DEVELOPMENTAL STUDIES OF *PHYLLANTHUS NIRURI* LINN. AND *P. RETICULATUS* POIR. (EUPHORBIACEÆ) WITH SPECIAL REFERENCE TO THE ORIGIN AND NATURE OF AXILLARY VEGETATIVE BUDS

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INTRODUCTION

PRAIN (1903) has listed ten Bengal species of *Phyllanthus* Linn. of which the following six are common in East Bengal: *P. niruri* Linn., *P. reticulatus* Poir., *P. Emblica* Linn., *P. urinaria* Linn., *P. simplex* Retz. and *P. distichous* Muell.

The primary branches of *P. niruri* often *resemble* pinnately compound leaves. But in the axil of each pinna (simple leaf) one (*P. niruri*), or a cluster (*P. reticulatus*) of flower-buds are borne. Moreover, a pair of scaly stipules are present at the base of the short petiole of these leaves. Most often in the axil of these primary branches, which are of limited growth, more than one vegetative buds (secondary and tertiary branches) arise slightly extra-axillary in position. The presence of these branches often misguides a casual observer in believing the primary branches as true compound leaves (Fig. 1).

The plant *P. niruri* is very often used in class rooms to demonstrate the differences between a compound leaf and a branch with simple leaves on account of flower buds or fruits borne in the axils of these leaves.

The present studies were undertaken especially to re-examine the morphological nature of these leaf-like branches on anatomical evidence.

MATERIALS AND METHODS

The following two species were studied anatomically: *P. niruri* and *P. reticulatus*. Materials of *P. niruri* were collected from Dacca University Botanical Garden and F.H.M. Hall compound, and those of *P. reticulatus* from different hedges in and around Dacca City.

For developmental studies, particularly of the axillary branches, the growing apex, nodes, branch-nodes and branch tips were killed and fixed

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in FAA solution, dehydrated and embedded in paraffin according to schedule. Microtome sections of these materials were cut at 6 to 15 μ with a rotary microtome. The sections, both t.s. and l.s., were stained with safranin and fast green combination and made permanent in canada balsam.

Freehand sections of the nodes of the main axis and branches were also cut to study the vascular supply to the leaves and buds. The sections were suitably stained, dehydrated and mounted in canada balsam. All figures have been drawn with a camera lucida.

OBSERVATIONS

Morphology

P. niruri Linn.—(Fig. 1)—An annual weed, 6–8 inches high with spirally arranged branches which are naked and smooth below. The branches arise in the axils of three-fid scaly structures, the leaves (Fig. 1 *c*). More than one branch buds are often seen to arise in the axils of these branches (Fig. 1 *a*). The simple leaves on the primary branches are arranged distichously on each branch which is of limited growth in *P. niruri*. Axillary buds of these leaves develop into single flowers but never into vegetative branches (Fig. 1 *b*).

P. reticulatus Poir.—(Fig. 2)—A large much branched diffuse subscandent shrub with slender branchlets. It resembles *P. niruri* in the origin and nature of its branches, arrangement of leaves, etc. It differs from *P. niruri* in its diffuse and robust habit. The bud in the axil of the leaves of its primary branches develops into a cluster of flowers but never into vegetative branches. During flowering the branch is seen terminated by flower clusters.

Organization of the vegetative shoot apices

The shoot apex of *P. niruri* (Fig. 3) is dome-shaped in resting stage but becomes asymmetrical during the laying down of a leaf primordium. It is occupied by the eumeristem. The outer layer is the typical *tunica* in which the cells divide by anticlinal walls only. Within this tunica layer just behind the extreme tip there is a layer which can easily be differentiated from the rest of the *corpus* cells by their cyto-histological behaviour. At the apex of the dome its cells are vertically elongated and characterized by anticlinal divisions. At the flanks the divisions are by periclinal walls. Both leaf and bud primordia appear to arise in this layer. Even quite early in bud development this layer is seen well organized (Fig. 3 *b*, *d*). In the rest of the corpus cells periclinal, anticlinal and irregular divisions occur. *Flank and rib meristem-like organizations are not noticed.*

The shoot apex organization of the main axis of *P. reticulatus* (Fig. 4) differs to a considerable extent from that of *P. niruri*. The tunica is uni-

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The shoot apex organization of the main axis of *P. reticulatus* (Fig. 4) differs to a considerable extent from that of *P. niruri*. The tunica is uniseriate but the corpus without any zonal organization, is more extensive and its cell arrangement is most irregular. The outermost layer of the corpus is not organized in the pattern of its counterpart in *P. niruri*, and periclinal divisions are less frequent at the flanks. A desmogen (provascular) strand is seen running up the apex to supply a leaf primordium which is being laid down.

Leaves and their vascular supply

Two types of leaves are found in both the species:

(1) Three-fid scale leaves on the main axis in the axils of which the primary branches arise, and (2) the foliage leaves which the primary branches bear.

The scale leaf and its vascular supply.—(Figs. 5–10)—The mature scale leaf of *P. niruri* is trifid (Fig. 1 *a*). It is supplied by a single trace bundle which causes only one gap in the axial cylinder (Fig. 5). Before entering the free limb of the leaf it divides into three parts, one central and two laterals (Fig. 7). The central enters the middle lobe of the scale and the two laterals, the two lobes of the same (Figs. 8–10). The trace is very feeble and when divides into three parts it becomes feebler, the further growth and development of the scale is therefore much arrested.

Figs. 6, 7, 8, 9 & 10 show a very notable feature which is worth mentioning here. The two bud traces are not branches given out from the two ends of the axial cylinder flanking the gap caused by the departure of the median trace bundle but they are parts of the main stele. Attached to the proximal end of each bud trace is noticed a constricted area which when compared with Fig. 13 (*P. reticulatus*) appears to be the lateral of the leaf trace. It seems that the two laterals instead of departing for the central limb of the scale leaf remain attached to the bud traces. When Figs. 8, 9 and 10 are examined it is further seen that these two constricted portions unite to form the trace of the secondary branch (see below).

The scale leaf of *P. reticulatus* is also trifid. It is supplied by three trace bundles which cause three gaps in the axial cylinder when they depart for the leaf. (Fig. 13). The median like that in *P. niruri* divides but the two lateral branches turn back and unite with the two incoming laterals (Fig. 14), and the central portion goes to supply the scaly leaf. The laterals give out a branch each to supply the lateral lobes with their traces (Fig. 14). The lateral lobes of the three-fid scaly leaf are, therefore, stipules and not the lobes of the scaly leaf (*cf.*, scaly leaf of *P. niruri*, Fig. 7). The composite bundles formed by the union of the lateral leaf traces and the lateral branches of the median do not enter the leaf but are lost in the leaf-cushion. Fig. 14 shows that the bud traces of the primary branch also remain united with these composite bundles for a short while before the latter are lost (Fig. 15).

