PHYLLOCLADE DEVELOPMENT IN THE ASPARAGACEAE

by

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RESUME

Les cladodes sont traditionnellement définis comme étant des tiges aplaties, à croissance déterminée, essentiellement à cause de leur position axiale. Cependent les écrits historiques traitant du sujet sont remplis de controverse sur l'interprétation morphologique de ces organes. Etant donné ces circonstances, une étude du développement du cladode en comparaison avec celui de la feuille et de la tige fut entreprise pour quatre espèces étroitement reliées d'Asparagacées : Ruscus aculeatus L., Danae racemosa Moench, Semele androgyna Kunth et Asparagus sprengeri Regel. Les résultats obtenus à l'aide de techniques de microscopie électronique à balayage, d'épi-illumination et de coupes semi-fines révèlent tout un continuum en ce qui a trait au développement du cladode: des formes de Danae ressemblant aux feuilles, aux formes intermédiares de cladodes fertiles et terminaux de Ruscus aux formes de Semele et d'Asparagus ressemblant aux tiges. Dans chaque espèce cependant, un mélange de caractères de feuilles et de tiges est observé. Ces caractères, s'il sont considerés également, nous démontrent que le cladode dans ce groupe est un organe intermédiaire partiellement homologue à une feuille et à une tige. Il est donc une forme d'innovation évolutionnaire et un exemple du phénomène d'homéose, qui signifie le transfert de caractères d'un organe à un autre.

ABSTRACT

Phylloclades are traditionally defined as flattened, determinate, leaf-like stems primarily on the basis of their axillary position. Historically, however, the literature is replete with controversy over what the morphological interpretation of these organs is. In view of this, a study of phylloclade development in comparison with leaf and stem development was undertaken in four closely related species of the Asparagaceae: Ruscus aculeatus L., Danaë racemosa Moench, Semele androgyna Kunth and Asparagus sprengeri Regel. Results of SEM, epi-illumination and thin plastic sectioning techniques reveal a continuum in phylloclade development from very leaf-like forms such as those of Danaë to more intermediate types such as the fertile and terminal phylloclades of Ruscus, to the gradually more shoot-like forms of Semele and Asparagus. In each species, however, a combination of shoot and leaf-like characteristics is seen, which when weighted equally, demonstrates that the phylloclade in this group is an intermediate organ, partially homologous to a leaf and a stem. It is a form of evolutionary novelty and exemplifies the phenomenon of homoeosis, which is the transference of characters from one organ to another.

CONTENTS

INTRODUCTION

According to classical plant morphology, the higher plant body is organized basically into three kinds of organs: root, stem (caulome) and leaf (phyllome) (Sattler 1974, Foster and Gifford, 1974; Cusset, 1982). These organ categories are considered as mutually exclusive and are distinguished on the basis of criteria such as position, symmetry (and thus also vascularization) and apical meristematic activity. Of these criteria, position has played the most central role in morphological interpretation. It is frequently invoked to discern the difference between organ categories. For example, stem and leaf may be distinguished by determining which is axillary (stem) and which is axillant (leaf).

Symmetry, which is also used in the discrimination between stems and leaves, can be described as the proportional distribution of material (such as that of an organ) about an axis such that all parts formed are equivalent and mirror images of one another (Bateson, 1894; Sinnott, 1960). Depending upon the number of proportional axes that may be drawn, three kinds of symmetry may be distinguished. When only one axis may be drawn through the structure, it is termed dorsiventral, typical examples of which are leaves and other phyllomes. If two axes of symmetry may be observed, the structure is termed bilateral, whereas if more than two axes can be recognized, it is radial. Typical examples of these latter include stems and other caulomes. In terms of internal morphology, symmetry can also be observed with regard to vascularization. The term vascularization can be used in this context both to indicate the arrangement of vascular bundles present and the orientation of xylem and phloem (inverted, in which the xylem is located abaxially versus the normal adaxial position). Leaves typically have a planar arrangement of vascular bundles with normally oriented xylem, in contrast to stems which have a radial endarch arrangement. Thus, symmetry can be distinguished either on the basis of external or internal morphology alone, or both. (See Table 1).

Another criterion often employed in the morphological distinction of organ categories is the phenomenon of apical meristematic activity, which for purposes of this work will be restricted to two aspects: duration and organogenetic potential. Of the two, duration necessarily implies a time reference and is used in a relative sense. Thus, organs may have determinate (limited) or indeterminate (unlimited) modes of growth. Organogenetic potential is a broader term which implies not only the ability to produce other organs but also the ability to branch. Typically, caulomes have indeterminate growth, give rise to other organs and are capable of branching. Conversely, phyllomes typically are of determinate growth, do not give rise to other organs or branch.

When an organ does not fit into one of the three aforementioned categories, it poses problems in terms of the classical shoot model. An example of such an organ is the phylloclade of the Asparagaceae (sensu Dahlgren and Clifford, 1982; = Asparagus and Ruscaceae, Dahlgren, Clifford, Yeo, 1985) which is traditionally considered a determinate leaf-like stem primarily on the basis of its position.

Terminologically, however, De Martius (cited in Clos, 1861) introduced the word cladode to emphasize the branch-like features of these structures. Later Bischoff (cited in Duchartre, 1885) coined the term phylloclade to denote the physiological and morphological resemblance to leaves and as a result, the two terms have often been used synonymously. Reinke (1898), in an exhaustive study of assimilatory organs in the Asparageae, tried to delimit the use of the two by suggesting that the term cladode be restricted to those instances where the assimilatory shoot represented a flattened internode alone, while the term phylloclade be used only in those cases in which the flattened assimilatory organ represented a "fusion" product of leaf and stem. Goebel (1905) similarly proposed that determinate stems with extreme resemblance to leaves be called phylloclades whereas other indeterminate flattened shoots or stems with less well developed similarities to leaves be termed cladodes. Troll (1937) accepted this but preferred to substitute the term platyclade ("Platykladium") for cladode ("Kladodium") since the literal meaning of cladode refers to structures that only resemble shoots but are not equivalent. For Troll, the term platyclade is used to signify flattened indeterminate shoots. In this work, for lack of a better word, the term phylloclade has been adopted. Its use, however, is meant to be in a neutral sense; by using the term no automatic homologization with shoots is intended. Rather it is hoped that by using the word phylloclade (leaf & stem) the acknowledgement of equal contributions of leaf and stem features will be denoted.

Historically, phylloclades have been the subject of much controversy in the literature. Their morphological interpretation has revolved around three main hypotheses which will now be reviewed.

Foliar Hypothesis. - The earliest known interpretation of the phylloclade was that of Theophrastus, who sometime in 300 B.C. wrote that "... some leaves are fruit bearing, ... as the Alexandrian laurel, which has its fruit attached to the leaves, "(Hort, 1916:77) and "the prickly myrtle (butcher's broom): both have their fruit on the midrib of the leaf." (Hort, 1916:267). In both these species of Ruscus, the fruit is inserted on the phylloclade, so for Theophrastus, phylloclades in these cases were leaves because they looked like leaves: they were dorsiventral, determinate, green (photosynthetic) structures whose position was irrelevant. Linné and Willdenow, several centuries later, interpreting the phylloclades of Ruscus arrived at the same conclusion (Schlittler, 1953:207).

Later botanists, however, were more mindful of the classical dictum of position that states leaves cannot axillate other leaves. To accomodate the leaf-like morphology of the phylloclade, yet remain within the framework of the classical model, required that the phylloclade be interpreted as a leaf born on an aborted, reduced or short shoot. Such an interpretation was advanced by De Candolle (1827) for Asparagus, by Duval-Jouve (1877) for the sterile phylloclade of Ruscus aculeatus and Velenovsky (1892, 1903, 1907) for Danaë and the sterile phylloclades of Semele and Ruscus, which were thought to be the terminal leaves of aborted short shoots. Troll (1937) subsequently re-examined Velenovsky's data and unable to accept the concept of terminal leaves considered the sterile phylloclades to be pseudo-terminal leaves. Joyeux (1928) studied the anatomy and morphology of both sterile and fertile phylloclades in

Ruscus, Semele and Danaë and concluded that the phylloclade in this group was the prophyll of an aborted axillary bud. Since, according to the classical model, leaves could not bear other organs, the position of the inflorescence on the phylloclade in Ruscus and Semele was described by Joyeux as being adventitious. Schlittler (1953) in a more comparative morphological approach, examined mature structures (stem, leaves and phylloclades) of the Asparagoidae in comparison with those of the Luzuriagoideae and agreed with earlier investigators that the sterile phylloclade represented a pseudo-terminal leaf of a reduced axillary shoot. Buscalioni (1914) earlier had also supported a foliar interpretation of the phylloclade as did Stefanoff (1932) who ignored the criterion of position, interpreting the phylloclade of Asparagus as being a phyllode because of its basal articulation and characteristic petiolar anatomy. Arber (1950) after re-reading Stefanoff's claims concurred with him, rejecting her two earlier interpretations. Finally, Van Iterson (1955) in an article on the unusual orientation of vascular strands in dorsiventral leaves, suggested that the phylloclades of Danaë, Ruscus and Semele be treated as leaves regardless of their inverted xylem.

Cauline View. - By far the most widely (and one might add, most tenaciously) held view, however, is that the phylloclade is a modified caulome with or without appendages. This interpretation began with Turpin who in 1820 stated that the lateral flattened leaf-like organs of Ruscus were branches because they were axillated by minute scale leaves and in some cases bore inflorescences. The presence of terminal non-axillated phylloclades offered further evidence for its cauline "nature". A. P. de Candolle (1827) and later De St. Hilaire (1840, cited in Arber, 1924a) supported this hypothesis although De Candolle attempted to explain the phylloclade's symmetry in terms of correlation by postulating the "abortion of true leaves" in Ruscus. The phylloclade's axillary position and its ability to give rise to other organs were the decisive factors in the cauline interpretations of the phylloclades of Danaë, Ruscus and Semele, by authors such as Clos (1861), Cauvet (1877), Dickson (1886), C. de Candolle (1890), Celakovsky (1893), Reinke (1898), Szafer (1910), Zweigelt (1913), Goebel (1905) and Motte (1938, 1939), all of whom only examined the mature structure.

The criterion of position has also been of prime importance in the interpretation of the phylloclades of Asparagus and Myrsiphyllum which have either been regarded as sterile pedicels or peduncles by Wydler (1845), Kunth (1850), Clos (1861), Duchartre (1885), Celakovsky (1893), Reinke (1898), Velenovsky (1903,1907), Goebel (1905) and Jessop (1966), or as naked vegetative axes (reduced shoots) by Van Tieghem (1884), Arber (1935) and Troll (1937). Arber (1935) rescinded her previous opinion (1924b), that the needles (phylloclades) of Asparagus bore vestigial leaves while Massart (1894) earlier had stated that the phylloclades of Asparagus represented the only known example of "basipetal branching".

More recent studies have focused on development as a basis for interpretation. Wenck (1935) examined the early development of phylloclades in Danaë, Ruscus, Semele and Myrsiphyllum yet still concluded that because the phylloclade (with the exception of the terminal phylloclade of Ruscus) was initiated in the axil of a bract, and because some phylloclades formed bracts in whose axils other organs developed, phylloclades were shoots. Troll (1937) especially agreed with this last point, considering the fertile phylloclades of Ruscus and Semele to be caulomes. Kaussmann (1955) in a most detailed comparative developmental study reinforced this interpretation, again emphasizing the criteria of position, and early shoot-like histogenesis. Hirsch (1977) concurred with both Wenck and Kaussmann in spite of admitting that "the intergradation of stem and leaf-like features can be clearly seen in the sequential development of the lateral appendages and terminal phylloclade of Ruscus".

Fusion Hypotheses. - At about the same time the cauline hypothesis was becoming established, another view of the phylloclade was emerging, which in some ways could be considered an outgrowth of the foliar hypotheses. In order to not only explain the position of the phylloclade in the axil of a reduced scale leaf and its ability to bear an inflorescence yet account for its extreme resemblance to a leaf, the prophyllar fusion hypothesis was proposed. Unlike the foliar interpretation, however, this hypothesis relies heavily upon the concept of "congenital" or phylogenetic fusion which is by definition a non-observable process. It is a necessary corollary of the classical model. (For a critique see Croizat, 1960, 1973; Sattler 1974 a,b,c; Dickinson and Sattler 1974).

Although no evidence was offered, Koch (1837, cited in Arber, 1924a) first put forth the idea that the basal half of the phylloclade, whether sterile or fertile, consisted of a fusion product of a leaf (prophyll) and an axillary branch, whereas the upper half of the phylloclade represented the leaf alone. It was left to Duval-Jouve (1877) to provide the first support for this interpretation in the form of the vascular anatomy of the mature structure. Because transverse sections of the basal half of the fertile phylloclade of Ruscus aculeatus L. exhibited a central vascular cylinder reminiscent of a stele and because the vasculature above the insertion of the inflorescence was leaf-like, i.e. a planar arrangement of vascular bundles, Duval-Jouve agreed with Koch that the fertile phylloclade was a congenital fusion product of an axillary branch with its prophyll. He saw additional confirmation of this in the epiphyllous inflorescences of Tilia, Bougainvillea, Thesium, Erythrochiton and Chailletia. In the case of the sterile phylloclade, as has already been mentioned, Duval-Jouve claimed it was entirely foliar. Van Tieghem (1884) also saw the sterile phylloclade as the prophyll of an aborted axillary shoot but considered it to be a "congenital fusion" product, stating that at its base one could see vascular evidence of the aborted axillary branch in the form of a central vascular cylinder. Further support for this interpretation was seen in the (inverted) orientation of the xylem of the phylloclade towards its axillant leaf, a point Van Tieghem criticized Duval-Jouve for not observing. Like both Duval-Jouve and Koch, Van Tieghem considered the fertile phylloclade to be a "congenital fusion" product, however, he saw an increase in complexity of the structure from Ruscus to Semele. Later, Velenovsky (1892, 1903, 1907, 1913) and

Danek (1919) expanded on these ideas (although no citation of Van Tieghem appeared), by interpreting the fertile phylloclade of Ruscus as a fusion product of a winged inflorescence axis and two median but unequal bracts. Transverse sections of the vascular anatomy of the mature fertile phylloclade as well as the venation pattern itself was submitted as evidence for this. Additionally, teratologies, in which the axial component was separate from the bract were taken as further confirmation. Like Van Tieghem, Velenovsky and Danek saw the fertile phylloclade of Semele as a complex structure, but instead of explaining it in terms of a repeating bifurcation pattern as had Van Tieghem, Danek and Velenovsky considered it to be composed of several congenitally fused units, each of which was equivalent to one fertile phylloclade of Ruscus.

Finally, Arber (1924a, 1925, 1950) recognized in the phylloclades of Ruscus, Danaë and Semele an example of her "partial shoot theory" in which "the leaf has an urge towards self-completion as a whole shoot" (Arber, 1950:93). She saw no difference between sterile and fertile phylloclades, stating that, "the phylloclade consists of a lateral shoot completely adnate to its own prophyll" (Arber, 1925:147) but that "the union which the adnation represents is a fusion of an excessively intimate nature, in which one partner - the prophyll - has gained such complete ascendancy that it is useless to look for the structural boundaries of the adnate axis; the prophyll has, as it were, absorbed the axis without making any concessions to it, and has retained its own foliar type of anatomy unaltered" (Arber, 1924a: 255). Thus for Arber the concept of congenital fusion does not include the usually implicit tenet of "vascular conservatism". As Croizat (1973), has noted, it is still nevertheless unfortunate that Arber chose the language she did to express herself.

Finally, Schlittler (1953) concluded that the fertile phylloclades of Ruscus, and Semele represented congenitally fused products of an axillary shoot with its prophyll.

Alternative Hypotheses. - The above three hypotheses, which have in various ways attempted to explain the unusual morphology of the phylloclade in terms of the classical model, have not gone unchallenged. Robert (1964) after an histological study of Ruscus aculeatus was not able to arrive at a conclusion of what the phylloclade was. Jeremie and Cusset (1972) in a detailed analysis of mitotic activity of the phylloclades of Asparagus densiflorus (Kunth) Jessop, concluded that the morphogenetic processes operating within these structures were not similar to those of typical stems or leaves and for this reason, the phylloclades were neither stems nor actual leaves. Croizat (1973) voiced the same opinion, although he offered no data, that the phylloclade in the Asparageae was the result of "the aggregation, at the meristem level" of potential foliar and axial "meristems in series which, failing to give origin to fully individualized bodies - "foliar" or "axial" - give origin to bodies that effectively belong neither to the category "Leaf" nor "Stem", but share in the two" (Croizat 1973:146-7). Sattler (1974a,1984) proposed that organs sharing characteristics of different categories be accepted as such. He argued that organs such as the phylloclades of

Ruscus and Asparagus be considered as intermediate organs in which total homologization with leaf or stem was not possible.

In light of this controversy a detailed developmental study of four species of the Asparagaceae; Ruscus aculeatus L., Semele androgyna Kunth, Danaë racemosa Moench and Asparagus sprengeri Regel was undertaken. The purpose of this investigation was to relate the development of phylloclades with that of more typical forms of plant construction such as stems and leaves in order to determine by which ontogentic and phylogenetic processes they may have arisen.

MATERIALS AND METHODS

Rhizome buds, young aerial shoots and mature phylloclades of *Ruscus aculeatus* L., *Danaë racemosa* Moench, *Semele androgyna* Kunth and *Asparagus sprengeri* Regel were collected periodically February through May 1982-1984 from plants grown in the McGill University Greenhouse. Two of the plants, *Danaë racemosa* and *Semele androgyna* originated from Kew Gardens in England and did not adapt well to growing conditions in Montreal. For this reason, a small amount of material was obtained from the Jardin des Plantes in Paris. Additionally, Dr. A. Siegert of the Universität Mainz and Dr. Rolf Rutishauser of the Universität Zurich each kindly supplied FAA fixed material of *Semele androgyna*. Of all the material available, over 100 shoot tips of *Ruscus aculeatus* L. and approximately 50 shoot tips of each of the three remaining species were examined.

