A morphological-anatomical classification of growth forms in monocotyledons

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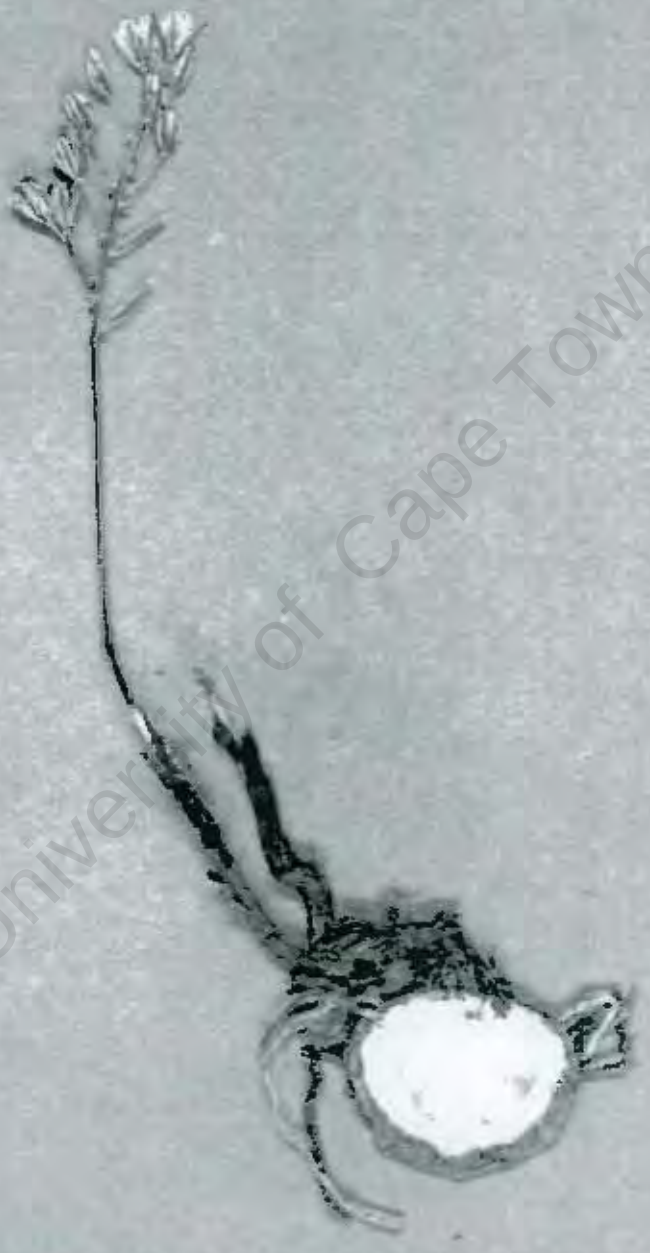

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Declaration

This thesis reports the results of my original research which I conducted in the Botany Department, University of Cape Town, under the supervision of Professor H. Peter Linder between 1996 and 2000. All the assistance that I have received has been fully acknowledged. This work has not been submitted for a degree at any other university.

Signed by candidate

Sioban Lucille Munro

Dedication

This thesis is dedicated to Andrew for teaching me to believe in myself and for all the support and love he has given me over the many years of my university career. And for my parents, Graeme and Paddy, whose own parents never afforded them the opportunity of university study.

Table of Contents

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Abstract

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Growth forms in monocots are diverse, ranging from arborescent forms to creeping, mat-forms. They show the whole spectrum of life forms described by Raunkiaer, but are most diverse as chamaephytes, hemicryptophytes, and cryptophytes. This diversity in form has been attributed to the constraints that a lack of true cambium (dicotyledon cambium) has placed on growth and therefore, the necessary evolution of the sympodial method of renewal growth. Many of the plants show modifications to the *stem-like* regions. These are thought to be an evolutionary response to seasonal habitats or an example of neotenous development.

Features such as morphology, anatomy, vascular construction and seedling development determine the growth form of monocotyledonous plants. The sympodial habit consists of a series of internodes which are either vertically or horizontally orientated (vegetative portion) and produce adventitious roots at their nodes. The internodes of the vegetative portion may or may not change growth direction, but will eventually terminate in a flower or inflorescence (reproductive portion). Subsequent growth is by axillary renewal, from axillary buds, which are most often distributed on the vegetative portion.

With such a diversity of forms it has been difficult to interpret the monocot habit in relation to the classical plant morphology model of de Candolle and to recognise the organs comprising the habit as "typical categories" - *stem (caulome)*, *root* and *leaf (phyllome)*. Interpreting monocots as "phytomers" - a series of repeating units, is equally difficult because the vascular system has been shown to be continuous throughout the axis of the monocot plant. The *stem* of monocots is usually composed of two functional portions: a vegetative and a reproductive portion. The classical term of *caulome* refers to both reproductive and vegetative *stems*, but is inadequate as a term for monocot *stems* because these two functional portions often show very distinct features and thus, may appear quite different from one another. Furthermore, the modified vegetative portions of the *stem* or so-called "storage organs" named *bulbs*, *tubers* and *corms*, adds confusion to the already imprecise terminology.

This thesis examines the morphology and anatomy of monocots from the standpoint of both taxic and growth form diversity and attempts to address the problems encountered in classifying and naming the structures which comprise the axial system of monocots.

