# THE LEAF-BASE AND THE INTERNODE — THEIR TRUE MORPHOLOGY[1]

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ABSTRACT

1. Development of the leaf primordium at the shoot apices of 14 species of dicotyledons has been studied.

2. These include exstipulate, stipulate and sheathing leaves with or without a free base.

3. The axial component which is laid down first during the initiation of a leaf development at the apex of a vegetative shoot is a part of the leaf and is to be considered as its base.

4. In species where a free base is wanting, the axial component represents the only base and the cauline and discontinuous stipular scar, which led Ponzo, Cross and others to doubt the origin of stipules from the leaf-base, is explained.

5. The development of a free base in the form of a sheath and/or a pair of stipules depends on the course and behaviour of the trace bundles through the axial component (e.g. in species of *Centella, Polygonum, Ixora, Ervatamia, Rosa, Morus, Calotropis, Artocarpus, Ficus, Paederia, Hibiscus* and *Pisum* ).

6. If the laterals change their vertical course, bend and follow an oblique horizontal course towards the median at the top of the axial component, the petiole appears to be inserted directly on the axis without any evident base ( free ) as in the species of *Ficus, Paederia, Jasminum, Hibiscus, Morus* and *Pisum* studied.

7. If during the horizontal course the laterals branch in the axial component, a single ( *Ficus elastica, Ervatamia divaricata, Polygonum orientale* ), or a pair of stipules ( *Ficus religiosa, Artocarpus integrifolia, Morus alba, Hibiscus rosa-sinensis, Pisum sativum* and *Rosa centifolia* ), or a composite stipule ( *Ixora parviflora* and *Paederia foetida* ), are formed with the branches as their traces, and the stipular scars appear cauline.

8. If the laterals, two or many, run almost parallel to one another and to the median, even after leaving the axial component for some time before they turn towards the median, a sheathing but free base is formed which partially or completely encloses the axis, depending on the number and nature of the course of the laterals ( e.g. *Centella* and *Rosa* ).

9. If in a multilacunar node the laterals branch during their horizontal course towards the median the stipule formed is either an ochrea ( *Polygonum* ), or bud scales ( species of *Ficus* and *Artocarpus* ).

10. If, however, the laterals do not branch and gradually shift towards the median where they form with the latter a ring of vascular bundles, the sheath becomes oblique and tapering without any stipule ( *Centella* ).

11. The base, i.e. the axial component, and its free portion, if there be any, can be anatomically distinguished by the nature and behaviour of the laterals, from the petiole: in the base they gradually approach the median without joining it and may branch, but in petiole they either join with the median ( *Rosa* ) or arrange themselves with the latter in the form of a ring of vascular bundles ( *Centella* ). They again branch in connection with leaflet and lamina formation.

12. The internode is made up of an axial core and a mantle derived from two different zones of the eumeristem — the corpus and the flank meristems. The mantle is made by base or bases ( axial component or components ) of the leaves, and extends radially up to the pith as suggested by Hofmeister.

## INTRODUCTION

THE idea of the nature and extent of the leaf-base, as we get it from the text-books, etc., is rather vague and indefinite. The base has been described as that " portion of the leaf which sits upon the vegetative point of the shoot " ( GOEBEL, 1907, p. 321 ), i.e. the region of its insertion on the axis; and only in a few cases, such as the pulvinus, leaf sheath, etc., the base is well developed ( VINES, STRASBURGER, SCOTT, GREEN *et al.*). In many cases, the petiole appears to be directly inserted on the axis and there is nothing free between the petiole and the axis that can be recognized as the leaf-base except the base of the petiole. Asa Gray ( 1879 ) would not recognize the existence of the base as a part of the leaf when he said that a typical leaf consists of *three* parts: a blade, the petiole and a pair of stipules ( p. 85 ) which are lateral appendages, one on each side of the base of the petiole ( p. 105 ). By the term ' leaf ' is at

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present understood the free lateral member of the shoot borne upon the stem but different from the latter in structure and form. It is admitted by all workers on organogeny that the leaf primordium ( limb ) in its initial stage of origin and development is undifferentiated, though the same is sometimes distinguished by its later behaviour, into two regions — an upper and a basal portion, as in the leaf of any grass ( GOEBEL, 1907, p. 304 ). The petiole is intercalated between the two later in the ontogeny of the leaf ( EICHLER, 1861 ).

This idea of the leaf-base, unless the latter is specially developed, has given rise to many controversies and the one that strikes us most is in connection with the origin of the stipules. After Sinnott and Bailey's ( 1914 ) classical studies and conclusions, the nature and origin of the stipules appeared to have been finally solved. According to them the stipules are leaf-base divergences being influenced in their development by the branches of the laterals of the trace bundles of a leaf. Without such branches no stipule is formed.

But in 1934 Ponzo, and later Cross (1937), doubted the leaf-base-divergence origin of the stipules at least in such cases where a free base is wanting, and consider the stipular scar to be cauline. As an alternative to the leaf-base-divergence theory in such cases Cross suggested that the region from which the stipules arise is not the base of the leaf but a leaf-stem transition region.

From a long time the phytonists held the view that the ' unit of growth ', i.e. each phyton, is made up of the leaf primordium and its base, the latter being incorporated in the axis (GAUDICHAUD, 1841 ; DE CANDOLLE, 1861; DELPINO, 1880, 1883; CELAKOVSKY, 1901; CHAUVEAUD, 1911; SCHUEPP, 1916; PRIESTLEY, 1929; GRIFFITH & MALLINS, 1930; SCHOUTE, 1931; PRIESTLEY & SCOTT, 1933; PRIESTLEY, SCOTT & GILLET, 1935; PRIESTLEY & MATTINSON, 1937; MAJUMDAR, 1942, 1947, 1949; *et al.*). Priestley defined the base ( axial component ) in *Vicia faba* as the " segment of the axis which subtends a leaf initial and surrounds the leaf trace as it differentiates ".

In 1851 Hofmeister propounded the Berindung theory to explain the nature of the shoot axis ( internode ). He visualized the internode as made up of an axial core surrounded by a mantle which develops from the leaf-base or bases. According to him the *core* in adult plants is represented by the pith and all the tissues outside the pith including the vascular bundles belong to the *mantle*. In 1922 Saunders revived this theory regarding the nature of the axis in her leaf-skin theory. She differed from the other theory only in one respect, namely the radial extent of the mantle, and thought that the epidermis and one or two hypodermal layers belong to the skin and the rest to the axial core. This skin she held as made up of the bases of leaves grown by the downward extension of the internode. Not much importance appears to have been given to this ' mantle-core ' nature of the internode.

In 1935 Grégoire and Louis for the first time showed that the initiation of a leaf development at the shoot apices of dicotyledons takes place by the formation of what they described as the *soubassement foliaire* which is incorporated in the axis and on which the free primordium ( limb ) is erected later. The later authors ( FOSTER, 1935; MAJUMDAR, 1942, 1947, 1948, 1949; MITRA, 1945, 1948, 1949; *et al.*) confirmed the formation of this foliar foundation, i.e. the axial component of the leaf, prior to its emergence ( free limb ) though Engard ( 1944 ) regards this as ' still hypothetical '. There are still many eminent botanists who are unwilling to accept this view of the origin of the leaf primordium at the growing apex of a vegetative shoot. Majumdar ( 1947 ) considered the axial component as the base of the leaf and thinks that the former cannot be omitted from the study of the latter. This has been shown to be the case in the species studied by the junior author ( MITRA, 1945, 1948, 1949 ).

During our studies we have noticed that the axis in the bud is made up of a core and a mantle ( leaf-base ) derived from two different zones of the apical meristem. The development of the internode is brought about by the united intercalary growth of the two. It was, therefore, thought necessary to re-examine the Berindung theory of Hofmeister and the leaf-skin theory of Saunders in the light of our observations.

The above facts amongst others led the junior author to study the shoot apices of diverse species of dicotyledons and the origin and development of the leaf and different types of stipules. The results whereof only in relation to the leaf-base and the nature of the internode are presented in this communication.

