I. INTRODUCTION

The symmetry of the aerial part of a vascular plant is determined by its lateral members of which the most important are the leaves and vegetative branches. The lateral branches repeat the essential morphogenetic features of the main axis. The great variety of plant form is a consequence not of any fundamental changes in this growth pattern but rather of relatively simple modifications, such as changes in the proportions of leaf and axis, in the length of internodes between successive leaves, in the degree of apical dominance, etc. (Allsopp, 1964). The endless form, size and shape of plants can, in one way or other, be traced back to the activity of the apical meristem of the plant. The shoot apex is concerned with the primary growth of the plant through a concerted activity of morphogenesis and histological differentiation. Thus, the most striking and fundamental
features of shoot morphogenesis are the 'continued embryogeny' (Bower, 1919) of the shoot apex and the ultimate display of the different categories of lateral members through which the plant exhibits its particular form, type of growth and symmetry. The basic morphogenetic problems are the inception of the lateral organs, their developmental potentialities and the factors determining their characteristic form and symmetry (Cutter, 1961).

The axillary bud meristem very often originates from the shoot apex and finally differentiates into a structure similar in function to the shoot apex. Hence, the importance of the study of the shoot apex for a better understanding of the origin and development of axillary buds is amply justified. Several workers (Philipsen, 1949; Popham and Chan, 1950; Popham, 1951, 1966; Gifford, 1954, 1963; Vertrees, 1959; Guttenberg, 1960; Paolille and Gifford, 1961; Cutter, 1961, 1965; Gifford and Tepper, 1962; Bowes, 1963; Philipsen and Balfour, 1963; Shah and Jani, 1964; Allsopp, 1964; Newman, 1965; Wardlaw, 1965; Mougarède, 1967) have contributed to the understanding of the various aspects of shoot morphogenesis.
The structural organization of the vegetative shoot apex has varying interpretations. The apical theory was replaced first by the histogen theory and later by the tunica-corpus theory of Schmidt (1924). The tunica-corpus theory is based on the different modes of cell divisions in the apex. The tunica shows predominant anticlinal divisions while the corpus exhibits various types of divisions. According to Gifford (1954) these two interdependent growth zones maintain the proper balance between the surface growth and growth in volume of the shoot apex.

The cytohistological heterogeneity in the shoot apex led to the recognition of three zones; peripheral meristem, central meristem and rib meristem superposed on the tunica-corpus organization (Foster, 1938; Beke, 1941; Majumdar, 1942; Philipson, 1949; Millington and Gunckel, 1950; Gifford, 1950, 1954; Rouffa and Gunckel, 1951; Allsopp, 1964). Esau (1965a) prefers the use of the terms distal axial zone, proximal axial zone and peripheral zone for central meristem, rib meristem and peripheral meristem respectively. The French School (Buvat, 1955) recognized "meristème d' attente", "l'anneau initial" and "meristème médullaire" in the shoot apex. Buvat (1955) attributed specific organogenetic functions to each zone. The méristème d' attente is
active only during the reproductive phase. Gifford (1954) considers that the central meristem (méristème d'attente of the French School) which includes tunica and corpus initials contributes to the reconstitution and growth of the peripheral and rib meristem zones. Wetmore (1959), Clowes (1961) and Shah and Jami (1964) do not subscribe to the existence of the inactive zone of the French School. Johnson and Telbert (1960) designated the central meristem as 'metrameristem'.

According to Clowes (1961, p. 30) the trouble with dividing an apical meristem into zones is that there is nothing very precise to say about the behaviour of the zones and nothing much on which to defend one's choice of boundaries to the zones. Despite the visible segregation into zones, an apical meristem grows as a whole with close co-ordination between the activities of the different parts and without a precise and rigid relationship between the planes of divisions at the apex and the genesis of tissues and organs (Esau, 1953).