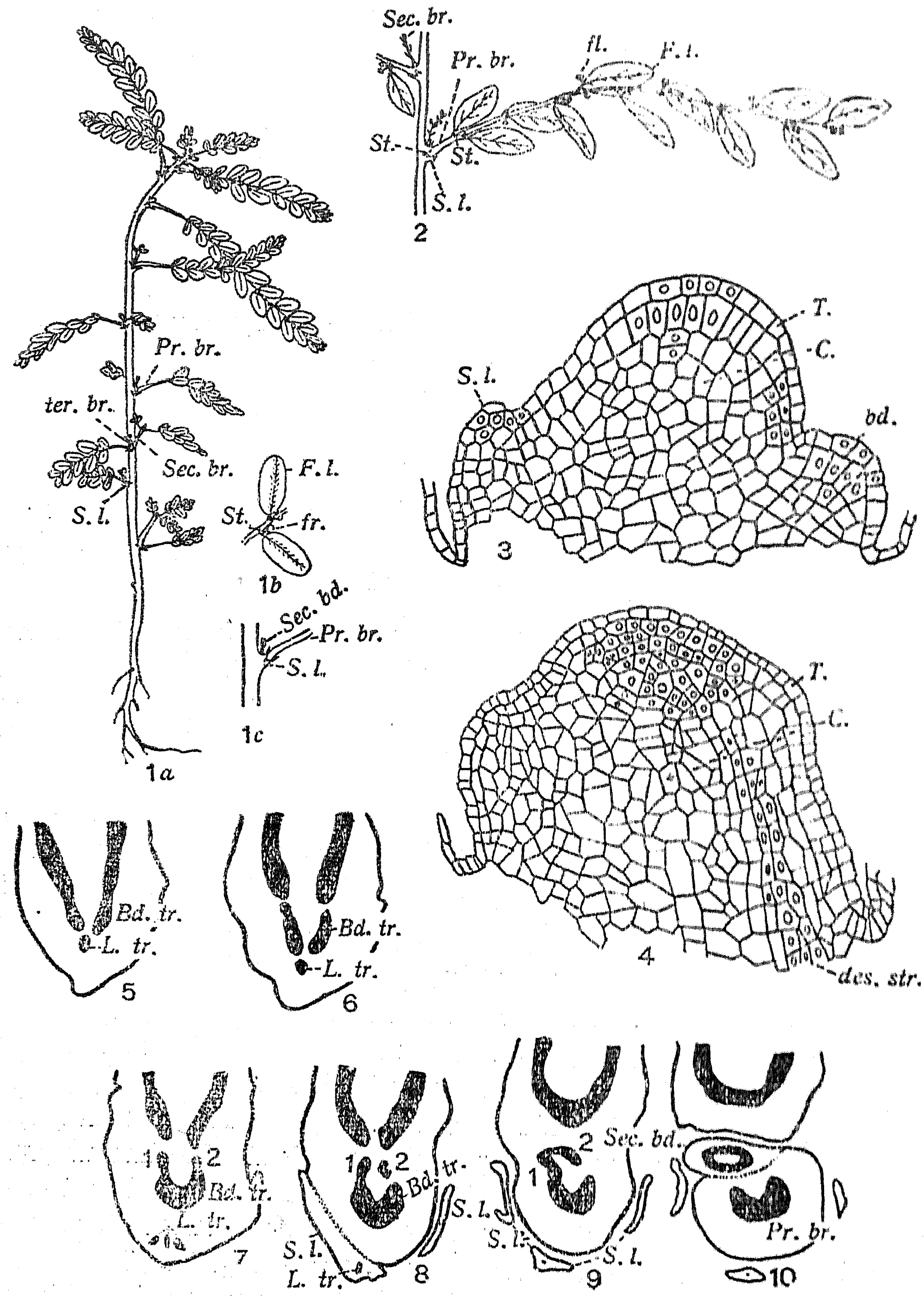


FIG. 1–10

The foliage leaf and its vascular supply.—The foliage leaves of these plants are simple and stipulate. They are borne only on the primary branches which terminate in growing points which are similar in organization to those of the main apices. In *P. niruri* (Fig. 18) these leaves are supplied by three trace bundles. The gap in the central cylinder caused by the departure of the median remains open and the stele in the branch assumes the form of a cup (*cf.*, rachis stele of a compound leaf) (Figs. 20, 21). The cup is later closed and the branch stele forms a cylinder a little beyond the divergence of the first leaf. During their movement towards the median the laterals send out a branch each to form the stipules and their traces on their corresponding sides (Figs. 19, 20).

Foliage leaves of *P. reticulatus* are also supplied by three trace bundles which cause three gaps in the axial cylinder (Figs. 22, 23). The laterals like those in *P. niruri* unite with the median and form an arc in the branch axis (Fig. 24). A branch from each lateral goes to supply the stipules (Figs. 24–26).