## MATERIALS AND METHODS

The vegetative buds of the following species were collected locally from different areas; fixed in FAA and other fixing fluids; and the usual schedule for microtome preparations was followed. Sections were cut between 8 and 10 $\mu$ in thickness, stained with safranin-haematoxylin (Heidenhain's), fast green-safranin, and ferric chloride-tannic acid-safranin combinations. All figures were drawn under camera lucida at magnifications noted against each.

| Species | Types of Leaf | |
|---|---|---|
| 1. *Calotropis procera* Br. | Exstipulate, subsessile | |
| 2. *Jasminum flexile* Vahl. | do | petiolate |
| 3. *Centella asiatica Urb.* | do | sheathing |
| 4. *Polygonum orientale* Linn. | Stipulate (ochreaceous) | |
| 5. *Ficus elastica* Roxb. | do | (bud scale) |
| 6. *Ficus religiosa* Linn. | do | do |
| 7. *Artocarpus integrifolia* Linn. | do | do |
| 8. *Ixora parviflora* Vahl. | do | (interpetiolar) |
| 9. *Paederia foetida* Linn. | do | do |
| 10. *Ervatamia divaricata* (L.) Burkill. | do | (intrapetiolar) |
| 11. *Rosa centifolia* Linn. | do | (adnate) |
| 12. *Morus alba* Linn. | do | (free lateral) |
| 13. *Hibiscus rosa-sinensis* Linn. | do | do |
| 14. *Pisum sativum* Linn. | do | (foliaceous) |

## EXTERNAL MORPHOLOGY

*Calotropis procera* — A shrub; belongs to the family Asclepiadaceae. Leaves are simple, opposite, decussate, subsessile, margin entire and exstipulate ( TEXT-FIG. 2 ).

Text-fig. 18 shows the arrangement of the leaf-bases in transection of a terminal vegetative bud.

*Jasminum flexile* — A climber; belongs to the family Oleaceae. Leaves compound, leaflets 3, alternate, petiolate, margin entire and exstipulate; petiole as well as the stalks of leaflets undergo torsion ( TEXT-FIG. 5 ).

Text-fig. 17 shows the arrangement of leaves in transection of a terminal vegetative bud.

*Centella asiatica* — A herbaceous member of the family Umbelliferae. Leaves simple, alternate, phyllotaxy two-fifths, petiolate, margin entire and exstipulate with sheathing leaf-base. In certain text-books the central part of the sheath is described as petiolar and the wings as stipules adnate to it (cf. *Rosa centifolia*, MITRA, 1949) (TEXT-FIG. 1).

Text-fig. 15 shows the arrangement of leaf-bases in transection of a terminal vegetative bud.

*Polygonum orientale* — An annual herb; belongs to the family Polygonaceae. Leaves simple, alternate, phyllotaxy two-fifths, petiolate, margin entire and stipulate ( ochreaceous ); the ochrea consists of two portions, the lower sheathing base and the upper sheathing stipule ( TEXT-FIG. 4 ).

Text-fig. 21 shows the arrangement of the leaves and the ochreas in transection of a terminal vegetative bud.

*Ficus elastica* — A tree; belongs to the family Moraceae. Leaves simple, alternate, petiolate, margin entire and stipulate ( bud scale); stipule single, sub-persistent, coloured, almost half as long as the leaves. The stipular scar is cauline and obliquely circular around the axis ( TEXT-FIG. 7 ).

Text-fig. 20 shows the arrangement of the leaves and the stipules in transection of a terminal vegetative bud.

*Ficus religiosa* — A large tree; belongs to the family Moraceae. Leaves simple, alternate, petiolate, margin entire, stipulate ( bud scales ); stipules a pair, caducous. The stipular scar is cauline ( TEXT-FIG. 6 ).

Text-fig. 19 shows the arrangement of the leaves and the stipules in transection of a terminal vegetative bud.

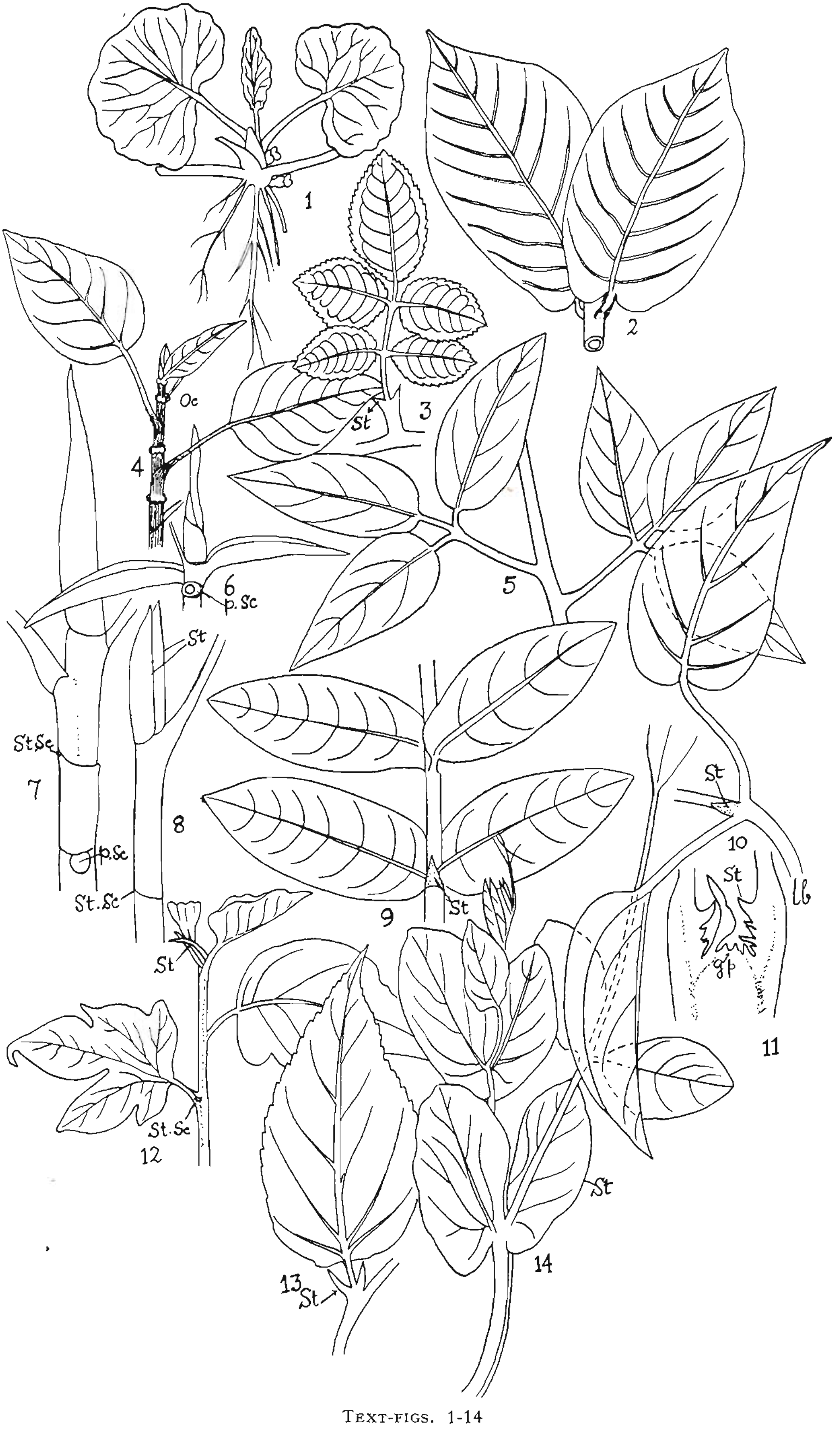
*Artocarpus integrifolia*—A large evergreen tree; belongs to the family Moraceae. Leaves simple, alternate, petiolate, margin entire, stipulate ( bud scale ); stipules a pair, caducous. The stipular scar is cauline ( TEXT-FIG. 8 ).

