DEVELOPMENTAL STUDIES : IV. THE ORIGIN AND VASCULARIZATION OF THE STIPULES AND AXILLARY BUDS OF *GARDENIA*, *PORTLANDIA*, *RANDIA*, *MUSSAENDA*, *LUCULIA*, *COFFEA*, *ADINA*, *MORINDA*, *HYMENODICTYON*, *HAMILTONIA* AND *RUBIA**

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ABSTRACT

The origin and vascularization of the stipules in 13 species, and those of the axillary buds in 24 species of the Rubiaceae have been reported in this paper. In 21 species the leaves are opposite, and only in 3 they are whorled.

At the initiation of a leaf at the shoot apex the first part to be laid down is the *leaf-base*, which at this stage is confluent with the axis. Two or three such leaf-bases at the node unite by their margins and form a *collar* round the axis. This collar grows with the axis for some time and then separate from the latter in the form of a tubular sheath. The stipules, *connate*, *interpetiolar* and *foliaceous*, develop as outgrowths of the collar after the petioles have separated from it. The stipules get their vascular supply (stipular trace) from the lateral leaf-trace bundles and/or their branches.

In the Rubiaceae the axillary buds are both *foliar* and *axial* in origin, and they occur in the same bud, sometimes at different nodes, in some cases at the same node in the axil of the same leaf. In almost all the species the foliar buds originate near the apex of the parent bud, and are ephemeral. Whereas the axial buds which develop into branches arise a few nodes below the apex and get their vascular supply directly from the central stele. On an adult axis there are always branchless nodes between two nodes with branches. The morphology of the axillary bud and its relationship with its axillant leaf have been discussed.

INTRODUCTION

This is a further contribution on the results of a systematic study of the origin, vascularization and morphology of the stipules and axillary buds of the Rubiaceae. Methods of studies followed are the same as in previous communications (Majumdar and Pal, 1958*a*, 1958*b*, 1959), but the materials are different.

OBSERVATIONS

1. *Gardenia lucida* Roxb.—Subarboreous shrubs, leaves opposite, decussate, rarely in whorls of three, stipules connate (annular), 'within the leaves', broadly ovate. All the leaves on a branch do not bear secondary branches in their axils. One to three branchless nodes intervene between two nodes bearing them (Fig. 1).

The node is trilacunar, the laterals are widely separated from the median. The *foliar foundations*** of the pair of opposite leaves at a node extend round the axis, their extending arms meet and coalesce to form a *collar*** confluent with the axis (Fig. 14).

The leaf-trace bundles move into the collar. The laterals branch, branches divert into the interpetiolar regions of the collar. On their way to the median

*Names of species studied are given under their description.

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***For the origin and description of the *foliar foundation* see Majumdar, 1942; and of *collar*, White, 1955, and Majumdar and Pal, 1958*a*.

the laterals send out a branch each to the adaxial face of the petiolar region. All the secondary bundles divide and spread uniformly round the axis and send out another series of bundles immediately below the adaxial epidermis. This vascular adjustment takes place in the collar after it has separated from the axis (Fig. 15).

Separation of the collar from the axis begins in its interpetiolar regions (Fig. 14). After separation the collar grows upwards in the form of a tubular sheath with the petiolar regions intact. During further development the petiolar region separates from the collar to give rise to the petiole with three bundles. Its separation begins from outside, passes between the laterals and their branches and leaves a strip of tissue with the outer series of secondary bundles continuous with the interpetiolar portions of the collar. The collar thus separated from the axis and the petiole grows into a connate stipule with only the hypodermal series of bundles as its trace (Fig. 16). The developing bud bursts through the connate stipule.

Near the apex of the terminal bud a few meristematic cells differentiate in the collar opposite the median and form the primordium of the *foliar bud*. They are seen at the second node from the apex and are soon lost. The branch buds are *axial* in origin and get their vascular supply from the axial stele. They develop into branches* (Figs. 14, 49, 50).

2. *Gardenia thunbergia* L.—Shrubs, leaves are in whorls of three, stipules large and connate (Fig. 2). In this species four to five branchless nodes come between two branch-bearing nodes.

The node is trilacunar as in the other species. The leaf-trace bundles are quite close to one another, and the subsequent behaviour of the laterals is similar to that in *G. lucida* (Fig. 17). The petiole separates with three bundles, and the collar develops into a connate stipule as in the other species.

The axillary bud is both *foliar* (Fig. 51) and *axial* in origin. In the shoot apex the buds remain foliar up to the next season, i.e., during the resting period, and when the buds unfold the branch buds develop in the lower nodes of the parent bud.

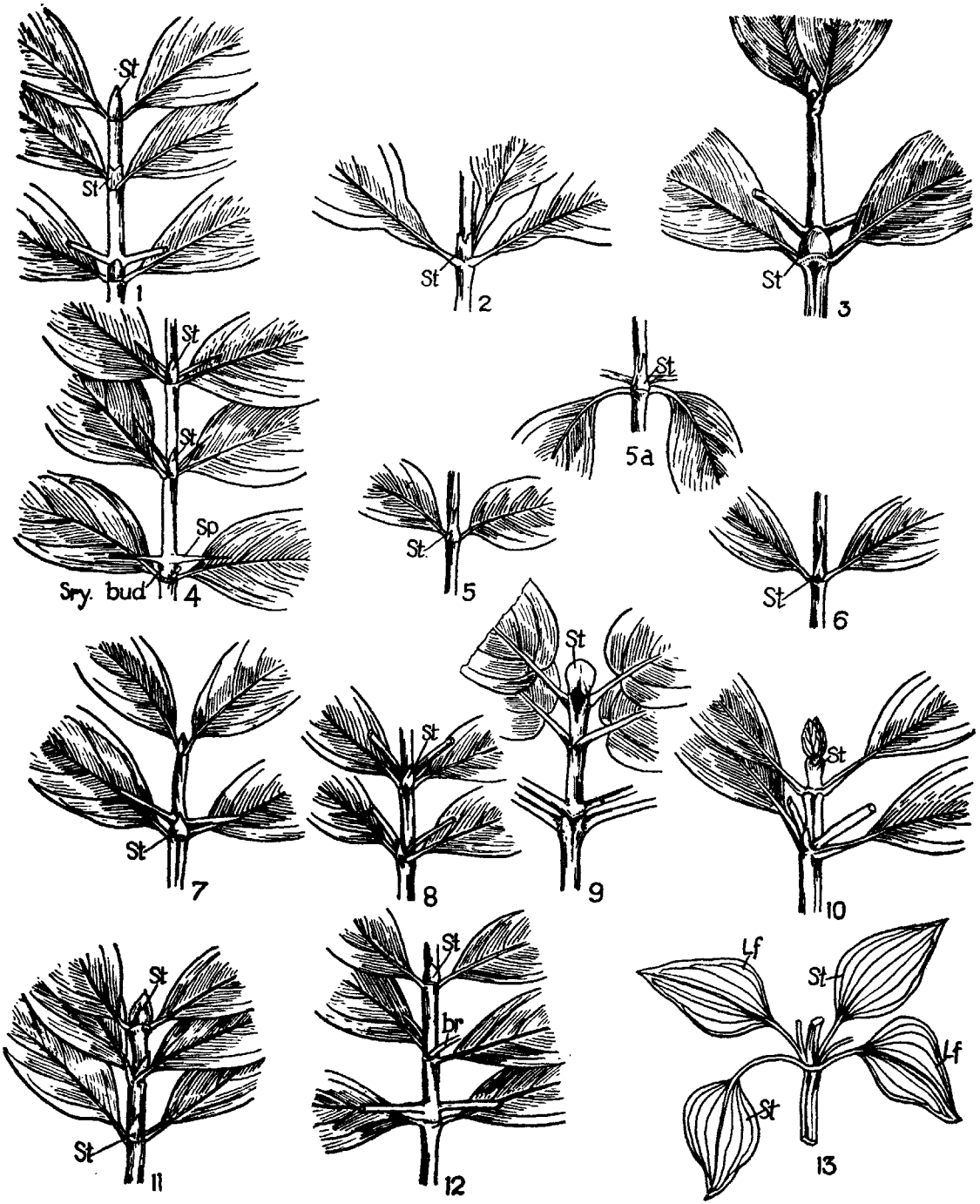
3. *Portlandia grandiflora* L.—Shrubs, leaves opposite, stipules connate at base, broad, rounded at apex, splits open into two interpetiolar stipules in the upper region (Fig. 3). In this species the primary branches, which are more or less vertical, have secondary branches at each node, but the secondary branches behave differently : they bear 2-5 branchless nodes between two nodes with branches.

