three species are either imperceptibly free (*A. integrifolia* and *F. religiosa*), or not at all (*F. elastica*), from the axis. In the case of *F. elastica* the stipule opens only at its posterior margins, whereas in the other two cases the pair of stipules open both at their posterior and anterior margins.

Origin and Early Development of the Leaf Primordium.

Figure 6 is a median longisection through the apex of a vegetative bud of *F. religiosa*. Similar sections through the shoot apices of the other two species show similarity in cellular organization and in the origin of leaf primordia. The meristem at the shoot apex consists of two tunica layers (T_1 and T_2) and a corpus (C) without any evident zonation. When a leaf is initiated transverse extension of the apical dome takes place in a particular sector. This extension is brought about by anticlinal divisions in the two layers of the tunica. This is closely followed by simultaneous periclinal divisions in the inner tunica derivatives and the outer corpus layer of this region resulting in a hump like outgrowth on the side of the apical dome (leaf emergence) (Fig. 6). The *erection* of the primordium progresses under the influence of the acropetally differentiating desmogen strand (its median bundle) coming up from the axial ring. The protoxylem is seen to differentiate in this desmogen strand at the base of the free limb and its progressive differentiation is acropetal in the latter and basipetal in the axis. Later on, as many as 15 or 17 lateral trace bundles enter the two arms of the base of the primordium as it extends tangentially around the axis. The two arms of the base at this stage show unequal

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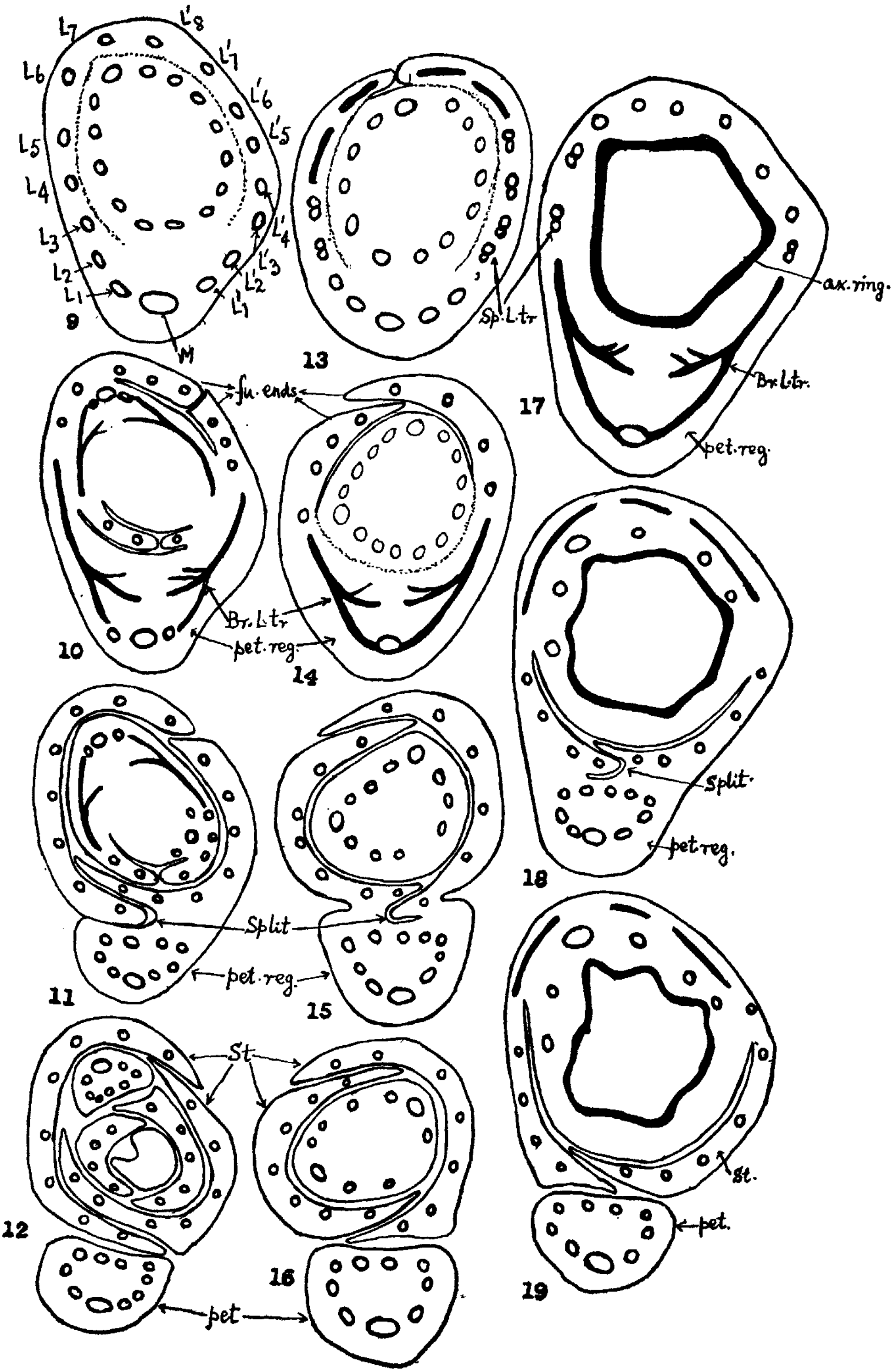
Explanation of Text-figs. 1–8 (p. 158).