Material was identified according to Thiselton-Dyer (1896), Hutchinson (1934), Yeo (1968), Dahlgren and Clifford (1982) and Dahlgren, Clifford and Yeo (1985). Voucher specimens of available material have been deposited in the McGill University Herbarium at Macdonald College, St. Anne de Bellevue, Quebec. Fresh material was first dissected out in cooled distilled water or buffer and then vacuum infiltrated in either formalin-acetic acid-alcohol (FAA) or 3% glutaraldehyde in 0.1 M sodium phosphate buffer at pH 7.2. The length of time in the fixative varied from indefinite storage in FAA to 6-12 hours in glutaraldehyde at 0° C. Some material was subsequently postfixed in buffered 1% osmium tetroxide for 2 hours at 0° C.

Mature phylloclades were fixed in FAA and cleared according to the technique of Fuchs (1963).

Light microscopy - Paraffin embedded material was first fixed in FAA and then stained in alcoholic acid fuchsin to facilitate orientation during embedding. Following dehydration through a graded tertiary butyl alcohol series the specimens were infiltrated with either Tissue Prep or Paraplast M.P. 61° C. Serial sections of 7 - 10 um were cut on an A.O. spencer rotary microtome, and stained with either Delafield's hematoxylin, Feulgen with fast green counterstain, or a modified Toluidine Blue O, in which slides were deparaffinized and oven dried prior to staining. This produced a more even and more enhanced metachromatic stain. Of the three methods, Delafield's gave the best results with meristematic tissue and Toluidine Blue O with differentiated material.

Material to be sectioned in plastic was usually fixed in glutaraldehyde with or without osmium postfixation. Several washes in cooled buffer followed by a rinse in distilled water were made before the specimens were dehydrated through a gradated ethanol series. In general, postfixation seemed to give better results in terms of contrast.

Infiltration was accomplished gradually over a period of 2-3 days for Spurr plastic (Spurr, 1969; O'Brien and McCully, 1981) and JB-4 embedding media (Polysciences, Inc. Data sheet 123). Material embedded in LR white resin (data sheet available from J.B. E.M. services, Inc.) was infiltrated for 2-3 weeks. This resin appears to be the best suited for plant tissue. It has a long shelf life and penetrates well. Spurr seems to give the clearest image once sectioned but its use is limited by its viscosity. Only extremely small pieces of tissue with thin cuticles infiltrate well. JB-4 gave results comparable to paraffin but was much more time consuming and difficult to section.

All plastic embedded material was sectioned at 2 μm using glass knives on a Sorval Porter Blum MT-2 ultramicrotome. Sections were floated onto beads of distilled water on cleaned glass slides. Slides were placed on a hot plate and sections were stretched using xylene fumes to eliminate wrinkles and insure adhesion. After drying they were stained with heat using either 0.1% Toluidine Blue O in 1% Borax or 0.1% Methylene Blue in 1% Borax.

Specimens for epi-illumination microscopy were fixed in FAA, dehydrated, stained and dissected according to the techniques of Sattler (1968) and Posluszny, Scott and Sattler (1980).

Scanning electron microscopy (SEM) - Material examined with SEM was fixed in glutaraldehyde with or without osmium post-fixation and prepared according to the techniques of Postek and Tucker (1977), Gersterberger and Leins (1978), and Anthony, Sattler and Cooney-Sovetts (1983).

OBSERVATIONS

Ruscus aculeatus L.

Organography - Ruscus aculeatus L. is a rhizomatous shrub of the Mediterranean region and the Middle East. Its plagiotropic rhizome is sympodially branched and in all the material examined, consists of usually five (or sometimes seven) completely ensheathing scale leaves per sympodium (Fig. 1). While the axils of the first two scale leaves are empty and that of the third sometimes contains a renewal bud, the fourth and fifth axils regularly do. (Fig. 1).

The branching pattern of the lateral dormant aerial shoot buds is the same as that of the main aerial shoot except that it is oriented in a plane perpendicular to the original. The aerial shoot buds remain dormant for the first year, usually growing out the following spring. If the main aerial shoot is damaged, however, one or both of the aerial shoot buds break dormancy and resume the growth of the plant.

The orthotropic aerial shoot is composed of lateral second order branches in its basal region with phylloclades distally (Fig. 8). Each second order branch is axillated by a scale leaf and in turn produces scale leaves in whose axils are located phylloclades (Fig. 8). Both the main aerial shoot and its lateral branches are of determinate growth, ending in a terminal phylloclade (Fig. 2).

Each lateral phylloclade undergoes a 90° torsion at its base and is axillated by a reduced scale leaf in contrast to the terminal phylloclade which is not (Fig. 2). All phylloclades whether lateral or terminal exhibit dorsiventral symmetry, determinate growth, ending in a spiny tip and may be either sterile or fertile. In the case of the fertile phylloclade, the inflorescence is inserted medianly on the adaxial surface of the phylloclade in the axil of the inflorescence bract (Fig. 2).

Shoot development - The shoot apex of the rhizome is broad and dome-shaped (Fig. 5). The scale leaves that ensheath it are initiated distichously and are of dorsiventral symmetry (Fig. 5). Histologically, the apex consists of a two layered tunica and a corpus (Fig. 25). Second order lateral aerial buds are initiated in the axils of the dorsiventral scale leaves by periclinal divisons within the corpus and are delimited by a shell zone (Fig. 25).

As the shoot apex becomes orthotropic, the phyllotaxis changes from distichous to a 2/5 spiral (Figs 5, 4, 6, 7) which secondarily becomes irregular. Second order branch primordia are initiated in the axils of dorsiventral scale leaves (Fig. 6). The morphology of the scale leaf of the orthotropic shoot changes from the ensheathing, hooded form characteristic of the rhizome, to a non-ensheathing more lanceolate form (compare Fig. 5 with Figs 6, 7). The scale leaf is dorsiventral from the beginning, whereas the lateral branch it subtends is bilateral (Fig. 6). As the branch grows, the symmetry changes from bilateral (Fig. 6) to dorsiventral (Fig. 7) and finally to radial (Fig. 13).

After producing several lateral branch primordia, the shoot apex becomes more dome-shaped, signaling the beginning of phylloclade production (Fig. 4). Because of irregularities in the transition zone it is difficult to determine which of the primordia will develop as branches or as phylloclades (Figs 7, 8). However, after more than three or four phylloclades have been produced in succession, the shoot apex usually only produces phylloclade primordia (Fig. 4).

The scale leaf primordia that subtend the phylloclades of the first order axis, are initiated in a spiral 3/8 phyllotaxis (Fig. 4). Each is first visible as a dorsiventral bulge on the periphery of the shoot apex (Fig. 4). During the third or fourth plastochron, a phylloclade primordium is seen within its axil (Fig. 4).

At the time phylloclade primordia begin to be initiated on the first order axis, the most basal second order branches begin to produce scale leaf and phylloclade primordia (Fig. 3). As on the rhizome, the scale leaf primordia of the second order branch are at first initiated distichously (Figs 3, 9) but in contrast to those of the rhizome a gradual spiral phyllotaxis with a divergence angle varying between 2/5 to 3/8 is achieved (Figs 10, 13). The shoot apex which is dome-shaped and somewhat triangular is approximately 200 um in diameter (Figs 10, 13). It is composed of a two layered tunica and corpus (Fig. 26). Periclinal divisions within the second tunica layer indicate the initiation of the scale leaf primordium (Fig. 26) which when visible externally manifests the same symmetry as that of the first order shoot (Figs 4, 7, 10, 13). Throughout its development, the scale leaf remains dorsiventrally symmetrical (Figs 13, 14, 26, 33) and receives only one median vascular trace (Fig. 30). The rate of development of the scale leaf primordium at first equals that of its axillary phylloclade (Figs 10, 13, 26) but later on, exceeds it (Fig. 33). More pronounced cell elongation along the abaxial side of the scale leaf primordium contributes to the upwards curvature and enclosure of the axillary phylloclade (Fig. 33).

Development of the lateral sterile phylloclades - The phylloclade primordium is initiated immediately after that of its subtending scale leaf (Figs 4, 10, 13) by periclinal divisions within the corpus and anticlinal divisions within the tunica (Fig. 26). Initially it is bilaterally symmetrical (Figs 10, 13) or perhaps slightly dorsiventral in the case of the first order axis (Fig. 4). Very quickly thereafter (within the second or third plastochron in the second order shoot) it becomes dorsiventral (Fig. 10). The young phylloclade primordium has two outer cell layers which at first divide only anticlinally (resembling somewhat the organization of a shoot apex) (Fig. 27). Additionally, a faint shell zone can be observed (Fig. 26). This shoot-like histological organization soon disappears leaving instead only a protodermal layer that divides anticlinally (Figs 33, 34). In cross section only the cell division pattern characteristic of a leaf is observed (Figs 30, 31). As the phylloclade grows further, a faster rate of maturation along the abaxial side contributes to its inward curvature, similar to that of its subtending leaf (Figs 33, 34). When the phylloclade is approximately 500 um in width (400 um in length) its distal portion begins to protrude (Fig. 18). At maturity, this region becomes sclerified (Fig. 39) resulting in a terminal spiny tip (Fig. 2) of radial symmetry. The middle and basal regions of the phylloclade, however, remain dorsiventrally symmetrical (Figs 35, 37).

In terms of vascularization, the phylloclade receives its first procambial strand within about the third plastochron. This procambial strand, which is median, differentiates acropetally from the provascular trace of the subtending scale leaf (Fig. 34). Somewhat later, two lateral traces depart from provascular strands within the stem, entering the phylloclade as do eventually other bundles, forming a dorsiventral arrangement (Figs 30-32). This dorsiventral arrangement is maintained in the mature form (Fig. 37). The median vascular bundles of the base are surrounded by an ellipse of sclerenchyma (Fig. 35). Above the base, the bundles are separate and are arranged in a venation pattern characteristic of monocotyledonous leaves (Fig. 37). The xylem of some, but not all, of the bundles is inverted (Figs 35, 37).

Development of the fertile phylloclade - Like the sterile phylloclade, the fertile is initiated in the axil of a scale leaf and its development thereafter is equivalent to that of the sterile except for the presence of the inflorescence. In *Ruscus hypophyllum* L. the inflorescence is initiated on the abaxial side of the phylloclade (Fig. 17), whereas in *Ruscus aculeatus* L. it is initiated adaxially (Figs 11, 12, 15, 16) although exceptions also occur (Fig. 23). The inflorescence bract primordium is initiated directly in a median position by anticlinal divisions within the protoderm and periclinal divisions within the subprotodermal layer of the phylloclade (Fig. 27). From the beginning, it is dorsiventrally symmetrical and remains so throughout its development (Figs. 12, 15, 16, 28, 29). Only one vascular trace is present which differentiates acropetally from the median procambial strand of the phylloclade (Figs 16, 28, 29). The inflorescence primordium is initiated in the axil of its bract as a result of deeply originating periclinal divisions (Fig. 28). The inflorescence apex is dome-shaped with a two layered tunica and corpus (Figs 16, 28, 29). Externally the struture is first visible as a flattened primordium with bilateral symmetry (Figs 15, 16).

At maturity, cross sections through the base of the fertile phylloclade show that the vascular bundles are in a more or less dorsiventral arrangement and are surrounded by sclerenchyma (Fig 36). The xylem of the bundles in the median region nearest the adaxial surface is inverted (Fig. 36). The xylem of the bundles nearest the abaxial surface is not (Fig. 36). Above the insertion of the inflorescence the vascular bundles are separate yet are still in a dorsiventral arrangement (Fig. 40). Only some of the bundles have inverted xylem (Fig. 38). At the tip of the fertile phylloclade the median and outer vascular bundles merge (Fig. 42).

<u>Development of the terminal phylloclade</u> - After each second and first order shoot apex has finished production of bract and lateral phylloclade primordia, as indicated by the basal elongation of the first order shoot, the terminal phylloclade primordium appears (Figs 14, 33). It results from the direct transformation of the shoot apex (Fig. 33), no subtending bract is initiated. The first indication of the terminal phylloclade primordium is an elongation of the shoot apex (Fig. 33). The symmetry of the apex at this time and thus the young phylloclade primordium is bilateral. As the shape becomes more triangular, the primordium becomes dorsiventral

(Fig. 14). As with the lateral phylloclade primordia, the terminal phylloclade maintains this dorsiventral symmetry at maturity except for its sclerified spiny tip which is radial (Figs 2, 19-21). Similarly, the terminal phylloclade may or may not be fertile (Figs 2,19,20,41) and displays the same histology as that of the lateral phylloclade primordia.

Abnormalities, variations - When the shoot apex is in transition as during the changeover from branch to phylloclade production and from lateral to terminal phylloclade production, morphological irregularities occur. In the first instance during the changeover from branch to phylloclade production, the irregularity may either be simply a phylloclade in a branch position (Fig. 8) (i.e. a complete transition) or more aberrant reflecting perhaps an incomplete transition. For example, where a branch would have been expected, structures that might be described as abnormal phylloclades (Fig 22) or abnormal branches (Figs. 24) may be present. Additionally, the terminal phylloclade itself may also exhibit similar irregularities such as variable inflorescence position, or it may even bear another phylloclade (Figs 19-21, 23).

Danaë racemosa Moench

Organography - Danaë racemosa Moench is a monotypic rhizomatous shrub occurring in southwest Asia and the Southeastern Balkan peninsula. The plagiotropic rhizome is sympodial and in the material examined, consists of five scale leaves[1] per sympodium (Fig. 43) that are ensheathing and are arranged distichously (Figs 47-49). The axils of the first two scale leaves appear empty, while those of the third and fourth contain buds (Figs 43, 47). The bud in axil five usually grows out as an aerial shoot following the emergence of the main aerial shoot.

The main aerial shoot is orthotropic and bears spirally arranged scale leaves in whose axils are usually located second order branches, not all of which reach maturity. In the first two leaf axils are shoots that bear third order branches. Occasionally the more apically located second order shoots also bear third order branches. Each shoot regardless of rank is of determinate growth and either remains sterile or produces a terminal raceme (Fig. 44). No terminal phylloclade is produced.

Phylloclades are found in the upper region of the first order shoot and along the second and third order shoot axes. The number of phylloclades per shoot varies from as few as two to as many as eight or more. Each phylloclade is subtended by a scarious scale leaf and usually undergoes torsion. All are sterile, of determinate growth and dorsiventral symmetry (Fig. 44).

[1] Although normal foliage leaves have been reported for both the seedling and mature plant by Arber (1924a), none were observed in the material examined for this study.

Shoot development - At the time of scale leaf initiation, the rhizome apex is broad and slightly convex (Fig. 48). The primordium arises as a crescent-shaped mound along the periphery of the rhizome apex (Fig. 48). Growth upwards below the tip results in the characteristic hood, while extension of the basal margins (Figs 47-49) eventually produces the ensheathing mature form. All of the scale leaf primordia are initiated in a distichous phyllotaxy and are of dorsiventral symmetry (Figs 47-49). During lateral bud initiation, the shoot apex is approximately 320 um in diameter and is composed of a two-layered tunica and a corpus (Fig. 59). Each lateral bud primordium originates in the axil of a scale leaf from divisions within the second tunica layer and corpus (Fig. 59).

As the shoot becomes orthotropic, a change in the size and shape of the apex is noticeable (Fig. 50). A corresponding change in the morphology of the scale leaves is also apparent. They become more reduced and non-ensheathing (Figs 50-53). Additionally, a change in phyllotaxy from distichous to a 1/3 spiral occurs (Fig. 50). The dorsiventral symmetry of the leaves, however, does not change, and they continue to originate as crescent shaped mounds along the periphery of the shoot apex (Figs 50, 53) and retain this symmetry throughout development (Figs 51-53).

Although at first second order branch primordia are not visible in the axils of the orthotropic scale leaves (Fig. 50), they later are clearly evident as bilaterally symmetrical structures that become slightly dorsiventral (Figs 51-53). After the first order shoot has finished producing lateral branch primordia, phylloclade primordia begin to be initiated in the leaf axils (Figs 51-53). Again there is a change in phyllotaxy, this time from spiral back to distichous (Fig. 53). Subsequently, (in the seventh or eighth plastochron) the young second order branches begin to initiate bract and phylloclade primordia (Figs 45, 57). The shoot apex is approximately 200 um in diameter and is composed of a two-layered tunica and a corpus (Fig. 57). The scale leaf primordia are initiated in a distichous phyllotaxy from periclinal divisions within the second tunica layer and concomitant anticlinal divisions in the outer layer (Figs 45, 57). Each is of dorsiventral symmetry (Figs 45, 57) and grows at a rate equal to or slightly faster than that of its axillary phylloclade (Figs 45, 46, 54, 57). A greater rate of elongation along the abaxial side of the scale leaf primordium contributes to its upward curvature (Fig. 57). During the third plastochron of the second order shoot, the bract primordium receives its first provascular trace. The procambial strand is median and is derived from an outer bundle within the stele (Fig. 66). After entering the bract, however, this strand sometimes branches (Fig. 65).

When the shoot apex has finished producing bract and phylloclade primordia, one of two things may occur. Either it remains sterile in which case the apex is gradually used up (Figs 54, 55, 60) or it becomes reproductive (Figs 46, 56, 58). The reproductive apex maintains the two-layered tunica and the corpus of the vegetative shoot but undergoes a noticeable change in size and shape (Figs 46, 56, 58). In the early stages of transition, the apex elongates considerably (Figs 46, 58), although its diameter is not much different from that of the vegetative state (176 um vs 200 um). With the production of flower primordia, however, the shape of the apex becomes more flattened, and its size gradually diminishes (Fig. 56). Like the phylloclade primordia, the flower primordia are initiated in the axils of scale leaves (Figs 46, 56, 58). They originate from divisions more deeply within the corpus than do the axillary bracts (Fig. 58) and are considerably more precocious in their development (Figs 46, 56, 58).

Phylloclade development - During the second plastochron of the second order shoot, the phylloclade primordium is already visible in the axil of the scale leaf as a conspicuous grouping of periclinal divisions within the second tunica layer with concomitant divisions within the corpus (Fig. 57). At its base, one can almost discern the cell division pattern characteristic of a shell zone (Fig. 57). This organization soon disappears, however, and in later plastochrons, there is a protodermal cell layer in which only anticlinal divisions occur (Figs 57, 58, 60). In cross section, the cell arrangement pattern is indistinguishable from that of a typical leaf(Figs 61, 62, 65).