Text-fig. 22 shows the arrangement of the leaves and the stipules in transection of a terminal vegetative bud.

*Ixora parviflora* — A branching shrub; belongs to the family Rubiaceae. Leaves simple, opposite, decussate, very shortly petiolate, margin entire, stipulate ( interpetiolar ); stipules minute, rigid and persistent ( TEXT-FIG. 9 ).

Text-fig. 25 shows the arrangement of the leaves and the stipules in transection of a terminal vegetative bud.

*Paederia foetida* — A slender twining shrub; belongs to the family Rubiaceae. Leaves simple, opposite, decussate, petiolate, margin entire, stipulate ( interpetiolar ); stipule minute and persistent ( TEXT-FIG. 10 ).




TEXT-FIGS. 1-14

Text-fig. 24 shows the arrangement of the leaves and the stipules in transection of a terminal vegetative bud.

*Ervatamia divaricata*—A shrub; appears to branch dichotomously and belongs to the family Apocynaceae. Leaves simple, opposite, decussate, petiolate, margin entire, stipulate (intrapetiolar, i.e. axillary); a single stipule growing out from the inner face of the sheathing base, minute, persistent (TEXT-FIG. 11).

Text-fig. 26 shows the arrangement of the leaves and their corresponding stipules in transection of a terminal vegetative bud.

*Rosa centifolia*—A scrambling prickly shrub; belongs to the family Rosaceae. Leaves compound, alternate, phyllotaxy two-fifths, petiolate, margin serrate, stipulate (adnate); the sheathing base along with two apical teeth is described as the adnate stipule (TEXT-FIG. 3).

Text-fig. 23 shows the arrangement of the leaf-bases in transection of a terminal vegetative bud.

*Morus alba*—A deciduous tree; belongs to the family Moraceae. Leaves simple, lobed, alternate, petiolate, margin serrate, stipulate (a pair of free lateral stipules); stipules minute and caducous. The stipular scar is cauline (TEXT-FIG. 12).

Text-fig. 28 shows the arrangement of the leaves and the stipules in transection of a terminal vegetative bud.

*Hibiscus rosa-sinensis* — A woody shrub; belongs to the family Malvaceae. Leaves simple, alternate, phyllotaxy two-fifths, petiolate, margin serrate, stipulate (free lateral); stipules minute and caducous. The stipular scar is cauline (TEXT-FIG. 13).

Text-fig. 16 shows the arrangement of the leaves and the stipules in transection of a terminal vegetative bud.

*Pisum sativum*—A cultivated annual herb; belongs to the family Leguminosae. Leaves compound, alternate, distichous, margin entire, stipulate (foliaceous); stipules large, leaf-like and persistent (TEXT-FIG. 14).

Text-fig. 27 shows the arrangement of the leaves and the stipules in transection of a terminal vegetative bud.

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TEXT-FIGS. 1-14. Show disposition of the leaves on the axis. Oc, ochrea; p.Sc, petiolar scar; St.Sc, stipular scar; St, stipule; lb, leaf-base; and gp, growing point. 1, *Centella asiatica*; 2, *Calotropis procera*; 3, *Rosa centifolia*; 4, *Polygonum orientale*; 5, *Jasminum flexile*; 6, *Ficus religiosa*; 7, *Ficus elastica*; 8, *Artocarpus integrifolia*, 9, *Ixora parviflora*; 10, *Paederia foetida*; 11, *Ervatamia divaricata*; 12, *Morus alba*; 13, *Hibiscus rosa-sinensis*; and 14, *Pisum sativum*. 11, a longitudinal section × 17; other figures, nat. size.

## OBSERVATIONS

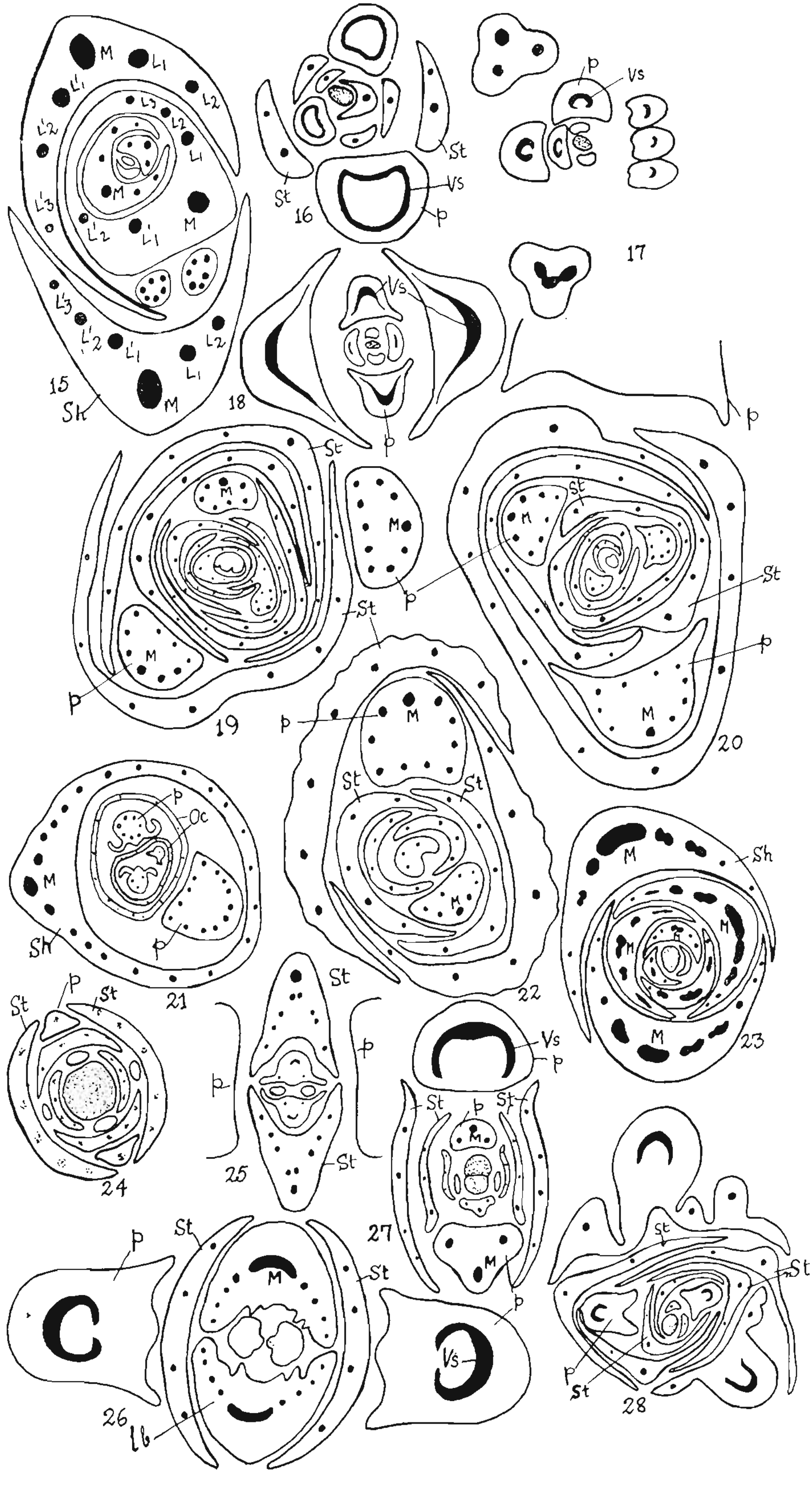
### SHOOT APEX: THE EUMERISTEM

In all the species studied and reported in this paper the free apical dome is occupied by the eumeristem which is generally made up of the *tunica* (1-3 layers) overlying the *corpus*. They have their distinctive mode of cell divisions. In some cases the eumeristem shows evident zonation: a zone each of the *central mother initials*, the *flank* meristem and the *file* meristem (the last is derived exclusively from the corpus cells). The central mother initials by slow divisions add to the flank and the file meristems; the flank meristem gives rise to the leaf primordia, and the file meristem, to the pith which helps in the development of the internode and forward growth of the shoot apex. Buds arise in the axils of the leaves far removed from the free apex.