The morphology and anatomy of the growth habits of a variety of monocots were described using standard sectioning and light microscope procedures. Monocot habits were interpreted without *a priori* recognition of "typical categories" in a non-typological comparative approach. Internodes were coded into binary variables and a similarity matrix constructed on the basis of the Jaccard co-efficient. Similarity between internodes was determined using the multivariate techniques of non-metric multidimensional scaling analysis (MDS) and cluster analysis. Equivalent structures comprising the axial system of monocots are recognised on the basis of this similarity. Using multivariate techniques it could be determined whether a basic pattern of growth form exists (both within and between plants) and whether sympodial growth could be described by sets of features or a series of processes. The axial system of a monocot plant may best be interpreted as consisting of serial homologues - the rhizome and inflorescence axis, each of which have distinctive features, but which are separated by a transition region. The axial system of a monocot plant represents a continuum. When equivalent structures between plants are

compared it is apparent that discrete categories cannot be erected and that intermediates between rhizomes and inflorescence axes must be recognised.

Two growth form models relating to the basic monocot growth habit are proposed, each of which is constructed on the basis of homologous structures. The models relate to the growth orientation of the axial system and are defined as a tufted model (orthotropic growth) and a rhizomatous model (plagiotropic growth). The basic growth form models proposed for monocots are most similar to growth habits in sister taxa e.g. some Piperales. Terms which refer to the determined equivalent structures (homologues) are proposed and aspects relating to the conflict between pattern and process in homology recognition are highlighted. Variations of these models represent the diversity in the axial system of monocots e.g. swollen internodes to form storage rhizomes or leafless, photosynthetic internodes of inflorescence axes, which determines the diversity in growth forms. Variations of the axial system represent modifications of a basic growth form pattern and thus terms which have referred to modified structures are simply "special terms".

CHAPTER 1

General Introduction: philosophical aspects of monocot growth form

"In botanical language, the stems of plants are not always called by the same name. The stems of trees, as the Oak, or of Palms, bear the name of trunk. The stems of Gramineae, commonly cylindrical, and nearly always indented by annular knots from which the leaves spring, are called the culm."

L. Figuier (1892)

THEORETICAL BACKGROUND

The difficulties in identifying portions and naming terms which refer to the stem of monocots, along with the philosophical interpretation of plant form are a central issue in this thesis. While this thesis concerns growth forms of monocots, philosophical issues relating to plant form in general and the process of typology cannot be ignored, because it has influenced the view that morphologists have about the construction of the monocot plant.

Monocot growth forms

Sympodial growth in the absence of cambium

The most coherent model of the sympodial monocot growth habit was developed by Holttum (1955) in which he proposed that the variation in growth forms (including the annual habit) evident in the monocots are modifications of a single basic growth pattern. Deviations from the theme are represented by the monopodial growth habit. The monocot growth habit is limited by the reduced occurrence of secondary growth which has placed a number of constraints on the development of various structures. The loss of cambium was related to a continuously growing habit (tropical) which ultimately resulted in sympodial growth. The basic monocot habit was proposed to consist of an axial system of compactly arranged nodes and internodes basally, with basal innovation buds that develop into vertical axes terminating in an inflorescence. This tufted growth form, could be modified in a number of ways in response to seasonality. The basal innovation buds were able to grow slightly laterally initially, to carry the new axis clear of the original one.

Gradually, a longer horizontal portion was maintained in the early stages of the axial development, which allowed separation between renewal axes and exploration of new soil. The horizontal portions of the axis would grow for some distance and then turn upwards developing into a vertical axis terminating in an inflorescence. This habit was adaptable to resting phases. The vertical axes could be produced on a seasonal basis, under favourable conditions from the axillary renewal buds positioned on the horizontal portions. Furthermore, the horizontal portions could undergo modification to form fleshy water and nutrient storage structures which could be utilised for the following season's growth. Most of the variation e.g. bulbs, tubers, pseudobulbs, corms etc. could be derived from this basic growth pattern.

The few exceptions that deviate from the basic theme, could be attributed to the presence of lateral inflorescence axes and monopodial growth. Holttum (1955) also recognised irregular sympodial growth and suggested that a precise description of the growth habit of plants with this method of sympodial growth was difficult. The example he offers as indicative of irregular sympodial growth is *Pandanus* which has terminal inflorescences and irregular lateral branching which is not related to flowering. Similar vegetative branching and irregular growth patterns are observable in terrestrial orchids of the Goodyera tribe.

Monopodial growth

The departure from basic sympodial growth is evident in some of the runners of Gramineae in which indefinite monopodial growth is displayed and erect leafy stems develop from lateral buds on the runners. Monopodial growth habits are also found in some orchids e.g. Sarcanthine orchids and Vandoid orchids, *Dipodium*, *Vanilla* and *Galeola*. The stem apex has indefinite growth and usually, the internodes are elongated and the stems are often climbers. Monopodial orchids can produce roots at all nodes along the stem, rather than just at the basal nodes and inflorescence axes are presented in a lateral position.

The annual habit

The annual habit in grasses is a development from the basic tufted habit of tropical grasses. The annual habit is thought to be an adaptation to climates with a long dry season. True annuals are found in the selected cereal crop plants of cultivation, but most grass "weeds" can develop from seed at any time (Holttum 1955). Few families of monocots include annual plants, representatives occurring mainly in Juncaceae,

Cyperaceae and Poaceae with fewer examples in Burmanniaceae, Centrolepidaceae, Commelinaceae and Liliaceae (Tomlinson 1980). Some aquatic families may contain annual representatives e.g. Potamogetonaceae, Najadaceae and Zannichelliaceae but, Tomlinson (1980), suggests that it is difficult to determine if this is an obligate habit or whether it is related to the seasonality of the habitat.