The node is trilacunar, the trace bundles are widely separated from one another. They move into the collar, and their behaviour in it is similar to that in the above species. The collar separates from the axis with the branches of the laterals and the petiole from the collar with the three leaf-trace bundles (Fig. 19). The collar now grows upwards in the form of a tubular sheath (Fig. 20). Its apical region separates into a pair of interpetiolar stipules (Fig. 21).

The bud primordia are both *axial* and *foliar* in origin. The foliar ones are ephemeral and leave socket-like depressions in the adaxial surface of the collar to indicate the position they occupied before falling off. The axial bud which develops into a branch separates from the collar and the axis by the formation of a *separation zone* developed completely surrounding it (Figs. 19, 52, 53).

4. *Randia dumetorum* Lamk.—Shrubs or trees, leaves opposite, stipules ovate, acuminate, 'within the leaves', large, tapering and caducous. In this species the primary axial buds develop into thorns, and the branch buds originate secondarily on the axis between the thorn and the leaf at lower nodes (Fig. 4).

*Glands are a characteristics feature of the Rubiaceae. They are formed on the adaxial surface of the collar, particularly confined to the stipular region, and are of the nature of emergences (Mitra, 1948; Metcalfe and Chalk, 1950; Majumdar and Pal, 1958*a*). As they occur in all the species described they will be omitted from the description.



TEXT-FIGS. 1-13.

Figs. 1–13. represent respectively a portion of the adult shoot of each of the following thirteen species described in the text : *Gardenia lucida, G. thunbergia, Portlandia grandiflora, Randia dumetorum, Mussaenda frondosa, Luculia gratissima, Coffea arabica, C. bengalensis, Adina cordifolia, Morinda citrifolia, Hymenodictyon excelsum, Hamiltonia suaveolens,* and *Rubia edgeworthii.* They have been drawn from live specimens to show the nature of the stipules and branchings in these species.

The node is unilacunar, but the three leaf-trace bundles are discrete and depart for the collar together. The collar now separates from the axis and grows upwards in the form of a sheath. The laterals diverge into the collar where they divide and give rise to eight bundles on each side, four from each lateral. Two contiguous bundles from the opposite laterals unite to form the midrib bundle (composite) of each of the two stipules, into which the sheath spilts up soon after. The stipules overlap by their free margins at the upper region. In this species the petiole gets only the median as its bundle (Figs. 22, 23).

The axillary buds are both *foliar* and *axial* in origin (Fig. 54). The foliar buds are ephemeral, and the axial buds develop into thorns (cf. *Catesbea spinosa*). The branch buds originate later in the adult region between the thorn and the axillant leaf (Fig. 4).

5. *Mussaenda frondosa* L.—Shruby, leaves opposite, stipules long or short bi-fid, no connate growth at base (Fig. 5). Branching is very interesting in this species. In a twig the fourth and fifth nodes bear branches (decussate), sixth, seventh and eighth do not bear them, ninth and tenth nodes bear branches again, but the next five nodes are branchless (Fig. 5*a*). In another twig it was found that branches do not develop up to the tenth node, sometimes in place of a pair of branches at a node, only one developed (cf. *Galium mollugo*).

The node is unilacunar, but the leaf-trace consists of three juxtaposed bundles They move into the collar without severing connection with the central cylinder. They cause a wide gap in the axial cylinder when they sever their connection with it. The laterals diverge into the collar and divide to form the stipular bundles. The petiole receives only the median bundle (Figs. 24, 25). Separation of the collar from the axis starts simultaneously laterally and in front of the median external to the bud primordium.

The collar after its separation, from the axis and the petiole, breaks up into two interpetiolar stipules with the branches of the laterals. Number of bundles received by each stipule is ten to twelve, 5-6 from each lateral. The contiguous bundles do not unite but remain separate and the stipule becomes bi-fid.

In this species the node becomes laterally extended and downwardly projected for about 40 μ below the level of the node (Fig. 24). After the separation from the collar the horizontally extended portion of the axis forms a ledge or buttress upon which the next pair of foliar primordia are erected (Fig. 25).

Axillary buds are both *foliar* and *axial* in origin (Fig. 55). Foliar buds are ephemeral.

6. *Luculia gratissima* Sweet—Shrubs, leaves opposite, stipules cuspidate, deciduous. 4-5 branchless nodes come between two nodes with branches (Fig. 6).

The node is unilacunar. The single leaf-trace bundle moves into the collar. For a long time it remains unbranched and the collar grows confluent with the axis. Two separation zones organize in the interpetiolar regions of the collar, one on each side. These extend, meet and completely surround the axis. Before the collar separates from the axis the interpetiolar regions outgrow with a tendency to cover the petiolar regions (cf. *Paederia foetida*, Mitra, 1948), but these ear-like outgrowths are soon cast off by the sheathing collar (Fig. 26).

The petiole separates from the collar with only the central part of the trace bundle, but before the separation it gives out two branches to the collar from its free ends which give rise to the stipular bundles (Fig. 27). Each stipule thus gets two bundles, one from each leaf-trace bundle. The two bundles ultimately unite to form the only bundle (composite) of each stipule. The sheathing stipule then splits up into a pair of interpetiolar stipules in the upper region (Figs. 27, 28).

The *foliar* bud primordium is organized in front of the trace bundle but it soon disappears (Figs. 27, 56). The *axial* bud primordium which gets its vascular supply from the central cylinder, is surrounded by its *own separation zone* before the collar

is separated from the axis (Fig. 57). These branch-buds differentiate in the fourth node down below the axis, whereas the first foliar bud is seen to organize in the third node.

7. *Coffea arabica* L.—Shrubs, leaves opposite, stipules broad (Fig. 7). On a secondary branch 9-10 branchless nodes intervene between two nodes with branches.

The node is unilacunar. The leaf-trace bundle moves into the collar; its two free ends extend and soon branch off from its central part (Fig. 29). These branch bundles divide unequally, the smaller ones remain with the central part and the bigger ones spread in the collar. Each petiole thus gets 3 bundles—the central part of the leaf-trace bundle and two secondary bundles. The interpetiolar portions of the collar gets 9 bundles each, of which the central one is composite (Fig. 30). They overlap by their free margins in the upper region.

The axillary buds are both *foliar* and *axial* in origin (Figs. 58-60). Vascular supply to the foliar bud is rather peculiar in this species : the axial bud gets its supply from the central cylinder, and the foliar buds from the axial bud trace before the collar separates from the axis. This species differs from others in another respect : at the same node of the bud in the axil of one leaf of the pair, both the axillary buds are foliar; and in the axil of the opposite leaf both are axial (Figs. 61-65). In one bud at the same node foliar bud was found to develop 220 μ higher up on the collar whereas the axial one was at the node.

8. *Coffea bengalensis* Roxb.—Trees or shrubs, leaves opposite, stipules subulate. On branches which are more or less horizontal every leaf bears a branch, but on these secondary branches 3-13 nodes without branches intervene between two nodes with branches (Fig. 8).

The node is unilacunar; behaviour of the trace bundle is similar to that in the other species. The petiole gets three bundles, and the stipule two bundles, one each from opposite trace bundles which ultimately unite with each other to form a single composite bundle (Figs. 31-33). Towards the upper region the pair of stipules overlap by their free margins (cf. bud scales). In this species unlike in others the separation of the collar from the axis begins opposite the petiolar regions (Fig. 69).