### ORIGIN OF THE LEAF PRIMORDIUM

In all the 14 species studied, the origin of a leaf primordium is initiated at the side of the free apex by the activity of the flank meristem in a particular sector at regular intervals or plastochrones leading to the formation of the "soubassement foliaire" (GREGOIRE, 1935; LOUIS, 1935) (TEXT-FIGS. 29-31). On this foliar foundation, which is a component of the axis at this stage of leaf development, the free limb of the primordium is erected under the influence of the acropetally differentiating desmogen strand coming up from below as its trace bundle (KOCH, 1891; THIESSEN, 1908; PRIESTLEY, SCOTT & GILLET, 1935; SMITH, 1941; CROSS, 1942; ESAU, 1942; CRAFT, 1943; ENGARD, 1944; STERLING, 1945, 1946; GUNCKEL & WETMORE, 1946; MAJUMDAR, 1942, 1947, 1948; MITRA, 1945, 1948, 1949; *et al.*) (TEXT-FIGS. 29-31).

*Calotropis procera* — By transverse extension of the free apex at two sectors of the apical dome a pair of opposite leaf primordia are laid down at the same time. The transverse extension is brought about by anticlinal and occasional periclinal divisions in the flank meristem. The leaf primordium at this stage consists of the base only (axial




TEXT-FIGS. 15-28

component ). The base of each primordium now extends tangentially half-way around the axis until their lateral ends meet and fuse to form a sheath around the axis ( TEXT-FIGS. 32-35 ). Pairs of primordia are laid down in quick succession at the shoot apex and the internodal space between two consecutive sets of primordia is occupied by their united bases enclosing the axial core in the form of a mantle. Elongation of the internode takes place by intercalary growth of this mantle and the axial core together as one organ ( TEXT-FIGS. 36, 37 ).

While the base of the primordium after its initiation is extending tangentially around the axis, its free limb grows out in the form of a hump at the side of the free apex under the influence of the acropetally differentiating desmogen strand coming up from the axis. The strand is a composite trace consisting of three bundles leaving the axial ring together and the node is unilacunar ( TEXT-FIG. 33 ).

The trace bundles do not branch during their upward courses through the axial component, at the top of which they spread laterally and form an open arc characteristic of the petiole and the latter appears directly inserted on the axis ( TEXT-FIG. 37 ).

There is no free growth of the leaf-base apart from what is included in the axis and when it separates from the latter, the three bundles of the trace have already formed an arc characteristic of a petiole grooved on its adaxial face.

*Jasminum flexile* — Primordia ( axial components ) of two leaves are almost simultaneously laid down at the free apex in the manner described for the above species ( TEXT-FIGS. 38, 42 ). The arm of each axial component extends and occupies about one-third of the circumference of the axis and continues its upward growth united with the latter for some distance. By the time the bases of two primordia separate from the axis, the trace, which is composite in nature ( three-bundled, but unilacunar node ), extends laterally to form an arc characteristic of the petiole ( TEXT-FIGS. 39, 41 ). When the two primordia are separating from the axis, the third is organized and after this one has separated from the axis, the next pair is laid down and the process is repeated ( TEXT-FIGS. 41, 42 ). In a transverse section the axis is seen to be composed of a mantle made up of three leaf-bases enclosing an axial core (TEXT-FIGS. 38, 42 ). The base is free from the axis for a very short distance, imperceptibly merging into the petiole which grows enormously by intercalary growth.

The apex in this species is characterized by the mode of laying down of the primordia and a very rapid elongation of the internode due to the active cell divisions of the file meristem.

*Centella asiatica* — The primordium in its earliest stage of initiation has only the axial component. When it is first laid down on the side of the free apex it occupies a sector. Its free limb is erected after the median has entered its base. Simultaneously with the growth of the free limb the base extends tangentially along the surface of the axis when more bundles enter it from the axial ring with the result that the base receives a large number of bundles (7) and the node becomes multilacunar ( TEXT-FIG. 43 ). The two arms ultimately meet on the opposite side of the axis and fuse to form a tubular sheath completely enclosing the latter. At this stage there is no petiole and the primordium consists of an upper free limb and a base enclosing the axis in the form of a mantle ( TEXT-FIGS. 43, 44 ).

From the axis the base becomes free as a tubular sheath. As the primordium elongates, the radial growth at the central region of the base takes place very rapidly. The trace bundles without branching gradually shift from their direct vertical courses and finally come to arrange themselves in the form of a ring in this region with the result that the margin of the base gradually recedes from their extreme ends and the free base forms an oblique sheath — widest at the node and tapering towards its upper limit ( TEXT-FIGS. 45-48 ). At the base of the petiole remnants of the two wings without any trace bundle are seen, and these are regarded by some as the stipules adnate to the petiole ( TEXT-FIGS. 48, 49). The base, therefore, in this case is partly included in

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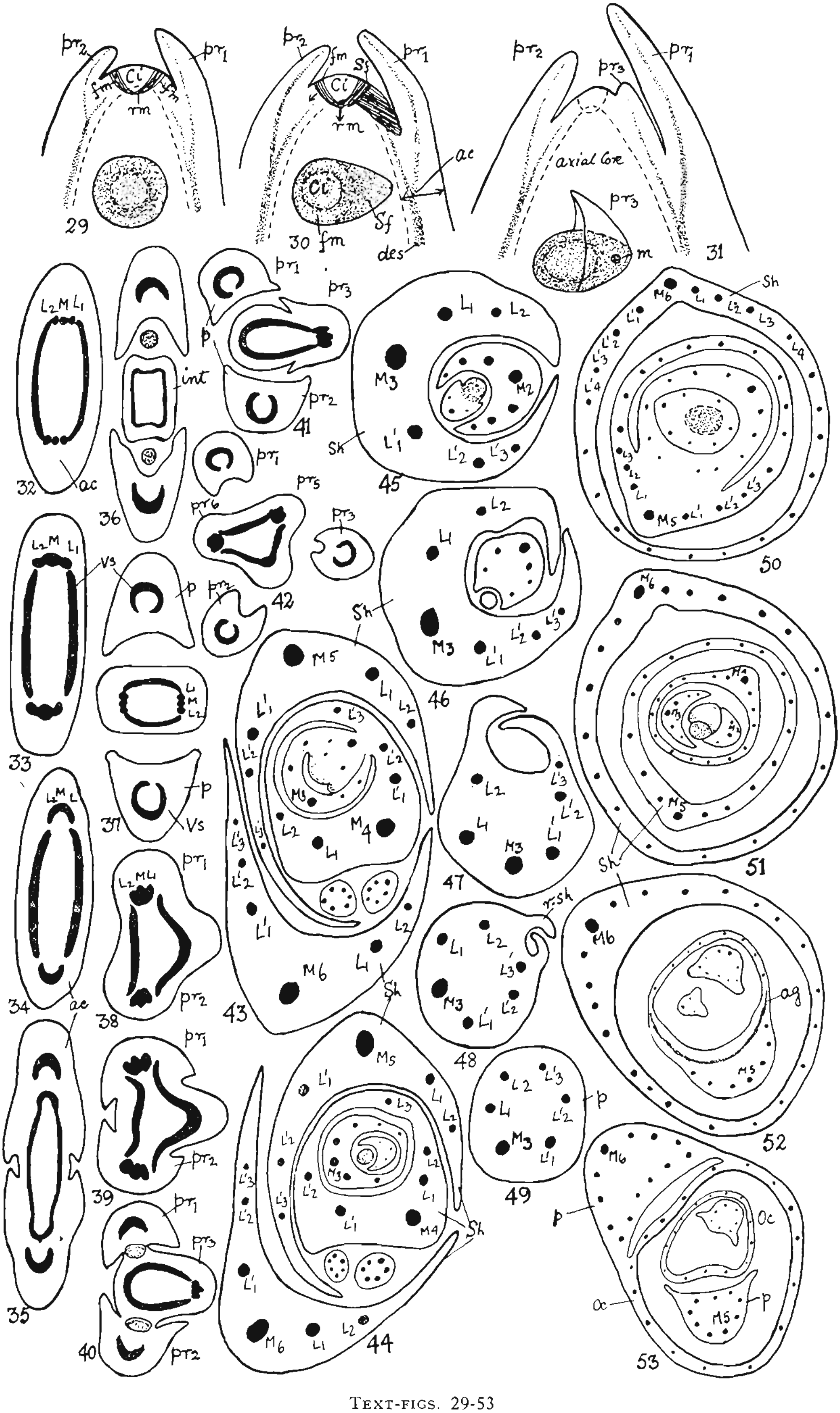
TEXT-FIGS. 15-28. Transections of terminal buds showing the arrangement of the leaves and the stipules. M, median trace bundle; L, $L_1$, $L_2$, etc., and $L'_1$, $L'_2$, $L'_3$, etc., lateral trace bundles; Vs, vascular bundle; Sh, sheath, p, petiole; and St, stipule. 15, *Centella asiatica* × 18, 16, *Hibiscus rosa-sinensis* × 18, 17, *Jasminum flexile* × 18, 18, *Calotropis procera* × 47, 19, *Ficus religiosa* × 49, 20, *Ficus elastica*, × 18; 21, *Polygonum orientale* × 46; 22, *Artocarpus integrifolia* × 49, 23, *Rosa centifolia* × 46; 24, *Paederia foetida* × 63; 25, *Ixora parviflora* × 47 , 26, *Ervatamia divaricata* × 46, 27, *Pisum sativum* × 46, and 28, *Morus alba* × 18.