In terms of symmetry, the phylloclade primordium first appears as a bilaterally symmetrical structure but rapidly becomes dorsiventral (Figs 45, 54, 65). This change in symmetry is at least in part related to an increased rate of cell elongation along the abaxial side which contributes to the phylloclade's inward curvature (Figs 58, 60). When a length of approximately 1 mm has been reached, the most distal portion of the phylloclade differentiates into a pointed tip. As growth proceeds, the phylloclade increases in length, the tip becomes narrower and more acuminate, while the blade increases in width becoming more ovate. The margins of the mature phylloclade may either curve upwards or remain flat in which case the base often undergoes torsion (Figs 44, 64).

The vascularisation of the phylloclade is independent of that of its subtending bract (Fig. 66). At the base of the young phylloclade primordium three procambial traces are visible (Fig. 66). Since the rate of differentiation of the median bundle is faster in comparison with that of the two lateral ones, only the median procambial strand is observable in cross sections through higher levels (Fig. 65).

At maturity only some of the xylem of the vascular bundles is inverted (Fig. 63). The orientation and distribution of the bundles gives rise to a parallel venation pattern typical of that seen in monocotyledonous leaves (Figs 62, 64).

Semele androgyna Kunth

Organography - Semele androgyna Kunth is a rhizomatous climbing shrub native to the Canary Islands and Madeira. Its plagiotropic sympodial rhizome consists of five or seven ensheathing scale leaves that are distichously arranged (Fig. 67). In the material examined all scale leaf-axils contain axillary buds (Fig. 67). If they develop, they have the same architectural branching pattern as the main sympodium except for the plane of orientation which has been turned ninety degrees.

In contrast to the rhizome, the main aerial shoot is orthotropic and at its base bears spirally arranged scale leaves in whose axils are located second order branches. Apically, the phyllotaxy reverts to distichy and the scale leaf axils contain phylloclades (Fig. 68). This same pattern of distichous phyllotaxy and phylloclade arrangement holds for the second order shoots as well (Figs 69-70). All shoots regardless of rank are of determinate growth ending with the production of lateral phylloclades. No terminal phylloclade was observed (Figs 68-70).

Lateral phylloclades, which are lanceolate, dorsiventral and determinate, usually undergo torsion at their base (Figs 68, 70). They may be either sterile (Fig. 68) or fertile (Figs 69-70,94). In the latter instance, the inflorescence is most commonly situated along the margin of the phylloclade in the axil of the inflorescence bract (Figs 69, 70), although other positions are occasionally observed (Fig. 69).

Shoot development - The rhizome shoot apex is approximately 150 um in diameter and is ensheathed by distichously arranged scale leaves (Fig. 71). Each scale leaf arises along the periphery of the apex as a crescent-shaped mound. The shape of the primordium gradually changes to a hooded ensheathing form (Fig. 71). Eventually the apex is totally enveloped by the dorsiventral leaves. The lateral bud primordia that are initiated in the axils of these scale leaves are also dorsiventrally symmetrical, at least at the beginning (Fig. 71).

When the first-order shoot becomes orthotropic, a noticeable change in the size and shape of the apex as well as leaf morphology occurs. The apex becomes rounder with age and attains a diameter of about 225 um (Fig. 72). It has a three-layered tunica and a corpus (Fig. 83). The scale leaf primordia that subtend branch primordia are initiated in 1/3 spiral phyllotaxy and are dorsiventrally symmetrical (Fig. 72). In comparison with those of the rhizome, they are more reduced, lanceolate in shape and are not ensheathing. Branch primordia are initiated in the axils of these scale leaves; they arise from anticlinal divisions in the tunica and periclinal divisions beneath the third tunica layer (Figs 72, 83). At first they appear as dorsiventral structures although in later development they are more bilateral (Figs 72, 77) and eventually their axis becomes radial (Fig. 76).

At the stage when bract and phylloclade primordia begin to form on the second order shoot, the apex of the latter is highly dome-shaped (250 um wide and 120 um high) and consists of a two-layered tunica and a corpus (Figs 74, 75, 85). Leaf primordia that subtend phylloclades are initiated from periclinal divisions within the second tunica layer and concomitant anticlinal divisions in the outer layer; they arise in a distichous phyllotaxy like those of the first order shoot (Figs 77, 85-87). Vacuolation and cellular differentiation occur first along the abaxial side (Figs 85, 87). Externally this process is reflected in the leaf's clearly dorsiventral form. In earliest stages it is visible as a crescent shaped bulge skirting the shoot apex (Figs 74-77). Both leaf initiation as well as rate of development are initially more advanced in relation to that of the phylloclade (Figs 73-78, 84-87). Throughout its development, the leaf receives only one median vascular trace. The procambium of this trace is formed acropetally during the second plastochron but is most conspicuous during the fourth (Fig. 87).

With further growth the scale leaves eventually enclose the shoot apex (Figs 73, 84). At the same time the apex diminishes in size as it is gradually used up in the production of leaf and phylloclade primordia (Figs 73, 84).

<u>Phylloclade development</u> - The phylloclade is initiated in the axil of its bract from anticlinal divisions within the second tunica layer and underlying divisions within the corpus (Figs 85-87). Concomitantly, anticlinal divisions occur in the outer tunica layer. Even though it is initiated during the second plastochron, the phylloclade primordium is not visible externally until the third or fourth (Fig. 74). It is a dorsiventral structure from the beginning and retains this symmetry throughout its development (Figs 76, 79-82, 92) thus resembling a leaf. Yet, in very early stages, it sometimes appears to have a faint shell zone, thus resembling the organization of a shoot apex (Figs 85, 87). This cellular division pattern, however, quickly disappears and in later stages the phylloclade primordium has only a one layered protoderm that divides anticlinally (Fig. 84). Although cells seem to differentiate more quickly along the abaxial side, thus contributing to the phylloclade's inward curvature, the overall rate of growth and eventual expansion of the primordium is delayed until the shoot apex is nearly exhausted (Figs 73, 84).

At the level of insertion on the stem, the vascularisation of the phylloclade is independent from that of its subtending bract (Figs 84, 89). Three provascular traces enter the base of the primordium from the stele (Fig. 89). The provascular bundles are thus initially arranged in a dorsiventral planar arrangement. Later, when the phylloclade matures, a flattened ellipse of vascular bundles somewhat resembling a stele is visible in its base (Fig. 92). The xylem of some of these bundles is inverted (Fig. 92). Above this region, the vascular bundles divide to form a parallel venation pattern typical of monocotyledonous leaves (Figs 90, 91, 93). At the tip of the phylloclade the outer vascular bundles of each margin converge. The median bundle ends blindly (Fig. 93).

Fertile phylloclade development – In terms of overall morphology, the fertile phylloclade primordium bears a striking resemblance to a young second order shoot (Figs 79, 80, 82). Bracts are initiated along the margins of the phylloclade in a more or less distichous phyllotaxy with two orthostiches (Fig. 82) although deviations in arrangement occur (Figs 79, 80). Each bract receives one median procambial trace that differentiates acropetally and is separate from that of the inflorescence primordium (Fig. 88). The inflorescence primordium is initiated in the axil of the bract directly on the phylloclade primordium (Figs 79, 80, 82, 88).

Asparagus Sprengeri Regel

Organography - *Asparagus Sprengeri* Regel is a widely cultivated ornamental whose plagiotropic rhizome produces orthotropic aerial shoots that bear scarious leaves more or less in a spiral phyllotaxy. The leaves have a thorny outgrowth at their abaxial base.

At the base of the aerial shoot, the lowermost leaf axils have axillary meristems that rarely if ever grow out. Above these in the middle region of the shoot, second order shoots and sometimes inflorescence buds are found in the leaf axils. Inflorescence buds appear to grow out in the early summer, one or two years after the aerial shoot has emerged from the ground. At the most distal portion of the shoot, clusters of phylloclades occur in the leaf axils.

The pattern of organization seen in the leaf axils shows a correlation with the location of the node on the plant (Fig. 95). In the middle region of the aerial shoot, nodes typically have the following pattern. In the axil of the subtending leaf is located the second order shoot (Fig. 95a). Lateral to the second order shoot on either side are two phylloclades, each axillated by a reduced scale leaf (Fig. 95a). Lateral to each of these is usually the inflorescence and its subtending bract (Fig. 95a). This architectural pattern is basically maintained for nodes in the apical region of the plant except that in the position occupied by the second order shoot, a phylloclade is observed (Fig. 95b). Similarly in the place where an inflorescence would be expected, a phylloclade is sometimes observed (Fig. 95b). Thus it is possible to have a cluster of five phylloclades instead of the usual three. In the literature even more (seven) have been reported (Arber, 1924b; Kausmann, 1955).

The branching pattern of the first order shoot is basically repeated in the second order shoot, except that inforescences and third order branches are less frequent. Inflorescences if present, grow out one or two months after those occurring on the first order shoot. All shoots whether first or second order are determinate, ending in a cluster of phylloclades.

Each phylloclade is of bilateral to dorsiventral symmetry, linear to strap shaped, and terminates in a spiny tip (Fig. 96). All are sterile (Fig. 96).

<u>Shoot development</u> - The apex of the young orthotropic first order shoot is approximately 125 μm in diameter and more broad than high (Fig. 97). Scale leaf primordia are initiated along the periphery of the apex in a spiral phyllotaxy (Fig. 97). Each is dorsiventral (Fig. 97). As the leaf grows, its basal abaxial portion protrudes forming at maturity a pointed sclerenchymatous thorn-like structure.

Second order shoots are initiated in the axils of the scale leaves as flattened structures with a bilateral to dorsiventral symmetry (Figs 97, 110). When they are about 130 μm wide, their lower flanks begin to bulge, indicating the initiation of two lateral bract primordia (Fig. 97). Adaxial growth between the two primordia leads to the formation of a semi-circular structure (Figs 110, 112) that has been interpreted as a prophyll (see, e.g., Wenck, 1935).

This structure is present only in basally located second order shoots (compare Figs 110-112 with Fig. 113). Lateral phylloclade primordia arise in the axils of the lobes of this structure at a very early stage (Fig. 111).

After a number of bract and second order branch primordia have been produced, the morphology of the first order shoot apex changes by becoming rounder and more dome-shaped (Fig. 98). This change correlates with the production of axillary meristems that give rise to bract and phylloclade primordia (Fig. 98). Both the first order shoot and its second order shoots appear to produce these structures during the same time period (Figs 98, 107, 113).

The shoot apex at this stage consists of a two-layered tunica and a corpus (Fig. 114). The scale leaf primordium that subtends the axillary meristem arises from anticlinal divisions within the first tunica layer and periclinal divisions within the second (Fig. 114). Like the leaf that subtends a second order shoot, it originates in a spiral phyllotaxy and is dorsiventral (Figs 98, 99). There is, however, a reduction in size. Each scale leaf receives one procambial trace which is median (Fig. 117). An axillary meristem is initiated in the axil of the scale leaf in the second or third plastochron (Figs 98, 114). It arises from anticlinal divisions within the tunica layers and concomitant divisions in various planes in the corpus (Fig. 114). In early stages, the external form of these structures is dorsiventral in first order shoots or perhaps almost bilateral in second order shoots (Figs 98, 101, 102, 107). Very quickly, however, these latter cases also become dorsiventral (Figs 99-102). The first procambial strand to the axillary meristem is median and is differentiated from that of the subtending leaf (Figs 117, 118).

As the shoot nears the end of its lifespan, the shape of the apex becomes triangular and its size is gradually reduced (Fig. 99). In its final phase, the last scale leaf primordium is initiated almost opposite to the penultimate one (Fig. 100). The remainder of the shoot apex is transformed into the last axillary meristem which then sequentially gives rise to the terminal cluster of phylloclade primordia and their subtending scale leaves (Figs 100-103, 108, 115).

Pattern of phylloclade initiation - When the axillary meristem is about 120 um wide, its distal region begins to protrude indicating the differentiation of the median phylloclade primordium (Figs 100, 102). Concurrently, the lateral flanks of the axillary meristem begin to form bract primordia (Figs 100, 102). The position of these primordia is slightly adaxial since the axillary meristem is slightly curved (Figs 100, 102). When the median phylloclade primordium is about 80 um wide and 70 u m high, lateral phylloclade primordia are initated in the axil of first one scale leaf primordium and then the other (Fig. 104). Later, as the lateral phylloclade primordia themselves reach 80-90 um length, cellular divisions can be observed at their bases more or less opposite to each phylloclade's subtending scale leaf (Fig. 106). These represent the initiation of two more bract primordia (Figs 105, 106, 109). In the axil of each bract primordium an axillary meristem arises that develops into another phylloclade or an inflorescence (Figs 109, 116). In some cases, the meristem appears not to develop, or becomes dormant (Fig. 108). Thus only three phylloclades per cluster would be formed instead of the usual four or five.

Phylloclade development - The phylloclade primordium is initally dorsiventral (Figs 100, 101, 119). By the time it has reached 70-80 um however, it is bilateral and dome-shaped (Figs 101, 103,104). The scale leaves that subtend phylloclades are dorsiventral from the beginning and remain so throughout their development (Figs 103, 105, 109, 114, 119, 121).

Histologically, the median phylloclade primordium at first has two outer cell layers that divide anticlinally (Figs 114, 115). At its base a cellular pattern that resembles a faint shell zone can be observed (Figs 114, 115). This shoot-like organization soon becomes transformed into a pattern that is characteristic for leaves (Figs 114, 116, 121).

The first procambial strand to the median phylloclade is itself median and is connected to that of the scale leaf subtending the axillary meristem from which the phylloclade primordia arises (Fig. 119). Each of the two lateral phylloclade primordia receives one procambial strand (Fig. 120). No provascular trace was observed in any of the lateral bract primordia.

When the phylloclade primordium has reached approximately 100 um in length, its most distal portion begins to extend (Figs 105, 106). The cells in this area continue to elongate until eventually a spiny tip with radial symmetry is formed (Figs 108, 109). At maturity it becomes sclerenchymatous. As the tip differentiates, the middle portion of the phylloclade expands laterally (Figs 105, 106, 108, 109). In cross-section the symmetry at this level is bilateral, and a large procambial bundle may be observed (Fig. 121). At maturity this solitary vascular bundle has an anomalous structure (Figs 122-124). In the mature phylloclade the basal region is dorsiventral in cross-section. Hence, the phylloclade as a whole is dorsiventral with a bilateral portion.

DISCUSSION

The present investigation demonstrates that the phylloclade in the Asparagaceae is a complex structure. On the one hand it resembles a shoot because of its position, early histogenesis and in some cases its initial bilateral symmetry and ability to produce other organs. Yet on the other hand, it is like a leaf because of its determinate growth and final dorsiventral symmetry. When all of these features of the space-time extension of the phylloclades are weighted equally, the natural conclusion one arrives at is that the phylloclade is an intermediate organ (Sattler, 1966, 1974a, 1984) that combines stem and leaf features (Jeremie and Cusset, 1972; Croizat, 1973). Interpreting the phylloclade in this manner not only provides a more comprehensive and dynamic explanation of morphogenesis but at the same time avoids the essentialistic trappings that plague other views. For example, proponents of the foliar hypothesis such as de Candolle (1827), Duval-Jouve (1877), Velenovsky (1892, 1903, 1907), Troll (1937), Joyeux (1928), Buscalioni (1914), Schlittler (1953) and at one point Arber (1950) have emphasized the phylloclade's leaf-like attributes in their interpretation; and to bring it into line with the accepted model of plant construction (the classical model), they have postulated that the phylloclade be the terminal or pseudo-terminal leaf of a reduced or aborted shoot. Yet no reduced or aborted shoot is observed during development. Phylloclades are either initiated directly in the axil of a scale leaf via divisions within the corpus and tunica as in the cases of lateral phylloclades or result from the direct transformation of either the shoot apex in the case of the terminal phylloclade of Ruscus. While one could argue (Rutishauser and Sattler, 1985) that this last point offers support for the interpretation of Schlittler (1953) and Arber (1950) that the terminal phylloclade in Ruscus is a leaf with "an urge towards whole shoot characters" (Arber, 1950), to do so would be limiting because it disregards its inception.

Likewise, those who advocate the opposite view that the phylloclade be equated with a caulome primarily because of its position (Turpin, 1820; A.P. de Candolle, 1827; Van Tieghem, 1884; Arber 1924b, 1935) or its ability to give rise to other structures (Clos, 1861; Cauvet, 1877; Dickson, 1886; C. de Candolle, 1890; Celakovsky, 1893; Reinke, 1898; Szafer, 1910; Zweigelt, 1913; Goebel, 1905; Mott, 1938, 1939) or because its initial histogenesis and symmetry is shoot-like (Wenck, 1935; Troll, 1937; Kaussmann, 1955; Hirsch, 1977) obtain an equally limiting view. Although phylloclades are initiated more or less like flattened shoot apices and at first appear to have a cell division pattern characteristic of a shell-zone, thus resembling the lateral branch initiation observed in Ruscus and Semele, they do not continue to develop like shoots. Very early in their development (sometimes even at inception) their symmetry becomes dorsiventral. In cross-section, the cell arrangement pattern characteristic of a leaf is observed. The pattern of vascularisation seen in the phylloclades of Ruscus, Danaë and Semele strongly resembles that found in monocotyledononous leaves. In terms of growth, phylloclades are determinate. Although certain phylloclades such as the fertile phylloclades of Ruscus and Semele do give rise to other organs, their ability to do so is by no means unique to shoots. Dickinson and Sattler (1974) have shown that leaf primordia in Phyllonoma give rise to bract and inflorescence primordia. Sattler and Maier (1977) have described the initiation of epiphyllous appendages in Begonia. Dickinson (1978) cites other examples and documents the widespread occurrence and significance of epiphylly in general.