Architecture and constructional constraints

Although the sympodial habit includes forms (e.g. arborescent forms) which are not constrained by the lack of secondary growth, the architecture that arborescent monocots can achieve is limited. This pattern in architecture is reflected in tree-like monocots with most of the arborescent forms conforming to only a few of the 23 models of tree architecture proposed by Hallé et al. (1978) (see Cremers & Edelin 1995; Mosbrugger 1990; Tomlinson 1980; Tomlinson 1982b). Monocots which have secondary growth do not have elaborate architecture or axis differentiation and conform to a single architectural model of Hallé et al., that of the monocaulous shrub (Tomlinson 1980; Tomlinson 1982b). The sympodial habit and construction of form in monocots appears to be deterministic. The nature of this open system of monocot growth habits is such that opportunistic growth is possible, which results in a plastic, basic constructional framework (Tomlinson 1982b). Despite the overall variation in monocotyledonous habits, they can be classified according to a single constructional principle i.e. where support is provided by isolated strengthening elements (Mosbrugger 1990). The exception is *Musa* where the support for the stem is provided by the overlapping of the sheathing leaf bases (see Mosbrugger 1990). The isolated strengthening elements lack secondary thickening and thus constructional design must be related to the low occurrence of secondary growth in monocots and this seems to be the case for most plants which lack secondary growth (see Mosbrugger 1990). Even in plants which have a secondary thickening meristem e.g. *Dracaena*, the same constructional principle is adhered to. The formation of a single leaf at each node is related to the growth form because the leaf sheath ensheaths the basal developing intercalary meristem and soft growing tissues (Fisher 1973a; Tomlinson 1980). This relationship has arisen in response to sympodial growth.

Vascular construction

The pattern of vascular construction is also associated with the growth form because the vascular arrangement is related to the connection between stem and ensheathing leaf (Tomlinson 1980). The vascular construction of axes in monocots has been examined in

arborescent forms such as palms which have served as a model system for comparative studies (e.g. Zimmermann & Tomlinson 1972). The pattern of vascular construction plays a role in maintaining the more constant features of monocot morphology i.e. axillary branch insertion and sheathing leaf bases at nodes on the stem (Zimmermann & Tomlinson 1972). The vascular patterns of monocots also represent a series of variations on a basic theme (Zimmermann & Tomlinson 1972). The variations in vascular construction are often related to the length of internodes and the method of attachment of lateral structures (Tomlinson 1995). The continuity in the vascular system of monocotyledonous stems is achieved by the branching of each vascular bundle at intervals associated with contact with the sheathing leaf (Tomlinson 1970a). One branch feeds the leaf directly (leaf trace), while the other continues to be axial and will serve to form a branch to the next leaf in the order. The leaf trace may branch further to form a leaf trace complex (satellite bundles) the component bundles of which also branch to form bridges which link to the vertical bundles. These observations have lead to the idea that the monocot axis is composed of a peripheral and central vascular system which is intricately linked to the functional whole of the growth form (Tomlinson & Zimmermann 1969; Zimmermann & Tomlinson 1972). This model of vascular construction applies to monocots which do not have horizontal nodal plexi. The nodal discontinuity is maintained by the presence of intercalary meristems in these nodal forms, but Tomlinson (1995) suggests that there is no reason why the constructional principles of the vascular system should be any different to that proposed for palms. The vascular supply to branching portions of the axis is predetermined early in the ontogeny of the plant and thus axillary buds will have a vascular connection to the main axis, whether they develop into branches or not (this is controlled by varying degrees in apical dominance) (LaFrankie 1985; Tomlinson 1995). Thus the overall form, degree of branching, both aerially and basally and root proliferation is determined by the vascular supply which is primary and predetermined.

Cheadle & Uhl (1948) described how the arrangement of xylem within the vascular bundle changed according to the organ that was examined e.g. roots, rhizomes and inflorescence axes. Zimmermann & Tomlinson (1967; 1972) examined the development of a single axial bundle within the axis of a palm and noted that the orientation of the xylem components changed according to the location of the bundle within the axis and the functional nature of the bundle e.g. whether the bundle branches to a leaf etc. Clearly the vascular bundle construction is related to the orientation and functional nature of the axis which is ultimately related to the growth form. This developmental variability of the

bundles is reflected in the pattern of vascular tissue arrangement in the various portions of the monocot axis e.g. internode of rhizome and inflorescence axis.

Branching

The development of a parent axis and the attachment of a branch to that axis in monocots is a primary process because of the lack of secondary growth (Tomlinson 1970a). Thus, branch attachment must be linked to the primary vascular system, which is predetermined in development. Branching is limited in distal parts in monocots due to problems of mechanical stability and no secondary vascular supply to distal parts of the plant (Holttum 1955; Tomlinson 1970a). But, aerial branching does occur, albeit limited and not widespread. Branching in arborescent forms is related to the degree of apical dominance (Fisher 1973a, Tomlinson 1970a). Branching in monocots is most usually by the development of axillary buds in the axil of a leaf on the dorsal side (Tomlinson 1973). Axillary buds are usually singular (Tomlinson 1973), but multiple buds may occur (e.g. Fisher & Moore 1977) as well as pseudomultiple buds (e.g. McClure 1993). Adventitious branching such as budding from leaves is restricted in monocots (Tomlinson 1973). True dichotomous branching is also rare in monocots occurring in *Flagellaria* (Tomlinson 1970b), *Strelitzia* (Fisher 1976), *Hyphaene* and *Nannorrhops*. Leaf opposed buds occur in *Musa* (Fisher 1978) and *Leptocarpus* (Restionaceae) (Tomlinson 1973) while in *Flickingeria* (Orchidaceae), buds are displaced and emerge on the abaxial side of the leaf base (Rasmussen 1982). Further examples of bud displacement are evident in palms, where adnation with inflorescence axes and leaf sheaths occurs (e.g. Fisher & Dransfield 1977) and where the buds are epiphyllous in *Chrysalidocarpus* (Fisher 1973b). Tomlinson (1973) proposes that the initiation of branches and the vascular supply is the same for all variations in branch attachment and that no difference really exists in vascularisation of distinct organs.