TEXT-FIGS. 29-53

the axis and partly free from the latter in the form of a sheath. The older morphologists regard this sheath as specially developed leaf-base.

*Polygonum orientale* — The initiation and development of the primordium at the shoot apex takes place in the same manner as in *Centella*. The primordium receives one median and many laterals and the node is multilacunar (TEXT-FIG. 50).

From the axis the base becomes free as a tubular sheath, and it continues its free upward growth till the laterals deviate from their vertical courses and bend to follow a united horizontal course towards the central region of the sheathing base (TEXT-FIGS. 51, 52). During the united horizontal course the laterals give out branches, and these branches maintain further upward growth of the sheath as the free upper tubular portion (stipule) (TEXT-FIGS. 53, 56). As in *Centella* the base forms a mantle enclosing the axial core in the internode. The ochrea is really the sheath plus the stipule.

*Ficus elastica*, *F. religiosa* and *Artocarpus integrifolia* — In these three species the initiation, further growth and differentiation of the primordium take place in a manner similar to that described for *Centella*. Each primordium receives many lateral trace bundles and the node is multilacunar. The base of a leaf or the axial component in each case completely encloses the axis and the internode is made up, as in the other cases, of a mantle and an axial core. The trace bundles, the median and the laterals, instead of diverging at once towards the periphery of the axial component which invests the axis in the form of a mantle, follow upward courses and form an outer series of bundles surrounding the axial ring of vascular bundles (TEXT-FIGS. 57, 61, 65). The internode is developed later by intercalary growth of the axial component and the core as one organ.

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

In *Ficus elastica* the base has no free growth and the laterals while following their upward course begin to branch one by one by turn — one branch of each continues its upward course while the other bends and joins the lateral next to it and the process is repeated (TEXT-FIGS. 65-67, 54). In this way all the laterals are linked up by one set of branches, the other set maintaining the forward growth of the lateral portions of the sheath as a *single stipule* (bud scale) (TEXT-FIG. 20). While in *Ficus religiosa* (TEXT-FIGS. 58-60) and *Artocarpus integrifolia* (TEXT-FIGS. 62-64) the base becomes free just for a little distance while the major portion remains incorporated in the axis. In the incorporated portion of the base near its top the laterals begin to branch one by one by turn — one branch follows its vertical course while the other bends and joins the lateral next to it as in *F. elastica* with this difference, that in these two species the branching proceeds from the laterals at the extreme ends (fused) (TEXT-FIG. 55) while in the former it starts from the laterals close to the median (TEXT-FIGS. 54, 65). The above branches maintain further upward growth of the sheathing base as *a pair* of free overlapping stipules (TEXT-FIGS. 60, 64) in *Ficus reli-*

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TEXT-FIGS. 29-53—29-31, longisections and corresponding transections of shoot apices showing the stages in the development of a leaf primordium at the free apex. Diagrammatic. For explanation see text.

$pr_1$, $pr_2$, $pr_3$, leaf primordia; Ci, central mother-initials; fm, flank meristem; rm, rippen or file meristem; Sf, " soubassement foliaires "; des, desmogen; ac, axial component; and m, median trace bundle.

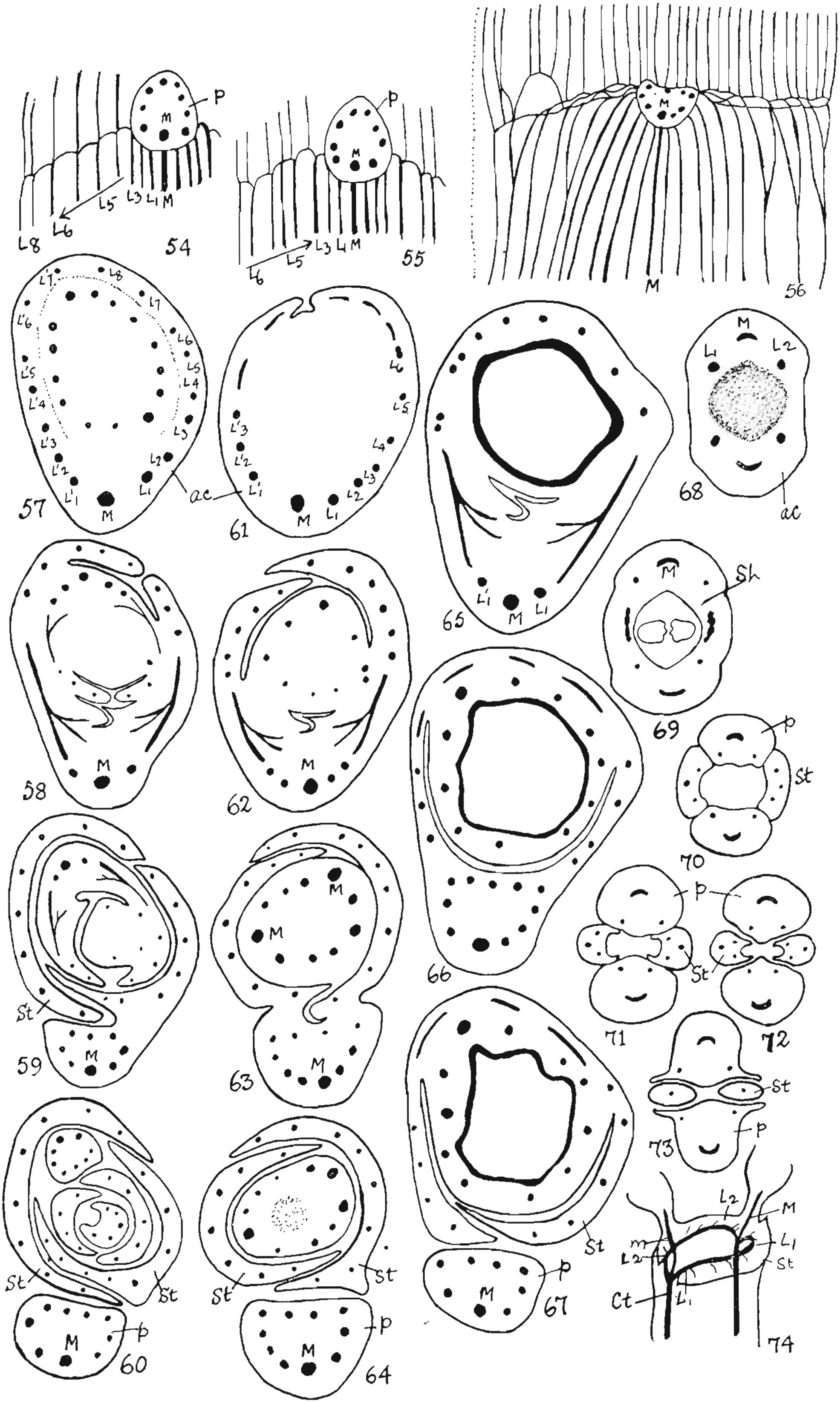
32-53, serial transections of terminal buds showing the development of the leaf-base, the stipules, if any, and the internode; the courses of the leaf trace bundles through the leaf-base are also shown. M, $M_6$, $M_5$, $M_4$, $M_3$, etc., median trace bundles; r.Sh, remnants of sheath; other legends as explained before.