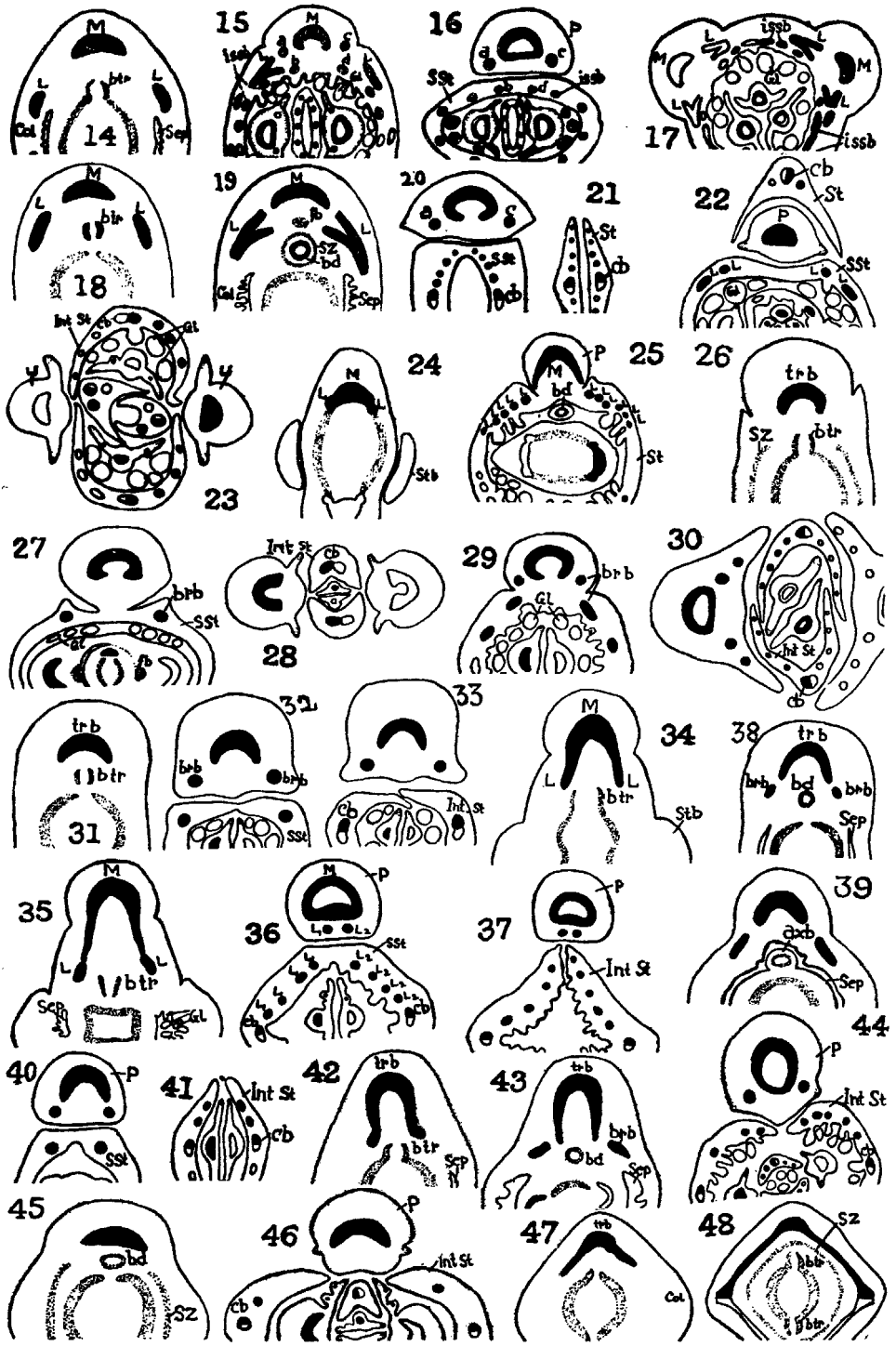
Foliar buds get their vascular supply from the axial cylinder, but they do not develop into branches (Fig. 67). Foliar bud is initiated at the second node from the apex and the *axial* bud in older nodes. But in one case both foliar and axial buds were seen at the same node in the axil of the same leaf (Figs. 68, 69),

9. *Adina cordifolia* Benth. and Hook.—Trees, leaves opposite, deciduous, stipules orbicular, or oblong. 2-6 nodes without branches intervene between 2 nodes with branches (Fig. 9).

The central cylinder is somewhat wavy, oblong, with four sharp ridges and corresponding furrows two of which are shallow (Fig. 71). The node is unilacunar, each leaf-trace bundle is constituted of an entire furrow with the ridges flanking it. The later behaviour shows that the furrowed portion represents the median and the short ridges, the laterals. The three never sever their connection with one another (Figs. 34, 35). The laterals extend into the interpetiolar regions of the collar, divide and the branch bundles behave as in previous species. The petiole gets three bundles, and the interpetiolar regions eleven bundles each, the middle one being a composite one (Figs. 36, 37).

In this species both the petiole and the stipule show downward projections just free from the axis (Figs. 70, 71). These projections are noticed even when they are examined with a hand lens.

The bud primordium is *foliar* in origin and gets its vascular supply directly from the axial cylinder. The foliar buds do not develop and branches are developed from *axial* buds taking their origin at the lower nodes (Fig. 72).



TEXT-FIGS. 14–48.

10. *Morinda citrifolia* L.—An elegant small tree, leaves opposite, short petioled, stipules large, broadly oblong, semilunar, entire, smooth or two fid. Normally one to three branchless nodes intervene between two nodes with branches. But in some branches all the nodes were found to bear lateral branches (Fig. 10).

The node is unilacunar, the single bundle of the leaf-trace moves into the collar from where it sends out branches into its interpetiolar regions (Fig. 38). The petiole receives three bundles. The collar separates from the axis and the petiole from the collar in the usual way. The stipule grows at first as a sheath and then splits up into a pair of interpetiolar stipules at the upper region. In the lower region each stipule gets five bundles with the central one composite, but their number is gradually reduced to three only, the composite midrib and two laterals (Fig. 40, 41).

Foliar buds originate at the third node and the *axial* at the fourth from the tip. The foliar bud gets its vascular supply from the central cylinder before the collar separates from the axis, but they do not develop into branches. Branch buds are always *axial* in origin (Figs. 39, 73).

11. *Hymenodictyon excelsum* Wall—Trees or shrubs, leaves opposite, stipules subentire. Seven to sixteen branchless nodes intervene between two nodes with branches (Fig. 11).

The node is unilacunar; the single trace bundle moves into the collar and its subsequent behaviour is similar to that of the previous species. The petiole separates with three bundles and the stipules get 7-9 bundles each, of which the central one is composite (Figs. 42-44).

Buds are both *foliar* (Fig. 74) and *axial* (Fig. 75) in origin. The foliar is ephemeral, the axial develops into a branch with vascular supply from the central cylinder.

12. *Hamiltonia suaveolens* Roxb.—An undershrub with spreading branches, leaves opposite, stipules short, acute. Prain describes the stipule as intrapetiolar and persistent. Two to ten branchless nodes intervene between two nodes with branches (Fig. 12).

The node is unilacunar. Trace bundle moves into the collar where its behaviour is similar to that in other species with one-bundle leaf-trace. A distinct but faint separation zone is formed between the axis and the collar. The petiole receives only the central part of the trace bundle and the interpetiolar regions of the collar four bundles on each side, but the interpetiolar stipules get three bundles each, the central one being composite (Figs. 45, 46).

EXPLANATION OF FIGURES

Figs. 14–48.—are camera lucida drawings, magnification of each figure has been noted against it. The figures are mostly from transverse sections (t.s.) of the shoot apices, and show the collar, the mode of its separation from the axis, the origin of sheathing and interpetiolar stipules, their vascularization, etc., and the glands.
Figs. 14–16.—*Gardenia lucida*, t.s. ×50.
Fig. 17. —*Gardenia thunbergia*, t.s. ×50.
Figs. 18–21.—*Portlandia grandiflora*, t.s. ×50. Fig. 19 also shows the axial bud, and its separation zone (*sz*).
Figs. 22–23.—*Randia dumetorum*, t.s. ×75.
Figs. 24–25.—*Mussaenda frondosa*, t.s. ×50.
Figs. 26–28.—*Luculia gratissima*, t.s. ×50.
Figs. 29–30.—*Coffea arabica*, t.s. ×100.
Figs. 31–33.—*Coffea bengalensis*, t.s. ×100.
Figs. 34–37.—*Adina cordifolia*, t.s. ×50.
Figs. 38–41.—*Morinda citrifolia*, t.s. ×30. Fig. 39 also shows axial bud.
Figs. 42–44.—*Hymenodictyon excelsum*, t.s. ×30.
Figs. 45–46.—*Hamiltonia suaveolens*, t.s. ×30.
Figs. 47–48.—*Rubia edgeworthii*, t.s. ×100.

The bud primordium is *foliar* in origin (Fig. 76). It receives its vascular supply from the axial cylinder before the collar separates from the axis. It is not always ephemeral. *Axial* buds originate from the lower nodes (Fig. 77).

13. *Rubia edgeworthii* Hook.—Herbs, scandent, leaves opposite, stipules stalked, foliaceous, morphologically similar to leaves in size, shape and vascularization. Branching regular (Fig. 13).

The node is unilacunar. The leaf-trace-bundle moves into the collar, but its behaviour is quite different from that in the species described with one-bundle leaf-trace. The trace bundles of the opposite pair of leaves extend by their arms which meet and fuse to form a complete girdle round the axis (cf. *Galium mollugo*, *Rubia cordifolia*). From the region of their union a branch (jointly contributed) is sent towards the periphery of the collar which enters the stipule as its trace (Figs. 47, 48).