1. *a–e*. Terminal buds of *F. religiosa* (Figs. *a–c*) and *A. integrifolia* (Figs. *d-e*), showing leaf scar (L.sc.) and the insertions of stipules at the nodes. Fig. *d*—stipules enclosing the shoot apex and the inflorescence while Fig. *e*—stipules enclosing the shoot apex only. All—$\frac{3}{4}$ Nat. Size.
2. *a* and *b*. Terminal bud of *F. elastica*; *a*, showing stipular scar (st.sc.) and leaf scar (L.sc.) and *b*, showing a single stipule (st.) with a split at its apical region and its parallel nervation. $\frac{3}{4}$ Nat. Size.
3. Transection of a terminal bud of *F. religiosa*. L_1, L_2, L_3, L_4, L_5 and L_6 are leaf primordia with their corresponding stipules (st_1, st_2, st_3, st_4, st_5 and st_6). $\times 11$.
4. Transection of a terminal bud of *A. integrifolia*. L_1, L_2, L_3 and L_4 are leaf primordia with their corresponding stipules (st_1, st_2, etc.). $\times 31$.
5. Transection of a terminal bud of *F. elastica*. L_1, L_2, etc., are leaf primordia with their corresponding stipules (st_1, st_2, etc.). $\times 11$.
6. A median longisection of *F. religiosa* showing cellular organisation and initiation of leaf primordium (Lp) at the apex. T_1 and T_2—the outer and inner layers of tunica respectively and C—the corpus. For explanation see text. $\times 477$.
7. Showing courses of the median (M) and the lateral traces (L_1, L_2, etc., and L'_1, L'_2, etc.) in the axial component of *F. religiosa* in a split condition.
   The splitting of the median trace has not been shown. Arrow indicates the progress of branching of the laterals of the arms and their gradual linking up. For explanation see text. Pet. reg.—central region of the base and st.tr.—stipular trace. Diagrammatic.
8. Showing courses of the median (M) and the lateral traces (as indicated by numbers in Fig. 7) in the axial component of *F. elastica* in a split condition. The splitting of the median trace has not been shown. Arrow indicates the progress of branching of the laterals of the arms and their gradual linking up. For explanation see text. Diagrammatic.



TEXT-FIGS. 9 to 19.