32-37, *Calotropis procera*. 32, 1026 $\mu$ below the free apex, 33, 110 $\mu$ above 32, 34, 70 $\mu$ above 33; 35, 190 $\mu$ above 34; 36, 110 $\mu$ above 35, and 37, 190 $\mu$ above 36. Each $\times$ 47.

38-42, *Jasminum flexile*. 38, 1700 $\mu$ below the free apex; Fig. 39, 60 $\mu$ above 38; 40, 60 $\mu$ above 39; 41, 180 $\mu$ above 40; and 42, 1040 $\mu$ above 41. Each $\times$ 18.

43-49, *Centella asiatica*. 43, 130 $\mu$ below the free apex; 44, 30 $\mu$ above 43; 45, 30 $\mu$ above 44; 46, 140 $\mu$ above 45; 47, 120 $\mu$ above 46; 48, 180 $\mu$ above 47; and 49, 180 $\mu$ above 48; 43, 44 $\times$ 18; and the rest $\times$ 47.

50-53, *Polygonum orientale*. 50, 90 $\mu$ below the free apex; 51, 40 $\mu$ above 50; 52, 110 $\mu$ above 51; and 53, 50 $\mu$ above 52. Each $\times$ 46.




Text-figs. 54-74

*giosa* and in *Artocarpus integrifolia*, while in *F. elastica* as a single stipule (TEXT-FIG. 20).

*Ixora parviflora* — A pair of foliar primordia is initiated by transverse extension of the free apex at two opposite sectors (TEXT-FIG. 68). The two primordia after being laid down extend laterally around the axis until their corresponding arms meet and fuse to form a tubular structure confluent with the axis. At this stage the axis is composed of a mantle formed by the two bases and an axial core, and the internode is developed later by their united intercalary growth. Being free from the axis the tubular structure continues its growth for some distance and then separates into 4 pieces — 2 central regions of the pair of opposite bases and 2 lateral pieces between the former pair composed of their fused arms (TEXT-FIGS. 69-73). The two lateral pieces now being free from the axis and from the central regions develop as the interpetiolar stipules which are composite structures (TEXT-FIGS. 72, 73).

Three bundles from the axis enter the base of each primordium leaving three gaps in the nodal ring (TEXT-FIG. 68). The laterals, while moving towards the median, branch in the arms of the axial component. The branches arrange themselves in the fused arms of the opposite primordia and influence their further development into the interpetiolar stipules.

*Paederia foetida* — The two primordia are initiated in the same manner as in *Ixora*. While the primordia are extending laterally, active cell divisions begin at three regions in each of them, namely, in the middle and near the two lateral ends (TEXT-FIGS. 75, 76). The shoot apex at this stage appears more or less hexagonal in transection, and the axis is made up of a mantle of the two opposite leaf-bases and a central core (TEXT-FIG. 76).

Owing to the difference in the rate of radial extension and vertical growth between the laterals and the median region in each primordium, the former gradually outgrow the latter and become free from it (TEXT-FIG. 77). Thus being separated from the middle region which now develops as the petiole, the two fused adjacent lateral arms of the opposite primordia develop as a single piece on each side of the axis forming a pair of interpetiolar stipules at each node (TEXT-FIGS. 77, 78).

In this case the base has no free growth. The whole of it is incorporated in the axis.

The trace is a composite bundle and on leaving the axial ring, where it forms a single gap, it follows its course in three directions (TEXT-FIG. 74). The median follows its undeviated course while the laterals follow oblique courses round the axis and form a girdle by the union of the corresponding laterals coming from the opposite side of the axis. The laterals during their oblique horizontal courses round the axis give out branches to the fused arms which now being influenced by these branches develop into interpetiolar stipules.

*Ervatamia divaricata* — By transverse extensions at opposite sectors of the free apex a pair of primordia are laid down. The two primordia exhaust the shoot apex which now appears as a cup-shaped structure (TEXT-FIG. 11). The plastochrone is fairly long and at the end of it the free apex becomes

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TEXT-FIGS. 54-74 — 54, 55, show longitudinal courses of the median and the lateral trace bundles in the axial component of *Ficus religiosa* (TEXT-FIG. 54), and of *Ficus elastica* (TEXT-FIG. 55). Arrow indicates the progress of branching of the laterals by turn. Diagrammatic. Explanation of legends as before.

56, shows longitudinal courses of the median and the lateral trace bundles in the leaf-base and the ochrea of *Polygonum orientale*. × 9.

57-73, serial transections of terminal buds showing the development of the leaf-base, the stipules, if any, and the internode, the courses of the leaf trace bundles through the leaf-base are also shown. Explanation of legends as before.

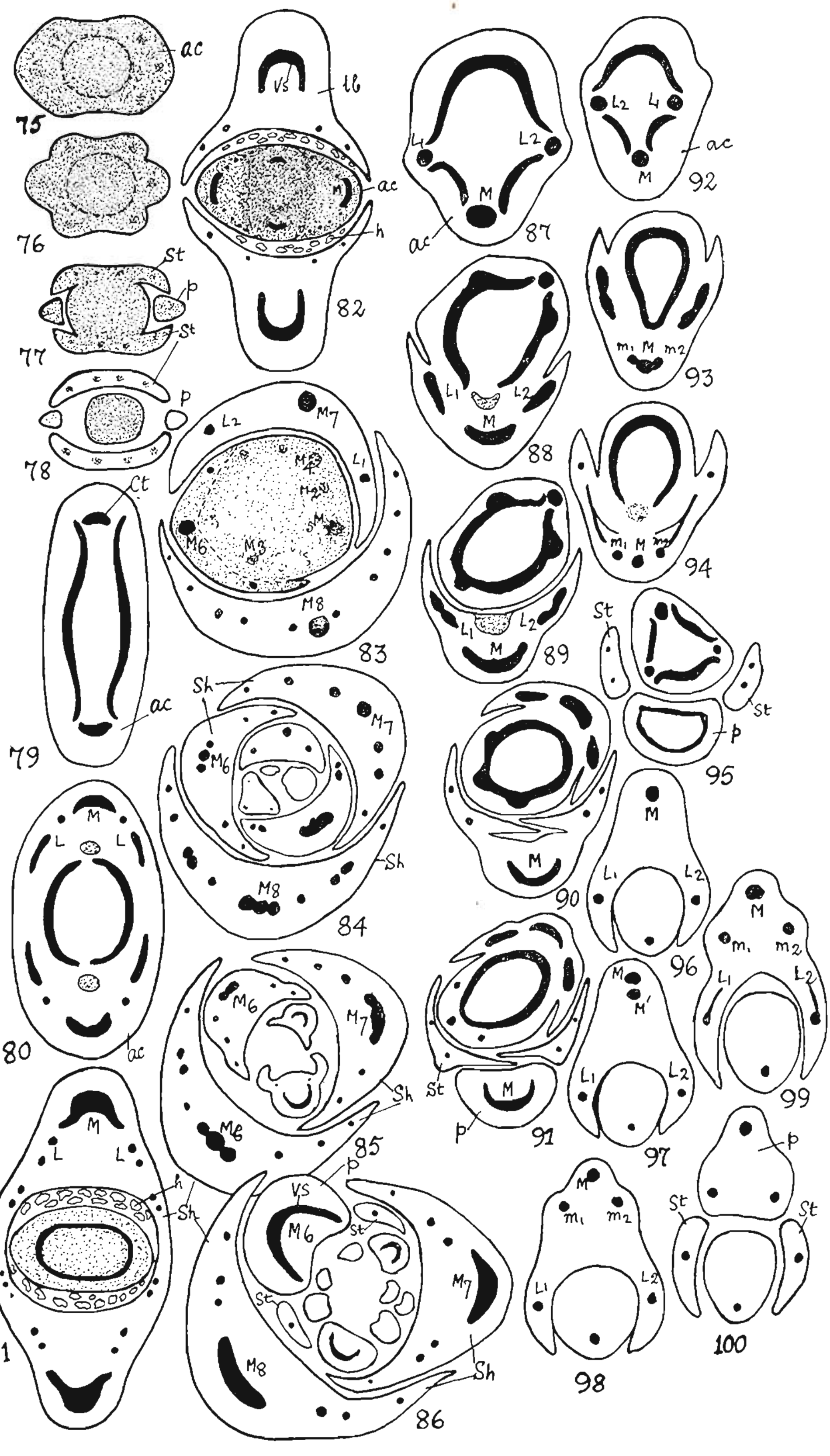
57-60, *Ficus religiosa*. 57, 170 μ below the free apex; 58, 20 μ above 57, 59, 30 μ above 58; and 60, 40 μ above 59. Each × 49.