A feeble separation zone is seen to differentiate at the junction of the collar and the axis, but actual separation starts external to the bud primordium, which is thus axial in origin and gets its vascular supply directly from the axial cylinder. *No foliar bud* has been seen to organize in this species (Fig. 78).

Discussion

I. The species studied show the following external features :

1. In habit they range from trees to scandent herbs.
2. Branching is noteworthy. All the leaves on the stem or parent axis do not bear secondary branches. Between two successive branch-bearing nodes come nodes, one to sixteen, without branches.
3. Leaves are petiolate, occur in pairs except in *Gardenia thunbergia* where they are normally in whorls of three, and in *G. lucida* which occasionally shows a node with three leaves.
4. All the leaves are stipulate. The stipules are *interpetiolar, sheathing* (connate), *partly sheathing* and *partly interpetiolar* and *foliaceous* (see under Stipules).
5. The leaves are all *complete*, i.e., each leaf consists of three parts : the *blade*, the *petiole* and the *leaf-base*.

II. *The Leaf-base :*

1. The foliar foundations unite by their extending arms around the axis and form a collar confluent with it. In all the species reported here the collar grows upwards, free from the axis, in the form of a tubular sheath. All vascular adjustments for the petiole and stipules take place in the collar. (Mitra and Majumdar 1952, Majumdar, 1955*a*, 1956; Majumdar and Pal, 1958*a*).

The foliar foundation represents the base of the leaf (leaf-base). This has been established on the evidence of its initiation, ontogeny, anatomy and vascularization at the shoot apex (Majumdar, 1955*a*, 1956; Mitra, 1949). Support for this finding comes very recently from White (1955) who states that leaf-bases of each pair (of decussate leaves) of *Acer pseudoplatanus* are extended laterally and fused to form a collar (or collet) surrounding the axis (P. 437). Long before Goebel (1889) and Ganong (1894) thought that only the leaf-base surrounded the stem (Boke, 1955, p. 1). Boke supports Ganong's conclusion that 'the stem is surrounded by decurrent leaf-bases' which in its turn supports the leaf-skin theory of Saunders (1922) (cf. berindung theory of Hofmeister, 1851, and mantle-core theory of Mitra and Majumdar, 1952, for the constitution of the internode). The collar in the Rubiaceae, therefore, represents the leaf-bases united by their outer margins. It consists of two parts : the lower confluent with the axis, and the upper free from it. When the free portion of the collar is absent, as in China-rose, Jasminum, etc.,

and its lower portion entirely incorporated in the axis as its outer mantle, the leaf is held without a base (as done by the American botanists, see Majumdar, 1955*a*) and the stipules, if present, are regarded as *cauline* (Parkin, 1948).

Strasburger (1930) stated that the petiole is never inserted directly on the axis. It appears to be correct only when the foliar foundation or the collar is taken to represent the leaf-base. In many cases the sheathing base of the leaf is described as the base of the petiole flattened or expanded. But this is not supported by the phylogeny and ontogeny of this organ. The petiole is a later addition to the leaf, and is intercalated between the blade and the leaf-base (Majumdar, 1957).

2. Each collar, confluent or free, has two regions : the *petiolar* and the *interpetiolar*. The petiolar region is radially extended and contains only the median, or the median and the laterals of a three-bundle leaf-trace, or in the case of a single-bundle leaf-trace, its central part with or without two other secondary bundles given out by the extended free ends of this bundle.

3. The petiolar region separates from the rest of the collar and grows into the petiole with three or one bundle as the case may be. The petiolar region, the petiole and the midrib of the blade are continuous, and the sheathing base, as we have mentioned before, is often mistaken for the petiole with expanded base (e.g. *Panax*, *Heracleum*, etc.).

4. After separation of the petioles (leaves opposite) the collar may immediately resolve into two interpetiolar stipules, or may grow up for some length before being split up into a pair of interpetiolar stipules, or may grow up and completely enclose the bud as a connate stipule, or may give rise to foliaceous stipules as lateral appendages like the leaves (see under Stipules).

III. *The Stipules :* Stipules are outgrowths of the leaf-base at and above the level of separation of the petiole from the former. In twelve species they are sessile when they may be regarded as the continued upgrowth of the collar, and in the thirteenth species, i.e., in *Rubia edgeworthii*, the stipules are stalked and lateral in origin like the leaves.

The stipules in all the thirteen species can be divided into the following types :

1. *Interpetiolar*—a pair of stipules, one from each leaf, on the same side of the axis, united by their outer margins. They may be :
   (i) *Triangular*—broad and/or acuminate or acute with receding margins towards the apex. There is no connate growth at the base, and the collar splits up and grow into a pair of stipules immediately after the separation of the petioles, e.g. *Mussaenda*, *Hymenodictyon* and *Hamiltonia*.
   (ii) *Connate at base*, split open into a pair of interpetiolar stipules near the upper region :
      (a) connate for a very short distance, about 20-25μ, e.g., *Coffea* spp., *Adina*, and *Morinda;*
      (b) connate for about 500μ above shoot apex—e.g. *Randia;*
      (c) connate for about 1000—1500μ above shoot apex—e.g. *Portlandia*, *Luculia;* or
      (d) overlapping by their inner margins near the tip : *Coffea arabica*—800μ, *Coffea bengalensis*—520μ, and *Randia dumetorum*—160μ above the shoot tip which they completely enclose.
2. *Sheathing :—Connate all throughout.* All the four (leaves opposite), or six (leaves in whorls of three) stipules are united by both the margins up to the tip. They form only one stipule which has been described as *connate*, e.g. *Gardenia lucida*, *G. thunbergia*.

Willis (1951) writes : the stipules in the Rubiaceae stand between the petioles (interpetiolar), or between the petioles and the axis (intrapetiolar or axillary), and are frequently united to one another and to the petiole, so that a sheath is formed round the stem (pp. 573-574).

But true intrapetiolar (axillary) stipules we have not found in the twenty-four species of the Rubiaceae so far studied by us. The sheath is not formed in the way suggested by Willis. In the species described the *sheath* and the *sheathing stipules* are formed in the following ways :

(i) *Sheath :* The collar after being free from the axis grows upwards in the form of a tubular sheath with the petiolar regions. The sheath is formed by the union of the leaf-bases, and the petiolar regions represent the foliar foundations (*Soubassement foliares* of Gregoire, 1935) at their initiation at the shoot apex.

(ii) *Sheathing stipule*—In the case of connate stipules the interpetiolar regions of the collar with a strip of the adaxial tissue of the petiolar regions separate from the petiolar regions (now petioles) and grows upwards in the form of a *sheathing stipule*, as in the *Gardenia* spp. In the case where the stipule is sheathing at the base but split open at the upper region the sheathing portion is formed in the way described above.

Willis made the evident mistake by confusing the petiolar region of the collar with the petiole proper. The nature of the foliar foundation as the base of leaves came to be realised only lately.

Whether the collar (united leaf-bases) would outgrow into a pair of interpetiolar stipules or a sheathing stipule after separation from the petioles depends on the disposition of branch bundles (stipular traces) in the adaxial face of the collar (see below).

3. *Foliaceous :* Foliaceous stipules are leaf-like in shape, size and vascularization and are stalked like the leaves of whose bases they are outgrowths, e.g. *Rubia* spp. The three genera, *Galium*, *Rubia* and *Asperula* 'are characterised by the resemblance of the stipules to the leaves'.

IV. *Vascular Supply to the Stipules :* Vascular supply to the leaf-base of which the stipules are outgrowths, may be described according to the number of bundles which constitute each leaf-trace. Thus :

(i) *Node trilacunar*—trace bundles three, widely separated from one another, e.g. *Gardenia lucida* and *Portlandia*, but they are closer in *G. thunbergia*.

(ii) *Node unilacunar*—trace bundles three, but they depart for the collar together leaving a wide gap in the axial stele, e.g. *Mussaenda*, *Randia*.

(iii) *Node unilacunar*—trace bundle consists of three juxtaposed bundles, e.g. *Adina*.

(iv) *Node unilacunar*—trace bundle one, e.g. *Luculia*, *Hymenodictyon*, *Hamiltonia*, *Coffea*, *Morinda* and *Rubia*.

From a close study of the distribution of trace bundles in the above species it would appear that there may be some truth in the statement of Sinnott and Bailey (1914) that the unilacunar condition of the node arose either by the approximation of the three trace bundles to one another, or by *complete merger* of the laterals with the median. Suppression of the laterals to give rise to the unilacunar condition has not been observed in any of the species studied.