Origin of Buds and their Vascular Supply

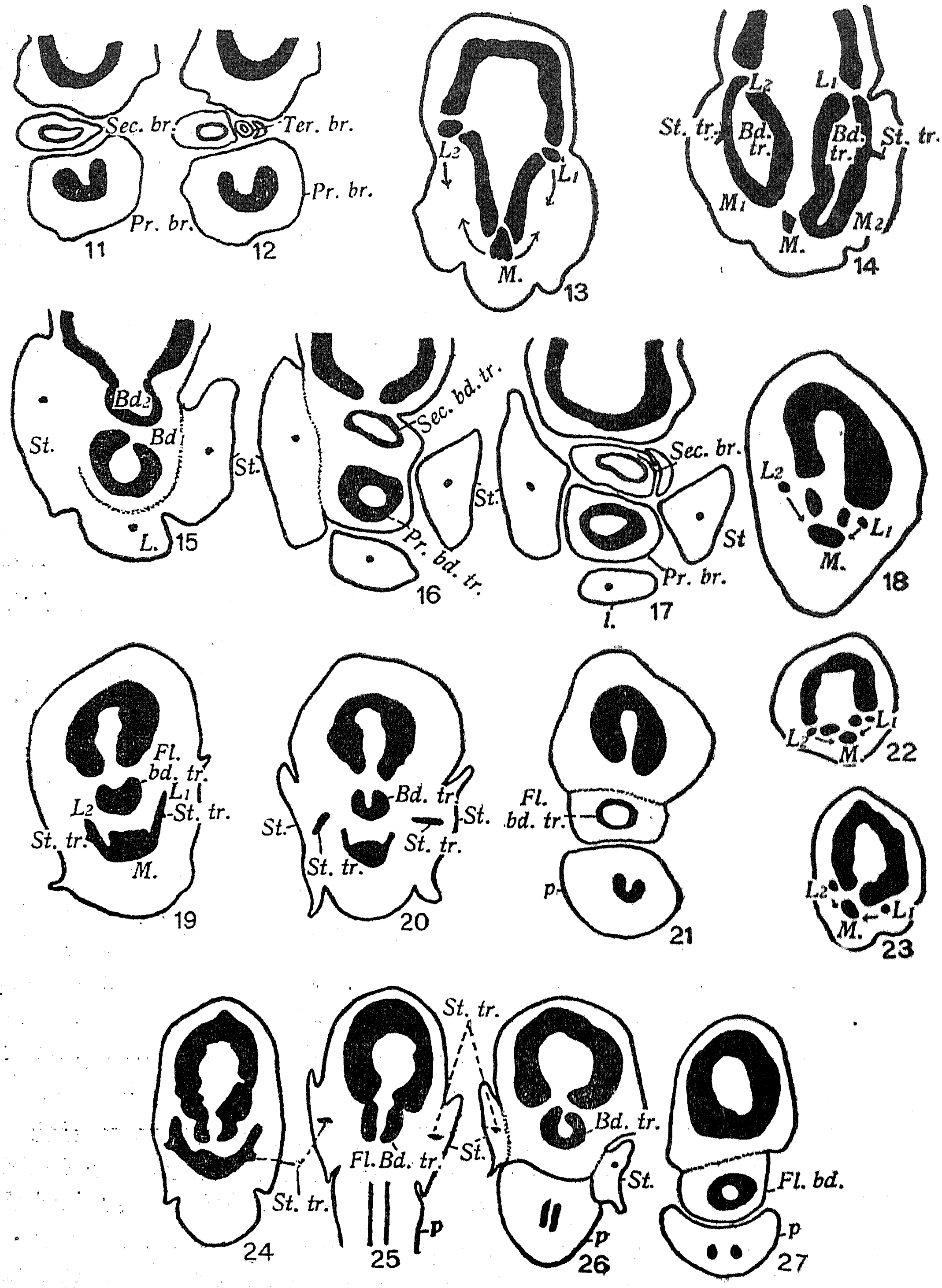
Origin of the primary bud in the axil of the scale-leaf and its vascular supply.—The buds in both the species studied originate in the tissues of the main axis and therefore their origin is *axial* and not foliar.

The first appearance of the bud in *P. niruri* is noticed in relation to the first or second scale leaf from the vegetative apex. The bud traces, two in number, are supplied from the vascular cylinder of the main axis flanking the gap caused by the departure of the median leaf trace bundle (Figs. 5, 6). These two traces run towards the base of the bud, unite by their posterior ends and remain cup-like for about $\frac{1}{2}$–1″ up the axis in mature branches, and then unite by their free ends to form a vascular cylinder (branch stele).

In *P. reticulatus* bud traces are also two in number, but instead of being branches from the free ends of the axial stele flanking the median leaf gap they are its portions between the median and lateral gaps on each side (Figs. 13, 14). Soon after the disappearance of the composite bundles (formed by the union of the laterals and lateral branches of the median) the bud traces unite to form a closed vascular cylinder at the base of the bud axis (Figs. 15, 16).

Origin of the secondary and tertiary buds (branches) in the axil of the primary bud and their vascular supply.—These buds arise in comparatably mature nodes (Figs. 1 *a* and 2). In *P. niruri* the second and third buds arise in slightly extra-axillary position (Figs. 10–12).

The origin of the two traces of the secondary bud in *P. niruri* as we have indicated before is rather interesting. Figs. 6 and 7 show two constricted areas (1, 2) at the distal ends of the two primary bud traces. They are



FIGS. 11–27

organized immediately after the separation of these traces from the main stele. When compared with Fig. 13 they appear to represent the two laterals of the three-bundle trace of *P. reticulatus*. If that is so then the two laterals of the leaf trace of *P. niruri* (unilacunar node) instead of departing for the median remain tagged to the tail ends of the primary bud traces and ultimately separate from the latter to form the traces of the secondary bud (Figs. 6–9). This appears to be a novel feature in the origin of traces of secondary bud (*cf.*, below for *P. reticulatus*) and further investigation is being carried on with other allied materials to verify the truth or otherwise of the method of origin of secondary bud traces noticed in this species.

The tertiary bud originates lateral to the secondary bud and gets its vascular supply from the axial stele of the latter (Figs. 11, 12). When Figs. 8–12 are examined the sequence of the origin and vascular supplies to the primary, secondary and tertiary buds of *P. niruri* are noticed as follows: The primary bud takes its origin in the tissues of the main axis and gets its vascular supply from the axial cylinder of the same. The secondary bud originates in the tissues of the primary bud and gets its vascular supply from the same, and the tertiary bud in its turn originates and gets its vascular supply from the secondary bud.

The origin of both the primary and secondary buds of *P. reticulatus* takes place in the tissues of the main axis and their vascular supplies are derived from the main stele (Figs. 14–17). *P. reticulatus* thus differs from *P. niruri* in the methods of the origin and vascular supplies to the secondary buds.

Origin of buds (flower) in the axils of the leaves of the primary branches and their vascular supplies.—The buds in both the species are axial in origin. These buds are invariably flower-buds. They generally arise in the axil of the second or third leaf primordium from the tip. In both the species the two bud traces originate from the vascular cylinder of the branch axis from the edges of the gap caused by the departure of the median leaf trace bundle. After separation from the branch stele they immediately unite to form a vascular cylinder and supply the flower bud (Figs. 18–21 and 24–27).

Discussion and Conclusions

The cellular organization at the vegetative shoot apices of both the species studied does not show an advanced type in dicotyledons. In *P. niruri* the tunica is uniseriate but the layer within (outer corpus layer) is rather peculiar in having two regions: the region immediately surmounting the apical dome is made up of vertically elongated prismatic cells bigger than other cells of the eumeristem, and its cells show slow anticlinal divisions;

in the region lower down in the flanks the cells are much smaller in size and divide mainly by periclinal walls. These along with the local tunica cells appear to be concerned in the origin of leaf and bud primordia. The rest of the corpus is a mass of cells without any organization or zonation.

The tunica in *P. reticulatus* is also uniseriate. The corpus in this case is extensive and the arrangement of the cells is most irregular. The desmogen strand is acropetal in its differentiation and appears directly concerned with the erection of the free limb of a leaf primordium on the side of the apical dome. In this case also the zonation of apical meristem is absent.