(See foot of p. 161 for Explanation.)

development and this appears to be due to unequal number of laterals (consequently food supply) they receive from the axial ring. The leaf-base shows considerable radial extension of its central region containing the median and immediate lateral traces.

Figures 11, 15 and 19 show that the base is never free (*F. elastica*) or free only for a very short length (*F. religiosa* and *A. integrifolia*) from the axis. The leaf-base, therefore, in these species, forms a thick mantle (skin) round the axis (internode); it grows and elongates unitedly with the growth and elongation of the axial core by intercalary growth of their cells. The internode in these species is thus made up of an axial core and a thick skin which belongs to the leaf. The base and the axial-component of the leaf are equivalent structures in each case and to an external morphologist the leaves of these species appear to consist of the blade and the petiole without any base, and it becomes difficult on external morphology alone to conceive the bud scales as leaf-base outgrowths, i.e., stipules.

Origin of the Stipules.

The leaf-base in *F. religiosa* and *A. integrifolia*, as we have just seen grows united with the axial core for the most part. During this united growth, the two laterally extending arms of the base meet and fuse on the side of the axis opposite to the median trace. After the fusion has been effected a branch from each of the extreme laterals L_7 and L'_8 (Figs. 7 and 13) enters this end. Then an oblique split appears between these two branches in the manner shown in figures 10 and 13 causing a separation of the fused ends which then overlap (Figs. 11 and 14). Separation of the base from the axis now proceeds from this end towards the central region of the base; its progress is always preceded by branches of corresponding laterals entering the arms (Figs. 11 and 15).

By the time a complete separation of the leaf-base is effected from the axis, the median and its branches, the laterals in the central region and branches coming from the proximate laterals of the arms, arrange themselves in the form of a ring in this region and a split now occurs on its adaxial side (Figs. 11 and 15). The split then extends both ways and the two arms not only become free from the axis and from each other but also cut off portions from the central region of the base which now develops as the petiole (Figs. 12 and 16).

The two arms thus being free grow directly into *a pair* of *stipules* without any pre-formed primordia. The vascular system of the stipules is formed by the branches of the laterals which run parallel to one another.

In *F. elastica*, on the other hand, after the fusion of the two laterally extending arms of the base, the regions of the arms adjacent to the central region of the base, but not the fused ends, are the first parts to receive branches from the laterals in

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Explanation of Text-figs. 9–19 (p. 160)

9–12. Serial transections of the shoot apex of *F. religiosa* showing the separations of the fused ends (fu. ends), of the base from the axis and of the arms from the central region; the origin of stipules (st) and the courses of the median (M) and the lateral traces (indicated by numbers) in the base of a primordium. pet.—petiole. For explanation see text. Br.L.tr.—branching of lateral traces.

Fig. 9 is 110μ below the extreme tip; Fig. 10, 20μ above Fig. 9; Fig. 11, 30μ above Fig. 10; and Fig. 12, 40μ above Fig. 11. Each $\times 50$.

13–16. Serial transections of the shoot apex of *A. integrifolia*. Description as given for the figures 9–12.

Fig. 13 is 170μ below the extreme tip; Fig. 14, 30μ above Fig. 13; Fig. 15, 40μ above Fig. 14; and Fig. 16, 20μ above Fig. 15. Each $\times 50$.

17–19. Serial transections of the shoot apex of *F. elastica* showing separation of the fused arms of the base from the axis and from the central region (pet.reg.); the origin of a single stipule and the courses of the median and lateral traces through the axial component. ax.ring—axial ring of vascular bundles; Br.L.tr.—branching of the lateral traces. Fig. 17 is 770μ below the extreme tip; Fig. 18, 250μ above Fig. 17; and Fig. 19, 110μ above Fig. 18. Each $\times 19$.