In the final disposition of the vascular bundles from the axial stele or cylinder the petiole in the majority of cases gets three bundles of which the central one is the median or its equivalent, and the stipule gets the laterals and/or their branches. The distribution is noted below :

Gardenia—in both the species the laterals send out branches (by division) to the interpetiolar regions of the collar and also to the adaxial side of its petiolar region. These branch bundles in their turn send branches to form a second series of bundles to run parallel to the inner face of the collar. The stipule (connate), however, gets only the second series of bundles, equally spaced all round, as its vascular system.

Portlandia—Each stipule gets 9 branch bundles of which the central one is a composite one. The branch bundles are not equally spaced, but leave a wide gap opposite the median. The stipule which is connate at the base splits open in this gap due perhaps to vigorous growth upwards round the midrib bundle.

Mussaenda—Each stipule gets 10 or 12 branch bundles the central ones do not unite but grow independently and a bi-fid stipule is formed.

Each stipule in *Randia* gets 7, in *Coffea arabica* 9, *Coffea bengalensis*–1, *Luculia*–1, *Adina*–11, *Morinda*–5, *Hymenodictyon*–7, *Hamiltonia*–3, and *Rubia*–1—the central bundle in all cases is a composite (contributed by two opposite laterals) one.

The stipules in twelve species are the results of vertical up-growth of the united leaf-bases with branches of the laterals or their equivalents as their vascular supply. In *Rubia*, however, the stipule is a stalked lateral outgrowth with a trace which is sent towards the periphery jointly by both the leaf-traces. The origin and development of the sheathing stipules can be compared with those (ochrea) of *Polygonum orientale* (Mitra, 1945; Majumdar, 1956).

V. *Methods of separation of the collar from the axis.*—In every species studied the collar separates from the axis and grows upwards in the form of a tubular sheath. In *Rubia* a distinct circular separation zone is formed at the junction of the collar and the axis. This zone also gives rise to glands (cf. *Galium*). In *Luculia* and *Hamiltonia* the origin of the separation zone is confined to the lateral regions. In the majority of cases the actual separation starts from the lateral regions but in *Coffea bengalensis* and *Rubia* the separation begins from opposite the median bundle.

In the majority of cases the separation of the leaf-base from the axis appears to be due to the unequal vertical growth of the axis and the collar. This fact also leads to the suggestion that the axis and the collar belong to different organizations. Kundu and Rao (1957) noticed in *Boehmeria* "differences in growth rates of the central and peripheral zones of the axis", the peripheral zone might mean the *collar*.

VI. *Separation of the petiole from the collar.*—After it has separated from the axis the collar grows upwards in the form of a connate sheath for some time before its petiolar regions separate to grow into the petioles. It separates from the collar in two ways:

(i) In *Mussaenda*, *Hymenodictyon* and *Hamiltonia* where the connate leaf-base after the separation of the petiolar regions directly grows into a pair of interpetiolar stipules, the separation starting from outside proceeds obliquely towards the centre of the petiolar region on the adaxial side and opens into the cavity just in front of the median bundle. The petiole assumes a biconvex shape, the inner more projecting and sharp than the outer one (Figs. 25, 44, 46).

(ii) In all the other species where the base of the stipule is connate, but splits up into two interpetiolar stipules at the upper region, the separation starts from outside and proceeds inwards between the laterals and their branches almost horizontally or slightly convexly leaving a strip of tissue with the branch bundles continuous with the interpetiolar regions of the collar (Figs. 21, 23, 28, 30, 33, 37, 41).

In the case of *Gardenia* stipular bundles are uniformly distributed in its tissue around the axis, and the upward growth of the stipule is without any break, but in the other species the bundles leave wide gap in front of the median, and the splitting takes place in this gap. In *Rubia* the origin and development of the stipule is like that in *Galium mollugo* (Majumdar and Pal, 1958*a*) and in *Rubia cordifolia* (Majumdar and Pal, 1958*b*).

The Axillary Bud

The axillary bud and its axillant leaf are closely associated together. These buds are important in the life of a plant as their presence or absence gives the latter its habit and form.

At least three problems relating to the axillary bud still remain unsolved and they are : its origin, vascularization and its morphology and relationship with its axillant leaf.

In the majority of cases so far investigated the origin of the axillary bud has been reported as *axial* from the 'detached meristem'** (Koch, 1893; Goebel, 1905, Louis, 1935; Reeve, 1943; Sifton, 1944; Miller and Wetmore, 1946; Garrison, 1949*a*, *b*; 1955; Philipson, 1949; Sterling, 1949; Gifford, 1951; Kundu and Rao, 1954, 1955, amongst others). *Foliar* origin has been reported only in a very few cases (Vöchting, 1873-74; Leinfellner, 1937; Majumdar, 1942; Majumdar and Datta, 1946). In monocotyledons, at least in the Gramineae, the axillary bud is axial in origin (Sharman, 1942, 1945; Hsü, 1944; Ledin, 1954; Saha, 1954).

Bud traces are mostly *acropetal* in differentiation from the central cylinder. In the majority of cases two bundles leave for the bud from the ends of the central cylinder flanking the gap caused in it by the departure of the median strand of the axillant leaf. Their *basipetal* differentiation has been reported in the case of foliar buds.

Garrison (1955) considers the above as 'contrasting viewpoints' (p. 263). I do not know if she meant that there should be only one type of origin and one type of vascularization for all axillary buds.

It is now agreed that axillary buds may originate close to the apical meristem of the parent shoot, or at some distance from the apical meristem. Esau (1953) relates this difference in origin to the time and position of bud development. Philipson (1949) has suggested that the bud-trace differentiation is related to time of bud development. He writes : In buds that develop simultaneously with the leaves (near the apex) the vascular strands arise acropetally, whereas traces of buds which develop long after the leaf, arise basipetally because they become seats of renewed meristematic activity located in vacuolated tissue.

Kundu and Rao (1955, 1957) have in their later contributions on the subject suggested that the origin of buds might be axillary, foliar and cauline, and each of them after their origin may assume any of the other positions by adjustment during growth and development. But the authors do not explain what they meant by cauline and axillary origin of buds. Esau points out that axillary buds generally arise on the stem, and therefore cauline in origin. (We are not dealing with extra-axillary, supra-axillary and accessory buds which are always cauline in origin). She thinks the term axillary is, therefore, somewhat inaccurate. But I think, at least for descriptive purposes, it is quite accurate if the bud is found in the axil of the axillant leaf.

But what is meant by *axil*? Axil (L. *axilla*—armpit) is the upper angle formed by a leaf and the supporting stem (Heinig, 1899), syn. intrafoliaceous. But at its insertion on the axis the free limb of a leaf embraces quite a portion of the axis. The axil, therefore, should be, as I think, the angle of contact between the leaf opposite its median bundle and the axis. Only the buds which occupy this angle are to be called axillary, whether the origin be foliar or axial, and other buds lateral to it should be regarded as accessory. Thus :

**'A group of cells which at one time formed part of the apical meristem and which have retained their meristematic potentialities' (Wardlaw, 1952).

Axillary bud	Axial (cauline)
(positional)	Foliar
	At the time of origin neither axial nor foliar.

The relationship with the axillant leaf is not clear. Warming (1872) suggested that the axillant leaf and its bud constitute one unit. According to him the axillant leaf might be treated as the first and only leaf of the axillary bud (see for further and fuller account, Arber, 1950; Majumdar, 1955*b*). No one seems to have pursued the theme further.

With regard to its morphological nature Arber (1950) offered a theory : According to her the axillary bud is the offspring of the leaf, the partial shoot, the product of its basal lobes (p. 126). The primitive leaf was taken to be a trilobed one. She elaborated the arguments on which she based her theory. Majumdar (1955*b*) suggested a theory alternative to that of Arber. According to him the axillant leaf and the axillary bud represent two primordia of the distal forking of a branch. The outer one (positional) develops quickly and rapidly to form the leaf primordium under the influence of its acropetally differentiating median strand which follows its erection closely. The other (inner) remains undeveloped until its trace comes from the axial cylinder a little later than the median trace bundle of the leaf' (1955*b*, pp. 91-92). Thus according to Majumdar the axillant leaf and its axillary bud represent a twin structure instead of the parent and its offspring. The position of the bud in relation to its primordium also appears to lend support to the theory of Majumdar.