61-64, *Artocarpus integrifolia*. 61 200 μ below the free apex; 62, 30 μ above 61; 63, 40 μ above 62; and 64, 20 μ above 63. Each × 49.

65-67, *Ficus elastica*. 65, 770 μ below the free apex; 66, 250 μ above 65; and 67, 110 μ above 66. Each × 18.

68-73, *Ixora parviflora*. 68, 100 μ below the free apex, 69, 40 μ above 68; 70, 50 μ above 69; 71, 30 μ above 70; 72, 20 μ above 71, and 73, 20 μ above 72. Each × 47.

74, shows longitudinal courses of the composite leaf trace bundles (Ct) in the axial component of *Paederia foetida*. The laterals ($L_1$ and $L_2$) of each of the opposite primordia form a girdle around the axis. Diagrammatic. For explanation see text.




Text-figs. 75-100

convex again when the next pair of primordia are laid down. The bases of a pair of primordia meet and fuse in the same manner as in *Ixora*, and have free growth in the form of a tubular sheath (TEXT-FIGS. 79-81). The sheath grows as such for some time and then separates into its component parts, i.e. into the bases of the pair of primordia at the fused margins (TEXT-FIG. 82). Then the arms of each free base, along with the adaxial portion of the central region, separate from the remaining portion of the latter and develop as an *intrapetiolar* (axillary) stipule while the central region develops as the petiole (TEXT-FIG. 26).

The incorporated bases of each pair of opposite primordia form a mantle around the central core of the axis and the internode develops later by the united intercalary growth of the two.

A composite trace of three bundles leaving a single gap in the nodal ring enters each primordium. The laterals of this trace during their upward course give out 8 branches, 4 on each side (TEXT-FIG. 81). These 8 bundles then unite in pairs to form 4 which arrange themselves along the inner face of the central region of each base (TEXT-FIG. 82). These branches influence this region to develop into the intrapetiolar or axillary stipule.

*Rosa centifolia* — By transverse extension of the free apex the primordium is laid down. The base extends tangentially about two-thirds of the circumference of the axis (TEXT-FIG. 83). Three or more leaf-bases together completely surround the axis in the form of a mantle enclosing the axial core.

The base being free from the axis continues its upward growth as a partly sheathing base and its apical region diverges as two teeth, one on each side of the base of the petiole (TEXT-FIGS. 84-86). The sheathing base along with its apical teeth cannot be regarded as an adnate stipule. The two apical teeth of the sheath being influenced to further growth by the branches of the laterals develop as a pair of free stipules (TEXT-FIG. 86).

Three bundles leaving three gaps in the nodal ring enter the base of each primordium (TEXT-FIG. 83). During their oblique courses through the sheathing base the two laterals give out branches and just below the level of divergence of the apical teeth unite with the median to form an arc (TEXT-FIG. 86). The branches influence the development of the two apical teeth as a pair of free stipules. The central region of the sheath after the formation of the vascular arc develops as the petiole.

*Morus alba* and *Hibiscus rosa-sinensis* — In both the species the primordia are initiated in the same manner as in *Rosa*. In both the base has no free growth and the whole of it is incorporated in the axis which is made up of an axial core surrounded by a mantle formed by the bases (TEXT-FIGS. 87, 92). The internode is developed later by united intercalary growth of the two.

Three trace bundles, leaving three gaps in the nodal ring, enter each primordium (TEXT-FIGS. 87, 92). The laterals follow a parallel course with the median for a very short distance and then they follow an oblique horizontal course towards the median giving out branches while doing so (TEXT-FIGS. 88-90; 93, 94). These branches influence the development of the arms of the base into a pair of free lateral stipules in these two species (TEXT-FIGS. 91, 95).

In *Morus* the nodal and subnodal regions, i.e. the axial component, are characterized by much radial growth opposite the three bundles of the trace and this gives rise to the ribbed appearance of the internode in young twigs (TEXT-FIG. 12). On the horizontal

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TEXT-FIGS. 75-100 — Serial transections of terminal buds showing the development of the leaf-base, the stipules, if any, and the internode; the courses of the leaf trace bundles through the leaf-base are also shown. $m_1$ and $m_2$, branches of the median; h, hairs; and explanation of other legends as before.

75-78, *Paederia foetida*. 75, 70 μ below the free apex; 76, 20 μ above 75; 77, 30 μ above 76; and 78, 20 μ above 77. Each × 63.

79-82, *Ervatamia divaricata*. 79, 1110 μ below the free apex; 80, 320 μ above 79; 81, 320 μ above 80; and 82, 470 μ above 81. Each × 34.

83-86, *Rosa centifolia*. Fig. 83, 190 μ below the free apex; 84, 270 μ above 83; 85, 70 μ above 84; and 86, 40 μ above 85. Each × 46.

87-91, *Morus alba*. 87, 200 μ below the free apex; 88, 40 μ above 87; 89, 24 μ above 88, 90, 40 μ above 89; and 91, 16 μ above 90. Each × 27.

92-95, *Hibiscus rosa-sinensis*. 92, 420 μ below the free apex; 93, 40 μ above 92; 94, 60 μ above 93; and 95, 130 μ above 94. Each × 18.

96-100, *Pisum sativum*. 96, 180 μ below the free apex; 97, 24 μ above 96; 98, 32 μ above 97; 99, 40 μ above 98; and 100, 24 μ above 99. Each × 47.

rims the stipules are borne. In other respects the origin and development of the leaf-base is similar in both the species.

*Pisum sativum* — A primordium is initiated at the free apex by transverse extension at a particular sector of the latter. This is soon followed by the initiation of a second primordium on the opposite side. The two leaf-bases enclose the axial core in the form of a mantle and the internode is developed later by the intercalary growth of the mantle and the core together. The base has just a free portion, the major portion being included in the axis. The lateral portions of the base after being free from its central region develop as a pair of foliaceous stipules ( TEXT-FIGS. 96-100 ).

Three bundles from the axis leaving three gaps in the nodal ring enter each primordium ( TEXT-FIG. 96 ). The laterals following a short parallel course with the median undergo much branching. The median also at the same time gives out branches ( TEXT-FIGS. 97-98 ). Some of the branches of the laterals enter the anterior lobe of the stipule while the posterior lobe receives its vascular supply from the united bundles of the branches of the median and of the laterals. The two wings of the stipule are unequal in development and the mesophyll is differentiated into palisade and spongy tissues.