this region and separate from the axis from this end. Meanwhile, the median and its branches, the laterals and their branches arrange themselves in the form of a ring in the central region of the base and its separations from the axis and into the petiole and the stipule, commence simultaneously. Separation of the base from the axis proceeds towards its opposite side and its progress is always preceded by the branches of the laterals entering the arms one after the other. While the base is becoming free from the axis the arms cut off portions from the central region of the base in the manner as described for the other two species. These cut ends (posterior) of the arms then grow and overlap and finally the arms separate from the axis as one piece without any split at the fused ends. The two arms thus being free as one piece with its overlapping posterior margins develop as a single stipule and the central region of the base as the petiole (Figs. 5 and 19). Thus it is seen that though the number of stipules in this species is one, it is a product of the two arms of the base. The stipular scar is also obliquely circular but the inclination is in this case upwards. Vascular system is formed exclusively, as in the other two species, by the branches of the laterals which run parallel to one another.

Courses of the Leaf Traces in the Base of the Leaf and the Vascular System of the Stipules.

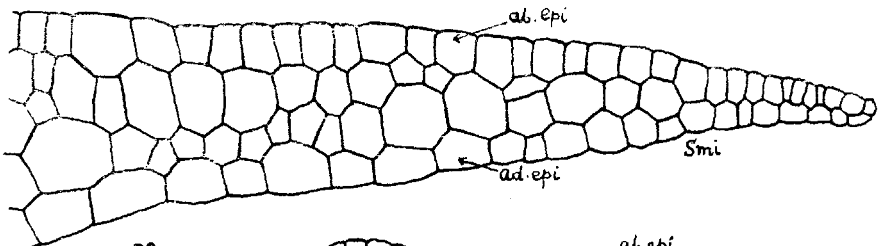
The node in each species is multilacunar, one median and 15 or 17 laterals enter the base which grows unitedly with the axial core. The median and the laterals depart from the axial ring, but instead of deviating at once towards the periphery they take vertical courses and form an outer series of bundles in the internode (Figs. 9, 13 and 17). The median continues its vertical course for some distance and then spreads laterally by giving off branches on its sides. Below the nodal region the median, its branches and 2 or 3 laterals on each side (L_1, L_2, and L'_1, L'_2 and L'_3, Fig. 7) enter directly the central region of the base. Up to this point the course of events is similar in all the three species but the subsequent behaviour of the remaining laterals is different in them.

In *F. religiosa* and *A. integrifolia* the remaining laterals begin to split one after the other, the splitting commencing from those at the extreme ends of the two arms. L_7 and L'_8 split simultaneously, one set of branches follows an oblique horizontal course to join L_6 and L'_7 respectively, while the other set continues through the fused ends which now begin to separate from the axis. L_6 and L'_7 then split in their turn and one set of their branches goes into the arms and the other set bends and joins L_5 and L'_6 respectively. In this way all the laterals (L_7 to L_3 and L'_8 to L'_4) are linked up with one another by their branches (Fig. 7), not at the same level but at different heights with the result that though they form a complete girdle round the axis, they are seen detached in a transverse section (Fig. 13).

L_3 and L'_4 are the last two of the laterals to split in the arms. In each case, one of the branches, as usual, goes into the arms and the other on entering the central region bifurcates: one branch of L_3 unites with L_2 and the other moves to the adaxial side and split here (Figs. 10 and 14). Same thing happens in the case of L'_4. These ultimate branches unite with each other. Thus the median, its branches, the laterals and their ultimate branches form a ring of vascular bundles in the central region of the base. By the time the leaf-base has completely separated from the axis. There now occurs an oblique split on the adaxial side of the leaf base which progresses both ways until the two arms completely cut off portions from the central region. The posterior margins of the two free arms now grow and overlap each other (Figs. 12 and 16).

In *F. elastica*, on the other hand, the oblique horizontal linking up of the split halves of the laterals starts from near the central region of the base and proceeds towards the fused ends of the arms. The organization of the vascular ring in the central region and the commencement of the branching of the laterals and their linking up to form a girdle around the axis take place in an order reverse of what has been described for the other two species. The separations of the base from the axis and of the arms from the central region by the formation of a split begin simultaneously at this end (Figs. 18 and 19), and the former proceeds towards the opposite side. As the progress of separation is contingent on the branching of the laterals by turn its beginning and completion, therefore, take place at different heights of the axis (Figs. 5, 8 and 17).