Cellular organization at the vegetative shoot apices of both the species therefore supports Sporne (1949) according to whom the Euphorbiaceæ to which these two species belong is a primitive family as its advancement index is only 25% (p. 273).

Neither Prain (1903) nor Willis (1951) has described the leaves on the main stem in the axils of which the primary vegetative buds arise. This omission appears to be due to the fact that these leaves are scaly and insignificant in nature. We have seen before that these features are related to their vascular supplies which are very feeble and slender.

The nodes of the main axis in *P. niruri* are unilacunar, and each lateral lobe of the scaly leaf receives its vascular supply from a branch of the median. The lateral lobes are, therefore, parts of the lamina (all the three lobes of the leaf getting their vascular supply from the same median), and are not a pair of stipules.

There are reported cases of a few dicotyledons in which though the nodes are unilacunar the leaves are stipulate. Sinnott and Bailey (1914) and Mitra (1949) who examined and reported on such nodes state that the so-called median bundle in many of them show indications of a composite nature as if formed by the fusion of the two laterals with the median of a three-bundle trace. Our present studies on the nodal anatomy of *P. niruri* give no indication of such fusion.

In *P. reticulatus* the nodes of the main axis are trilacunar and the leaf trace consists of three bundles—the median and the two laterals. The two laterals after giving out a branch each to the two lateral lobes of the scaly leaf disappear in the leaf cushion. The two lobes in the case of this species are, therefore, a pair of stipules (Colomb, 1887; Sinnott and Bailey, 1914; Mitra and Majumdar, 1952, and others).

The above observations on the two species of the Euphorbiaceæ support Sinnott and Bailey (1914) who state that in the Euphorbiaceæ the species are both uni- and tri-lacunar with exstipulate and stipulate leaves. It is however to be noted that the traces of the leaves on the primary branches in both the species consist of three bundles—one median and two laterals, and the nodes are trilacunar.

P. niruri and *P. reticulatus* belong to the same genus and in great many features resemble each other. The scaly leaf on the main axis are trifid in both the species, but in one case its lateral lobes are *leaf lobes* and in the other species they are *stipules*. This distinction has been made only on the basis of their vascularization. A pertinent question may be raised here: Are the *stipules* and the pair of basal lobes of a leaf (particularly in these cases) equivalent organs? Sinnott and Bailey (1914) suggested that the stipules may be "considered as homologous with the two basal leaf lobes or the earliest leaf teeth". In the first case the difference is one of degree than of kind, and in the second case their position is determined by the branches of the two lateral leaf traces of a three-bundle leaf trace (p. 451).

Let us examine the suggestions of Sinnott and Bailey in the light of the evidence presented in this paper: The leaves on the primary branches of both the species are simple and stipulate, the leaf trace is made up of three bundles—the median and the two laterals and the nodes are trilacunar. The axillary buds are all flower-buds.

Both the species agree in having scaly trilobed leaves on the main axis and there the common feature ends. In *P. niruri* the leaf trace consists of the median only and the node is unilacular. In *P. reticulatus* on the other hand three bundles, the median and two laterals, constitute the leaf trace and the node is trilacunar. The median in both the species divide into three parts—a central and two lateral branches. In both of them the central portion goes to the central lobe but the behaviour of the two laterals is different in the two species. In *P. niruri* they go to supply the two basal lobes, but in *P. reticulatus* they turn back and join the incoming laterals of the leaf trace which have already sent out branches to the two basal lobes, and finally lost in the leaf cushion. Only on the nature of the vascular supply the basal lobes in one case is described as leaf lobes and in the other case a pair of stipules.

Trilacunar condition of the node and the three-bundle leaf trace go together. Therefore the only difference noticed in the two species is the absence of the laterals in one case and their presence in the other. In the first case the median divides to supply the lateral leaf lobes and in the other case the laterals give out branches to these leaf lobes. On the basis of this difference it may be said that in the present case the difference between the pair of lateral basal lobes and the pair of stipules " is one of degree than of kind".

Primary buds in both the species arise in the tissues of the main axis and receive their vascular supplies from the main stele (Sterling, 1945; Garrison, 1949 *a*, 1949 *b*; Gifford, 1951; Miller and Wetmore, 1946; White, 1955). The two bud traces in both the cases instead of being branches appear to be portions of the central cylinder between the gaps caused by the departure of the median and the laterals.

The position of the secondary buds in both the species is axillary or slightly extra-axillary to the primary buds. In *P. reticulatus* its origin is in the tissues of the main axis like that of the primary buds, but in *P. niruri* it is in the tissues of the primary bud axis. The vascular supply also appears different in the two species. In *P. niruri* the supply comes from the two free ends of the cup-shaped primary bud trace. Immediately after the separation of the two bud traces from the main cylinder two constricted areas appear at their distal ends. These look like the two laterals of the scale leaf suppressed in this species. These two areas separate from the primary bud traces which meanwhile unite by their proximal ends and form the trace of the secondary bud.

The origin of the secondary bud in *P. reticulatus* is axial (main axis) like that of the primary buds and its vascular supply also comes from the central cylinder. From the very beginning it forms a loop opposite the median gap and after separation from the main cylinder form a closed stele at the base of the bud.

Tertiary buds are extra-axillary in position being situated laterally to the secondary bud, and were found developed only in *P. niruri*. Its origin is in the tissues of the axis of the secondary bud and its vascular supply also comes from the axial stele of the former in the form of a loop as seen in the origin of the trace of the secondary bud in *P. reticulatus*.

The buds in the axils of the leaves on the primary branches develop into flowers without any exception. They get their vascular supply from the stele of the primary branches and not from the stele of the main axis. As the primary branches bear only flower-buds, either singly or in clusters, it is suggested that these branches should be called *inflorescences* and not vegetative branches. The simple stipulate leaves are therefore bracts.

SUMMARY

The apical organizations of the vegetative shoot apices have been studied in *P. niruri* and *P. reticulatus* (Euphorbiaceæ). The uniseriate tunica and

he massive corpus without any zonation in both the species indicate a less advanced apical organization among dicotyledons.

Two types of leaves are borne by both the plants: scaly on the main axis and foliage on the primary branches. The foliage leaves of both the plants are simple and stipulate, and are characterized by a three-bundle leaf trace, trilacunar nodes which bear them, and presence of only flower-buds in their axils. The scale leaves, on the other hand, are three-lobed in both the species, but they differ in the constitution of their traces and nodal anatomy. In *P. niruri* the leaf trace consists of only one bundle, the median, and the node is unilacunar, whereas in *P. reticulatus* the leaf trace is constituted of three bundles and the node is trilacunar.