Meristems

Lateral meristems

Lateral meristems in monocots also play an important role in establishing the growth form of the plant. Two kinds of lateral meristems occur in the stems of monocots. The first is a primary tissue - the primary thickening meristem (PTM), responsible for the increase in stem girth and is located close to the proximity of the crown (DeMason 1983; Rudall 1991). The PTM is also responsible for the production of adventitious root primordia and the formation of linkages in the vascular system between the axial system and the leaf

sheaths (Rudall 1991). The second lateral meristem is a tissue which is morphologically and developmentally related to the PTM and is located in more distal portions of the stem (Diggle & DeMason 1983; Stevenson & Fisher 1980; Rudall 1991; see also Cheadle 1937). This meristem - the secondary thickening meristem (STM), is found in a few members of the Liliiflorae (e.g. Liliaceae (Rudall 1984) - *Aloe*, *Aphyllanthes, Gasteria*, *Haworthia*; Agavaceae (Diggle & DeMason 1983; Rudall 1984; Stevenson 1980; Stevenson & Fisher 1980- *Agave*, *Beaucarnea*, *Cordyline*, *Dracaena*, *Dasylirion, Furcraea, Yucca*; Iridaceae (Rudall 1984) - *Klattia, Nivenia, Patersonia, Witsenia;* Xanthorrhoeaceae (Diggle & DeMason 1983; Rudall 1984) - *Xanthorrhoea*; Lomandraceae - *Lomandra* (Diggle & DeMason 1983) and is responsible for radial growth in shrubby and arborescent forms (Tomlinson & Zimmermann 1969; Rudall 1991).

Internodal meristems

Holttum (1955) described intercalary growth and suggested that the sheathing leaf base of the monocot habit allows for this kind of stem growth. The extreme example illustrating the supporting role of the leaf sheaths is the growth habit of *Musa*. Intercalary growth is an expression of intensified primary growth (Esau 1953; Evans 1965) and is brought about by localised meristem activity in the internodes. Internodal meristems are responsible for internode elongation in many monocots and may be linked to the establishment of shoot form (Fisher & French 1978). Internodal meristems are located in two areas: at the base of the internodes and displaying basipetal cell maturation is the intercalary meristem (IM), while towards the upper portion of developing internodes an uninterrupted meristem (UM) is found and cell maturation is acropetal (Fisher and French 1976). Intercalary meristems do not have a widespread taxonomic distribution. Uninterrupted meristems, on the other hand seem to be taxonomically more widespread. The internodal meristem type is not generally correlated to morphology of particular species, although forms which lack a sheathing leaf base lack IM's (Fisher & French 1976). Similarly, monocots which do not have distinct nodes typically lack IM's (Fisher & French 1976).

Seedlings

Seedling morphology

The embryo also reflects the monocotyledonous growth form. The single cotyledon is a single leaf which is homologous to a prophyll (= a reduced leaf, the first on a branch)(Tomlinson 1980). Monocot seedling structure is highly variable and is related in

part to phylogeny and the growth habit of adult plants e.g. climbers (Tillich 1995). In the monocot seedling, the leaf morphology of the adult (i.e. leaf divided into sheath plus blade) is recognisable, with the seedling having a single cotyledon which is divided into a sheath and a hyperphyll (terms *sensu* Tillich 1995). Tillich (1995) has described the seedling structure in monocots as follows: the primary shoot may consist of reduced internodes; the first internode above the cotyledonary node is termed the epicotyl and is rarely elongated; the internode portion that is most frequently elongated or modified is the hypocotyl; internodes that elongate above the cotyledon occur frequently in climbing plants; primary leaves may be produced first, but scale leaves can develop initially, followed by primary leaves and then mature leaves; and the primary root of monocotyledons is produced exogenously in the embryo while shoot borne roots arise endogenously.

Establishment growth

While some monocot seedlings show precocial development and flower within the first year after germination, others take several years to develop the structures seen in adult forms (see Chapter 2; Tomlinson 1970a; 1980). This particular, long developmental phase which is required by some monocots (particularly arborescent forms) has been referred to as the establishment phase or growth (Tomlinson & Zimmermann 1966). The establishment phase is necessary in the monocot growth habit because of the primary vascular supply (Tomlinson 1980). This developmental phase (establishment growth) is extended in arborescent monocotyledons so that the massive single axis (such as in palms) can be formed (Tomlinson & Esler 1973). In the developmental phase of forms with primary axes, an obconical seedling axis is formed by the initial development of successively wider internodes which do not elongate (Tomlinson & Esler 1973). There is a concomitant rapid increase in the total number of vascular bundles and abundant root development (Tomlinson 1980). This overcomes the mechanical and physiological restrictions that would otherwise be placed on the tree habit. But, other forms also have an extended developmental phase (see Tomlinson 1990). This varies from the formation of basal suckers in multiple stemmed monocotyledons (Tomlinson 1970a), to the expansion of the hypocotyl internode in tuberous seedlings (Tillich 1995, Chapter 2), to the proliferation of seedling "leaves" for three years before single aerial axes and a stout, branched rhizome are formed in Restionaceae (Chapter 2) and to the negatively geotropic subterranean axis in *Cordyline* (Fisher & Tomlinson 1972).