The Rubiaceae appear to be unique in so far that the origin of the axillary bud is definitely both *foliar* and *axial* in origin, and they occur in the same bud, and sometimes at the same node. The foliar buds are mostly ephemeral, and branches develop from the axial buds which always receive their vascular supply from the central stele. At least in half a dozen species, in the axils of the same leaf, twin foliar buds, twin axial buds and both foliar and axial buds occur at the same node. Another noted fact is that bud initials arise by de-differentiation of vacuolating dividing cells of the leaves (foliar) and axis (axial).

The following account gives a summary of observations of 24* species so far studied :

I. Origin of the bud : Either axial or foliar, but not both in the same bud

Species	Origin	Vascularization	Development
1. *Rubia edgeworthii* (Fig. 78)	Axial	Acropetal	into a branch
2. *R. cordifolia* (Fig. 79) (Majumdar and Pal, 1958*b*)	Axial	Acropetal	,, branch
3. *Catesbea spinosa* (Figs. 80-82) (Majumdar and Pal, 1958*b*)	Axial	Acropetal	,, spine; branch-buds arise secondarily between the spines and the leaf at node 6 below (cf. Randia)
4. *Anthocephalus cadamba* (Fig. 83) (Majumdar and Pal, 1959)	Foliar	Acropetal	into a branch
5. *Cinchona ledgeriana* (Figs. 84,85) (Majumdar and Pal, 1958*b*)	Foliar	Acropetal	,, branch

*Thirteen species have been described in this paper, the rest are from papers already published (Majumdar and Pal, 1958*a*, 1958*b*).

In all the five species the bud primordium differentiates in the ground tissue at the junction of the axis and the collar. Separation of the collar from the axis starts in the interpetiolar regions and proceeds towards the median bundles of the leaf-traces. If the line of separation passes external to the bud primordium it becomes *axial*, if internal to it the bud primordium goes with the collar and becomes *foliar*. In the earlier stages of bud initiation it can not, therefore, be strictly assigned either to leaf or to the axis.

II. Origin of the bud : Axial or foliar at the same or different nodes of the same bud

6. *Gardenia lucida* (Figs. 49-50) — At the same or different nodes :
Foliar—a few meristematic cells, no vascular supply, ephemeral, first appearance at second node from apex.
Axial—acropetal vas. supply, develops into branch, in lower nodes.
Branching—1-3 branchless nodes between 2 nodes with branches.

7. *G. thunbergia* (Fig. 51) — Foliar—acropetal, soon falls off, at upper nodes.
Axial—acropetal, develops into branch, at lower nodes.
Branching—4-5 branchless nodes intervene between 2 nodes with branches.

8. *G. florida* (Fig. 86, 87) (Majumdar and Pal, 1958*b*) — Foliar—at the upper node, ephemeral.
Axial—at lower nodes, acropetal vascular supply, develops into branch.
Branching—1-3 branchless nodes intervene between two nodes with branches.

9. *Portlandia grandiflora* (Fig. 52-53) — At different and same nodes :
Foliar—only a few meristematic cells, no vascular supply, ephemeral, upper node.
Axial—bud primordium originates at junction of collar and axis ; it separates from both collar and axis by a separation zone of its own, vascular supply acropetal, develops into a branch. From the manner of origin and separation it can not properly be referred to either axis or leaf.
Branching—2-5 branchless nodes come between two nodes with branches.

10. *Randia dumetorum* (Fig. 54) — Same and different nodes :
Foliar—no vascular supply, ephemeral.
Axial—acropetal vas supply, develops into thorn.
Axial—secondary in origin between the thorn and the leaf in lower nodes which develops into branches.

11. *Mussaenda frondosa* (Fig. 55) — origin at different nodes:
Foliar—no vascular supply, ephemeral, arises at upper nodes.
Axial—acropetal, at lower nodes, develops into branches.
Branching—3-10 branchless nodes between 2 nodes with branches.

12. *Luculia gratissima* (Fig. 56, 57) — at different nodes:
Foliar—no vascular supply, ephemeral, at upper nodes.
Axial—acropetal vas. supply, the bud separates from the axis and the leaf by the formation of a separation zone around itself. Therefore, like that in *Portlandia* its origin is independent (?) of the leaf and the axis.
Branching—4-5 branchless nodes come between two nodes with branches.

13. *Coffea arabica* (Figs. 58-65): This species is unique among the species so far examined. It shows three types of axillary buds in the same bud:
(i) Foliar and foliar as twin buds in the axil of the same leaf of a node, the distal gets vascular supply from the axial cylinder, and the proximal from the distal (Figs. 61-63).
(ii) Axial and axial as twin buds in the axil of the opposite leaf of the above node; the proximal gets its vascular supply from the axial cylinder and the distal from the proximal bud, (Figs. 64, 65) and
(iii) Foliar and axial at a different node with vascular supply from the axial cylinder (Figs. 58-60).

14. *Coffea bengalensis* (Figs. 66-69) — Foliar—acropetal, at upper node.
Foliar and axial—at the same node, as *twin* in the axil of the same leaf; the distal gets its vascular supply from the axial cylinder and the foliar from the axial bud trace.

15. *Adina cordifolia* (Fig. 72) — at different nodes—
Foliar—acropetal vas. supply, falls off soon, at upper nodes.
Axial—acropetal, develops into a branch, at lower nodes.
Branching—2-6 branchless nodes between two nodes with branches.

16. *Morinda citrifolia* (Figs. 39, 73) — at different nodes:
Foliar—acropetal vas. supply, falls off soon, at upper nodes.
Axial—acropetal, develops into a branch, origin at lower nodes.
Branching—1-3 branchless nodes between 2 nodes with branches.

17. *Hymenodictyon excelsum* (Figs. 74, 75) — at different nodes:
Foliar—acropetal vas. supply, falls off soon, at upper nodes.
Axial—acropetal, develops into branch, at lower nodes.
Branching—7-16 branchless nodes between 2 nodes with branches.

18. *Hamiltonia suaveolens* (Figs. 76, 77) — at different nodes:
Foliar—acropetal vas. supply, falls off soon, at upper nodes.
Axial—acropetal, develops into branch, at lower nodes.
Branching—2-10 branchless nodes between 2 nodes with branches.

19. *Hamelia patens* (Figs. 88-91) (Majumdar and Pal, 1959)
at different nodes—Buds originate at junction of axis and collar, axial or foliar is determined by the line of separation passing external or internal to it (cf. spp. 1-5 above)
Foliar—acropetal vas. supply, falls off soon, first seen at node three from tip (Figs. 88-90).
Axial—acropetal, develops into branch, at 6th node below (Fig. 91).
Branching—2-4 branchless nodes between 2 nodes with branches.

20. *H. sphaerocarpa* (Figs. 92, 93) (Majumdar and Pal, 1959)
as in the other species.
Foliar—acroptel vas. supply, ephemeral, first noticed at node 2 (Fig. 92).
Axial—acropetal, develops into branch, at 6th node (Fig. 93).