The two lobes of the scale leaf, on the basis of their vascularization, are described as a pair of basal leaf lobes in *P. niruri*, and a pair of stipules in *P. reticulatus*. The probable homologies of these two structures *in these plants* have been discussed.

The origin and vascularization of the primary, secondary and tertiary buds—the last only in *P. niruri*, have been studied and discussed. The origin of the secondary and tertiary buds and their vascular supplies appear to be novel features not so far as the authors are aware, recorded before.

As the primary branches bear only flower-buds it is suggested that they should be called *inflorescence axes* and the foliage leaves, bracts. This also appears to be a primitive character.

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EXPLANATION OF TEXT-FIGURES

FIG. 1 *a, b, c*. Habit sketch of *Phyllanthus niruri* showing primary, secondary and tertiary branches, scale leaf, foliage leaf, stipules, fruits, etc. 1 *a*, $\times\frac{1}{2}$; 1 *b*, $\times 1$; 1 *c*, $\times 2$.

FIG. 2. A portion of *P. reticulatus* showing primary and secondary branches, scale leaf, stipules, foliage leaves, flowers, fruits, etc., $\times\frac{1}{2}$.

FIG. 3. Median longitudinal section of the shoot apex of *P. niruri* showing uniseriate tunica, massive corpus, outer corpus layer, bud initiation at the right flank and a scale leaf in development at left, $\times 562 \cdot 5$.

FIG. 4. Median longitudinal section of the shoot apex of *P. reticulatus* showing uniseriate tunica enclosing extensive corpus, desmogen strand of a new leaf primordium continuous with the eumeristem at its right flank, $\times 362 \cdot 5$.

FIGS. 5–12. Serial transverse sections through the nodal region of the main axis of *P. niruri* showing unilacunar node, one-bundle (median) leaf trace, origin of traces of the primary, secondary and tertiary buds, vascular supply to the lobes of the scale leaf, etc., $\times 23 \cdot 8$.

FIGS. 13–17. Serial t.s. through the nodal region of the main axis of *P. reticulatus* showing trilacunar node, three-bundle leaf trace, stipular trace, traces of primary and secondary branches, etc., $\times 27 \cdot 5$.

FIGS. 18–21. Serial t.s. through the node of a primary branch of *P. niruri* showing trilacunar node, three-bundle leaf trace, stipules with their traces, traces of flower-bud, etc., $\times 23 \cdot 8$.

FIGS. 22–27. Serial t.s. through the node of a primary branch of *P. reticulatus* showing trilacunar node, three-bundle leaf trace, stipules with their traces, petiole and its trace, flower-bud and its trace, $\times 23 \cdot 8$.

Pr.br., *Sec.br.* and *ter.br.*, primary, secondary and tertiary branches respectively; *s.l.*, scale leaf; *F.l.*, foliage leaf; *st.*, stipule; *p.*, petiole; *Fl.*, flower; *fr.*, fruit; *bud*, bud primordium; *Fl.bd.tr.*, flower-bud trace; *T.*, tunica; *C.*, corpus; *des.str.*, desmogen strand; *l.tr.*, leaf trace; *Bd.tr.*, bud trace; *M.* and L_1, L_2, median and lateral leaf trace; *l.*, leaf; *St.tr.*, stipular trace; *op.cup.*, open cup-shaped bud trace.

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of the median do not enter the leaf but are lost in the leaf-cushion. Fig. 14 shows that the bud traces of the primary branch also remain united with these composite bundles for a short while before the latter are lost (Fig. 15).