In the present study central meristem, peripheral meristem and rib meristem are recognised if the shoot apex shows distinct cytohistological heterogeneity. In its absence, terms central region, peripheral region and rib meristem are used to indicate broad topographical positions in the shoot apex.
The shoot apex shows considerable changes in size, shape and structure during a plastochron. These are expressed in different phases of a plastochron (Reeve, 1942; Gifford, 1954; Paolillo and Gifford, 1961). According to Schmidt (1924), during the beginning of leaf initiation the shoot apex attains a maximal area and after the appearance of a definable primordium it is reduced to a minimal area. Reeve (1942) described maximal area phase and minimal area phase during a plastochron in Garrya elliptica. An increase in the number of stratified layers is reported in the maximal area phase of the plastochron (Cross and Johnson, 1941; Reeve, 1942; Gifford, 1950). Certain amount of fluctuations in the number of tunica layers is reported in some members of Rosaceae (Rouffa and Gunckel, 1951). According to Zimmerman (1928) in Hypericum uralum the tunica layers do not fluctuate but the apparent changes in stratification is attributed to the variations in the activity of the corpus. In Drimys winteri and D. lanceolata Gifford (1950) reported the stratification of the corpus during the maximal area phase. Paolillo and Gifford (1961) recognized maximal, minimal, early post-minimal, late post-minimal and pre-maximal phases in Ephedra altissima. In the present investigation the five phases of the plastochron are distinguished on the basis of height, width,
cytohistological sensation, number of stratified layers and the developmental stage of the youngest visible leaf primordium. In some of the investigated species the apex is flat or slightly concave during certain phases of the plastochron where the height measurements have not been possible. In such cases all the above mentioned features except the height are taken into consideration.

The primary vascular system is an important feature which determines the structural organisation of the plant. The developmental anatomists are interested in the pattern of the primary vascular differentiation in the plant because of its importance in phylogenetic and taxonomic studies. According to Esau (1965b) the concept of stele emphasises the unity of the vascular system of the axis while the concept of leaf trace stresses the relation between the axial and foliar vascular systems. She also states that the primary vascular system in shoots of most seed plants can be interpreted in terms of leaf traces and their sympodia (Esau, 1965b). There are two basic types of leaf trace interconnections. In one the leaf traces diverge from a sympodium on one side only, so that the sympodia remain independent of one another. In the other type a leaf trace is related to more than
one sympodium and the sympodia are connected with one another (Esau, 1965b). According to Berner (1945) they are 'open' and 'closed' systems. According to Philipson and Balfour (1963) these two types correspond to the sympodial and reticulate types of de Bary (1884). The open and closed systems are closely linked. The former is shown to precede the latter in its ontogeny in Linum (Esau, 1965b) and Helianthus (Esau, 1954). The primary vascular system of Arthrocnemum is mainly open and partly closed (Bisalputra, 1962).

The pattern of nodal vascular system is of great importance in the study of the primary vascular differentiation. Marsden and Bailey (1955) reported a fourth type of nodal structure in Clerodendron trichotomum in addition to the three common types described by Simnot (1914). Carlquist (1961) enumerated five different nodal types and their probable phylogenetic relationship in angiosperms. Bailey and Swamy (1949) reported that the leaf trace in Astrobailalea arises as two strands from the same leaf gap but from distinct sectors of the vascular cylinder and these two strands remain separate for varying distances in the lamina. This condition is also observed in Sarcandra (Swamy and Bailey, 1950),
Trimeria and Piptocalyx (Money, Bailey and Swamy, 1950) and Calicanthus and Chimonanthus (Pahn and Bailey, 1957). It is important that the pattern of the primary vascular system of the stem should also be studied in relation to the vascular supply of the axillary or lateral buds.

The locus of origin of axillary buds varies in angiosperms. The change of position during development is also very common. In most of the reported cases the bud meristem is differentiated from the apical meristem (Garrison, 1949a, 1949b; Gifford, 1951; Kundu and Rao, 1955). Esau (1953, 1965a) does not fully agree with the use of the term axillary bud as it does not reveal the correct place of origin of the bud. Most of the workers (Miller and Wetmore, 1946; Garrison, 1949a; 1949b, 1955; Gifford, 1951; Kundu and Rao, 1955, 1957; Ramji and Parameswaran, 1961; Tucker, 1963; Shah et al., 1967) prefer to use the term axillary bud. In the present study the terms 'axillary bud' and 'lateral bud' are used as synonyms. It generally denotes those buds which originate either from the peripheral meristem of the shoot apex or its immediate derivatives. The buds may be cauline, lateral, axillary or foliar in the early or/and final positions.
The first formed bud is designated as the main bud and the successively formed ones as the accessory.

