SHOOT APEX OF *EUPHORBIA NERIFOLIA* L.

by J. J. Shah,\(^1\) Department of Botany, University School of Sciences, 
Gujarat University, Ahmedabad 9

and

P. M. Jani, Department of Biology, Mahendrasinhji Science College, 
Morvi, Gujarat

(Communicated by P. Maheshwari, F.N.I.)

(Received November 16, 1963)

The structure and organization of the shoot apex of *Euphorbia neriifolia* L. are described. Its structure is interpreted in terms of tunica-corpus theory and cytobhistological zonation. The tunica is one-layered though the second layer simulates it. The central meristem is prominent throughout plasto-chronic phases. The close histogenic relationship between the central and peripheral meristem is indicated. The precocious development of the leaf trace is observed. Periclinal divisions in the third or and fourth layers of peripheral meristem initiate the leaf. The leaf bears at its base two types of appendages, one pair each of auricle-like scales and spines. On the basis of development it is shown that the two spines at the leaf base in *E. neriifolia* are not the stipular outgrowths as generally believed. The former appendages are interpreted as stipules.

The studies on the structure and organization of the shoot apex of members of Euphorbiaceae are few (Gifford 1954; Majumdar and Ali 1956; Soma 1958). *Euphorbia neriifolia* \(^2\) is a common hedge plant. According to Saxton and Sedgwick (1918) the plant is very common in North Gujarat though Santapau (1954) notes that it is replaced by *E. ligularia* in this part of Gujarat State. It is a shrub about 2 metres high with thick almost rounded green stems which, when old, appear woody. New leaves appear to arise at the end of old branches in the beginning of every monsoon, i.e. in the month of May, and remain on the plants till October.

Later the axillary inflorescences begin to appear on almost leafless branches. The vegetative buds on the branch ends usually remain dormant.

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\(^1\) Present address: University Department of Botany, Sardar Vallabh bhai Vidyapeeth, Vallabh Vidyanagar, Dist. Kaira, Gujarat.

\(^2\) According to Dr. G. L. Shah (personal communication) the *E. neriifolia* referred to in this paper is *E. nivula* Ham. The change in the nomenclature is now suggested (Santapau 1954).

In Saxton's collections of plants of North Gujarat deposited in Gujarat College, Ahmedabad (Saxton and Sedgwick 1918), *E. nivula* Ham, (W. T. Saxton, No. 701) is reported from Abu and *E. neriifolia* (W. T. Saxton, No. 178) is very common in Ahmedabad. The former specimen shows mucronate leaves while according to Hooker (1885) *E. nivula* has rounded leaf tips. The change in the nomenclature of this plant does not affect the content of this paper.

VOL. 30, B, No. 2.
through winter and part of the summer and are reactivated in May. The leaves are fleshy, alternate, obovate and glabrous. The angle of divergence in the plants observed was 138°. Santapau and Shah (1958) reported variation in the phyllotaxy of plants growing at Purandhar and Western Ghat. They observed that some plants had five strong spirals going counter-clockwise while the others had a clockwise direction. But some of the younger plants showed a double twist, i.e. phyllotaxy 'twisting to the right and to the left on one and the same plant'. Similar observations could not be noted in E. nerifolia growing in the University Campus. Each leaf normally bears at its base two types of appendages, a pair of spines (described as 'stipular thorns' by Santapan and Shah 1958) and a pair of auricle-like scaly appendages (not reported by Santapau and Shah 1958) (Fig. 1). The latter appear as lateral appendages of the leaf base. The spines are below the leaf scar which appears as a white or brown depressed patch with a circular or triangular outline (Fig. 2). The spines appear to arise on the brownish spine shields of the tubercle (Fig. 2). The leaves on the lower part of the branches are sometimes without spines.

**Material and Methods**

The shoot tips were fixed in a standard FAA solution. The usual histological techniques were used to obtain the stained sections (Sass 1958). Photomicrographs were obtained with Leitz Ortholux microscope with fluorite objectives and Mikas attachment.