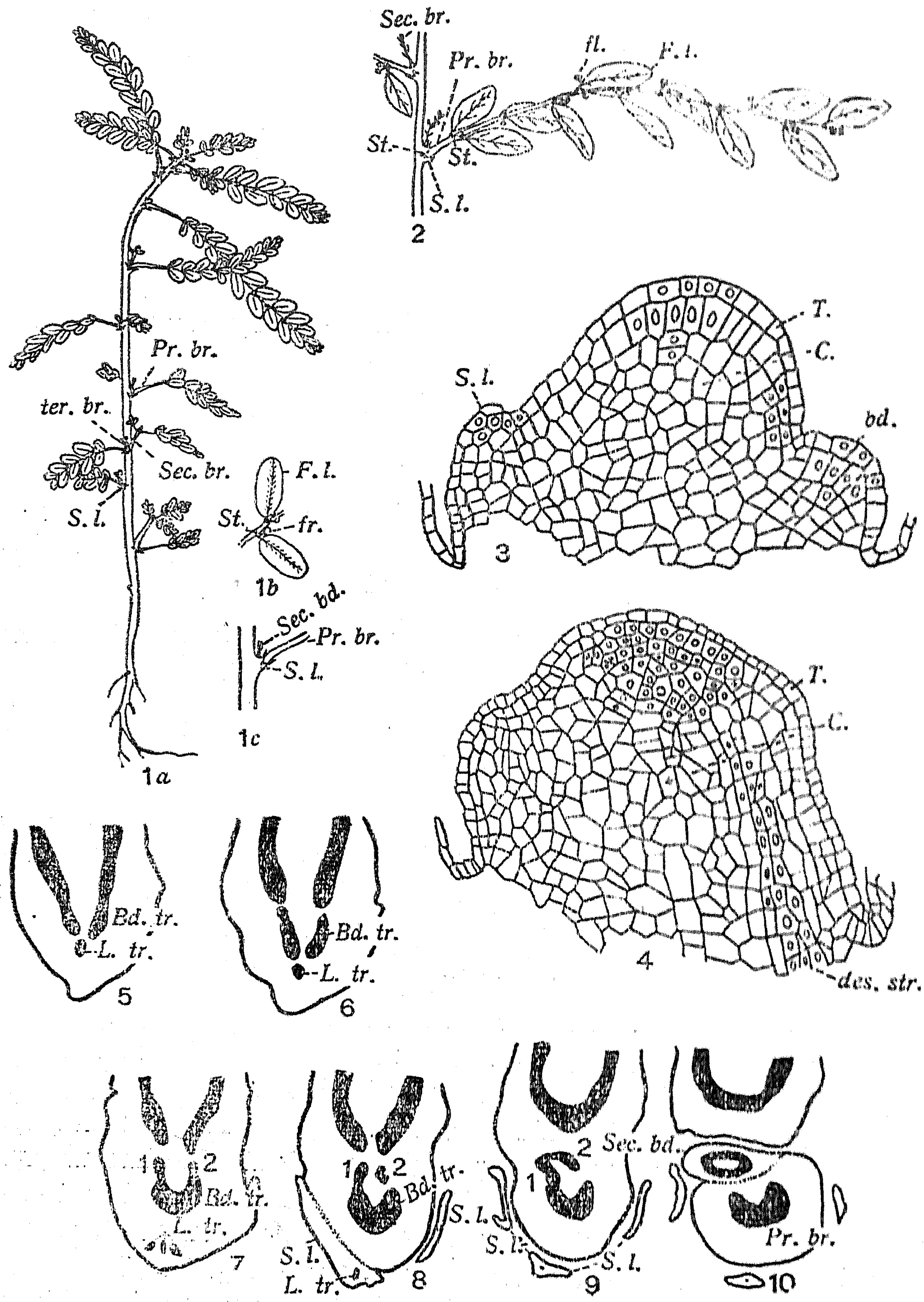


FIG. 1–10

The foliage leaf and its vascular supply.—The foliage leaves of these plants are simple and stipulate. They are borne only on the primary branches which terminate in growing points which are similar in organization to those of the main apices. In *P. niruri* (Fig. 18) these leaves are supplied by three trace bundles. The gap in the central cylinder caused by the departure of the median remains open and the stele in the branch assumes the form of a cup (*cf.*, rachis stele of a compound leaf) (Figs. 20, 21). The cup is later closed and the branch stele forms a cylinder a little beyond the divergence of the first leaf. During their movement towards the median the laterals send out a branch each to form the stipules and their traces on their corresponding sides (Figs. 19, 20).

Foliage leaves of *P. reticulatus* are also supplied by three trace bundles which cause three gaps in the axial cylinder (Figs. 22, 23). The laterals like those in *P. niruri* unite with the median and form an arc in the branch axis (Fig. 24). A branch from each lateral goes to supply the stipules (Figs. 24–26).

Origin of Buds and their Vascular Supply

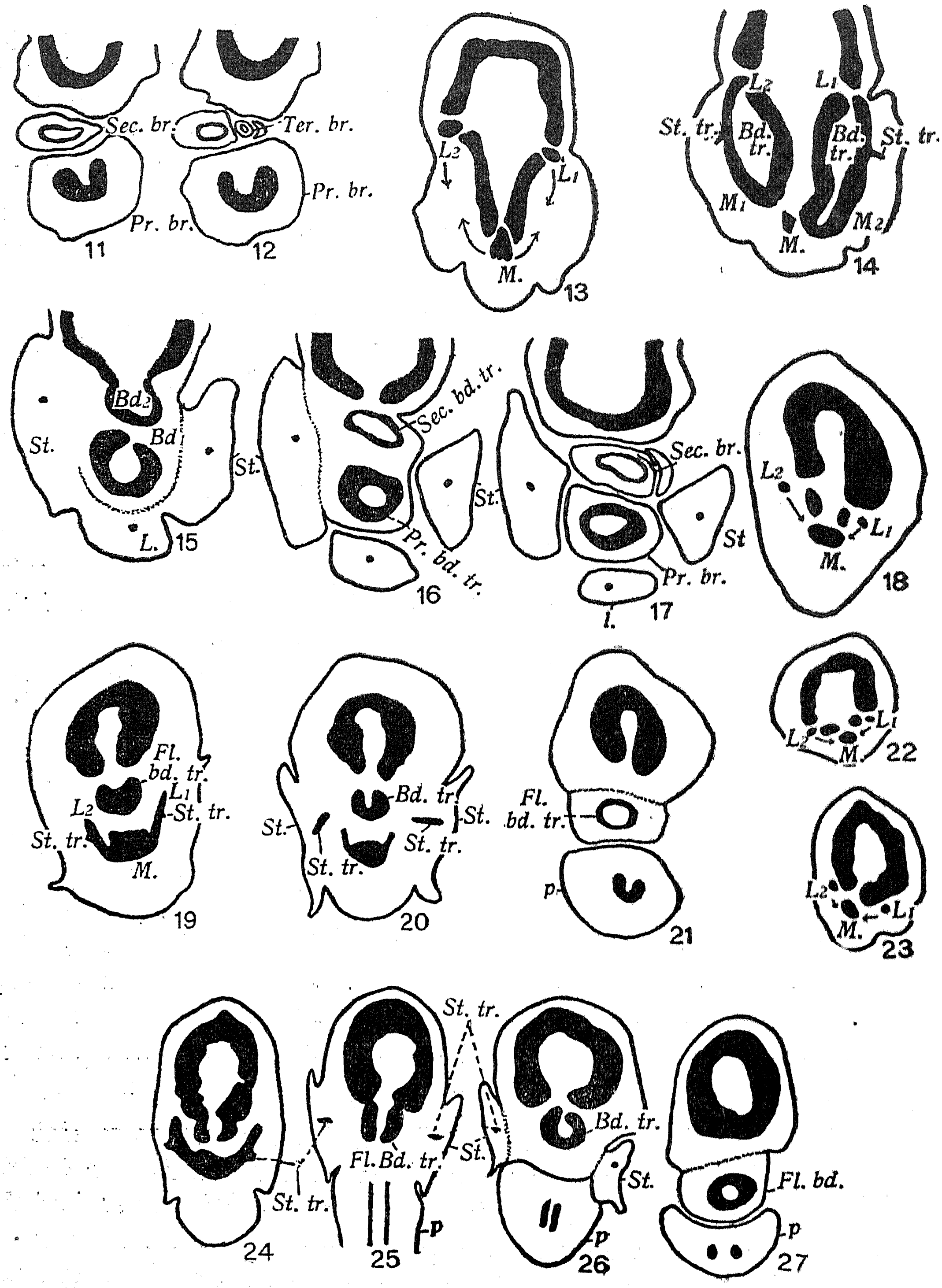
Origin of the primary bud in the axil of the scale-leaf and its vascular supply.—The buds in both the species studied originate in the tissues of the main axis and therefore their origin is *axial* and not foliar.

The first appearance of the bud in *P. niruri* is noticed in relation to the first or second scale leaf from the vegetative apex. The bud traces, two in number, are supplied from the vascular cylinder of the main axis flanking the gap caused by the departure of the median leaf trace bundle (Figs. 5, 6). These two traces run towards the base of the bud, unite by their posterior ends and remain cup-like for about ½–1″ up the axis in mature branches, and then unite by their free ends to form a vascular cylinder (branch stele).

In *P. reticulatus* bud traces are also two in number, but instead of being branches from the free ends of the axial stele flanking the median leaf gap they are its portions between the median and lateral gaps on each side (Figs. 13, 14). Soon after the disappearance of the composite bundles (formed by the union of the laterals and lateral branches of the median) the bud traces unite to form a closed vascular cylinder at the base of the bud axis (Figs. 15, 16).