Philosophy of plant form in relation to monocots

Monocot plant form, while being demonstrably different in many aspects to dicot plant form (Corner 1954; Holttum 1955; Tomlinson 1970a; 1995), has been examined in light of the many theories of plant morphology. When monocot form is considered, a single question comes to mind - what is the basic monocot form? No answer seems to be forthcoming and while many aspects relating to growth form have been considered (e.g. vascularisation, meristems, habit, architecture, seedlings) there is still no consensus (see Arber 1925; Boyd 1932; Corner 1954; Holttum 1955; Madison 1970; Sargant 1903; Tillich 1995; Tomlinson 1970a) or comprehensive overview. Monocot form has been considered idealistically (e.g. Troll 1937), with Candollean concepts (e.g. Hallé, Sattler, Tomlinson) and from the viewpoint of phytonic doctrines (colonial or metameric in approach). Concepts of plant form are steeped in philosophical interpretation and abstraction and as a result are complex. Bloch (1952) and Wardlaw (1951) highlight that the problems of trying to classify form are possibly a result of the inherent complexity of biological form.

Idealism, typology and categories

Goethe is usually given credit for being the first plant morphologist to have considered the elements of plant construction to explain the metamorphosis of plants (see Arber 1946; Sattler 1974; Hagemann 1992). Cusset (1982) has categorised the approach to plant morphology that Goethe proposed as an idealistic doctrine. Goethe established the method of typology by comparing plant organs and determining equivalent structures (see Hagemann 1992). The typological approach is philosophically based on essentialism which can be traced back to Plato, who's philosophy was to view real things as material manifestations of essences (see Sattler 1974). Within the typological framework, each organ being compared must represent the essence of one thing (type) or another (Sattler 1974). Troll and followers adopted the typological approach of Goethe with some modifications of the concept of the type (Cusset 1982). The typological approach of Troll (1937-1943) brought about the idealistic notion of the type as being a realistic entity and not just a representation of essences (Hagemann 1992). In addition to this Troll rejected the notion of causality and thus morphology was considered in isolation of anatomy and physiological experimentation by ideal morphologists (Hagemann 1992). The approach of Goethe and his ideas of the construction of the plant body were refined by de Candolle (Sattler 1974) and as a result a whole new concept of plant morphology came about, which Cusset (1982) has categorised as the Candollean doctrines. Goethe and de Candolle were instrumental in laying the foundations of plant morphological concepts.

The classical plant morphology model

The Candollean concept of plant form has caught the attention of plant morphologists for over a century and has influenced many modern plant morphologists (e.g. Arber, Croizat, Cusset, Goebel, Hallé, Jeune, Sattler, Tomlinson, Van Tieghem, Wardlaw, Zimmermann - see Cusset (1982)). From this concept, two main theories of plant construction have influenced the thinking of plant morphologists and have persisted for decades. These are the models of angiosperm construction (classical model of de Candolle 1827) and that of the telome theory of Zimmermann for lower vascular plants (Sattler 1974). Candollean concepts of form proceed from observable reality towards abstraction (Cusset 1982). De Candolle viewed plants as having a regular plan of construction with symmetrical appendages. Plants could be characterised by the factors responsible for the symmetry and each plant family could be characterised by a regular "kind"- this was de Candolle's type (Cusset 1982). This concept of type is clearly different from a Goethean type because it is a concrete type and not an abstraction (Cusset 1982). De Candolle also proposed three organs, root, stem and leaf, but not from a categorical point of view (Cusset 1982). The Candollean approach was extended into phyllotactic geometry and has been taken up with a mathematical approach today and many models of plant architecture, symmetry and branching have their bases in Candollean theory (Cusset 1982). Similarly, the Candollean approach has influenced plant form concepts based on morphology and function (e.g. Sachs 1982).

In the classical model of the shoot (de Candolle 1827), the "shoot" is composed of two fundamental units (categories): the caulome (stem) and phyllome (leaf). Within this conceptual framework, adventitious roots could also be present on the shoot (Troll 1937). Two assumptions follow this classical model and these are 1) that the two organ categories caulome and phyllome are mutually exclusive and 2) that phyllomes and caulomes are inserted on the caulome (Sattler 1974). Sattler (1974) has proposed that these categories are too rigid and do not allow for the categorisation of structures with combined features of both categories. However, it should be highlighted, that the categorical approach has been established over the years by morphologists utilising Troll's typology, and that such rigid definitions of categories may not have been advocated by Troll (Weber, pers. comm.). Sattler (1974) proposes a "relaxation" of the mutual exclusivity of the categories so that intermediate structures are not forcibly categorised. Arber (1950) also proposed a shoot model (the partial shoot model) with the recognition of intermediate structures. Sattler's (1974) conception of the shoot of higher plants opens interesting considerations about the derivation of intermediate structures and the ecological and physiological factors that play a role in

their development. Similarly, evolutionary questions about homologues are also challenged by Sattler's (1974) "shoot" conception (continuum morphology - Sattler (1996)). The logic which has been carried through time with regards to the recognition of homologues can be traced back to Aristotle i.e. *either* this *or* that and thus, degrees of homology cannot be recognised (Sattler 1994; Sattler 1996).