The above has shown that by weighting criteria or restricting an investigation to only one morphological feature or developmental stage only a partial understanding of phylloclade morphogenesis is possible. The following illustrates how science can actually be hampered by such an approach. Proponents of the prophyllar fusion hypothesis, such as Koch (1837, cited in Arber, 1924a), Duval-Jouve (1877), Van Tieghem (1884), and with modifications, Velenovsky (1892, 1903, 1907, 1913), Danek (1919), Arber (1924a, 1925, 1950) and Schlittler (1953), postulate in various ways that the phylloclade in Ruscus and Semele is a congenital fusion product of a lateral branch with its attendant prophyll. Evidence to support this contention is offered in the form of the vascular anatomy of the mature structure. Cross-sections taken through the bases of both sterile and fertile phylloclades in Ruscus show a more or less flattened vascular cylinder that somewhat resembles a stele thus indicating supposedly where the branch and leaf had fused. Above the insertion of the inflorescence and above the base in the case of the sterile phylloclade, the vascular bundles are arranged in a plane like a leaf, yet some of the xylem is inverted, serving as it were as a kind of vestigial reminder of the fusion. While congenital fusion is by definition a non-observable process, it nevertheless must be pointed out that no ontogenetic evidence for fusion exists. Firstly, as has already been stated, phylloclades are initiated directly as a continuous transformation of the apical or axillary meristem. Furthermore, in the case of the fertile phylloclade, the inflorescence is initiated in the axil of the inflorescence bract directly on the adaxial surface of the phylloclade primordium in Ruscus and along the margin in Semele. Secondly with regard to vasculature, the process of vascular development occurring in Ruscus, Danaë, Semele and Asparagus does not support such an hypothesis, neither in terms of organisational pattern nor tissue differentiation. In Ruscus, the first procambial trace to the phyllocade is median and differentiates acropetally. Shortly thereafter two lateral strands differentiate on either side. At the base of the young phyllocade primordium in Danaë and Semele, three procambial traces in a dorsiventral arrangement are also observed. This pattern of organisation is consistent with that reported by Fisher (1971) for the leaf of Cladium.

In the mature sterile phylloclades of Ruscus, Semele and Danaë, the vascular bundles, although more numerous, are still maintained in this more or less dorsiventral arrangement, even in the base of the phylloclade. A superficial resemblance to a stele results because a flattened cylinder of sclerenchyma surrounds the bundles in the base. More of a case could be made for the fertile phylloclade of Ruscus in which major "axial" bundles are arranged dorsiventrally, while smaller cortical bundles and sclerenchyma surround them in a somewhat elliptical pattern. The vascular arrangement in both types of phylloclades, however, can be explained in a developmental fashion according to ideas expressed by Zimmermann and Tomlinson (1972). These authors have demonstrated that the pattern of vascular connection in monocotyledons is a complicated process related not only to the presence and size of certain physiological "growth centers" (i.e., lateral appendage primordia -leaf and branch) but also to the timing of their initiation (see also Maze, 1977). Axillary primordia that are initiated relatively early, i.e., in close proximity to the meristematic cap act as a kind of "sink" in attracting part of the axial vascular system. The phylloclade primordia in Danaë, Ruscus and Semele originate within the second or third plastochron and thus may act as a "sink". Since vascular connection between an axillary structure and the axis can occur over a long period of time, more than one type of vascular connection is possible (Zimmermann and Tomlinson, 1972). This would tend to support the presence and arrangement of the cortical bundles in the sterile phylloclades. Additionally, if another "growth center" (the bract and inflorescence primordia) were to initiate on the young phylloclade primordium while it was still close to the meristematic cap, perhaps even more axial vasculature would be diverted into the phylloclade. That the inflorescence does initiate relatively early and that there are more vascular bundles seen at the base of the mature fertile phylloclade of Ruscus would seem in agreement with this. Conversely, the presence of only one vascular bundle in the phylloclade of Asparagus, which has been part of the basis for its interpretation as a phyllode, may simply be the

the result of a later initiation, smaller primordial size and lessened physiological requirements (for further criticism of the phyllode hypothesis in relation to monocotyledons, see Tomlinson, 1970).

Finally as a last point, the presence of inverted xylem in the mature phylloclades of Ruscus and Danaë may also be explained in terms of development. Fisher (1971) has elegantly shown that the inverted vascular bundles found in Cladium result when procambial strands differentiate in close proximity to one another. In contrast when procambium differentiated in isolation the xylem was oriented in its normal adaxial position. One may assume that similar developmental mechanisms may occur in Ruscus, Danaë, Semele and Asparagus. Thus when the presence or absence of inverted xylem can be explained in morphogenetic terms, the reliance upon the principle of vascular conservatism whereby the inverted xylem is a vestige of the presumed congenital fusion seems not only unnecessary but also misleading.

The foregoing discussion has illustrated some of the inadequacies of thinking in terms of either/or (Sattler, 1974 a, b, c, 1984, 1986). The weakness of the foliar and cauline hypotheses is that they are limited. Each alone leads to only a fragmented or partial understanding of the morphology of the phylloclade. Schüepp (1969), Rutishauser (1983), Sattler (1984, 1986) and Rutishauser and Sattler (1985) have proposed that contrasting points of view be regarded as different perspectives of the same phenomenon, and thus as complementary to one another rather than antagonistic. By viewing the foliar and cauline views in this manner we obtain at once a resolution of the conflict and a more comprehensive account of phylloclade morphogenesis. Phylloclades become/are neither stems nor leaves but something that incorporates features of both.

Sattler (1974 a, 1984) has proposed a new model of the shoot of higher plants that takes situations such as these into consideration. Thus the three fundamental organ categories of the classical model, root, stem and leaf are not considered as mutually exclusive but rather as end points along a morphological continuum. Graphically this can be visualized as a pyramid (see Sattler, 1986) whose four corners are occupied by the following categories: caulome (stem), phyllome (leaf), shoot (stem and leaf) and trichome. Intermediates (i.e., organs sharing features of one or more of the above) are accepted as such and are perceived as occupying a portion of a face or the interior of the pyramid.

According to this model, the phylloclades of the Asparagaceae as well as those of Phyllocladus (Keng, 1974, 1977; Bergrenn, 1980) and Phyllanthus; (Roux, 1968; Banchilhon, 1972) fall within the shoot-phyllome-caulome continuum. In the Asparagaceae, the sterile phylloclades of Danaë, Ruscus and Semele occupy the more leaf-like region of the continuum. They become dorsiventral very early in their development, their anatomy is like that of a leaf, they are of determinate growth and no other structures are initiated on them. More towards the middle of the continuum are the fertile phylloclades of Ruscus. They share all of the leaf-like features of the preceeding group except for the initiation of a bract and an inflorescence primordium on the adaxial surface. Towards the shoot-like region of the continuum are the phylloclades of Asparagus and the fertile phylloclades of <u>Semele</u>. The latter, while primordia, give rise to bract and flower primordia along their margins and thus bear a striking resemblance to the young flat second order shoots of <u>Semele</u>, <u>Danaë</u> and to a lesser extent <u>Ruscus</u>. The phylloclades of <u>Asparagus</u> are included in the shoot-like region of the continuum because of their pattern of initiation and organogenetic potential. The axillary meristem that gives rise to these phylloclades is in a continuous state of morphological fluidity, so much so that it is difficult to describe in terms of conventional concepts of plant morphology. As soon as the apical portion of the axillary meristem begins to form a median phylloclade, a 90° switch in polarity occurs and its flanks begin to protrude, forming lateral bract primordia. In the axils of these bract primordia, lateral phylloclade primordia develop which then go on to partially repeat this pattern (i.e., they give rise to bract primordia at the base of one of their margins). In the axils of these latter bracts, other phylloclades or sometimes inflorescences develop. The axillary meristems thus exhibit a certain plasticity or morphogenetic potentiality for following different developmental pathways. This plasticity is also reflected in the morphogenetic potentiality of the axillary meristems in general. While in <u>Danaë</u> and <u>Semele</u> the axillary meristems appear to produce either rhizome buds, second order shoots or phylloclades in a characteristic order with little deviation[1], the axillary meristems of <u>Asparagus</u> do not. In

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[1] A similar situation with regard to potentiality has been observed in <u>Flickigeria</u> a sympodial rhizomatous orchid, where buds developed as main shoots, branches or inflorescences in correlation with the location on the plant (Rasmussen, 1982).

some instances they differentiate into a second order shoot and two lateral phylloclades and in others, into a median phylloclade with two lateral phylloclades. This morphogenetic potentiality to undergo different types of development is similar to that observed in the areole of Opuntia polycantha (Mauseth and Halperin, 1975). The axillary meristem in this species normally gives rise to an areole that in some cases develops as a leafy shoot and in others as spines. The axillary meristems of Ruscus can switch back and forth between branch and phylloclade production especially in the transition region where structures intermediate between the two are somtimes produced.

All of these situations are interesting in light of the switches in developmental pathways between leaves and stems that have been observed in surgical experiments on ferns (Warlaw, 1949; Cutter, 1956; Steeves, 1961, 1966; Haight and Kuehnart, 1971; Von Aderkas and Hicks, 1985) and recently angiosperms (Smith, 1984). While in the majority of cases complete leaf to shoot interconversion is accomplished, intermediate organs sharing leaf and stem features are sometimes produced (Haight and Kuehnart, 1969; Sussex, 1955; Snow and Snow, 1959; Hanawa, 1961).

Changes in developmental integration that lead to the expression of different developmental pathways and thus intermediate organs may be examples of the phenomenon of homeosis. First defined by Bateson (1894) and later elaborated on by Leavitt (1909), homeosis is the assumption by one part of an organism of the likeness characteristic of another part such that developmental processes common to one organ category appear in a new location (Corner, 1958; Zimmermann, 1961; Sattler, 1974b; Ouweneel, 1976; Sachs, 1982). The second order shoots and the phylloclades of the Asparagaceae could thus be thought of as examples of where leaf developmental processes have been expressed in locations characteristic of shoots. The integration of leaf developmental processes in the cases of the second order shoots has only been slight, as evidenced by the expression of only a few leaf features (i.e., determinate growth and early dorsiventral symmetry). A greater integration of leaf developmental processes is suggested by the phylloclades, especially the sterile phylloclades of Danaë, Semele and Ruscus. Less integration is suggested in the cases of the fertile phylloclade of Semele and the phylloclades of Asparagus, especially in the case of A. plumosus where the phylloclades have a radial symmetry (Kaussmann, 1955).

The progression of integration seen in these phylloclades may be suggestive of an evolutionary trend within this group. For example, one could postulate that since most of the Asparagaceae's close relatives have typical leaves and axillary shoots, that plants with phylloclades could have evolved from plants having typical axillary shoots. It should be kept in mind, however, that structures (i.e., phylloclades) do not evolve from the modification of other structures (leaf or shoot) but through the combination or integration of developmental processes typical of different organ cagetories. In this respect, the phylloclade is an example of morphological novelty and is not an ancient or relic structure as has been proposed in the case of Phyllocladus (Keng, 1974, 1977).

Homeosis may also be useful in explaining other organs that combine leaf and shoot features such as the phyllomorph of

Streptocarpus (Jong and Burtt, 1975; Rosenblume and Basile, 1984). The "indeterminate leaves" of Lygodium (Bierhorst, 1971; Mueller, 1982, 1983), Guaria (Mabberly, 1979; Fisher, 1984) and Chisocheton (Fisher, 1984; Rutishauser and Sattler, in prep.) for example may be cases where developmental processes characteristic of caulomes have combined with those typical of leaf sites. Conversely, the appearance of non-appendicular fronds (i.e., leaves that are the direct continuation of the stem) in certain ferns (Bierhorst, 1973, 1974) may be situations where leaf developmental processes combine with those of the apical meristem and thus would be similar to the condition in the terminal phylloclade of Ruscus.

Homeotic transformations such as these not only provide insight into how instances of evolutionary novelty can arise but at the same time point out inadequacies of traditional definitions of homology that require 1:1 correspondences (Stevens, 1984). Lodkina (1983) has addressed the problems encountered when organs sharing characteristics common to different organ categories are homologized. Sachs (1982) has proposed that the term "hybrid" organ be used to describe these situations. Sattler (1984) has argued that homology should be based on the "hybridization" of the developmental processes that lead to these kinds of organs, rather than on the final structure. This type of approach is obviously one of degree and supports the notion of a partial (Meyen, 1973) or semi-quantitative homology (Sattler, 1966, 1974 a, 1984, 1986). The phylloclades of the Asparagaceae are illustrative of this. They are partially homologous to both stems and leaves because they share developmental processes characteristic of both. This important realization allows for a more flexible and holistic morphology (Cusset, 1982) that does not force atypical forms such as phylloclades into fundamental molds of organ categorization.

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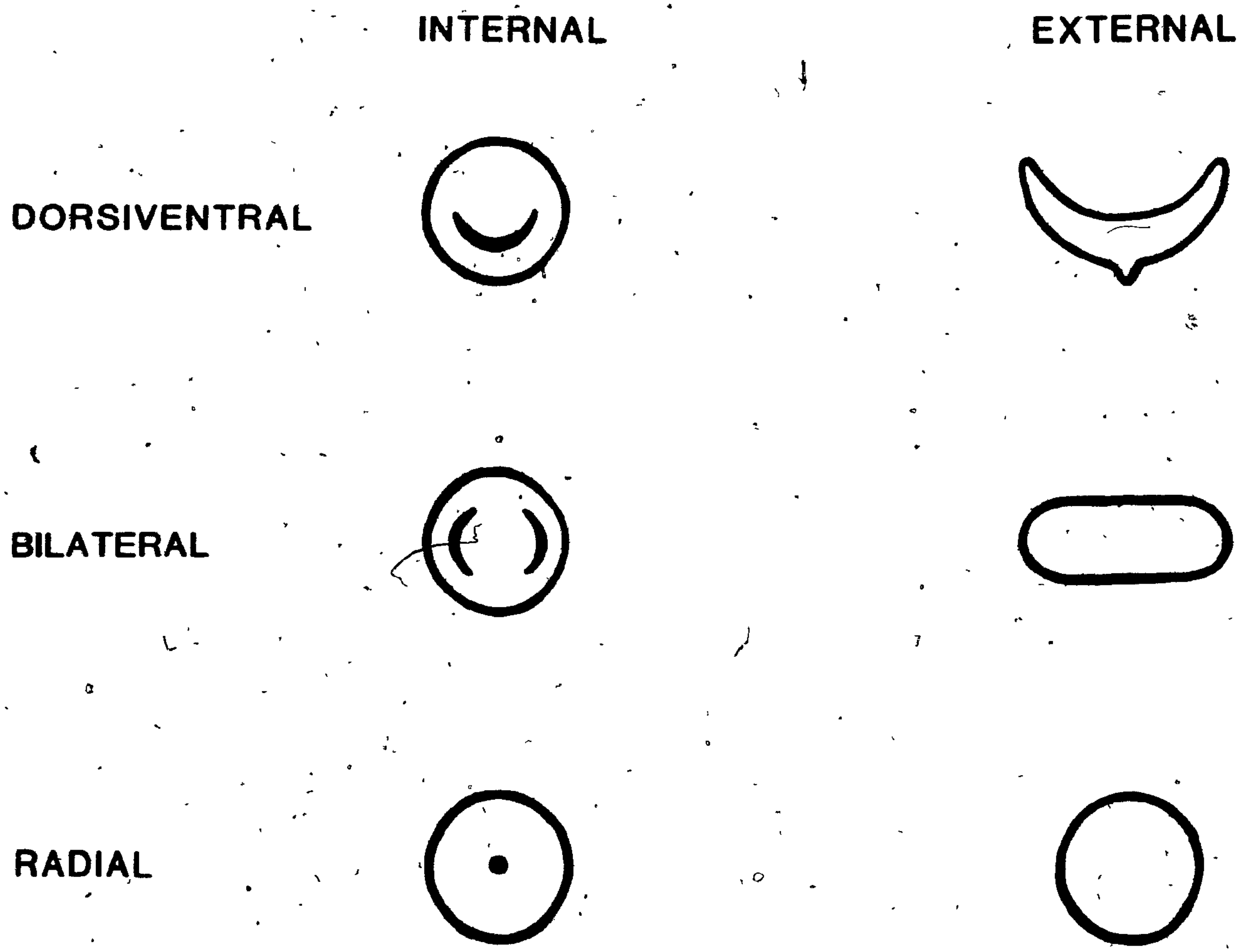
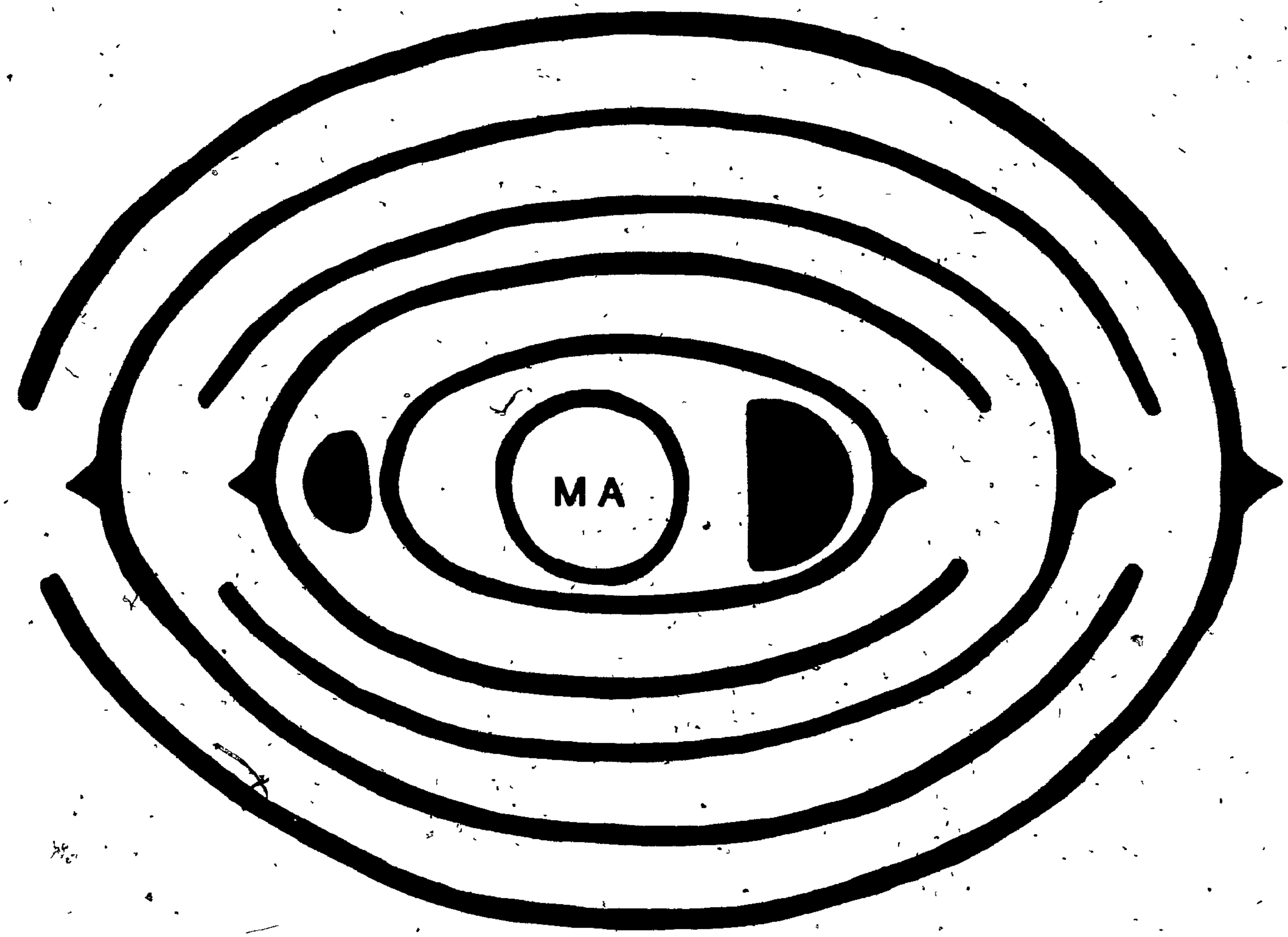


TABLE 1. Types of symmetry based on internal and/or external morphology

Figure 1 Diagrammatic representation of one sympodium of the rhizome of Ruscus aculeatus L. Scale leaf axils one, two and three are empty. Dormant renewal shoot buds (shaded) are found in leaf axils four and five. MA, main aerial shoot axis.