In all the three species the arms of the leaf-base directly develop as a *pair* or a *single* stipule as the case may be under the influence of the branches of the laterals going straight into these organs while the other set by linking up with one another form the oblique horizontal girdle round the axis. It is also to be noted that the arms cut off portions from the central region of the base only after the median, its branches, the laterals and their branches have arranged themselves in the form of a ring. The separation of the base from the axis starts with the running of branches from the pair of laterals to branch in the arms first and is completed with the



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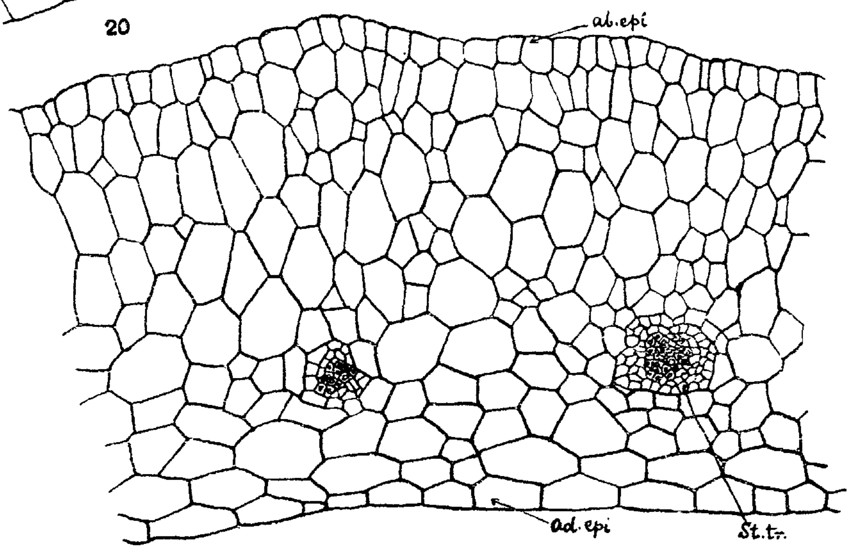

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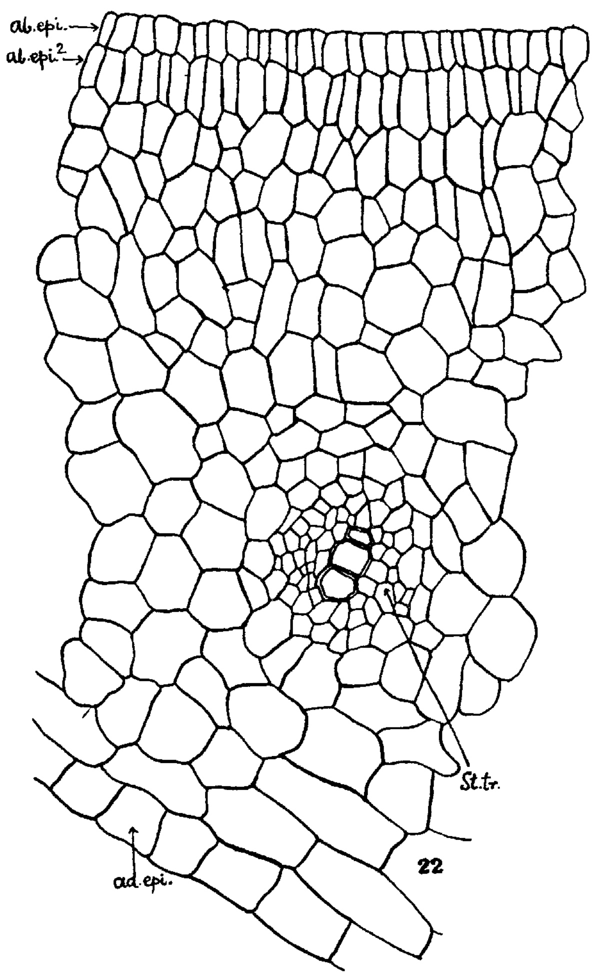
TEXT-FIGS. 20–21.