Phytonic doctrines

In phytonic approaches the plant is viewed as consisting of a number of units or phytons assembled according to the same plan, or natural type (Cusset 1982). In its very basic conception, the phyton concept was applied to both lower vascular plants and angiosperms (Cusset 1982). With time, the phytonic approach took on the idea of a Goethean type e.g. Meyer proposed that the stem was composed of a succession of internodes each giving rise to one or several leaves (Cusset 1982). In all of the phytonic concepts, there is the notion of discontinuity between units (Cusset 1982). Phytonic approaches have been very popular, especially with respect to nodal forms of monocots. In this view, monocots may be modular organisms composed of repeating units. Such units have been termed phyton units - composed of a leaf, internode, shoot bud, and basal node with adventitious root buds (Madison 1970). The phyton unit was proposed early in the history of plant morphology (Madison 1970) and over the years the interpretation of the composition of the phyton unit has varied (e.g. Etter 1951; Evans & Grover 1940; Gray 1879; Priestley et al. 1935; Skutch 1927; Weatherwax 1923). Madison (1970) proposed that the location of the intercalary meristem acts to divide up the repeating units. Sharman (1942) and Zimmermann & Tomlinson (1972) have shown that the vascular system is continuous throughout the axis in monocots with the vasculature consisting of a complex network of branches which supply the nodal structures (phyton units) providing a link between the vascular systems of stem and leaf.

Typology and pattern versus process in monocot growth forms

Typology and idealistic notions about morphology have influenced the interpretation of plant structure in many plant groups. Hagemann (1992) has preferred a different notion of plant growth and development as it pertains to lower plants (similar to the telome theory) and relies on the inter-relationship of anatomy and morphology at the cellular level. The thallus form is maintained by the differential development of the adaxial and abaxial surface resulting in dorsiventrality, and branching is the result of inequal develeopment of thallus tips. The classical categories of phyllome and caulome have been applied to both monocotyledons and dicotyledons. The recognition of monocot axial organs has been problematic (Rasmussen 1985; Tomlinson 1987), suffering from the points that Sattler (1974) raises about categorisation. The trend has been to realise that caulome refers to both vegetative and reproductive

axes in monocots. However, the practise has been to refer to the two axes as separate entities e.g. rhizome and aerial axis (See Tables 4.2 and 4.3, Chapter 4). Anatomical descriptions are a very clear example of the separate consideration of the monocot axis where rhizome (or stem) is treated differently from inflorescence axis (or flowering stem) e.g. Metcalfe/Cutler monocot anatomy series.

The aerial portion has been subject to much interpretation and as a result many terms have been proposed for this axis. A few morphologists e.g. Rasmussen (1985) and Tomlinson (1987) have preferred to consider the axis of monocots as a whole representing a process, that of branching. The difference in perception of the plant body in monocots is due to the importance that is placed on either a pattern based interpretation or a process (functionally) based approach. There is no doubt that the external morphology of monocots displays a specific repeated set of features (pattern) which could easily be interpreted as sets of repeating units (e.g. phyton units). However, if the development and vasculature of the plant body is considered in the interpretation, the monocot plant has to be considered holistically. This is because the axillary bud which gives rise to the axial system is one process (i.e. formation of a branch) and the vascular system is continuous within the axial system. LaFrankie (1985) has demonstrated the vascular connection of the preceding axis with the renewal bud for the following season's growth. The preceding discussion on the various aspects of philosophy of plant form and how the interpretation is affected suggests that plant form, complex as it is with a diversity of facets, may be best viewed pluralistically. Sattler (1996) has proposed a similar notion for classical and continuum morphological concepts.

Current terminology

Rasmussen (1985) has suggested that morphological terminology of plants is necessary to make non-conflicting descriptions of plants and this is important in any comparative assessment of plant form. Terms must apply to the same structures so that there is consensus on their meaning. Thus, terms have to be representative of equivalent structures. The equivalence of structures must be determined as homologues by some of the similarity methods proposed by Kaplan (1984) or using cladistic methodology (e.g. Patterson 1982, de Pinna 1991). However, homology of parts implies a 1:1 correspondence (sameness of parts), which is discrete and therefore categorical in approach (Sattler 1994). For this reason, homologues must be either similar or dissimilar. The result is that intermediate structures cannot be categorised in a 1:1 similarity system. This is problematic because, if terms represent homologues, then there can be no term

for intermediate structures and intermediates must be forced into one category or the other. This has been the problem with idealistic methods of typology in the past when intermediate structures have been categorised.

Rasmussen (1985) highlights that the aerial part of the stem in sympodial orchids which bears lateral leafy appendages seems to lack any consistency in terminology. In fact, so many terms have been proposed for this region of the plant in orchids, that she suggests there is no specific term in use. Rasmussen suggests that this problem applies generally to monocots with sympodial growth habit, but is most problematic in sympodial epiphytic orchids in which the use of the word aerial is inappropriate. Part of the problem of naming structures lies in the conflict between pattern and process in homology recognition. The rhizome plus aerial portions are viewed by some as being part of a series of processes i.e. a branch and its development (see Rasmussen 1985; Tomlinson 1987). Others (e.g. Stern & Pridgeon 1984) have recognised that the aerial axes have a different set of attributes (pattern) from the rhizome portion and thus, warrant a name due to their distinctness. The other problem which is associated with naming structures is preconceived notions of structural categories. Using the classical plant morphology model and the proposed categories with their restrictive definitions can lead to misnaming of structures. An example frequently cited is the phylloclade of Asparagaceae which, due to its position on the axis has to be considered as a stem. However as Cooney-Sovetts & Sattler (1986) have shown, the dorsiventrality of the structure is leaf-like in nature and thus a name for this structure becomes problematic because it can be termed neither stem nor leaf.