Origin of the secondary and tertiary buds (branches) in the axil of the primary bud and their vascular supply.—These buds arise in comparatably mature nodes (Figs. 1 *a* and 2). In *P. niruri* the second and third buds arise in slightly extra-axillary position (Figs. 10–12).

The origin of the two traces of the secondary bud in *P. niruri* as we have indicated before is rather interesting. Figs. 6 and 7 show two constricted areas (1, 2) at the distal ends of the two primary bud traces. They are



FIGS. 11–27

organized immediately after the separation of these traces from the main stele. When compared with Fig. 13 they appear to represent the two laterals of the three-bundle trace of *P. reticulatus*. If that is so then the two laterals of the leaf trace of *P. niruri* (unilacunar node) instead of departing for the median remain tagged to the tail ends of the primary bud traces and ultimately separate from the latter to form the traces of the secondary bud (Figs. 6–9). This appears to be a novel feature in the origin of traces of secondary bud (*cf.*, below for *P. reticulatus*) and further investigation is being carried on with other allied materials to verify the truth or otherwise of the method of origin of secondary bud traces noticed in this species.

The tertiary bud originates lateral to the secondary bud and gets its vascular supply from the axial stele of the latter (Figs. 11, 12). When Figs. 8–12 are examined the sequence of the origin and vascular supplies to the primary, secondary and tertiary buds of *P. niruri* are noticed as follows: The primary bud takes its origin in the tissues of the main axis and gets its vascular supply from the axial cylinder of the same. The secondary bud originates in the tissues of the primary bud and gets its vascular supply from the same, and the tertiary bud in its turn originates and gets its vascular supply from the secondary bud.

The origin of both the primary and secondary buds of *P. reticulatus* takes place in the tissues of the main axis and their vascular supplies are derived from the main stele (Figs. 14–17). *P. reticulatus* thus differs from *P. niruri* in the methods of the origin and vascular supplies to the secondary buds.

Origin of buds (flower) in the axils of the leaves of the primary branches and their vascular supplies.—The buds in both the species are axial in origin. These buds are invariably flower-buds. They generally arise in the axil of the second or third leaf primordium from the tip. In both the species the two bud traces originate from the vascular cylinder of the branch axis from the edges of the gap caused by the departure of the median leaf trace bundle. After separation from the branch stele they immediately unite to form a vascular cylinder and supply the flower bud (Figs. 18–21 and 24–27).

Discussion and Conclusions

The cellular organization at the vegetative shoot apices of both the species studied does not show an advanced type in dicotyledons. In *P. niruri* the tunica is uniseriate but the layer within (outer corpus layer) is rather peculiar in having two regions: the region immediately surmounting the apical dome is made up of vertically elongated prismatic cells bigger than other cells of the eumeristem, and its cells show slow anticlinal divisions;

in the region lower down in the flanks the cells are much smaller in size and divide mainly by periclinal walls. These along with the local tunica cells appear to be concerned in the origin of leaf and bud primordia. The rest of the corpus is a mass of cells without any organization or zonation.

The tunica in *P. reticulatus* is also uniseriate. The corpus in this case is extensive and the arrangement of the cells is most irregular. The desmogen strand is acropetal in its differentiation and appears directly concerned with the erection of the free limb of a leaf primordium on the side of the apical dome. In this case also the zonation of apical meristem is absent.

Cellular organization at the vegetative shoot apices of both the species therefore supports Sporne (1949) according to whom the Euphorbiaceæ to which these two species belong is a primitive family as its advancement index is only 25% (p. 273).

Neither Prain (1903) nor Willis (1951) has described the leaves on the main stem in the axils of which the primary vegetative buds arise. This omission appears to be due to the fact that these leaves are scaly and insignificant in nature. We have seen before that these features are related to their vascular supplies which are very feeble and slender.

The nodes of the main axis in *P. niruri* are unilacunar, and each lateral lobe of the scaly leaf receives its vascular supply from a branch of the median. The lateral lobes are, therefore, parts of the lamina (all the three lobes of the leaf getting their vascular supply from the same median), and are not a pair of stipules.

There are reported cases of a few dicotyledons in which though the nodes are unilacunar the leaves are stipulate. Sinnott and Bailey (1914) and Mitra (1949) who examined and reported on such nodes state that the so-called median bundle in many of them show indications of a composite nature as if formed by the fusion of the two laterals with the median of a three-bundle trace. Our present studies on the nodal anatomy of *P. niruri* give no indication of such fusion.

In *P. reticulatus* the nodes of the main axis are trilacunar and the leaf trace consists of three bundles—the median and the two laterals. The two laterals after giving out a branch each to the two lateral lobes of the scaly leaf disappear in the leaf cushion. The two lobes in the case of this species are, therefore, a pair of stipules (Colomb, 1887; Sinnott and Bailey, 1914; Mitra and Majumdar, 1952, and others).

The above observations on the two species of the Euphorbiaceæ support Sinnott and Bailey (1914) who state that in the Euphorbiaceæ the species are both uni- and tri-lacunar with exstipulate and stipulate leaves. It is however to be noted that the traces of the leaves on the primary branches in both the species consist of three bundles—one median and two laterals, and the nodes are trilacunar.

P. niruri and *P. reticulatus* belong to the same genus and in great many features resemble each other. The scaly leaf on the main axis are trifid in both the species, but in one case its lateral lobes are *leaf lobes* and in the other species they are *stipules*. This distinction has been made only on the basis of their vascularization. A pertinent question may be raised here: Are the *stipules* and the pair of basal lobes of a leaf (particularly in these cases) equivalent organs? Sinnott and Bailey (1914) suggested that the stipules may be "considered as homologous with the two basal leaf lobes or the earliest leaf teeth". In the first case the difference is one of degree than of kind, and in the second case their position is determined by the branches of the two lateral leaf traces of a three-bundle leaf trace (p. 451).

Let us examine the suggestions of Sinnott and Bailey in the light of the evidence presented in this paper: The leaves on the primary branches of both the species are simple and stipulate, the leaf trace is made up of three bundles—the median and the two laterals and the nodes are trilacunar. The axillary buds are all flower-buds.

Both the species agree in having scaly trilobed leaves on the main axis and there the common feature ends. In *P. niruri* the leaf trace consists of the median only and the node is unilacular. In *P. reticulatus* on the other hand three bundles, the median and two laterals, constitute the leaf trace and the node is trilacunar. The median in both the species divide into three parts—a central and two lateral branches. In both of them the central portion goes to the central lobe but the behaviour of the two laterals is different in the two species. In *P. niruri* they go to supply the two basal lobes, but in *P. reticulatus* they turn back and join the incoming laterals of the leaf trace which have already sent out branches to the two basal lobes, and finally lost in the leaf cushion. Only on the nature of the vascular supply the basal lobes in one case is described as leaf lobes and in the other case a pair of stipules.