RUSCUS ACULEATUS L.

shoot with phylloclades. The terminal phylloclade (TP) is fertile. A lateral phylloclade (P) is located in the axil of its bract (B).

Figures 3-7 Scanning electron micrographs (SEM) of developing shoots. Fig. 3. Side view of a young second order shoot in which a bract primordium (b) and phylloclade primordium (p) are initiating. Fig. 4. Top view of the apex of a first order shoot that is initiating bract (b) and phylloclade (p) primordia. Fig. 5. Oblique top view of the rhizome apex with developing scale leaf primordia, (b) one of which has been removed. Fig. 6. Oblique top view of a first order shoot apex when it becomes orthotropic. Bilateral second order shoot primordia (s) are axillated by dorsiventral scale leaves (b). Fig. 7. Top view of a first order shoot apex during the changeover from production of second order shoot primordia (s) to phylloclade primordia. It is uncertain whether the primordium in the axil of the bract primordium (b) is that of a branch or a phylloclade.

Figure 8. Portion of the transition zone in the mature plant. A second order shoot (S) has formed in the site normally occupied by a phylloclade (P). Arrowhead indicates scar of deciduous scale leaf.

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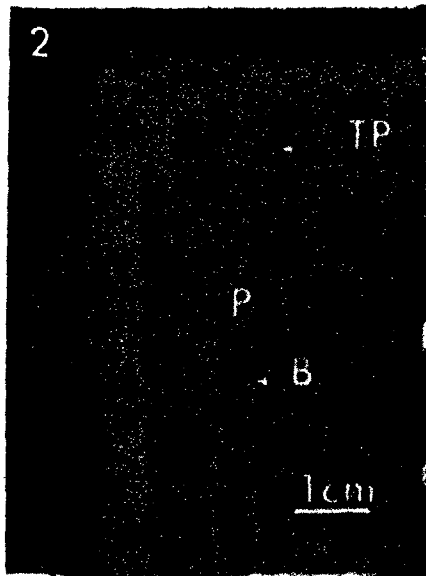

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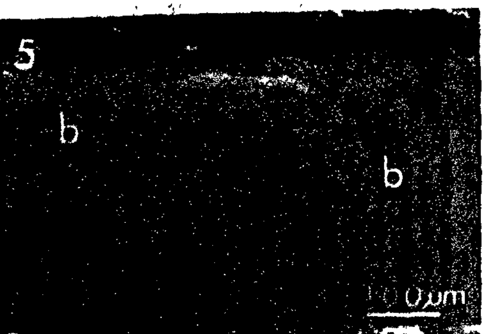

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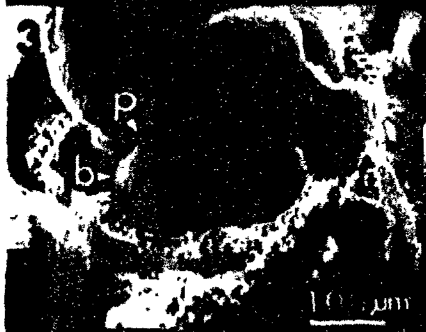

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Figures 9-10 SEM of second order shoot apices with developing phylloclade (p) and bract (b) primordia. Fig. 9. A young shoot in which the phyllotaxis is distichous. Fig. 10. Older shoot with spiral phyllotaxis showing inception of a bilateral phylloclade primordium in the axil of its dorsiventral bract primordium.

Figures 11-12 SEM of fertile phylloclade primordia where an inflorescence bract primordium (rb) has been initiated. Fig. 11. Side view. Fig. 12. Adaxial view.

9

Figures 13-14 Epi-illumination microscopic views of second order shoots. Fig. 13. Top views of a shoot apex that is slightly older than the stage seen in Fig. 10. Note precocious initiation of the phylloclade primordium (p) in relation to the subtending bract primordium (b). Fig. 14. Top view of an apex that has transformed into a terminal phylloclade primordium (tp). Lateral phylloclade primordia are located on either side of the terminal phylloclade in the axils of scale leaves that have been removed.

Figures 15-18 Epi-illumination microscopic views of phylloclades of <u>Ruscus</u>. Fig. 15. Early stage of the initiation of the inflorescence primordium (r) in the axil of its bract primordium (rb) on the adaxial surface of the dorsiventral phylloclade primordium (p) of <u>R. aculeatus</u> L. A portion of the bract (B) that subtends the phylloclade primordium is remaining. Fig. 16. Older developmental stage of the fertile phylloclade (P) of <u>R. aculeatus</u> L. The bract (rb) of the inflorescence primordium (r) has only one procambial trace (arrowhead). Fig. 17. Young fertile phylloclade of <u>R. hypophyllum</u> L. The inflorescence primordium (r) is initiated in the axil of the inflorescence bract primordium (rb) on the abaxial surface of the phylloclade (P). Fig. 18. Adaxial view of young sterile phylloclade of <u>R. aculeatus</u> L. Note leaf-like appearance.

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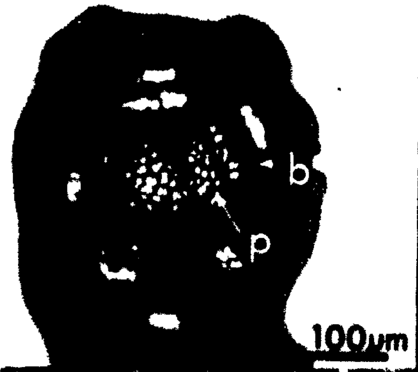
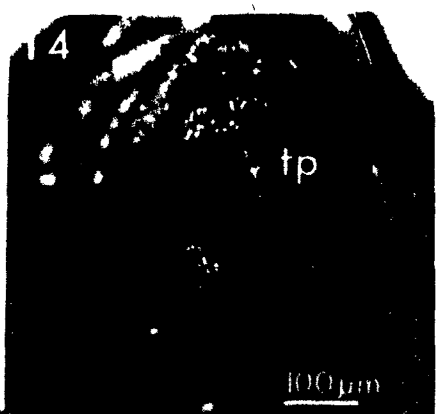
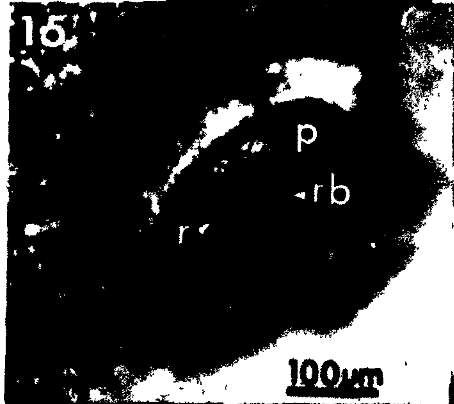
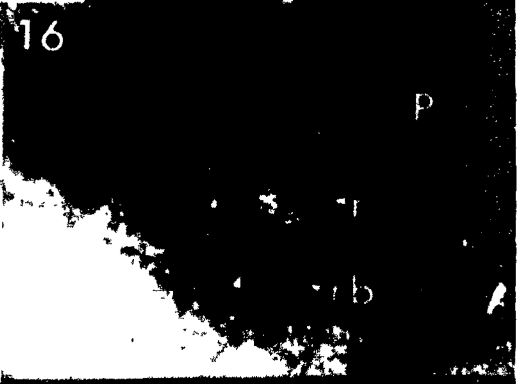
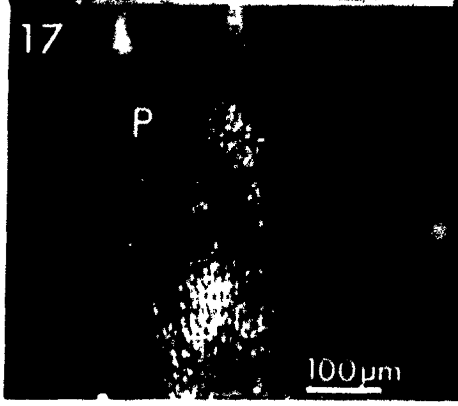
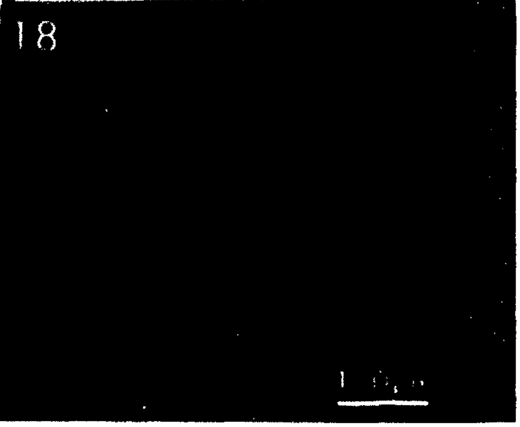






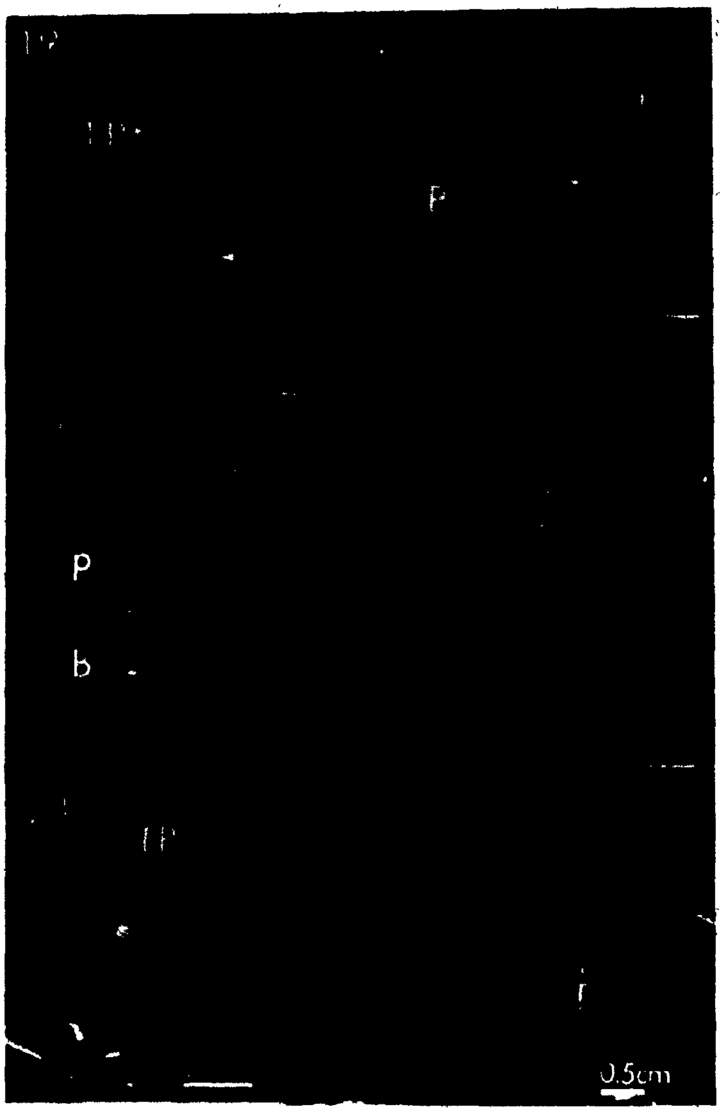






Figures 19-23 Morphological variations or abnormalities in mature phylloclades. Figs. 19-21, 23. Abnormal terminal phylloclades. Fig. 19. Terminal phylloclade (TP) that is fertile, with unusual notched and decurrent margin (arrowhead). Fig. 20. Terminal phylloclade (TP) that bears a lateral phylloclade (p) on its lower surface and has an unusual outgrowth along its mid-rib (arrowhead). Fig. 21. Terminal phylloclade (TP) bearing lateral phylloclade (P) in the axil of bract (B). Fig. 23. Fertile terminal phylloclade (TP) with unusual outgrowth along its lower surface. The tip of the terminal phylloclade is not tapered and spiny but rounded. Fig. 22. Lateral phylloclade taken from transition region of shoot. The inflorescence is inserted on the adaxial surface near a notch in the margin.

Figure 24 Structure from transition region of shoot that could be interpreted either as an abnormal petiolate phylloclade or an abnormal branch. R = inflorescence.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P
p
b
IP
r
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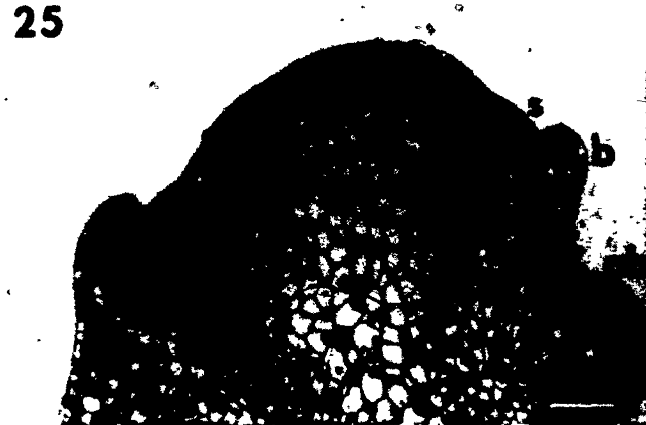
Figures 25-26 Longitudinal sections of plastic embedded shoot apices. Fig. 25. Median section through the rhizome apex as it becomes orthotropic. Two lateral aerial bud primordia (ab) have been initiated. Arrows indicate shell zone underlying younger unlabelled aerial bud primordium. A second order shoot primordium (s) is initiating in the axil of its bract (b). Fig. 26. Near median section of a second order shoot showing the initiation of a phylloclade primordium (p) in the axil of the subtending bract primordium (b). Arrows indicate cell division pattern that resembles a shell zone. An older phylloclade and bract have been labelled to the right.

Figures 27-29 Longitudinal sections of developing fertile phylloclades. Fig. 27. The initiation of the inflorescence bract (arrowhead). Fig. 28. The inflorescence primordium (r) is initiated in the axil of its bract primordium (rb) on the adaxial surface of the phylloclade primordium (p). Fig. 29. Older stage.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Figures 30-32 Cross-sections through developing phylloclades showing dorsiventral symmetry and leaf-like organization. Figs. 30-31. Sections through the middle of the phylloclade. Fig. 30. A lateral sterile phylloclade in the axil of its bract (b) that has one vascular trace (black arrowhead). Three procambial traces are visible in the phylloclade (white arrowheads). Fig. 31. A lateral fertile phylloclade slightly younger than that in Fig. 16. The bract that subtends the inflorescence primordium (r) has only one procambial strand (arrowhead). Three procambial traces are visible in the phylloclade (white arrows). Fig. 32. Cross-section through the bases of the phylloclade and its subtending bract (b). Only one procambial strand (arrow) is present in the bract; the phylloclade has three (arrowheads).

Figure 33 Median longitudinal section through a shoot apex that has transformed into a terminal phylloclade primordium (TP).

Figure 34 Median longitudinal section through a young sterile phylloclade showing vascular connection with its subtending bract (B).

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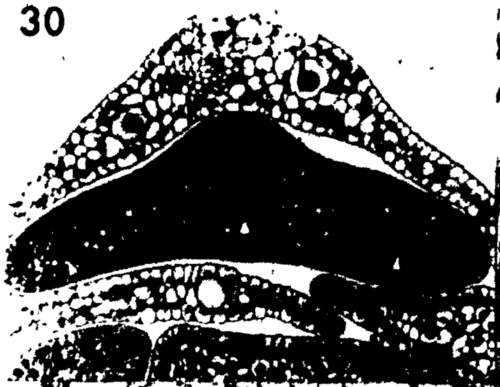

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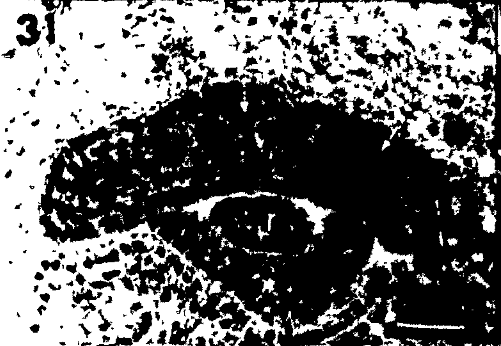

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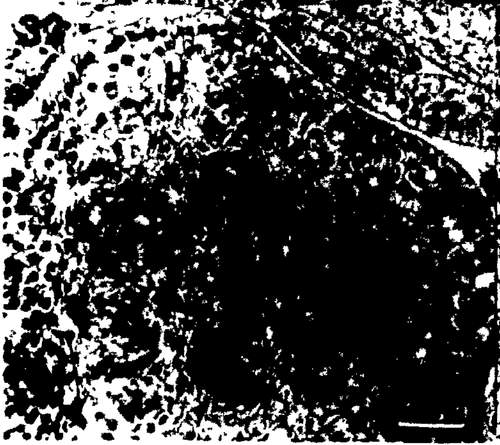

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Figures 35, 37, 39 Cross-sections through the mature sterile phylloclade. Fig. 35. In the base an ellipse of sclerenchyma surrounds the vascular bundles. Arrows indicate the direction of the xylem. Fig. 37. Section through the middle region showing typical leaf-like anatomy and symmetry. The xylem of the median vascular bundle and the one to the left of it is inverted. Fig. 39. Section just beneath the tip still shows dorsiventral symmetry. Cells in the middle region of the section are differentiating as sclerenchyma.