There are two views regarding the nature of the tissue associated with the inception of the axillary bud. The bud meristem is derived from the peripheral region of the apical meristem or its immediate derivatives (Wardlaw, 1943; Miller and Wetmore, 1946; Garrison, 1949a, 1949b, 1955; Gifford, 1951; Kondur and Rao, 1955, 1957; Ramji and Parameswaran, 1961; Shah et al., 1967). On the other hand some buds arise from vacuolated parenchyma by dedifferentiation and redifferentiation (Majumdar, 1942; Majumdar and Datta, 1946). In Boehmeria nivea, Kondur and Rao (1957) reported the origin of buds from meristematic cells in the second layer of the subtending leaf primordium. The foliar origin of bud is reported in Heracleum and Leonurus (Majumdar and Datta, 1946).

In majority of the reported cases axillary or lateral buds originate after the differentiation of the subtending leaf. In most of the cases the initiation of the bud is in the second, third or fourth node from the shoot apex (Miller and Wetmore, 1946; Garrison, 1949a, 1949b; Gifford, 1951; Kondur and Rao, 1955, 1957). In Caryatia carnosa the origin of the bud and
its subtending leaf is simultaneous (Shah, 1960).

The earliest bud meristem is a deep stained or light stained zone. In majority of the reported cases it is a deep stained zone. Shah et al. (1967) reported the light stained nature of the early bud meristem in Dioscorea alata.

The early bud meristem is designated as shell zone in Garrya elliptica (Reeve, 1943), Drimys winteri (Gifford, 1951), Cayratia cariosa (Shah, 1960) and Michelia fascata (Tucker, 1963). The term shell zone was originally coined by Schmidt (1924). In the early stage orderly divisions along the basal and lateral limits of the bud result in the formation of a zone of parallel curving layers and it is termed as shell zone (Esau, 1962, 1965a). The shell zone as conceived by Garrison (1949a, 1949b), Boke (1960) and Ramji and Parameswaran (1961) is the histological region which delimits the bud meristem from the axial tissue. In the present study the term is used to designate the arcuate band of narrow, elongated and generally vacuolated cells which delimit the bud from the surrounding tissue.
The development of the bud after its histological inception is the result of the co-ordinated growth of its tunica and corpus cells (Garrison, 1949a, 1949b; Gifford, 1951; Sussex, 1955). In Dioscorea alata the second tunica layer along with the corpus take active part in the development of the bud (Shah et al., 1967).

The early bud meristem may be a 'detached meristem' devoid of any vascular connection with the axis or it may be connected to the axis from its very inception by residual meristem strands. In Phlox (Miller and Wetmore, 1946), Drimys (Gifford, 1951) and Clerodendron (Ramji and Parameswaran, 1961) the early bud meristem is a detached meristem. In Syringa (Garrison, 1949a) Magnolia and Liriodendron (Garrison, 1955) and Hibiscus (Kundu and Rao, 1955) the early bud meristem is connected by residual meristem with the axial vasculature. The residual meristem strands later differentiate into procambium.

There are varying reports regarding the direction of differentiation of bud traces. The acropetal differentiation is most commonly reported in dicotyledons (Reeve, 1943; Sterling, 1945; Miller and Wetmore, 1946; Garrison, 1949a, 1949b; Sussex, 1955; Kundu and Rao,
Majumdar and Datta (1946) reported the basipetal differentiation of bud traces in *Heraeleum* and *Leonurus*. In *Primus* the procambium of the axillary bud differentiates basipetally but the procambium from the axis develops acropetally and joins with the basipetally developed one (Gifford, 1951). In *Clerodendron aculeatum* both acropetal and basipetal differentiation of the bud trace procambium is observed (Ramji and Parameswaran, 1961). According to Vaughan (1955) the differentiation of bud trace procambium in *Arabidopsis*, *Capsella* and *Anagallis* is basipetal. According to Esma (1962) if the axillary buds arise close to the apex they may be connected by discernible bud traces to the main axis from the earliest stages of vacuolation in the peripheral meristem.