Trilacunar condition of the node and the three-bundle leaf trace go together. Therefore the only difference noticed in the two species is the absence of the laterals in one case and their presence in the other. In the first case the median divides to supply the lateral leaf lobes and in the other case the laterals give out branches to these leaf lobes. On the basis of this difference it may be said that in the present case the difference between the pair of lateral basal lobes and the pair of stipules " is one of degree than of kind".

Primary buds in both the species arise in the tissues of the main axis and receive their vascular supplies from the main stele (Sterling, 1945; Garrison, 1949 *a*, 1949 *b*; Gifford, 1951; Miller and Wetmore, 1946; White, 1955). The two bud traces in both the cases instead of being branches appear to be portions of the central cylinder between the gaps caused by the departure of the median and the laterals.

The position of the secondary buds in both the species is axillary or slightly extra-axillary to the primary buds. In *P. reticulatus* its origin is in the tissues of the main axis like that of the primary buds, but in *P. niruri* it is in the tissues of the primary bud axis. The vascular supply also appears different in the two species. In *P. niruri* the supply comes from the two free ends of the cup-shaped primary bud trace. Immediately after the separation of the two bud traces from the main cylinder two constricted areas appear at their distal ends. These look like the two laterals of the scale leaf suppressed in this species. These two areas separate from the primary bud traces which meanwhile unite by their proximal ends and form the trace of the secondary bud.

The origin of the secondary bud in *P. reticulatus* is axial (main axis) like that of the primary buds and its vascular supply also comes from the central cylinder. From the very beginning it forms a loop opposite the median gap and after separation from the main cylinder form a closed stele at the base of the bud.

Tertiary buds are extra-axillary in position being situated laterally to the secondary bud, and were found developed only in *P. niruri*. Its origin is in the tissues of the axis of the secondary bud and its vascular supply also comes from the axial stele of the former in the form of a loop as seen in the origin of the trace of the secondary bud in *P. reticulatus*.

The buds in the axils of the leaves on the primary branches develop into flowers without any exception. They get their vascular supply from the stele of the primary branches and not from the stele of the main axis. As the primary branches bear only flower-buds, either singly or in clusters, it is suggested that these branches should be called *inflorescences* and not vegetative branches. The simple stipulate leaves are therefore bracts.

SUMMARY

The apical organizations of the vegetative shoot apices have been studied in *P. niruri* and *P. reticulatus* (Euphorbiaceæ). The uniseriate tunica and

he massive corpus without any zonation in both the species indicate a less advanced apical organization among dicotyledons.

Two types of leaves are borne by both the plants: scaly on the main axis and foliage on the primary branches. The foliage leaves of both the plants are simple and stipulate, and are characterized by a three-bundle leaf trace, trilacunar nodes which bear them, and presence of only flower-buds in their axils. The scale leaves, on the other hand, are three-lobed in both the species, but they differ in the constitution of their traces and nodal anatomy. In *P. niruri* the leaf trace consists of only one bundle, the median, and the node is unilacunar, whereas in *P. reticulatus* the leaf trace is constituted of three bundles and the node is trilacunar.

The two lobes of the scale leaf, on the basis of their vascularization, are described as a pair of basal leaf lobes in *P. niruri*, and a pair of stipules in *P. reticulatus*. The probable homologies of these two structures *in these plants* have been discussed.

The origin and vascularization of the primary, secondary and tertiary buds—the last only in *P. niruri*, have been studied and discussed. The origin of the secondary and tertiary buds and their vascular supplies appear to be novel features not so far as the authors are aware, recorded before.

As the primary branches bear only flower-buds it is suggested that they should be called *inflorescence axes* and the foliage leaves, bracts. This also appears to be a primitive character.

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EXPLANATION OF TEXT-FIGURES

FIG. 1 *a, b, c*. Habit sketch of *Phyllanthus niruri* showing primary, secondary and tertiary branches, scale leaf, foliage leaf, stipules, fruits, etc. 1 *a*, $\times\frac{1}{2}$; 1 *b*, $\times 1$; 1 *c*, $\times 2$.

FIG. 2. A portion of *P. reticulatus* showing primary and secondary branches, scale leaf, stipules, foliage leaves, flowers, fruits, etc., $\times\frac{1}{2}$.

FIG. 3. Median longitudinal section of the shoot apex of *P. niruri* showing uniseriate tunica, massive corpus, outer corpus layer, bud initiation at the right flank and a scale leaf in development at left, $\times 562 \cdot 5$.

FIG. 4. Median longitudinal section of the shoot apex of *P. reticulatus* showing uniseriate tunica enclosing extensive corpus, desmogen strand of a new leaf primordium continuous with the eumeristem at its right flank, $\times 362 \cdot 5$.

FIGS. 5–12. Serial transverse sections through the nodal region of the main axis of *P. niruri* showing unilacunar node, one-bundle (median) leaf trace, origin of traces of the primary, secondary and tertiary buds, vascular supply to the lobes of the scale leaf, etc., $\times 23 \cdot 8$.

FIGS. 13–17. Serial t.s. through the nodal region of the main axis of *P. reticulatus* showing trilacunar node, three-bundle leaf trace, stipular trace, traces of primary and secondary branches, etc., $\times 27 \cdot 5$.

FIGS. 18–21. Serial t.s. through the node of a primary branch of *P. niruri* showing trilacunar node, three-bundle leaf trace, stipules with their traces, traces of flower-bud, etc., $\times 23 \cdot 8$.

FIGS. 22–27. Serial t.s. through the node of a primary branch of *P. reticulatus* showing trilacunar node, three-bundle leaf trace, stipules with their traces, petiole and its trace, flower-bud and its trace, $\times 23 \cdot 8$.

Pr.br., *Sec.br.* and *ter.br.*, primary, secondary and tertiary branches respectively; *s.l.*, scale leaf; *F.l.*, foliage leaf; *st.*, stipule; *p.*, petiole; *Fl.*, flower; *fr.*, fruit; *bud*, bud primordium; *Fl.bd.tr.*, flower-bud trace; *T.*, tunica; *C.*, corpus; *des.str.*, desmogen strand; *l.tr.*, leaf trace; *Bd.tr.*, bud trace; *M.* and L_1, L_2, median and lateral leaf trace; *l.*, leaf; *St.tr.*, stipular trace; *op.cup.*, open cup-shaped bud trace.

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