Figures 36, 38, 40 Cross-sections through the mature fertile phylloclade. Fig. 36. Through the base, arrows indicate direction of xylem. Fig. 38. Section through the region just beneath the insertion of the inflorescence. Traces that supply the inflorescence are visible. Fig. 40. Section above the insertion of the inflorescence. The vascular bundles are in a dorsiventral arrangement.

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Figures 41-42 Clearings of mature phylloclades showing leaf-like venation patterns. Fig. 41. Sterile terminal phylloclade. Fig. 42. Lateral fertile phylloclade.

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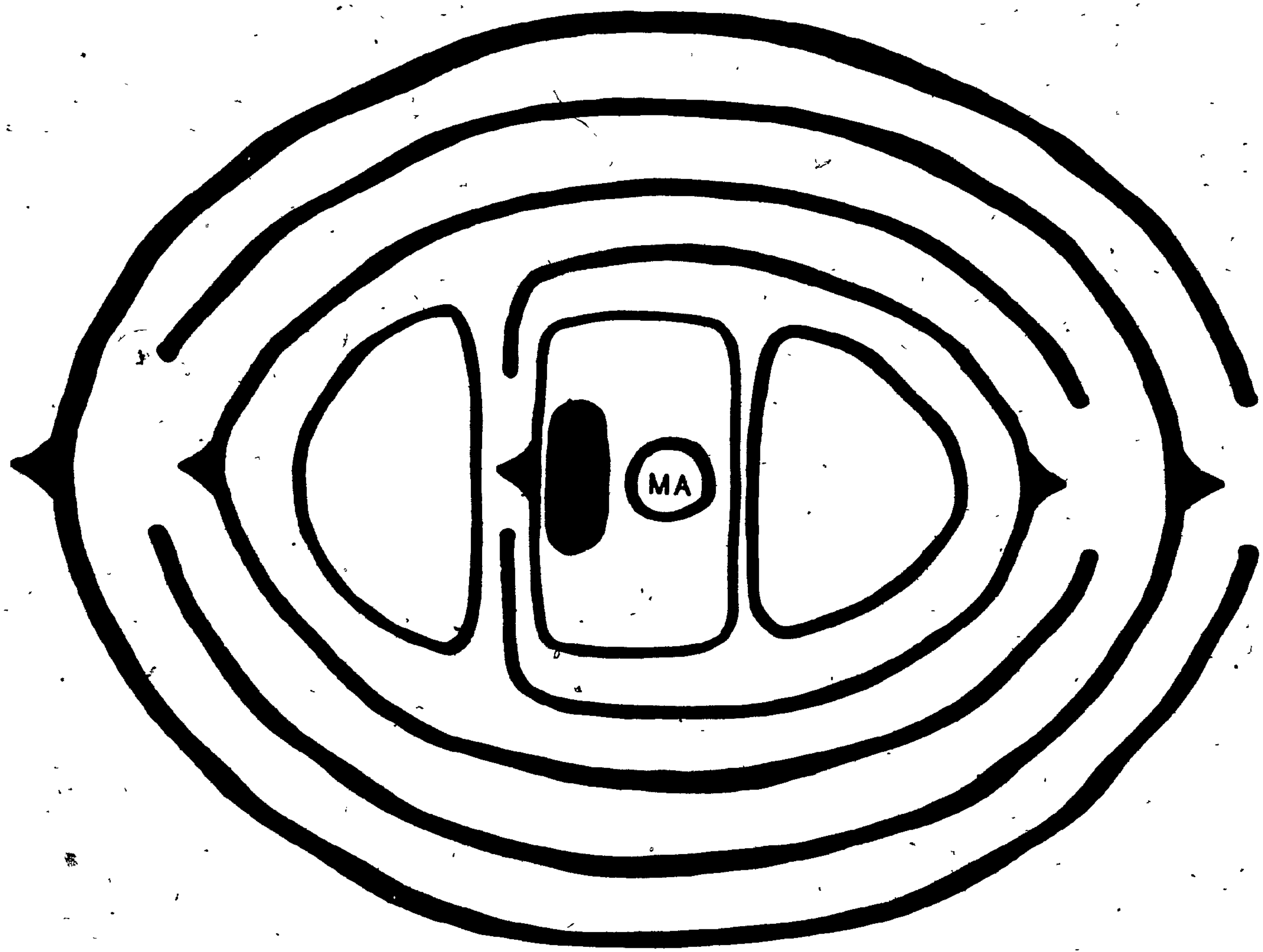
Figure 43 Diagrammatic representation of one sympodium of the rhizome of *Danaë racemosa* Moench. Scale leaf axils one and two are empty. Dormant renewal buds (unshaded) are found in the axils of scale leaves three and four. A dormant aerial shoot bud is found in leaf axil five. MA, main aerial shoot axis.



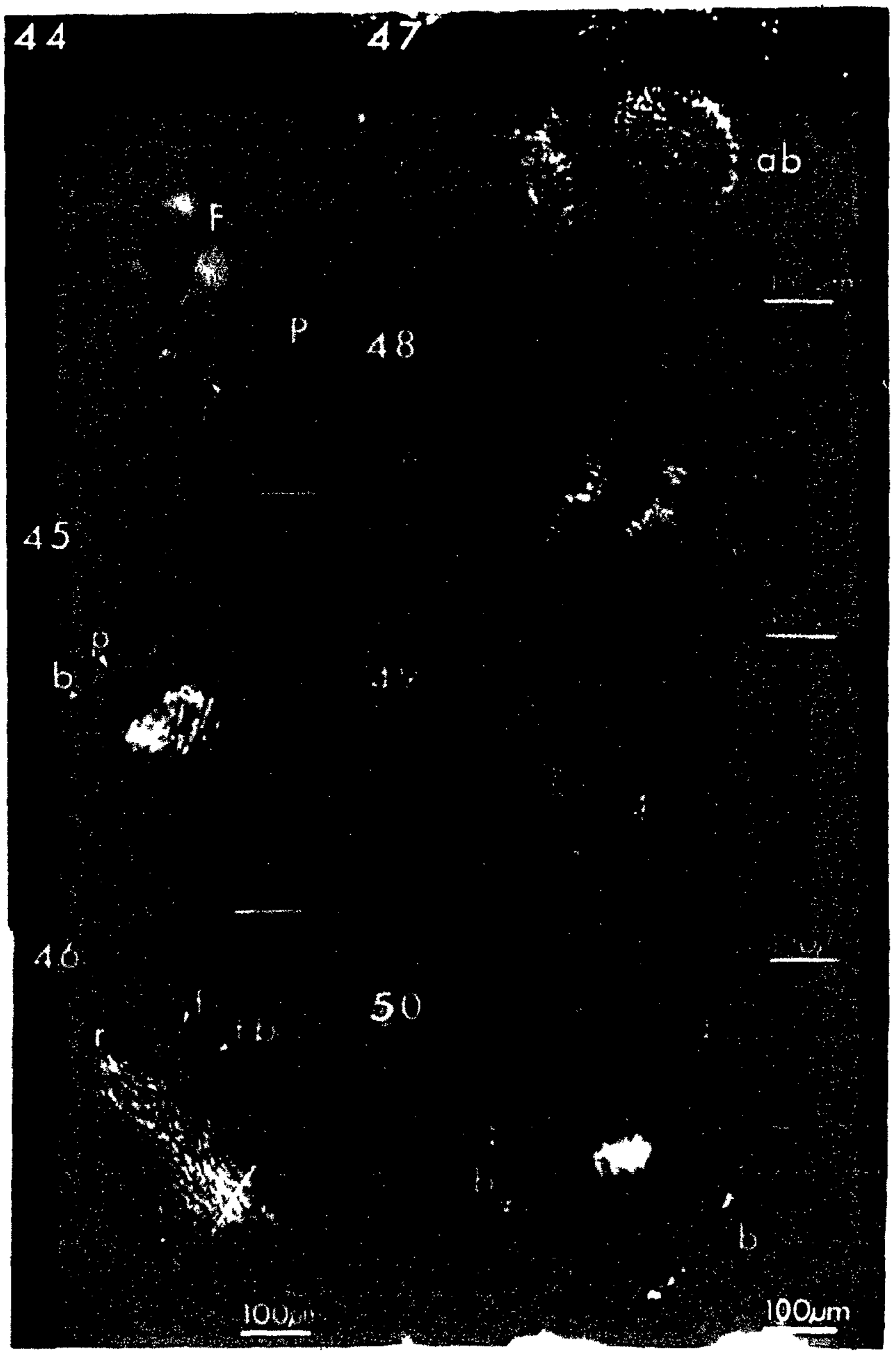
DANAE RACEMOSA MOENCH

Figure 44 Portion of a mature fertile shoot of Danaë racemosa Moench. A bract (arrowhead) subtends a lateral phylloclade (P). F, flower.

Figures 45–46 Side views taken with epi-illumination microscopy showing developing second order shoots. Fig. 45. A young sterile shoot showing the inception of a phylloclade primordium (p) in the axil of a bract primordium (b). Fig. 46. Slightly older stage of a fertile second order shoot with reproductive apex (r). A flower primordium (f) is initiating in the axil of its bract (fb).

Figures 47–49 Top views of developing rhizome with epi-illumination microscopy. Fig. 47. The rhizome apex remains covered by the developing hooded scale leaf primordium (b). The scale leaf subtending the axillary bud (ab) has been removed. Fig. 48. The rhizome apex (v) with developing bract primordium (b). Fig. 49. The rhizome apex just prior to becoming orthotropic. At this stage the scale leaf primordia (b) are still distichously arranged.

Figure 50 Top view of the young orthotropic first order shoot apex. The phyllotaxy of the scale leaf primordia (b) is spiral.


44
F
P
47
ab
48
45
p
b
46
r
50
b
b
100μm
100μm

Figures 51-53 SEM from various angles of the first order shoot apex in transition from the production of branch primordia (s) to phylloclade primordia (p). Fig. 51. Side view showing the associated change from spiral to distichous phyllotaxy. The scale leaf (b) subtends the last formed second order shoot primordium. Fig. 52. The same apex viewed 90 degrees opposite to scale leaf (b) in Fig. 51. A phylloclade primordium (p) is located in the axil of a scale leaf promordium (b). Fig. 53. Top view of the same apex. The phylloclade primordium (p) has the same dorsiventral symmetry as the primordium of its scale leaf (b).

Figure 54 SEM of a sterile second order shoot that is becoming determinate. v, vegetative apex; p, developing phylloclade; b, developing bract.

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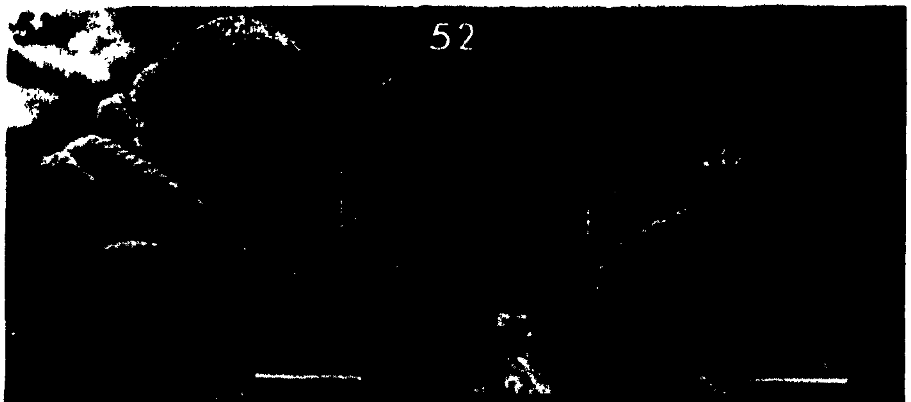

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Figures 55–56 Side views of second order shoots that are becoming determinate, taken with epi-illumination microscopy.

Fig. 55. Slightly older stage than that of Fig. 54. v, vegetative apex remnant; p, phylloclade; b, bract.

Fig. 56. Fertile shoot of an older stage than that of Fig. 46. The reproductive apex (r) has produced three flower primordia, two of which are labelled (f), one with a subtending bract primordium (fb). A phylloclade primordium (p) and the primordium of subtending bract (b) have been labelled for comparison.

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Figures 57-60 Median longitudinal sections through the shoot apex. Fig. 57. A young second order shoot showing early stages of the initiation of a bract primordium (b) to the left and simultaneously to the right the inception of a phylloclade primordium (p) in the axil of its bract primordium (b). Arrows indicate cell division pattern resembling a shell zone. Fig. 58. Reproductive apex of a similar stage as that in Fig. 46, f, flower primordium; p, last formed phylloclade primordium. Fig. 59. A younger stage of the rhizome apex than in Fig. 47, showing the initiation of a lateral bud primordium (s) in the axil of its bract (b). Fig. 60. Determinate sterile second order shoot of the same stage as that in Fig. 55. p, developing phylloclades, v, remnant of vegetative apex.


57
58
P
f
7

Figures 61-63 Cross-sections through the mature phylloclade showing leaf-like symmetry and anatomy. Fig. 61. From the tip of the phylloclade. Fig. 62. From the middle region of the phylloclade. The xylem of the vascular bundles is inverted. Fig. 63. In the base of the phylloclade an ellipse of sclerenchyma surrounds the vascular bundles. Arrows indicate direction of xylem.

Figure 64 Clearing of mature phylloclade demonstrating leaf-like venation pattern. The sclerenchymatous basal portion referred to in Fig. 63 has fallen off.

Figure 65-66 Cross-sections of a developing phylloclade showing dorsiventral symmetry and leaf-like organization. Fig. 65. Above the base of the phylloclade only one procambial bundle is visible (white arrowhead). The bract subtending the phylloclade has one trace that branches (arrows). Fig. 66. At the level of insertion on the stem. Arrow indicates separate trace to the subtending bract. Arrowheads, the three procambial bundles that enter the base of the primordium of the phylloclade.

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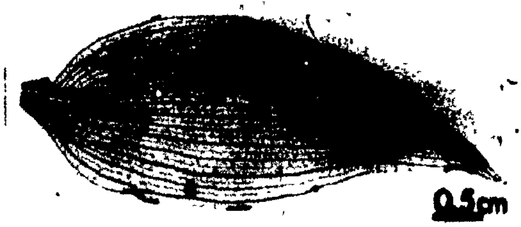

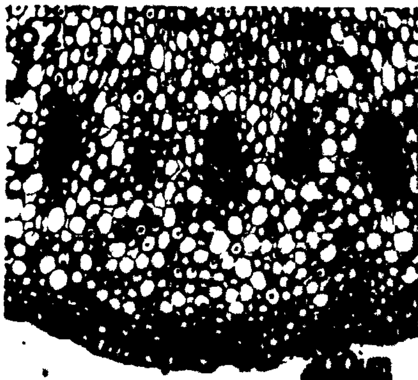

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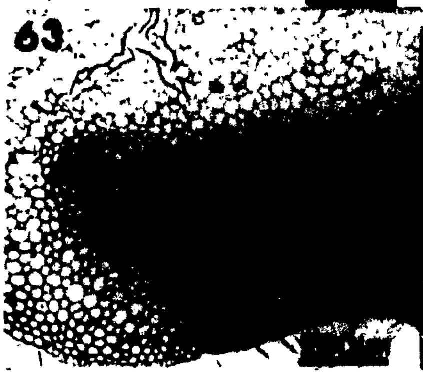
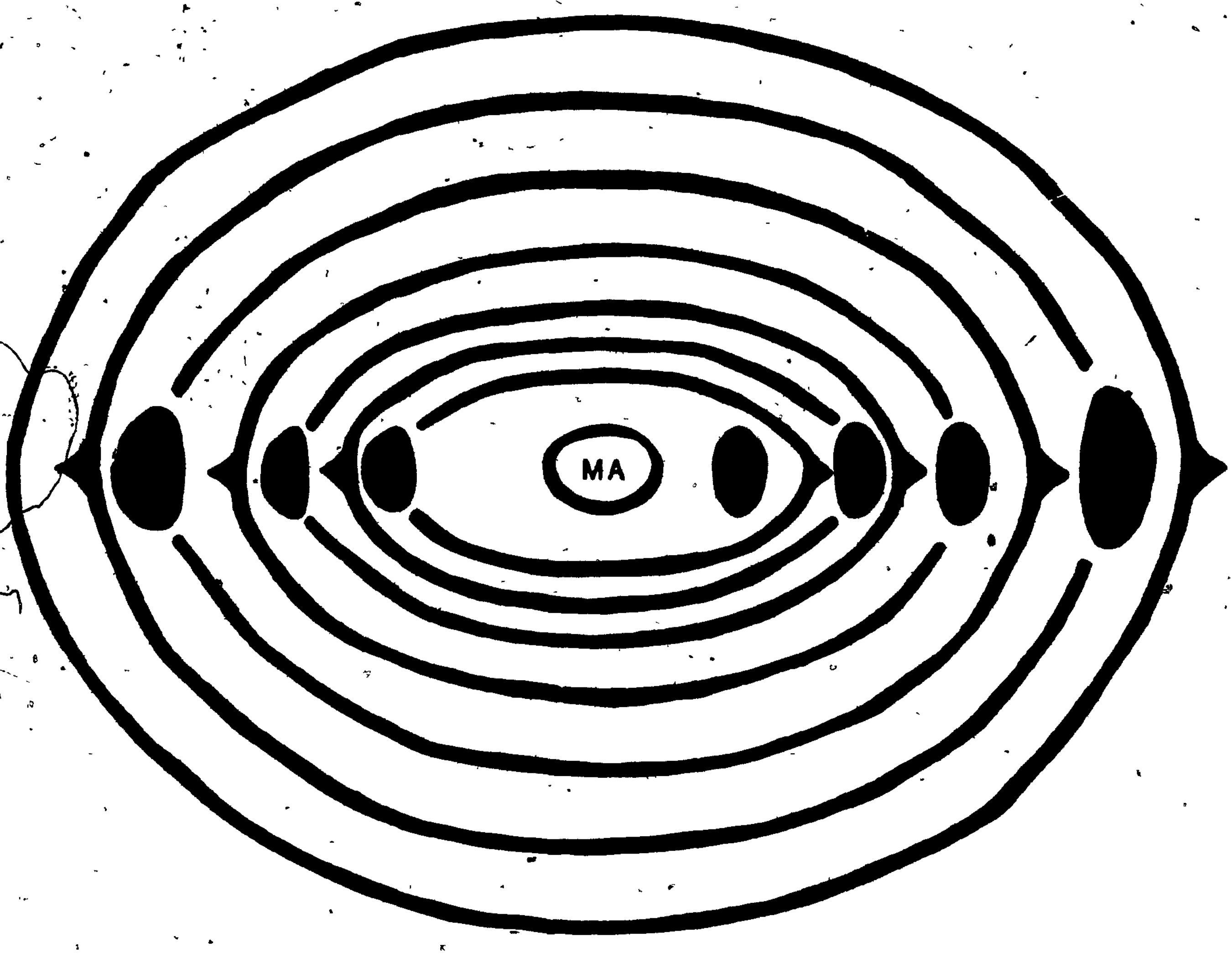


Figure 67 Diagrammatic representation of one sympodium of the rhizome of *Semele androgyna* Kunth. All scale leaf axils contain dormant axillary buds. MA, main aerial shoot axis.