Equally controversial is the term rhizome, which refers to the usually subterranean, prostrate, scale-leaf bearing part of the stem. Burkill (1960) suggests that over the years the use of the term has been exceptionally loose so that much confusion exists over exactly what a rhizome is. He proposes that three features are most important in recognising rhizomes: (I) cauline nature; (ii) horizontal orientation; and (iii) thickness. He argues that the underground stem of *Paris quadrifolia* is not a rhizome, but a stolon because it lacks thickness, whereas the underground stem of *Aspidistra* is a rhizome because it has all three qualities. If all of these qualities are applied to all monocot underground stems, we would not be able to recognise many rhizomes, because they may not be "thick". In addition, aerial stems of palms and Araceae could not be recognised as rhizomes because they are not horizontal, and storage axes such as corms cannot be recognised. Categorising organs into rigid terms in this way leads to the recognition of narrow types e.g. synflorescence axis (see Rua & Gróttola 1997), which is

undesirable. On the other hand, too loose a definition for particular structures may also lead to confusion e.g. "root - stem tubers" of Orchidoideae (see Pridgeon & Chase 1995). Bell & Tomlinson (1980) offer a broad and general definition for the term "rhizome" as it relates to the architecture of these axes. They define "rhizome" as: "... indicative of vegetative extension over or within the substrate by means of axis elongation, and include(s) organs which may be distinguished more precisely as stolons, offsets or suckers and which may intergrade with tubers and corms". Monocot growth habits are well known for displaying a high degree of variation in their underground stem components, as well as aerial stems and by adopting an idealistic approach, much of the variability won't be accounted for. This ultimately leads to a greater confusion in terminology of various (or modified) plant parts such as stolons, bulbs or corms.

If there was some notion of what the basic monocot growth habit is, then some idea of appropriate terms could be considered. The basic monocot form is an idea of the general condition, or the most simple form. If a set of terms could be established for the parts comprising the basic habit this could serve as the "prototype" to which all modified structures could be compared and thus, homologues could be determined. Without the basic idea of a type, any comparative approach is impossible. It is important, however, to elucidate the concept of type. The type should be determined *a posteriori*, after considerable examination of form has been undertaken. The type should be representative, but real forms may conform to the structure proposed by the type. The type should as far as possible not be rigidly defined so that categorical structures are recognised. The type should not be conceptually devoid of processes such as genetic modification; extrinsically controlled factors and physiological functioning.

AIMS AND OBJECTIVES OF THE THESIS

From the preceding discussion of monocot growth forms, it becomes apparent that several aspects relating to monocot growth form require further investigation including:

- a consolidation and overall view of the variation in growth habits that exists;
- a summary of the basic morphology and anatomy of the various structures that comprise the monocot plant, from the rhizome right through to the inflorescence axis;
- a general picture of the morphology and anatomy of monocot vegetative structures within single plants as well as between different taxa;
- an examination of the variation of structures within and between plants without the rigidity of *a priori* notions of categories;

- an evaluation of the structures to determine which are equivalent structures (homologues);
- a basic monocot habit derived from the relation between homologous structures and
- a simple terminology based on these homologues to serve as a workable basis for further comparative approaches.

The focus of this thesis is the pattern observable in the morphology of various monocotyledonous growth forms and the main goals are:

(1) to attempt to understand the variation in form by examining morphological (overall form) and anatomical (internal structure) attributes of plants [which may indicate separate levels of organisation e.g. Kaplan & Hagemann (1991); Kaplan 1992]

(2) to propose a classification of the growth forms and associated structures without *a priori* categorisation of structures

(3) to obtain a broad overview of monocot growth forms using a sampling procedure that is designed to observe a diversity of form as well as taxonomic variability. Many of the selected plants are representatives of the Cape Flora and were chosen because of the adaptations they show in relation to seasonal water inundation coupled with summer dry periods, the low nutrient status of the soils, and periodic fires. Habitats such as this often contain plants with elaborate storage mechanisms or water use specialisations. Monocots that have received detailed study in terms of growth habit previously, such as arborescent forms (palms and other woody representatives), Iridaceae, Zingiberales, Orchidaceae and pasture grasses are either not included in this study or are not sampled widely

(3) to be able to recognise homologous structures within the variety of growth forms in monocotyledons. The concept of homology recognition is based on topographic and/or special similarity

(4) to propose a simple terminology once the homologues have been established; and

(5) with an idea of which structures are homologous simple models of the monocot growth form are proposed which may well represent the basic monocotyledonous plan.

ORGANISATION OF THE THESIS

Excluding the general introduction (Chapter 1) and the synthesis (Chapter 5), this thesis is composed of three main chapters. Chapter 2 consists of observations of monocot growth form diversity within and between plants and is the examination of morphology

and anatomy of structures from a diversity of growth habits within a whole range of taxa. Chapter 3 is an analytical chapter and illustrates the use of multivariate methods in the analysis of monocot growth form. The analyses are based on the descriptive data obtained from the observations in Chapter 2. Chapter 4 is the interpretation and discussion of the results from Chapters 2 and 3. Chapter 4 attempts to establish homologues of monocot structures both within and between plants. Homology recognition is based on similarity of parts identifiable from the multivariate analysis in Chapter 3. Growth form models constructed on the basis of homologues are also proposed in Chapter 4 with the overall intention of presenting a simple terminology of monocot structures.