20. Transection through the margin of a stipule showing marginal growth. ab.epi.—abaxial epidermis. ad.epi.—adaxial epidermis, and Smi.—submarginal initial. For explanation see text. ×460.
21. Transection of a mature stipule of *F. religiosa* through the median region of the lamina showing cellular differentiation and vascular bundles. ab.epi.—abaxial epidermis; ad.epi.—adaxial epidermis and st.tr.—stipular trace which is a branch of a lateral trace. ×223.

branches from the pair to remain and split in the arms last. The formation of a stipule takes place by gradual separation of the arms of the leaf-base and without any pre-formed primordium which might be identified as stipular primordium.

TISSUE DIFFERENTIATION IN THE STIPULES.

In all the three species marginal growth of the stipules takes place in the same manner. The marginal meristem (*perinome* of Lund, *vide* McNab, 1873) is continuous over the edge and by dividing anticlinally forms the adaxial and abaxial epidermi. At the extreme edge, however, the marginal meristem forms a biseriate plate of cells (Fig. 20). The submarginal meristem (*pycnome* of Lund, *vide* McNab, 1873) divides periclinally, and subsequent oblique divisions of the derivatives give



TEXT-FIG. 22.

22. Transection of a mature stipule of *F. elastica* near the median region of the lamina showing the cellular differentiation and vascular bundle. ab.epi.—abaxial epidermis; ab.epi.²—second layer of abaxial epidermis; ad.epi.—adaxial epidermis and st.tr.—stipular trace. ×492.

rise to the many layered mesophyll (Fig. 21). In *F. elastica* the abaxial subepidermal cells divide regularly by anticlinal walls and appear as a second layer of epidermis (Fig. 22). The mesophyll of the stipule is not differentiated into the spongy and palisade tissues (Figs. 21 and 22). The vascular system of the stipules, as we have already seen, is made up of branches from the laterals running parallel to one another.

Discussion.*

Developmental studies of the vegetative shoot apices of the three species of *Moraceae*, namely *Artocarpus integrifolia*, *Ficus religiosa* and *Ficus elastica*, show that though they present similarity in cellular organization, foliar initiation and internodal development, *F. elastica* differs from the other two species in the method of origin of the stipules and their separation from the axis.

The stipules in these species have no separate primordia, but the arms of the leaf base including the adaxial portions of its central region, as they separate from the axis, develop into these structures. The separation is gradual because the branches of the laterals enter the arms one after the other and not simultaneously, and that is why the stipular scar is oblique instead of being horizontal in these cases.

Stipules are leaf-base divergences. In *F. elastica* the studies show the absence of a free base, though in the other two species its development is very slight, almost imperceptible to the naked eye. It appears that most of the previous workers have not taken into their consideration the axial-component of the leaf while describing the origin and development of a leaf primordium. Our studies show that the axial-component cannot be omitted from the studies of leaf development. They prove conclusively that the base of the leaf may be (1) completely incorporated in the axis, i.e., internode, as is illustrated in *F. elastica* (cf. also *Paederia foetida*, Mitra, 1948); (2) for the most part included in the axis, and free for a very short length, as in *F. religiosa* and *A. integrifolia*; and (3) partly included in the axis, but free for some considerable length, as in *Heracleum* (Majumdar, 1942, 1947 and 1949), *Polygonum* (Mitra, 1945), *Rosa* (Mitra, 1949), and others with free sheathing bases.