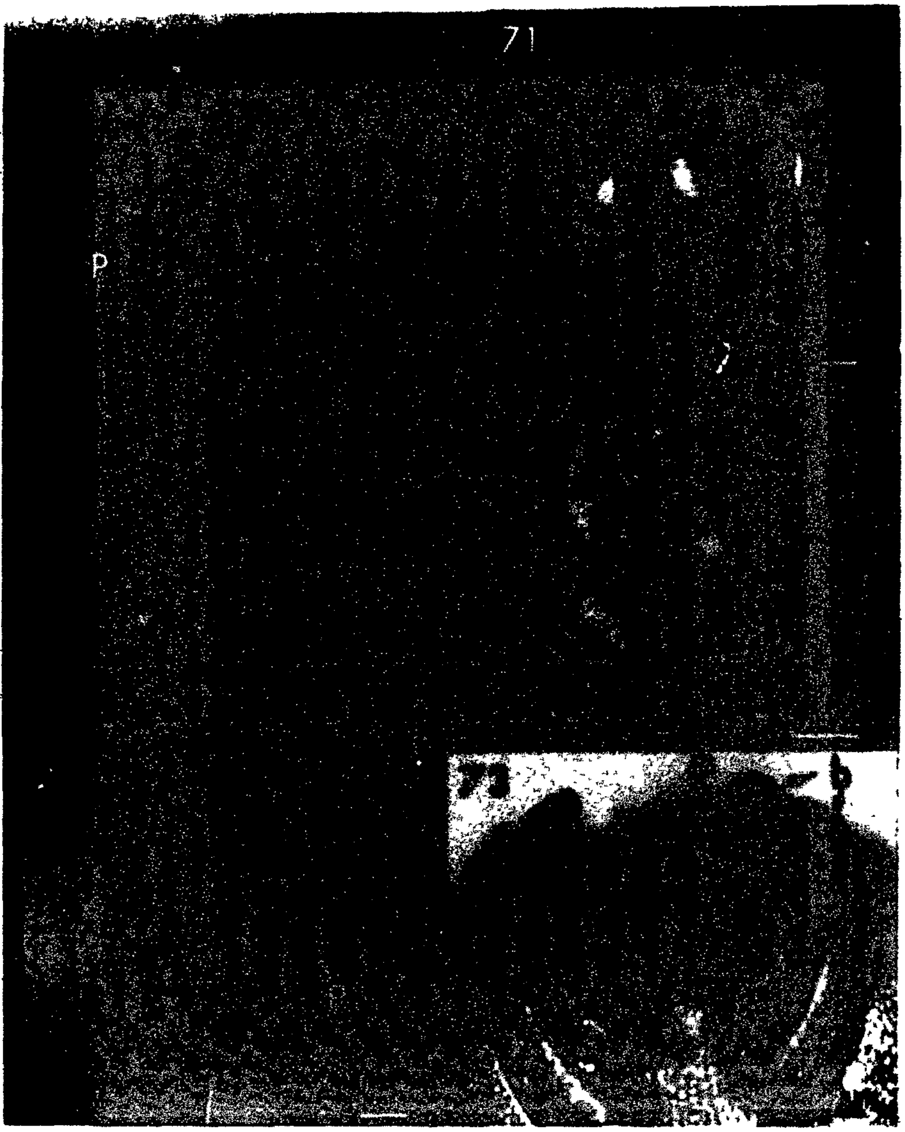


SEMELE ANDROGYNA KUNTH

Figure 68 Portion of the mature shoot of Semele androgyna Kunth in which all phylloclades (P) are sterile. Arrowhead indicates the subtending scale leaf of the phylloclade.

Figures 69-70 Mature fertile phylloclades. Inflorescences (arrowheads) are usually inserted in notches along the margin of the phylloclade. In Fig. 69 an abnormal position is indicated by an arrow.

Figures 71-73 Epi-illumination microscopic views of the shoot apex. Fig. 71. The rhizome apex with scale leaf primordium (b) and an axillary bud (ab) whose subtending scale leaf has been removed. Fig. 72. The orthotropic first order aerial shoot with spirally arranged scale leaf primordia. In the axil of one scale leaf primordium (b) a dorsiventral second order shoot primordium (s) is visible. Fig. 73. A second order shoot that is becoming determinate. The vegetative apex (v) has produced the last phylloclade (p). The rate of development of the scale leaves (b) is greater than that of the phylloclades they subtend.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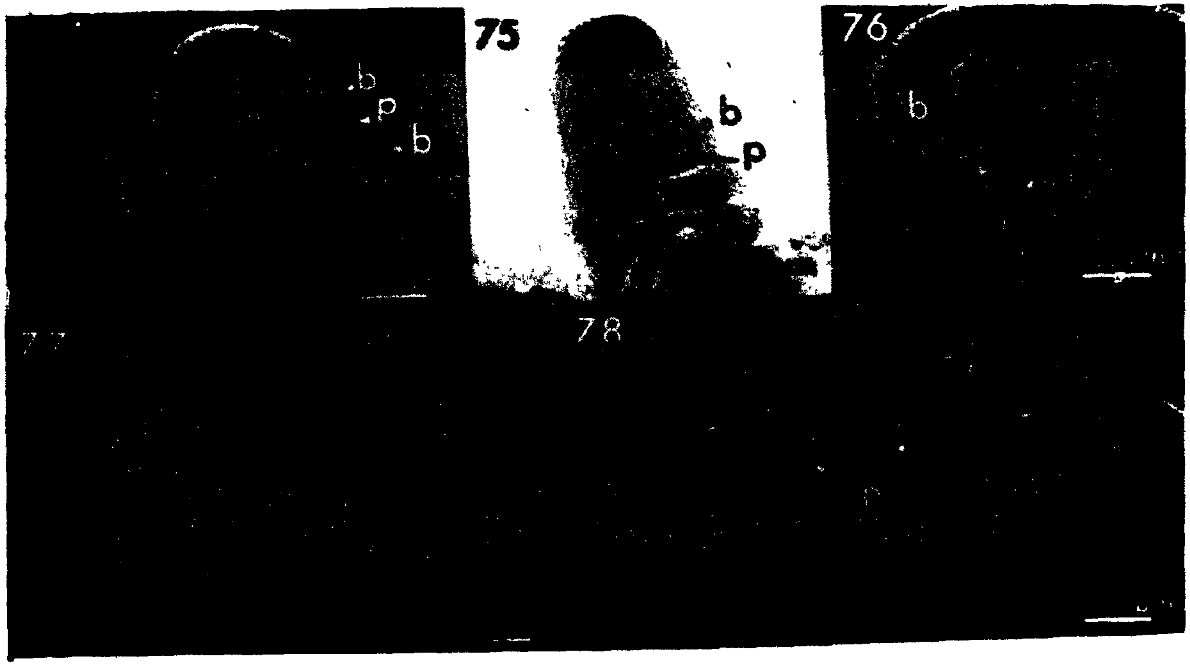
P
73

Figures 74-78 SEM views of developing second order shoots. Figs. 74-75. Side and lateral views of a young apex showing the initiation and subsequent development of bract primordia (b) and the inception of a phylloclade primordium (p). Fig. 76. Top view of an older shoot apex that is becoming determinate. The phylloclade primordia (p) have the same dorsiventral symmetry as their subtending bracts (b). Fig. 77. Top view of a shoot apex younger than that of Figs. 74-75. showing distichous phyllotaxy. Fig. 78. Side view of a stage similar to that in Fig. 76. p, phylloclade primordia; b, bract primordia that subtend the phylloclade primordia.


75
b
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b
b
p
76
b
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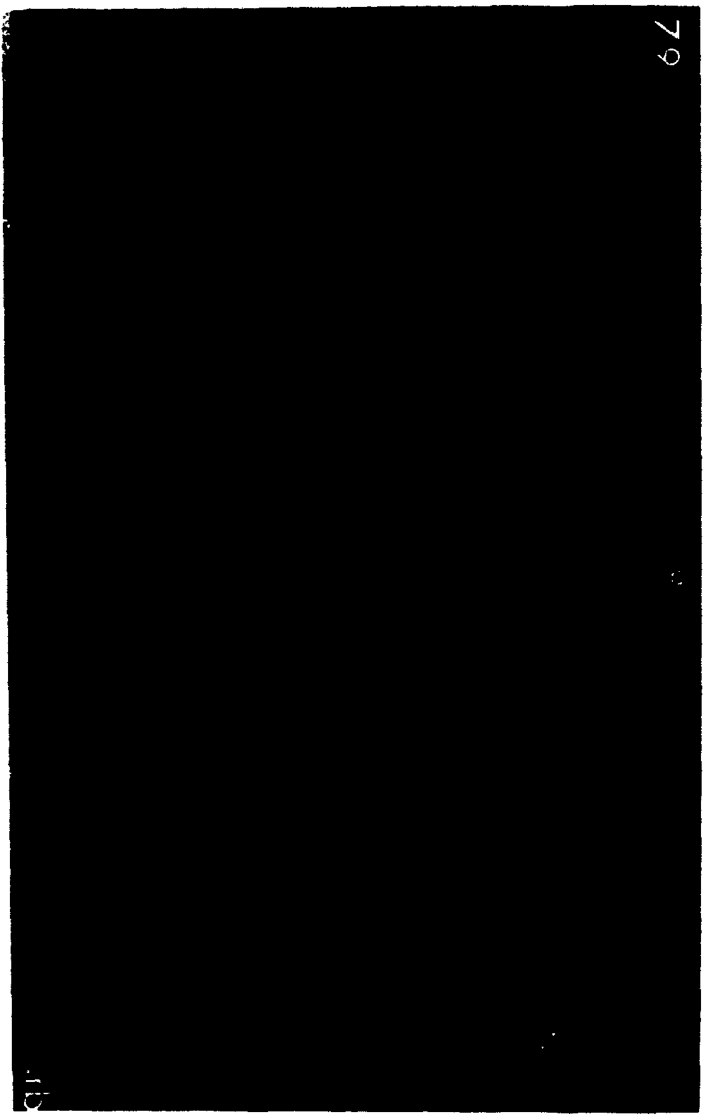
78

Figures 79-82 SEM views of phylloclade primordia. Figs. 79, 80, 82. Fertile phylloclade primordia that bear a striking resemblance to young second order shoot primordia. Inflorescence primordia (r) are initiated in the axils of developing inflorescence bracts (rb). Figs. 79-80 show disruption of the distichous phyllotaxy of the infloresence bracts. Fig. 82 shows usual arrangement. Fig. 81. Young sterile phylloclade (p) with dorsiventral symmetry.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Figures 83-85 Median longitudinal sections through the shoot apex. Fig. 83. First order shoot apex showing the inception of a second order shoot primordium (s) in the axil of its subtending bract primordium (b). Fig. 84. A second order shoot of a similar stage to that in Fig.73 showing the diminution of the shoot apex and the development of young phylloclades (p) in relation to their subtending bracts (b). Fig. 85. Young second order shoot showing the inception of bract (b) and phylloclade (p) primordia.

Figures 86-87 Early stages of the inception of bract (b) and phylloclade (p) primordia. Fig. 86. Magnified view of the right side of the apex in Fig. 85. The arrow points to narrow cells that may have divided recently and be the earliest indication of the initiation of a bract primordium. A phylloclade primordium has not yet been initiated in the axil of the more developed bract primordium (b) but is perhaps being initiated (p) beneath it. Fig. 87. Magnified portion of another second order shoot apex. A phylloclade primordium (p) seems to be initiating in the axil of the lower bract primordium (b). Black arrows indicate a cellular division pattern resembling a shell zone. White arrow points to procambial trace to the bract primordium (b).


83
50µm
84
85
50µm
b
p
87
b
p
b

Figure 88 Median longitudinal section of one side of a fertile phylloclade similar in stage to that in Figs. 79-80, showing the inception and subsequent development of inflorescence primordia (r) in the axils of inflorescence bracts (rb).

Figure 89 Cross-section through the base of a sterile phylloclade primordium and its subtending bract (b). One procambial bundle is present in the bract (arrowhead) while three enter the base of the phylloclade primordium (arrowheads).


88
r
rb
r
rb

Figures 90-92 Cross-sections through the mature sterile phylloclade showing dorsiventral symmetry and leaf-like anatomy. Fig. 90. Section taken through the region of the tip. Three vascular bundles are present. Fig. 91. Section taken through the middle region showing presence of chlorenchyma and stomata along the adaxial surface. The xylem of the vascular bundle is inverted. Fig. 92. Section through the base. The vascular bundles are embedded in a dorsiventral band of sclerenchyma . Arrows indicate the direction of the xylem.

Figures 93-94 Clearings of mature phylloclades with venation pattern characteristic of monocotyledonous leaves. Fig. 93. Sterile phylloclade. Fig. 94. Fertile phylloclades. R, inflorescence.

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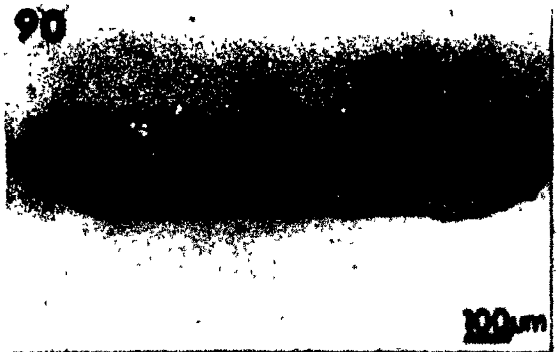

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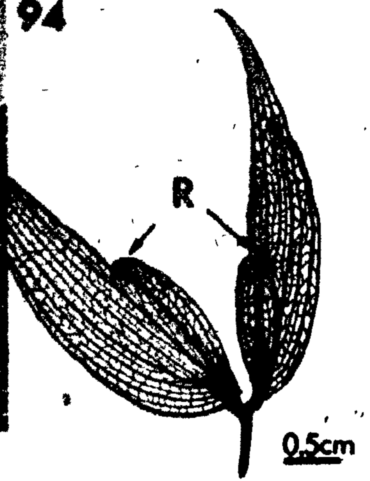
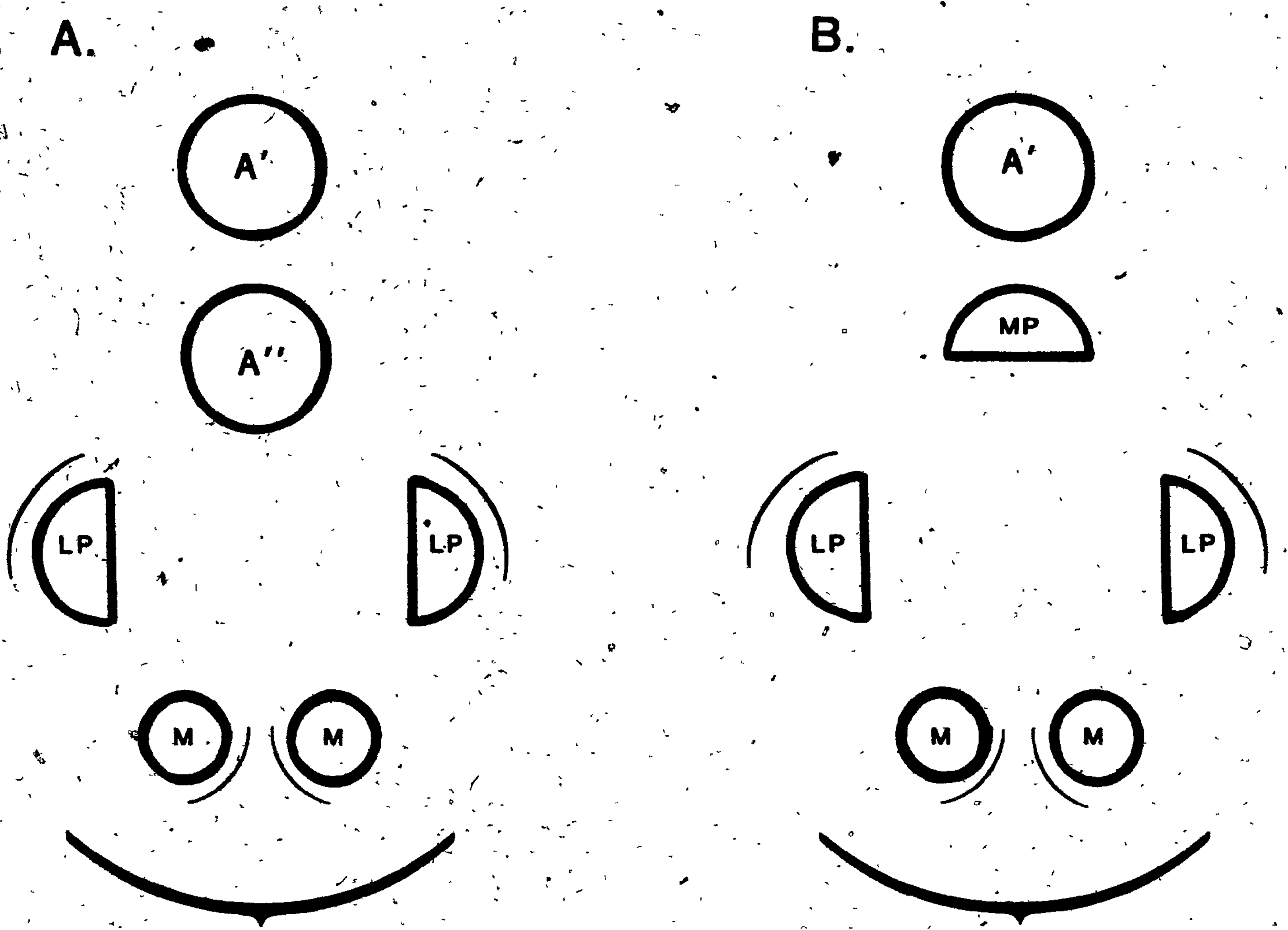