## DISCUSSION

*The Leaf-base* — We have seen that at the growing apices of the species studied a leaf primordium is initiated by transverse extension of the free apex at a particular sector at regular intervals, or by plastochrones which seem to be specific for each species. This horizontally extended portion of the apical dome at leaf initiation has been variously named as *soubassement foliaires*, *foliar buttress*, *foliar foundation*, *axial component* or *leaf cushion*. The axial component soon extends laterally around the free apex either partly or completely as the case may be. Simultaneously with the lateral extension the axial component also grows in vertical extent unitedly with the axis. During its further development it may or may not develop into a base free from the axis. In many cases, as for example, in *Ficus elastica*, *Paederia foetida*, *Hibiscus rosa-sinensis* and *Jasminum flexile*, it has been observed that the whole of the base is incorporated in the axis in the form of a mantle leaving no part of it free from the axis. In such cases, if the leaf is stipulate, the arms of the axial component directly develop into a single or a pair of stipules, as the case may be, and the stipular scar appears cauline and may be formed completely or partially round the axis, e.g. *F. elastica* and *Hibiscus rosa-sinensis*. In other cases, as for example, in *Ficus religiosa*, *Artocarpus integrifolia*, *Morus alba*, *Pisum sativum* and *Calotropis procera* the major portion of the axial component is incorporated in the axis and is free from the latter only for a very short distance as a short rim which is almost imperceptible to the naked eye. In such cases, if the leaf is stipulate, the stipular scar is either circular or obliquely left on the axis due to gradual separation of the stipule from the axis. This is an additional evidence to show that the leaf-base, of which the stipules are outgrowths, has no separate existence apart from the axial component in such cases. Lastly, in the third group of plants, as for example, in *Centella asiatica*, *Ixora parviflora*, *Polygonum orientale*, *Ervatamia divaricata* and *Rosa centifolia* only a small portion of the base is incorporated in the axis of the bud and the major portion develops as a free organ. In such cases, the bases are sheathing for a greater or less extent and may entirely enclose the axis ( in a multilacunar node ), or enclose one half or two-thirds of the circumference of the latter according to the number of leaves at the node. And if in the free sheath the laterals branch while moving towards the median in the central region stipules are formed as in *Polygonum*, *Rosa*, *Ixora* and *Ervatamia*.

*The Number and the Behaviour of the Leaf Trace Bundles, particularly of the Laterals, through the Axial Component determine the Nature of the Leaf-base* — Where the trace bundles are many and the node is multilacunar as in *Centella*, *Polygonum*, *Ficus elastica*, *F. religiosa* and *Artocarpus* the behaviour of the laterals in the axial component determines the nature of the base as to whether it will remain entirely incorporated in the axis as its component, or will develop in addition as a free base. Where the lateral trace bundles 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 for example, in *Polygonum* and *Centella*. In the rest of the above species the laterals, after running parallel for a short distance in the axial component, follow an oblique horizontal course towards the median before they leave the axial component, and the base has no free growth except for an imperceptibly short distance, as in the species of *Ficus religiosa* and *Artocarpus*. In all these cases the laterals ultimately move towards the median with which they form a ring of vascular bundles in the petiole. Where the laterals give out branches while following a united horizontal course the base gives rise either to a single (*Ficus elastica*), or to a pair of stipules (*Ficus religiosa* and *Artocarpus integrifolia*), or to a tubular stipule (*Polygonum orientale*), with the branches as their traces.

Where the trace bundles are three and the node is *trilacunar*, as for example, in *Rosa*, *Morus*, *Hibiscus*, *Pisum* and *Ixora* the axial component of a leaf encloses about two-thirds (but one half in the case of *Ixora*) of the circumference of the axis and may or may not develop into a free base. Where the lateral trace bundles run parallel to one another beyond the axial component the base develops into a free sheath (partial), as for example, in *Rosa* and *Ixora*. Where the laterals follow an oblique course in the axial component itself the base has no free growth, as for example, in the rest of the above species. In all these species the laterals during their oblique horizontal courses give out branches and the axial component develops into a pair of stipules or interpetiolar stipules, as in *Ixora* with these branches as their vascular system.

Where the leaf receives a *composite* trace and the node is *unilacunar*, as for example, in *Calotropis*, *Jasminum*, *Paederia* and *Ervatamia*, the base has no, or very little, free growth which is almost imperceptible to the naked eye. Their later behaviour shows that the composite trace is composed of three bundles. In *Calotropis* and *Jasminum* the trace forms an arc without branching, and soon spreads laterally forming an open cylinder whose free ends face each other. This region of the primordium develops into the petiole. But in *Ervatamia* and *Paederia* the laterals soon separate from the median and give off branches in the axial component with the result that the stipules are developed. Ponzo and Cross noticed cauline and discontinuous stipular scars because in these species there is no free base development apart from the axial component.

It is seen in all the above species that the bundle or bundles on leaving the nodal ring follow an upward course for a short or greater distance as the case may be. Then they follow oblique horizontal courses towards the median with which they either form a ring or unite to form an open or closed arc. This region containing either the ring of trace bundles or an open arc develops into the petiole. As soon as the bundles leave the petiole the laterals and the median again branch in connection with leaflet or lamina development.

Anatomically, therefore, the three regions of a typical leaf, namely the base, the petiole and the upper leaf, can 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 an arc or arrange themselves in a ring without branching and in the upper leaf they again branch in connection with leaflet or lamina development.

*The Internode: The Mantle-core Theory is Revived* — In serial transections of a terminal bud the axis is seen to consist of a *peripheral mantle* composed either of *a single* axial component, as in *Polygonum*, *Centella*, *Ficus elastica*, *F. religiosa* and *Artocarpus integrifolia*, or of *two opposite* axial components, as in *Paederia*, *Ixora*, *Ervatamia*, *Calotropis* and *Pisum*, or of *more than two* axial components as in *Hibiscus*, *Morus*, *Jasminum* and *Rosa*. These components enclose in each case an axial core of vacuolating dividing cells. Developmental studies show that the axial component with its vascular bundles is derived from the flank meristem, and the axial core exclusively from the corpus cells of the apical meristem. The internode is developed later during the unfolding of the vegetative bud by the united intercalary growth of the axial component or components and the axial core which they enclose as one organ. The internodal development is found to take place below the lowest leaf of a complete cycle of primordia of the respective phyllotaxy from the apex and its axil usually bears a bud for the first time. The axial core is characterized by exclusive transverse and less frequent longitudinal divisions of its cells while the mantle, in addition to keeping pace with the elongation of the axial core, also extends in radial direction by longitudinal and irregular divisions of its cells.

Thus in the study of a leaf development the axial component cannot be omitted from being regarded as a part of the leaf, and in consequence the internode is to be recognized as composed of a mantle ( axial component or components ) and an axial core surrounded by the former. The axial component should be regarded as the base of a leaf.

In 1922 Saunders revived the Berindung theory of Hofmeister ( 1851 ) and propounded her leaf-skin theory to explain the make-up of the axis bearing leaves. Both of them visualized a *core* ( axial ) enclosed by a *skin* ( 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.

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. The present study, however, does not support this view of the nature and formation of the skin. We have seen that the axial component or components, soon after their initiation at the side of the free apex, enclose the latter and later in ontogeny the internode is developed by their united intercalary growth, and not by the downward growth and extension of the leaf-base or bases. In this connection 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.

While speaking of its vertical extent, Priestley ( 1929 ) says that in an adult shoot it runs downwards from a leaf insertion to the foliar gap above the insertion of the next vertically below ( p. 7 ), and it corresponds with the mericyclic shoot segment ( *Spross-gleider* of Celakovsky ).

What is the radial extent of the mantle? The tissue of the axial core is a cell lineage of the transverse divisions of the file meristem while the mantle including the desmogen strands is derived from the flank meristem by tangential and periclinal divisions of its derivatives. Thus the two ( i.e. the mantle and the axial core ) are derived from two different zones of meristem ( shown by later development ) at the shoot apex. Therefore, the radial extent of the mantle appears to extend up to the pith as suggested by Hofmeister. Priestley's view that in dicotyledons it radially extends right up to the centre of the axis is not supported by an examination of the shoot apices in development in the present study.

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