If stipules are leaf-base divergences, and they certainly are, unless the axial-component is recognized as a part of the leaf-base, *bud scales* of these species, and particularly of *F. elastica*, cannot be regarded as stipules. Therefore, we are perfectly justified in recognizing the base as comprising of two regions: one incorporated into the axis (axial-component), and the other free. The free portion is very slightly developed in *F. religiosa* and *A. integrifolia*, and undeveloped in *F. elastica*.

The origin and behaviour of the leaf traces and their branches also support the conclusion that the axial-component is a part of the leaf-base. It can be safely postulated that the laterals branch only in the leaf-base below the petiole and beyond the petiole in connection with the development of leaflets and lamina. The branches in the leaf-base cause the development of its laminar wings, teeth or stipules, and in their absence these structures will not develop in the base. In our studies we find the laterals branch in the axial-component, and one set of branches stimulate the arms of the latter beyond the level of branching to develop further into the stipules. All these facts show that the axial-component of a leaf is part and parcel of its base. Moreover, the courses of the laterals after departing from axial ring determine the nature of the base whether it will continue its united growth with the axis for a short or greater length, or be immediately free from the latter and give rise to simple or sheathing leaf-bases.

Saunders in 1922 revived the Berindung Theory of Hofmeister (1851) and propounded her Leaf-skin Theory, both of which visualized a core (axial) and a skin

* In this discussion leaf-base and axial-component are used synonymously.

(leaf-base), the radial, tangential and vertical extent of the latter varying. According to Hofmeister all the tissues external to the pith belong to the leaf. Saunders, on the other hand, thinks the epidermis and one or two hypodermal layers belong to this organ. The present studies, however, support the view of Hofmeister.

According to Saunders the leaf-skin is formed by a downward growth and extension of the leaf primordium keeping pace with the extension of the central axis with which it is fused. This is not supported by our observation. We have seen that the axial-component soon after its initiation encloses the axial core and later in ontogeny by their united intercalary growth the internode is developed. In this connection the observation of Sharman (1942) on the development of the internode of Maize from the lower half of the 'disc of insertion' of the primordium may be referred to. Once more the dual nature of the axis (leaf-base+axial core) is revived. It is desirable that further extensive developmental studies should be made to establish the true morphology of the axis.

It is proved once again that the branches of the lateral traces are the determining factor for the development of the stipules from the leaf-base. Normally a stipulate leaf has a pair of stipules and they diverge symmetrically from the base on the two sides of the petiole. Stipules of *F. religiosa* and *A. integrifolia* conform to this rule, and in *F. elastica* though a single stipule is formed the developmental studies establish its double nature, i.e., the product of the fusion of the two arms which do not free and overlap in the region of fusion of their ends. Its double nature is also indicated by the short split at the apical portion of the adult stipule along the line of fusion.

It is difficult to suggest any explanation as to why the fused margins in this case do not separate and overlap in the manner noticed in the other two species, unless the nature of the splitting is different. In all the three cases the wings or arms of the base meet on the opposite side of the axis and remain united with the latter for some length. In their subsequent development *F. elastica* differs from the other two species in one important aspect, namely, that the branching of the laterals and the separation of the base from the axis, as we have noticed, take place in reverse order.

The stipules of these species have been described as axillary by Goebel and others but their ontogeny, however, shows that they are lateral outgrowths, only a portion, i.e., the extreme posterior margins is derived from the central region of the base.

Summary.

Developmental studies of the vegetative shoot apices of the three species, namely *Artocarpus integrifolia, Ficus religiosa* and *Ficus elastica* show similarity in cellular organization and in the initiation and early development of leaf primordia.

During foliar development the two sides of the axial-component extend tangentially around the apical dome and completely enclose the latter. They meet on the opposite side of the axis and fuse with each other by their ends. At first, the median and then gradually 7 or 8 laterals on each side of the median enter the axial-component as its two arms extend round the axis. These trace bundles, median and laterals, instead of diverging at once towards the periphery of the axial-component which now invest the axis in the form of a mantle (skin), follow upward courses and form an outer series of bundles surrounding the axial ring. The internode is developed later by the intercalary growth of the axial-component and the central core of the axis as one organ.