Usually there are two bud traces (branch traces) in dicotyledons. Considerable variations are observed in the nodal structure and relationship between the vasculature of the axis and that of the bud. Ezalarab and Dörmer (1963) reported five types of vascular connections in Ranunculaceae. According to them the branch traces are related (a) to the median leaf trace (*Berberis* condition), (b) to the median and lateral leaf traces (*Thalictrum* condition, (c) only to
the lateral leaf traces (*Lepidium* condition),
(d) to the bundles bordering the median leaf gap
(normal condition) and (e) to the bundles bordering
the median and lateral leaf gaps (*Petasites* condition).

The morphogenetic development of the lateral
buds into thorns has received scant attention. The
detailed development of thorn is studied in *Sedumsia*
(Blaser, 1956). Recently Bieriek and Millington
(1967) described the development of spines in *Ulex*
europeaus.

Thus a brief survey of available literature on
the morphogenesis of shoot apex and axillary buds
reveals the inadequacy of knowledge regarding certain
morpho-histogenetic problems of the axillary or lateral
buds. Hence the necessity for a detailed investigation
on the origin, development and vascularization of the
bud and its modification was felt.

The following plants, belonging to various families
and with different habits and varying phylletaxy are
selected for the present study.

1. *Ipomoea cairica* Sw.
2. *Ipomoea quamoclit* L.
4. *Vitex negundo* L.
5. *Salvadora oleoides* Donn.
6. *Euphorbia tirucalli* L.
7. *Michelia champaca* L.
8. *Sesamum indicum* L.
9. *Peronia lémonia* L.
11. *Leonurus sibiricus* L.

The ontogeny of axillary buds in *Leonurus sibiricus* is studied by Majumdar and Datta (1946) and that of *Buchmeria nivea* by Kundu and Rao (1957). The present study on these two species is a reinvestigation.

The salient aspects of the present study are:

1) structure, organization and plastochronic changes in the vegetative shoot apex,
2) primary vascular differentiation at the young shoot,
3) inception of the early bud meristem,
4) further development of the bud and prophyllic initiation,

5) early procambialization of the bud,

6) differentiation of the prevascular or primary vascular system of the bud,

7) ontogeny and development of accessory buds, if any,

8) early procambialization of the accessory bud,

9) differentiation of the prevascular system of the accessory bud,

10) vascular relationship between the axis, lateral branches (buds) and the subtending leaf with special reference to nodal anatomy and the nature of bud trace connections,

11) comparative ontogeny of the vegetative and floral buds in *Ipomoea calirica* and *I. quamoclit,*
12) comparative vascular features of vegetative and floral branches in *I. quamoclit*.

13) the pattern of vegetative branching and growth habit in *Sesamum indicum*.

14) early developmental changes in the differentiation of an axillary or a lateral thorn in *Feronia limonia* and *Bougainvillea spectabilis*.

15) the ontogeny and vascularization of the peculiarly positioned prophyll buds in *Feronia limonia*.

16) relationship between the anomalous vascular bundles and bud traces in *Bougainvillea spectabilis*.

17) differentiation of the vascular plexus and the relation of bud traces to the plexus in *Muehlenbeckia platyclada*.

18) reinvestigation of the origin of early bud meristem in *Leonurus sibiricus* (Majumdar and Batta, 1946) and
19) reinvestigation of the ontogeny of early bud meristem in Bechmeria nivea (Kundu and Rae, 1955).

The meaning attributed to certain selected terms used in this thesis is as follows. The uniformity in use of these terms is maintained as far as possible but some of them have been used in a different context in the absence of any other suitable usage.

Accessory bud: The bud which is differentiated subsequently from the main axillary or lateral bud.

Anomalous vascular strands: The vascular strands differentiated from the cortical parenchyma at the seventh or eighth node from the shoot apex in Bougainvillea spectabilis.

Bud trace: The vascular strand connected with the trace of the subtending leaf or any other vascular strand of the axis and bridging the primary vascular system of the bud.

Bud trace complex: The vascular strand or strands from which the traces of the main and accessory buds are differentiated.
**Residual meristem:** The tissue derived from the apical meristem of the axis or bud which appears relatively more meristematic than the other surrounding tissues of the axis and the bud. It gives rise to either procambium or ground tissue.

**Trace complex:** The vascular strand of the axis below the subtending node, which is associated with the traces of the main and accessory buds at the node and other vascular strand traversing in the next internode above.