**Observations**

*Shoot apex.*—The shoot apex is surrounded by a few foliar primordia, some of which are in conduplicate vernation (Fig. 1). It is a flattened somewhat elevated mound (Figs. 3, 8). Its height and contour vary during its plastochronic development. Following the concept of Gifford (1954), the structure of the shoot apex is interpreted in terms of tunica-corpus theory and cytöhistological zonation. The height of the apex from the rib meristem zone to outer tunica is about 125 μ and width varies from 190 μ to 385 μ (the foliar buttress is not included). The tunica is one-layered, though the second

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**Plate XI**

**Figs. 1-7**—Fig. 1. Shoot tip (a, leaf primordia; b, spine; c, auricle-like stipules). Fig. 2. Leaf base of an old stem (a, leaf scar; b, spines; c, stipules; d, tubercle; e, axillary bud). Fig. 3. L.s. shoot apex (a and b, central meristem; c, peripheral meristem; d, rib meristem). × 245. Figs. 4, 5. T.s. central and peripheral meristem from the uppermost region of the shoot apex. The nucleated cells and peripherally stippled cells in Fig. 4 are respectively the initials and derivatives of the central meristem. Thick lines in Fig. 4 indicate the probable cell lineages and cell complexes in the peripheral meristem presumably derived histologically from the central meristem. Also refer Fig. 13. × 245. Fig. 6. Young leaf primordium (b, spine primordium; c, stipules; d, median trace). × 19. Fig. 7. Initiation of the stipule. × 315.
layer simulates it. The occurrence of periclinal divisions in the second layer is infrequent. The outer tunica cells divide anticlinally though a periclinal division in a solitary cell of the peripheral meristem was observed.

The term central meristem is used here to include the initials and their immediate derivatives of tunica and corpus (Figs. 3–5, 8, 13). The central meristem is almost a permanent feature of the apex in all its histogenic phases (Figs. 8–10, 14). Its depth varies from 80 to 125 μ and diameter 85 to 125 μ. The central meristem cells, both of tunica and corpus, are polygonal, prominently vacuolated, larger, lighter stained, comparatively thick-walled and sometimes with conspicuous angular thickening (Figs. 4, 5, 8, 11, 13). They may appear to be arranged either with or without any distinct pattern. There is a single prominent vacuole. The outer tangential walls of the tunica are prominently thickened. About four centrally situated cells in the first two layers of the central meristem appear larger than the other adjacent cells (Fig. 13). The peripheral meristem consists of comparatively smaller, thinly-walled and densely staining cells (Figs. 8, 15, 16). They are arranged in 9-10 stratified layers (Figs. 8, 11). Their cytonuclear ratio is small. Occasional thickening of the cell walls was also observed. The radial width of the peripheral meristem, i.e. its extent around the central zone, is subject to plastochnic changes (Figs. 8–10, 14). Its development is well marked at maximal phase (Fig. 8), but varies during minimal phase (Fig. 9). The peripheral meristem is the organogenic centre for the foliar primordia (Fig. 14). Figs. 4 and 13 show the close histogenic relationships between the central and peripheral meristems. Figs. 15–18 illustrate the close histogenic relationships among central, peripheral and residual meristems and procambium. Fig. 15 illustrates the central meristem flanked by peripheral meristem in a semicircular way, i.e. opposite to the empty space formed by two flanking foliar primordia. In the shoot apex the former is slightly projected upwards beyond the peripheral meristem. The radial extent and alignment of the cells of the peripheral zone are conspicuous (Figs. 4, 15–17). That the central meristem consists of initials and derivatives and the cells of the peripheral meristem have a histogenic relation with them are evident (Figs. 4, 5, 13). The changes in the cytohistological features, like the disappearance of vacuole, increased selectivity for certain stains and decrease in size, in the central

PLATE XII

Figs. 8–14—(l, leaf primordia; m, mitotic division; p, procambium). Fig. 8. L.s. shoot apex, maximal phase. Note the distinct central, peripheral and rib meristem zones. ×110. Fig. 9. L.s. shoot apex, minimal phase. ×110. Fig. 10. L.s. shoot apex, maximal phase, ×110. Fig. 11. T.s. shoot apex. ×110. Fig. 12. Part of Fig. 10 magnified. ×526. Fig. 13. T.s. part of central and peripheral meristems showing the histogenic relationship between the large vacuolated central initial cells and the peripheral meristem of the first tunica layer. ×750. Fig. 14. Initiation of leaf. ×110.
meristem cells are gradual (Figs. 4, 13). The other notable feature is the close approximation of the procambium to the peripheral meristem (Figs. 8, 12, 15). In fact, histological distinction between the two is not always evident (Fig. 12). Occasionally a section of the peripheral meristem which is in continuity with the subjacent procambium shows densely staining and shrunken cells. This histological differentiation is generally a prelude to the procambium initiation and establishment of a foliar centre (Figs. 12, 14). Figs. 17 and 18 show that the part of the peripheral meristem persists at the lower levels of the apex, i.e. below the few nodes. At this level it may be identified as residual meristem, though such delimitation between the peripheral and residual meristems is difficult here. The close histogenic relationship between peripheral meristem, residual meristem and procambium is evident. The three meristems delimit the pattern of the primary vascular system of the axis at this level (Fig. 18).