All these features concerning the origin and development of leaf primordia and the internode up to a point are common to all the three species but the subsequent development and differentiation is different in them.

In *A. integrifolia* and *F. religiosa* the branching of the laterals, which is not simultaneous but takes place one after the other begins with the pair of laterals at the extreme ends of the two arms and stops with the laterals just outside the central region of the base. Of the two branches of each lateral one goes up into the arms and the other bends obliquely to join the lateral next to it. In this way all the laterals of the arms are linked up gradually by one set of their branches to form an oblique horizontal girdle round the axis, the other set goes directly into the arms of the base above the region of branching. By this time radial extension

of the central region of the base in the form of an abaxial bulge has formed due to the activity of the abaxial meristem.

The branching of the laterals is followed by the separation of the base from the axis which begins at the fused ends. An oblique split occurs at this end and later development of the split ends cause their overlapping. Vertical growth of the axis (i.e., of the combined axial-component and central core) continues until a complete separation of the base from the axis is effected. By this time the median, its branches, the laterals and their branches have arranged themselves in the form of a ring in the central region of the base—a feature characteristic of a cylindrical petiole. An oblique adaxial split now occurs at this region which cause overlapping of the split margins. The free arms now cut off portions from the central region of the base and the three organs, viz., the central region and the two free arms overlapping by both their margins continue their vertical growth and development under the influence of their respective vascular supply as the petiole and a pair of stipules respectively. The pair of stipules enclose and protect the buds as bud scales. The stipular scar is obliquely circular, the inclination being towards the lower internode.

In *F. elastica* the story of the branching of the laterals and the separation of the base from the axis, is the reverse of what has been noticed in the above two species. The branching of the laterals begins at the central region of the base and proceeds from one lateral to the other by turn towards the opposite side of the axis. In a similar way, as what has been noticed in the other two species, one set of branches of the laterals run vertically into the arms and the other set link up with one another to form an oblique horizontal girdle round the axis. The central region, as in the other two species, grows radially in the form of a bulge.

The separation of the base from the axis and of the arms from the central region begin at the latter region but not at the fused ends of the arms as is seen in the other two species, and after the first pair of branches of the laterals have entered the arms and the median, the laterals and their branches have arranged themselves in the form of a closed ring in the central region of the base. The separation then proceeds towards the opposite side of the axis. The fused arms with its posterior margins overlapping and except for a very short split at its apex, separate as one piece from the axis with the result that the stipule is single and sheathing in this species. The posterior margins of the stipule which are adaxial portions of the central region of the base being cut off in a manner as described for the other two species, due to active growth overlap each other and enclose and protect the buds as bud scales. The stipular scar is obliquely circular but the inclination is towards the upper internode.

The present studies prove that—

(1) The leaf-base includes the axial-component which should be regarded as an integral part of the leaf:
  - (i) when it consists of the axial-component only as in *F. elastica* the free base is absent;
  - (ii) when it is axial-component for the most part and free only for a very short length as in *F. religiosa* and *A. integrifolia*, the base has just a free portion;
  - and (iii) when it is axial-component for comparatively a short length (leaf cushion) and free for a considerable length as in *Heracleum*, *Polygonum*, etc., the free portion of the base is sheathing.

(2) The internode of the axis is structurally dual in nature being composed of an axial core enveloped by the axial-component (base or bases of leaves).

(3) For the development of stipules branches from the lateral traces are essential but pre-formed primordia are not necessary.

Acknowledgments.

The author is indebted to Prof. G. P. Majumdar, Ph.D., F.N.I., Professor of Botany, Presidency College, Calcutta, for his guidance in the work and for valuable assistance in preparing the manuscript.

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