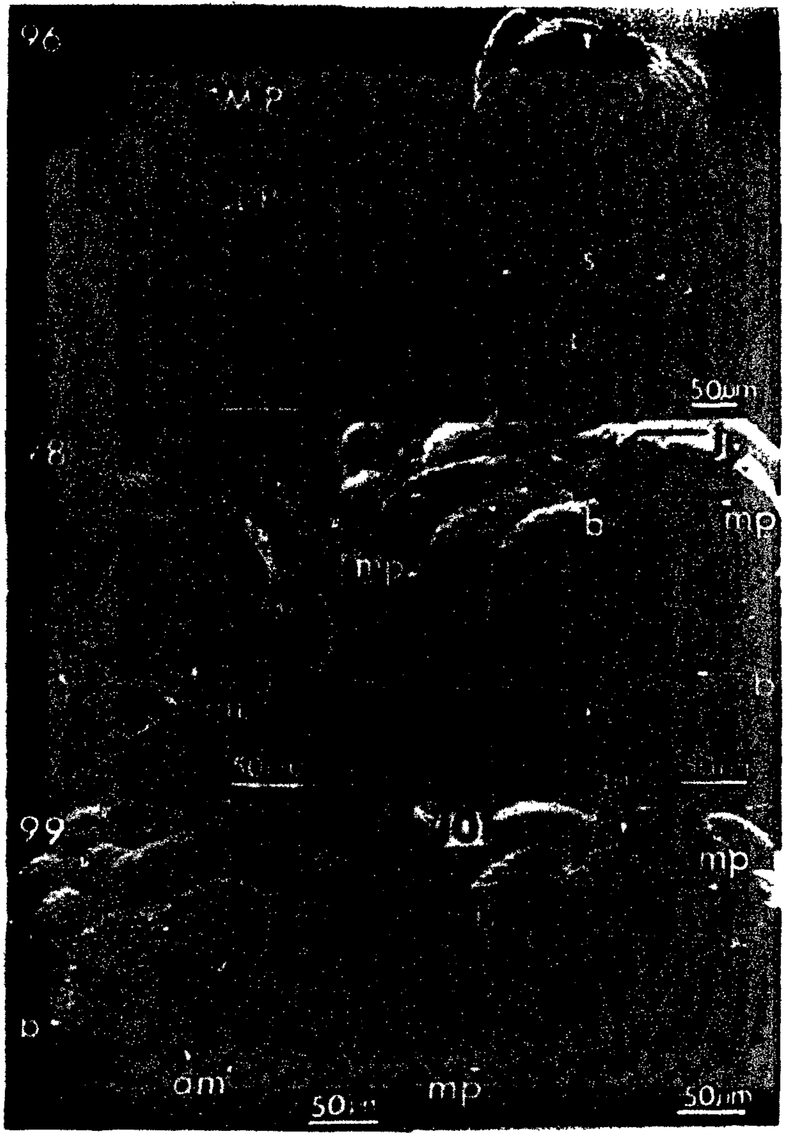
Figure 95 Diagrammatic representation of the nodes of the first order shoot of Asparagus Sprengeri Regel. A.) From the middle region of the aerial shoot. A', the first order aerial shoot axis; A", the second order shoot axis; LP, lateral phylloclade; M, meristem that remains dormant or produces an inflorescence. B.) From the apical portion of the aerial shoot. A', first order shoot axis, MP, median phylloclade; LP, lateral phylloclade, M, meristem that may either remain dormant or produce an inflorescence or another phylloclade.



ASPARAGUS SPRENGERI REGEL

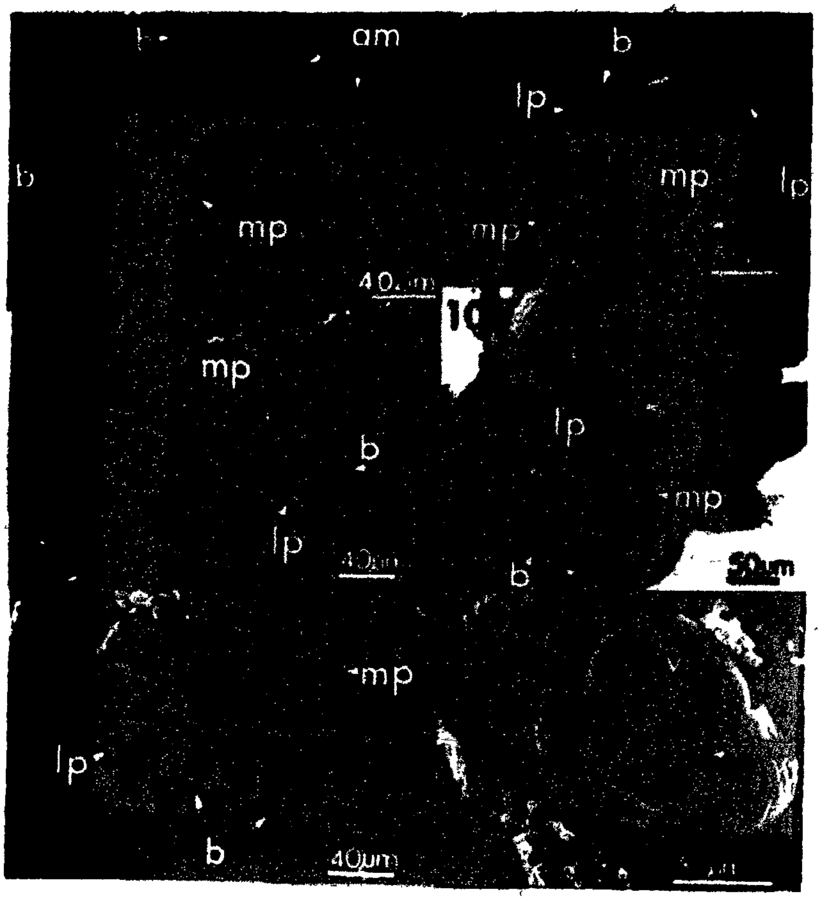
Figure 96 Portion of the mature shoot of Asparagus Sprengeri Regel. A median phylloclade (MP) is situated between two lateral phylloclades one of which has been labelled (LP).

Figures 97-101 SEM of shoot apices. Fig. 97. Side view of a first order shoot apex that is producing scale leaves and in their axils second order shoot primordia. An older second order shoot primordium (s) is initiating lateral bract primordia (arrowheads) along its flanks. The scale leaf that subtended (s) has been removed (b). Fig. 98. Top view of a first order apex initiating scale leaf primordia (b) in a spiral phyllotaxy. The axillary meristems (am) of these bract primordia are dorsiventral. Fig. 99. Top view of a second order shoot in which the apex (v) is starting to become determinate. am, axillary meristem; b, bract primordium. Fig. 100 Second order shoot. The axillary meristem (unlabelled) of the youngest bract primordium (b) represents all that is left of the vegetative apex. The axillary meristem of scale leaves 3 and 4 have begun to form median phylloclade primordia (mp), lateral scale leaf primordia (b) and in the axil of one of these, a lateral phylloclade primordium (lp). Fig. 101. Older stage than Fig. 100. The axillary meristem opposite bract primordium (b) is forming a median phylloclade primordium (mp) at the same time its lower flanks are bulging (arrowhead). An older median phylloclade primordium has been labelled in the lower portion of the photograph.


96
mp
mp
s
50µm
98
jp
b
mp
mp
b
50µm
50µm
99
100
mp
b
am
50µm
mp
50µm

Figures 102-106 SEM of developing phylloclade primordia. Fig. 102. The two youngest axillary meristems have not yet begun to form median and lateral phylloclade primordia. The axillary meristem of the partially dissected bract primordium (b) is forming a median phylloclade primordium (mp). Fig. 103. Older stage in the development of the terminal cluster of phylloclades. The axillary meristems (am) of Fig. 102 have formed median phylloclades (mp) and lateral phylloclades (lp). The subtending scale leaf of one of the lateral phylloclades has been labelled (b). Fig. 104. Formation of phylloclade cluster. Side view of developing median phylloclade (mp), a lateral scale leaf primordium (b) and in its axil, the inception of a lateral phylloclade primordium (lp). Fig. 105. Older stages in the formation of the phylloclade cluster. The median phylloclade primordium (mp) is becoming pointed. Scale leaf primordia (b) are located at the base of lateral phylloclade primordia (lp). Fig. 106. The inception of the lateral scale leaf primordia (b). mp, median phylloclade primordium; lp, lateral phylloclade primordium.

Figure 107 Abaxial SEM view of a second order shoot with young axillary meristem (am) that is slightly bilateral. v, shoot apex; b, scale leaf primordium.


am
b
lp
b
mp
lp
mp
mp
40 μm
10
mp
b
lp
mp
lp
40μm
b
50μm
mp
lp
b
40μm

Figures 108-109 SEM views of older stages in the formation of phylloclade clusters. Fig. 108. Older stage of Fig. 103. The cells in the tip of the median phylloclade (mp) are elongating. The tips of the lateral phyllocaldes (lp) are becoming pointed. Arrowhead indicates possible dormant meristem. Fig. 109. Older stage of Figs. 105-106. mp, median phylloclade; lp, lateral phylloclade subtended by a scale leaf (b). Another scale leaf primordium (b) is located more or less opposite. In its axil is a meristem (arrowhead) that may give rise to an inflorescence or a phylloclade primordium.

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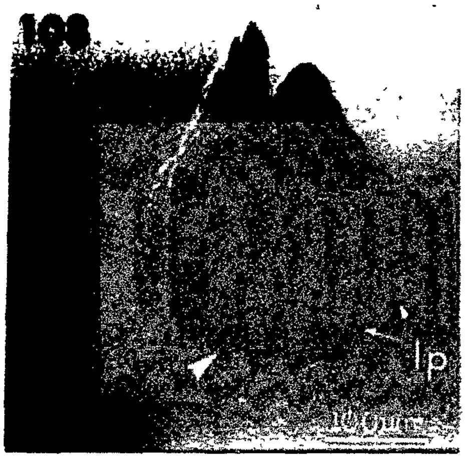

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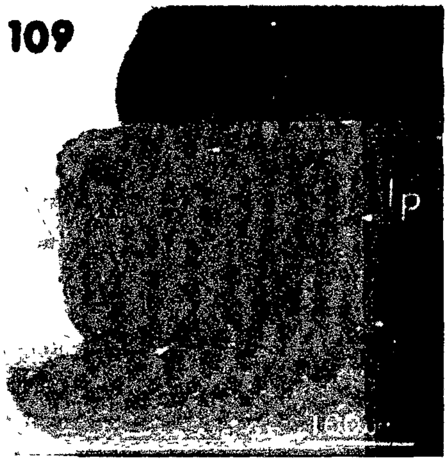
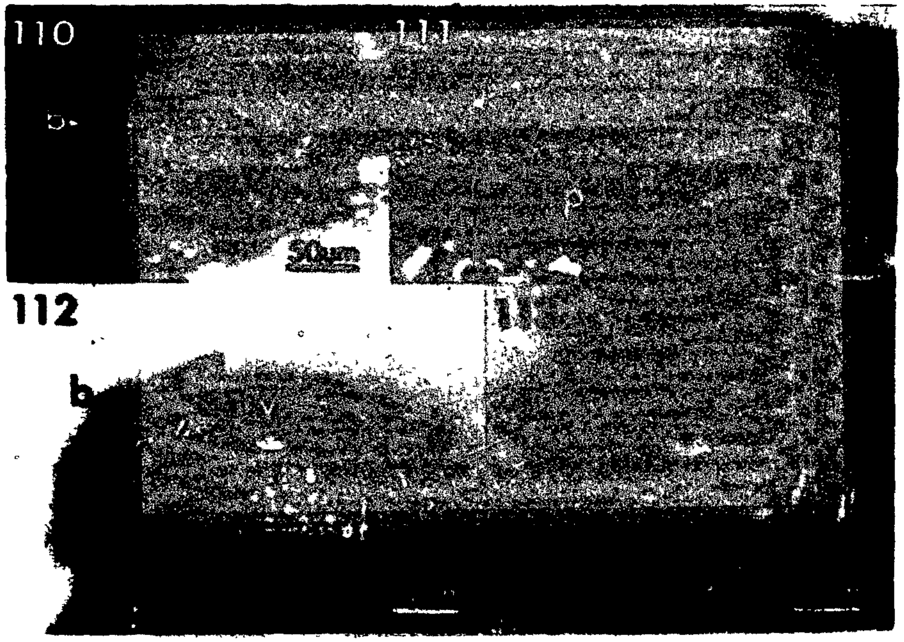


Figures 110-113 Epi-illumination microscopic views of second order shoots. Figs. 110-112. Young shoots from the basal portion of the aerial shoot showing the development of a semi-circular structure (b) that has been interpreted as a prophyll, v, shoot apex. Fig. 110. Top view of the inception of (b). Fig. 111. Top view of older stage. The semi-circular structure has been removed. A phylloclade primordium (p) is in the axil of one of the removed lobes. Fig. 112. Side view of the developing semi-circular structure (b). Fig. 113. Adaxial view of a shoot from the upper region of the aerial shoot showing two separate scale leaves. v, shoot apex.


110
b
111
50um
p
112
b
v

Figures 114-115 Median longitudinal sections through the shoot tip. Fig. 114. Slightly older stage than that of Fig. 98 showing the initiation of an axillary meristem (am); b, subtending scale leaf primordium; mp, median phylloclade primordium. Arrows indicate cell division pattern faintly resembling a shell zone. Fig. 115 Similar stage to that in Fig. 101. mp, median phylloclade primordium; b, youngest scale leaf primordium.

Fig. 116 Slightly oblique longitudinal section through a lateral phylloclade (lp) younger than that in Fig. 109. Arrowhead indicates axillary meristem that may give rise to an inflorescence or phylloclade primordium.

Fig. 117 Cross-section through the base of an axillary meristem. Arrow points to provascular trace.

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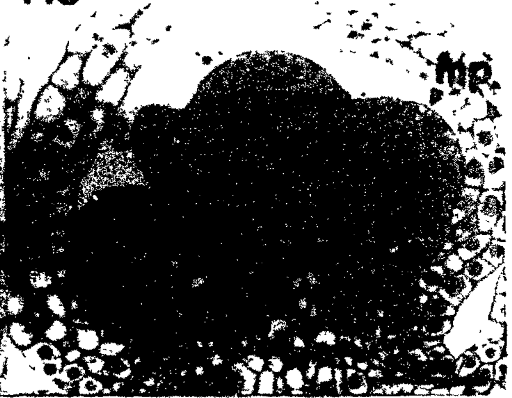

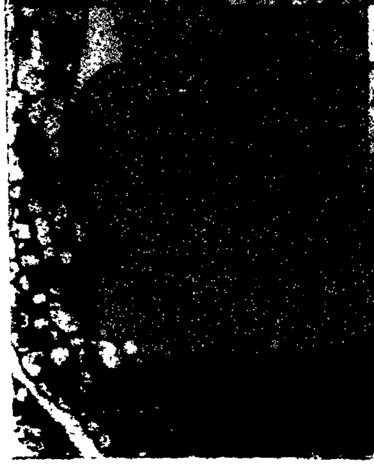

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Figure 118 Cross-section through young axillary meristem with one procambial bundle (white arrowhead). Black arrowhead indicates procambial strand of the subtending bract.

Figure 119 Cross-section through an axillary meristem that has formed a median phylloclade primordium and two lateral phylloclade primordia (lp). White arrowhead points to solitary provascular bundle in the median phylloclade. b, subtending scale-leaf.

Figures 120–121 Cross-sections through older phylloclades. Fig. 120. Through the base of a phylloclade cluster. Arrows indicate procambial strands to lateral phylloclade primordia. Fig. 121. Through the middle region of a median phylloclade primordium (mp). Arrow indicates anomalous provascular bundle.

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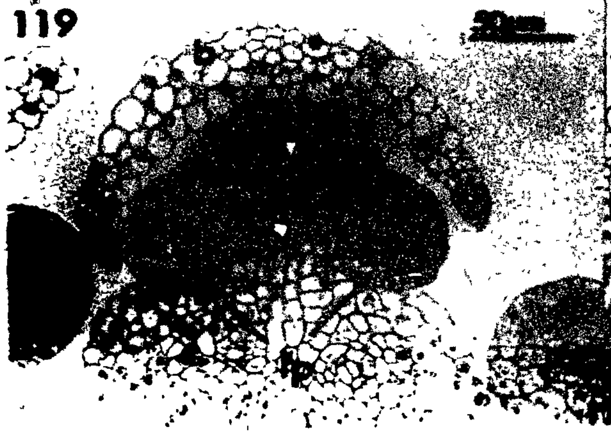

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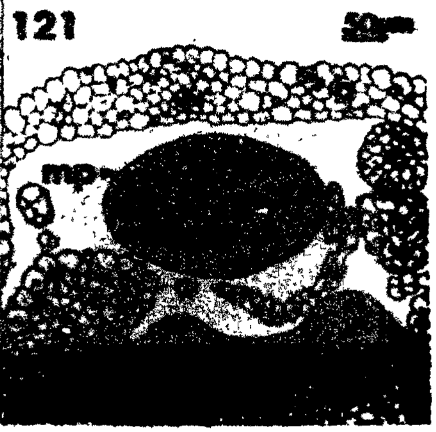

Figures 122-124 Cross-sections through a mature phylloclade showing leaf-like symmetry and anatomy. The solitary vascular bundle has an anomalous structure. Fig. 122. Taken from a region near the tip. Fig. 123. Through the middle. Fig. 124. Through the base.

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124