The rib meristem is situated below the few early nodes (Figs. 3, 8). It is distinct below the central meristem and it ultimately differentiates into the broad pith. There is some evidence to believe that some of the rib meristem or pith cells are also differentiated from the peripheral meristem (Fig. 3). The histogenesis of the rib meristem and the resultant pattern of arrangement of cells are subject to plastochoic stages of the shoot apex (Figs. 8–10, 14).

Initiation of the leaf, scaly appendage and spine.—At the maximal phase, the peripheral meristem appears stratified and well differentiated (Fig. 8). The development of procambial strands of the first leaf traces is precocious and acropetal (Figs. 8, 10, 12). Each procambial strand extends to a group of corpus cells belonging to the third or/and fourth layers of the peripheral meristem, which divide periclinally, thus differentiating the foliar buttress (Fig. 14). The central meristem of the shoot apex appears flattened and a portion of the peripheral meristem appears distinct from the foliar buttress (Fig. 14).

As noted earlier, two types of appendages are present at the leaf base, i.e. a pair of auricle-like scaly appendages and a pair of spines. The initiation and development of the former is much earlier than the latter (Figs. 1, 6). Fig. 6 illustrates a foliar primordium with prominent auricles. The two stippled areas represent the spine primordia. Fig. 7 illustrates the early development of the scaly appendage of a leaf 187 μ high. It develops from the lateral side of the leaf base, due to the activity of the marginal meristem. At this stage the groups of cells initiating the spine primordia are not present.

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PLATE XIII

Figs. 15–20—(a, leaf trace bundles; t, leaf primordia; s, spine primordium). Figs. 15–18. T.S. of shoot apex. Note the lightly stained central meristem and densely stained peripheral meristem cells arranged in radial rows. In Figs. 17 and 18 close histogenic relationships among peripheral meristem, residual meristem and procambium are evident. ×36. Figs. 19, 20. L.S. spine primordium, ×110.
The appendages become auricular in shape with a wavy margin. The epidermal cells are markedly elongated. In the mature leaf they shrivel and become inconspicuous (Fig. 2).

As already stated, the development of the spines is very late. Their position is not on either side of the leaf base but more or less in front (Figs. 1, 2). The group of densely staining cells, just below a sector of the protoderm of the leaf base, represents an early spine primordium (Figs. 19, 20). The height of the leaf at this stage varies from about 900-0 μ to 1-5 mm. Due to further meristematic activity at this site, a protuberance comes out which ultimately develops into a spine. On a leafless stem, it appears to arise on the brownish spine shield of the tubercle (Fig. 2).

**Discussion**

Soma (1958) has studied the morphogenesis of shoot apex of *Euphorbia lathyris*. It has opposite decussate phyllotaxy while *E. neriifolia* has alternate. The shoot apex of *E. lathyris*, apart from size and genetic variations, appears to differ from that of *E. neriifolia* in having sometimes three tunica layers, an indistinct central meristem, except at maximal phase, and an indiscernible rib meristem. The tunica in *Phyllanthus niruri* and *P. reticulatus* is one-layered and no cytobiological zonation occurs (Majumdar and Ali 1956).

The variations in the structure and organization of the shoot apex, i.e. size-volume variations and clarity of zonal variations during its morphogenetic phases, are well known (Gifford 1954; Popham 1960; Clowes 1961). They are reported to be either related or unrelated to the plastochronic stages (Clowes 1961). A correlation between the different mature leaf forms and shoot apex size and organization is not found in the members of Ericaceae (Hara 1958). The shoot apex of *E. lathyris*, because of its opposite decussate phyllotaxy, shows distinct plastochronic variations (Soma 1958). No information is available on the relationship between the types of plastochronic variations and the alternate phyllotaxis with varying angles of divergence. The absence and presence of sectors of peripheral meristem at various depths of the shoot apex in *E. neriifolia* are a feature which may be correlated with its particular phyllotaxy.