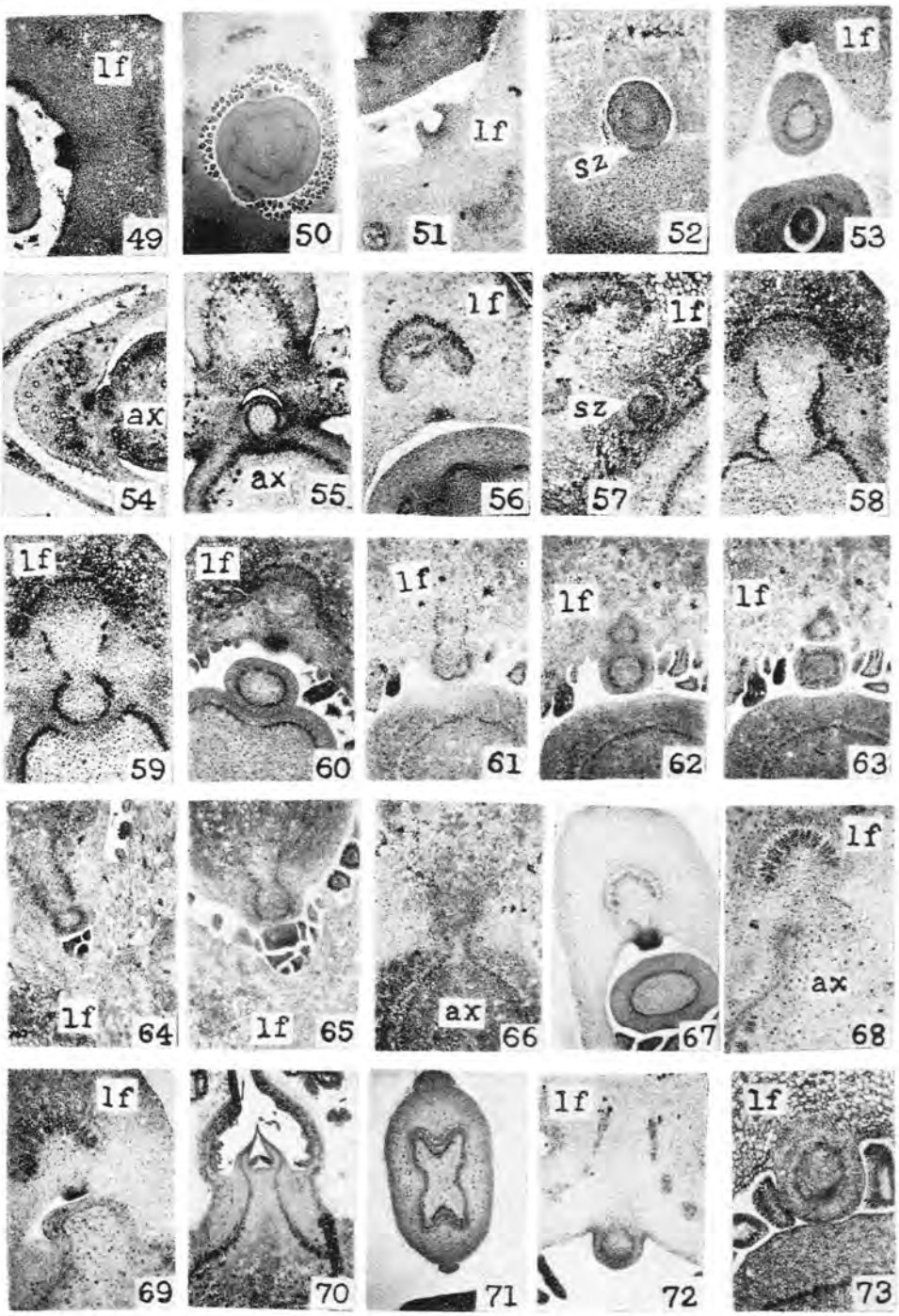
21. *Galium mollugo* (Figs. 94. 95) (Majumdar and Pal, 1958*a*)
Three types of bud formation are noticed in this species :
(i) Foliar—at the same node, one each in the axils of the pair of opposite leaves.
(ii) Axial—at the same node, one each in the axil of the pair of opposite leaves (Fig. 94).
(iii) Foliar and foliar as a *twin* at the same node in the axil of the same leaf (Fig. 95).

22. *Oldenlandia Heynii* (Figs. 96-98) (Majumdar and Pal, 1958*b*)
Foliar—Two foliar buds (*twin*) organize at the same node in the axil of the same leaf; the distal one gets its vascular supply from the axial cylinder, and the other represented by a few meristematic cells gets its very feeble vascular supply from the median trace bundle. The distal bud develops into a very small bud (Figs. 96, 97).
Axial—acropetal, develops into a branch, arises in the lower nodes (Fig. 98).
Branching—double branches are found in the axil of the same leaf, one remains small.

EXPLANATION OF PLATE XI.

(*Axillary Buds*)

Figs. 49–73.—are microphotographs of transverse (t.s.) and longitudinal (l.s.) sections of the apical bud to show particularly the origin, development and vascularization of the axillary buds, foliar and axial, For details see text.
Figs. 49–50.—*Gardenia lucida*, t.s.
Fig. 51. —*Gardenia thunbergia*, t.s.
Figs. 52–53.—*Portlandia grandiflora*, t.s.
Fig. 54. —*Randia dumetorum*, t.s.
Fig. 55. —*Mussaenda frondosa*, t.s.
Figs. 56–57.—*Luculia gratissima*, t.s.
Figs. 58–65.—*Coffea arabica*, t.s.
Figs. 66–69.—*Coffea bengalensis*, t.s.
Figs. 70–72.—*Adina cordifolia*, t.s., but fig. 70 is a logisection to show the stipule bases free from axis.
Figs. 73. —*Morinda citrifolia*, t.s.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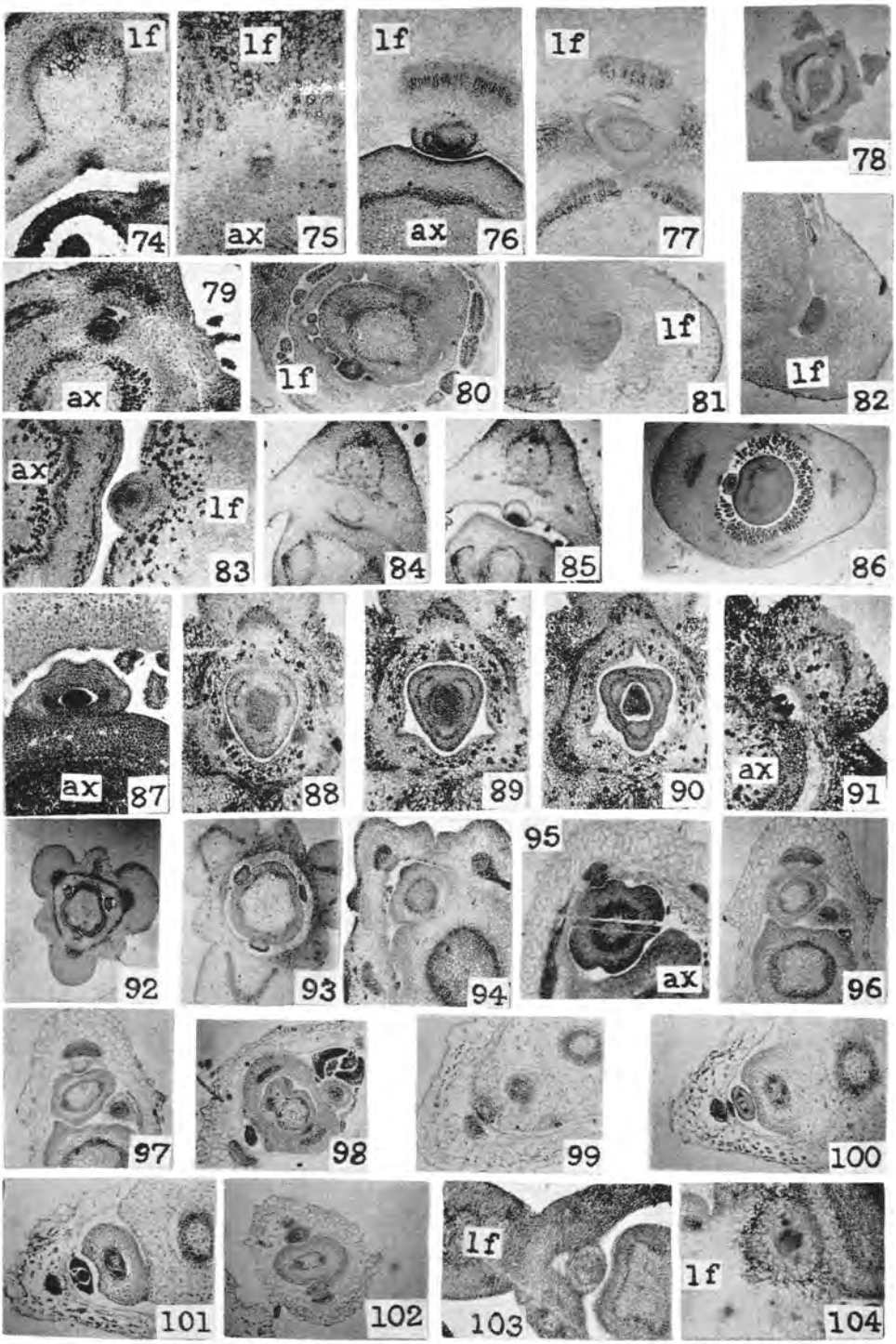
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23. *Dentella repens* (Figs. 99-102) (Majumdar and Pal, 1958*b*)

Foliar—ephemeral at upper nodes (Fig. 102).

Branches—double are found at each node, one remains small. Axial and axial as a pair of *twin* and foliar buds originate at the same node, the proximal gets its vascular supply from the axial cylinder, and the distal from the bud trace. The foliar is represented only by a few meristematic cells (Figs. 99-101).

24. *Stephagyne parviflora* (Figs. 103-104) (Majumdar and Pal, 1958*b*)

Foliar (?)—originates at the junction of the leaf and axis, vascular supply from the axial cylinder, a separation zone separates it from the axis, falls off soon (Fig. 103).