According to Gifford (1954) the shoot apex of a dicotyledon shows four zones: 1, tunica initials; 2, corpus initials; 3, peripheral meristem; 4, rib meristem. Philipson (1954) considers zones 1 and 2 as a central meristem (Wetmore et al. 1959). It is recently named as ‘metameristem’ (Gr. metra: womb + meristem) by Johnson and Tolbert (1960). Clowes (1961) considered these zones somewhat arbitrary as the state of differentiation and cell size partly decide them. The shoot apex of *E. neriifolia* broadly conforms to Gifford’s type. In *E. lathyris* the central meristem zone is obscure at minimal phase (Soma 1958). The presence and function of the central meristem in
the angiosperm shoot apex are a matter of serious discussion (Buvat 1952; Wetmore et al. 1959; Johnson and Tolbert 1960; Clowes 1961). It is broadly distinguished histologically by certain cell features (Gifford 1954; Wetmore et al. 1959). In E. nerifolia the tunica and corpus of the central meristem are vacuolated. In E. lathyrous, only its corpus cells are large and vacuolated though Soma (1958) also includes the tunica cells above them as part of the central zone. At the maximal phase of the shoot apex, Soma (1958) considers the light staining zone consisting of ‘corpus initials’. In Polygonia longisofia and Chenopodium album only the tunica cells of this zone show vacuolation (Ramji 1960; Gifford and Tepper 1961). The central zone is not distinct in the shoot apex of Aquilegia, Ranunculus and Clematis (Tepfer 1960). On the other hand, due to its dominance in Bombax, it is called a ‘metrameristem’ which ‘literally implies organic and topographic relationship to the remainder of the shoot apex’ (Johnson and Tolbert 1960). This zone is the seat of origin of all cells of the primary body and hence consists of tunica and corpus initials (Gifford 1954; Tepfer 1960; Tolbert 1961). By correlating the number of distal mitoses and the differentiation of derivatives of the distal cells with stages of the plastochronic cycle, Paolillo and Gifford (1961) have shown that the sub-apical initials of Ephedra altissima are self-perpetuating and must be regarded as a dynamic entity. Figs. 4, 5 and 13 distinctly show the alignment and probable cell lineages in the cells of $T_2$ (?) (Fig. 4) and $T_1$ (Figs. 5, 13) of the central and peripheral meristem of the shoot apex of E. nerifolia. The early derivatives of the tunica initials are vacuolated while those differentiating into peripheral meristem gradually appear densely staining. This justifies the above-mentioned morphogenic status of the central meristem. The central meristem in E. nerifolia appears to consist of tunica and corpus initials and their immediate derivatives. Boke (1960) refers them jointly as promeristem. Clowes (1961) prefers to use this term only for initials but admits practical difficulty in delimiting them. The shoot apex of E. nerifolia therefore does not conform to the model of shoot apex showing a ‘meristème d’attente’ as visualized by Buvat (1952). It cannot also be defined as in Hibiscus syriacus (Tolbert 1961) as the portion of the apical meristem lying above the axil of the first visible foliar primordium.

The spines at the bases of the leaf of E. nerifolia are morphologically considered stipular outgrowths (Hooker 1885; d’Almeida and Mullan 1946; Santapau and Shah 1968). Though White and others (1941) remark that the origin of such a principal pair of spines in spine-paired Euphorbias is ‘not definitely understood but in the absence of a better interpretation they are also frequently spoken of as stipular outgrowths’. That their present morphology is confused and questionable is evident from the fact that some of the spine-paired Euphorbias bear ‘two additional prickles, one on either side of the base
of the leaf, corresponding in position to the stipules in *E. ingens* E. Mey. Because of their position these prickles are believed to be modified stipules’ (White et al. 1941). The auricular appendages of *E. neriifolia* are also placed one on either side of the leaf base. The present study clearly indicates that the auricular scaly appendages are the true stipules and that the pair of spines on the shield of the tubercle represent pointed outgrowths. It is possible that this conclusion based on the developmental studies of a single species of spine-paired Euphorbias may not be readily acceptable and it may be that the only way to solve the problem is by a comparative study of a considerable number of species. The stipules and spines of *E. neriifolia* are without any vascular tissues. According to Majumdar (1955, 1956) the branch or branches of the lateral leaf traces initiate the stipules. As previously discussed (Shah 1969), this view does not appear to indicate the correct morphogenetic situation for the initiation of the stipule.

**ACKNOWLEDGEMENTS**

Thanks are due to Professor J. J. Chinoy, Head of the Department, for facilities, Professor P. Maheshwari, Delhi University, for help and interest, Dr. G. L. Shah, Sardar Vallabhbhai Vidyapeeth, Vallabh Vidyanagar, for help in identification and taxonomic literature, and Mr. Y. S. Dave in drawing.

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