Axial and axial as twin buds arise at the same node in the axil of the same leaf, the distal degenerates and the proximal develops into a branch. The distal gets its vascular supply from the proximal, and both separate from the axis and the collar by their own separation zone formed round them (Fig. 104).

From the foregoing account of the origin and vascularization of the axillary buds in twenty-four species of the Rubiaceae the following conclusions are inevitable :

I. *Their origin :* Axillary buds may be *foliar* and/or *axial* in origin.

1. In some cases the foliar or axial origin of the bud is determined by the line separating the collar from the axis passing external (axial) or internal (foliar) to the bud which takes its origin in the ground tissue at the junction of the two organs. The buds receive their vascular supply from the axial cylinder as in *Rubia, Catesbea, Anthocephalus, Cinchona, Stephagyne, Hamelia, Gardenia, Mussaenda, Adina, Morinda, Hymenodictyon* and *Hamiltonia.*

2. In some cases the origin of the bud is similar to that in (1). but they separate from the axis and the collar by the formation of a separation zone round each of them as in *Portlandia* and *Luculia.*

N.B.—In (1) and (2) at the time of the origin a bud is neither axial nor foliar.

3. The foliar buds, which in most cases appear at upper nodes of the bud, are mostly ephemeral, with or without vascular supply, whereas the axial buds which appear at lower nodes of the same bud with vascular supply from the axial cylinder, develop into branches. This is reflected in the nature of branching on adult stems.

4. In some species, e.g. *Catesbea* and *Randia,* the branch buds arise secondarily on the axis between the spine or thorn and the leaf at the node.

EXPLANATION OF PLATE XII

(*Auxiliary Buds* continued)

Figs. 74–75.—*Hymenodictyon excelsum,* t.s.
Figs. 76–77.—*Hamiltonia suaveolens,* t.s.
Fig. 78. —*Rubia edgeworthii,* t.s.
Fig. 79. —*Rubia cordifolia,* t.s.
Figs. 80–82.—*Catesbea spinosa,* t.s.
Fig. 83. —*Anthocephalus cadamba,* t.s.
Figs. 84–85.—*Cinchona ledgeriana,* t.s.
Figs. 86–87.—*Gardenia florida,* t.s.
Figs. 88–91.—*Hamelia patens,* t.s.
Figs. 92–93.—*Hamelia sphaerocarpa,* t.s.
Figs. 94–95.—*Galium mollugo,* t.s.
Figs. 96–98.—*Oldenlandia Heynii,* t.s.
Figs. 99–102.—*Dentella repens,* t.s.
Figs. 103–104.—*Stephagyne parviflora,* t.s.

5. In some species, e.g. the foliar and axial buds originate as twins at the same node and in the axil of the same leaf, e.g. *Randia, Coffea arabica, C. bengalensis* and *Portlandia*.

6. In some species, e.g. *Oldenlandia, Galium, Coffea arabica*, foliar and foliar buds originate as twins at the same node in the axil of the same leaf.

7. In some species, such as, *Dentella, Stephagyne* and *C. arabica*, axial and axial buds as twins arise at the same node in the axil of the same leaf.

8. In *Dentella* there occur three buds, foliar, axial and axial in the axil of the same leaf.

II. *Their relationship with the axillant leaves, and morphological nature :*

It is indeed difficult to suggest any relationship between the axillant leaf and its bud. In a few species the bud at its initiation is not at all connected directly with the axis or the leaf. In the majority of cases the foliar buds take their origin in the tissues of the leaf, and the axial in the tissues of the axis. In one case a foliar bud has been seen to take origin 220μ above the shoot apex (e.g. *Coffea arabica*). The axillant leaf cannot, therefore, be regarded as the first leaf of the bud as suggested by Warming (1872).

Arber's (1950) parent-offspring theory is not supported. There is no indication that the bud is produced by the face to face union of the basal lobes of the axillant leaf. Our observations, however, to some extent, support Majumdar's (1955) theory that the axillant leaf and the axillary bud may represent the two forks of a dichotomous branching of an axis.

The origin of axillary buds reported in *Galium, Oldenlandia, Dentella, Stephagyne, Coffea bengalensis*, and particularly in *Coffea arabica*, are very interesting. The twin buds, foliar and foliar, axial and axial, and foliar and axial, and their vascular supply appear to point to the identical nature of the foliar and axial buds. Their origin, position, with reference to one another and their vascularization point to the following conclusions :

(i) The leaf and the axis, both of which bear the axillary buds, are equivalent organs. This lends support to Arber's (1950) partial-shoot theory of the leaf with 'an inherent urge towards the development of whole-shoot character' (p. 78). Recently Wardlaw (1949, 1957) and Cutter (1956) have shown that bud could be induced in a leaf-site, and an undetermined leaf primordium could be transformed into a bud.

(ii) In many species the bud initiation takes place in the tissue at the junction of the collar and the axis before the former separates from the latter. The collar then separates from the axis, and during the process if the line of separation passes external to the bud primordium it becomes axial, and if internal to it, it becomes foliar. In some species a separation zone organises surrounding the bud primordium to separate it both from the collar and the axis.

(iii) The buds appear to be twin products of ultimate dichotomy of an axis.

(iv) The foliar buds normally do not develop into branches because of their position and vascularization to which may be added the hereditary factor controlling the system of branching in these species.

(v) The axillary buds originate in the vacuolating dividing cells of the ground tissue. This is supported by Vöchting (1874), Priestley and Swingle (1929), Majumdar (1942), Sharman (1942), and Kundu and Rao in unbranched jute (1954), though the majority of investigators reported their origin from 'detached meristem'.

(vi) The branch buds, whether axial or foliar in origin, always receive their vascular supply from the central stele, whereas the foliar buds which are mostly ephemeral, are without any vascular supply, or get supplies from the median bundle of the leaf-trace, or secondarily from the axial bud-trace.

Conclusion

1. The collar of the Rubiaceae represents the united bases of the leaves, two or three as the case may be. It has two parts : one or the lower included in the axis as its outer component, and the other free from it and grows upwards in the form of a tubular sheath.

2. The collar is differentiated into two regions : the *petiolar regions* which contain the median bundle of the leaf-trace or its equivalent, and is radially extended; and the *interpetiolar regions* forming its lateral parts which generally contain the laterals and/or their branches.

3. The sheathing leaf-base or the free collar extends up to the region of separation of the petiole which is continuous or the prolongation of the petiolar regions (*soubassements foliares* of Gregoire, 1935) free from the collar.

4. The interpetiolar regions of the collar in continuation with the adaxial strip of the petiolar region after the separation of the petiole grows upwards in the form of a connate stipule, as in *Gardenia* spp. No inter-or intra-petiolar stipules are formed in this case.

Or, the collar may grow into a pair of interpetiolar stipules immediately after the separation of the petiole from it, or the collar may grow upwards as a sheathing base before it separates into a pair of interpetiolar stipules, or the collar by local outgrowth under the influence of a composite bundle may give rise to the stalked foliaceous stipules of the genus *Rubia*.

5. The stipules, connate or interpetiolar, receive their vascular supply from the laterals and/or their branches. Their development and vascularization have been followed and described in detail.

6. The Rubiaceous species are unique in having both foliar and axial bud primordia developed in the same parent bud, sometimes at different nodes, and in some cases at the same node in the axil of the same leaf. The foliar buds are formed near the apex and are ephemeral whereas the axial buds which normally develop into branches originate a few nodes below the growing point, and get their vascular supply directly from the axial cylinder.

Another unique feature has been noticed and reported in the previous pages : the bud primordium originates in the ground tissue at the junction of the collar and the axis, it separates from both by the formation of a separation zone round it. For other points of interest see under The Axillary Bud.

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Abbreviations used :

ax. axis; *axb.*, axial bud; *bd.*, bud; *br.*, branch; *btr.*, bud-trace; *brb.*, branch bundle of the leaf-trace; *cb.*, composite bundle; *col.*, collar; *fb.*, foliar bud; *gl.*, gland; *int. st.*, interpetiolar stipule; *issb.*, inner series of secondary bundles; L., lateral leaf-trace bundle; L_1, L_2, *a*, *b*, *c.*, branches of *L.*; *Lf*, *lf.*, leaf; *M.*, median trace bundle; *p.*, petiole; *sep.*, separation of the collar from the axis; *sp.*, spine; *sry. bud*, secondary bud; *sst.*, sheathing stipule; *st.*, stipule; *stb.*, base of the stipule; *st. tp.*, stipule tip; *trb.*, leaf-trace bundle; *sz.*, separation zone.