The structure of this thesis is such that all chapters are naturally dependent on those preceding them. Thus, Chapter 2 forms the basis to the issues addressed in this thesis and should be read in its entirety so that a full understanding of growth form morphology, anatomy and biology of the plants examined is obtained. Chapter 3 is really the analysis of this observational data in Chapter 2, and Chapter 4 could be viewed as a general discussion of the observations in Chapter 2 and the results of Chapter 3. Although the intention of this thesis is to examine structures of monocot growth form and to establish homology as well as ultimately, a working terminology, it must be stressed that the approach utilised in this thesis does not rely on the *a priori* construction of categories for the various structures. The focus of the thesis is a pattern based approach to recognising the attributes of various growth forms. Many of the attributes may relate to growth processes and thus, process is not excluded from the recognition of pattern relating to form. However, process assumptions about form are not utilised in initial hypotheses about form. Although pattern is the central theme of the approach to analysing growth forms in monocots, other aspects such as the habitats and ecology that are important in the life history of specific plants are also discussed.

CHAPTER 2

Growth form morphology and anatomy of selected monocots

INTRODUCTION

The monocotyledonous growth form is distinctive, lacking a cambium which precludes true secondary thickening growth (Arber 1925; Holttum 1955; Madison 1970; Tomlinson 1970a). This has resulted in sympodial growth, where roots arise at the nodes along sympodia, the occurrence of renewal growth from axillary buds, and a unique vascular construction which ultimately has been shaped by the sympodial habit. Secondary growth may occur, but arises from a specialised meristem called a secondary thickening meristem (STM) *sensu* Rudall (1991) and is restricted to a few taxa within Liliaceae (Tomlinson & Zimmermann 1969; Coetzee & van der Schijff 1969), Agavaceae (Stevenson 1980; Stevenson & Fisher 1980), Iridaceae (Rudall 1984; 1989; 1995), Xanthorrhoeaceae (Diggle & DeMason 1983) and *Aphyllanthes monspeliensis* (Chakroun & Hébant 1983). Similarly, secondary growth in roots is rare, occurring only in *Dracaena* (Tomlinson 1980).

The sympodial habit has numerous features associated with it. These include the terminal position of flowering units, the presence of axillary buds and the location of adventitious roots at nodes. Monocots are generally described as being composed of a series of sympodial units, separated by nodes and each portion consisting of one or more internodes. The feature of axillary buds is very important in the sympodial habit, allowing for indeterminate growth, in an otherwise determinate system. The axillary buds are usually located on the stem (which may be a horizontal subterranean rhizome or an aerial trunk with vertical orientation) directly in the axil of a sheathing leaf base. The axillary buds allow for the continued renewal of sympodial units. The axillary bud (or renewal bud) in the case of a rhizomatous growth form, initially grows horizontally for a portion, and may be composed of two to three internodes with adventitious roots located at the nodes and then turns upright to form a leafy aerial portion which terminates in an inflorescence, which develops directly from the apical meristem. The lifespan of each aerial portion is therefore limited.

The general consideration of terms for these parts of the sympodium has been rhizome, for the horizontal portion, roots for the adventitious roots and inflorescence axis

or leafy stem for the aerial portion. There exists a profusion of terms for monocot organs, which has been previously considered (Chapter 1) and will be further discussed in Chapter 4. The Holttum model of growth for monocots centres around the rhizome and inflorescence axis (or leafy stem), which is a result of the basic pattern of sympodial growth. Holttum attributed the variation in the basic pattern that is seen in monocots to seasonality and the need for "resting" phases in non-constant environments. Tomlinson and others (Tomlinson 1970a; 1990; 1995 and Tomlinson & Zimmermann 1969 and Tomlinson & Vincent 1984 and Zimmermann & Tomlinson 1968, 1972 and French & Tomlinson 1980 and Bell 1980a; 1980b and LaFrankie 1985) examined the vascular construction and organisation in monocot stems starting with large arborescent monocot stems and then examining other forms. There is a basic vascular construction which is present in arborescent monocotyledons and can be generalised to most monocotyledonous stems. The basic construction of the vascular system is also hypothesised to be closely linked with the sympodial habit, as well as the establishment phase of many monocot seedlings.

In the study of monocot growth form, there exist few broad based comparative studies apart from that of Arber (1925), Holttum (1955) and Tomlinson (1970a; 1973; 1995). The morphology of seedlings on the other hand has generally been examined in a comparative manner (Sargant 1903, Boyd 1932, Tillich 1995). A model organism approach of vascular construction has been developed by Tomlinson & co-workers who examined the vasculature and architecture of palm stems with one or two examples of other monocots. A few studies have been conducted where growth forms are compared within largely circumscribed, diverse taxa e.g. palms (Fisher & Dransfield 1977; Fisher & Moore 1977; Tomlinson 1990), bamboos (McClure 1993; Wong 1986), orchids (Withner 1959; 1974, Dressler 1981, Rasmussen 1985; 1986, Kurzweil et al. 1991, 1995, Pridgeon & Chase 1995), Zingiberales (Fisher 1978), grasses (Hoshikawa 1969; Clark & Fisher 1986) and Iridaceae (Rudall 1995) or monocots occurring within a specific area (e.g. Tomlinson & Esler 1973; Staff & Waterhouse 1981; Pate & Dixon 1982; Wong 1986). Many studies have focused on individual species and/or peculiar growth forms (see Results and Discussion for citations), where the morphology and anatomy of specific structures are described in detail (Troll 1937 in particular). What is lacking are detailed morphological and anatomical descriptions of a wide variety of monocotyledonous growth forms as a synthesis that will allow for a comparative approach to considering form as a whole. This chapter explores the general morphology and anatomy of a variety of monocotyledons including diverse growth forms as well as unrelated taxa.

In this chapter the aims are:

(i) to describe the growth habits of a variety of monocots so that a comparison can be made among forms ensuring that similar features are being compared;

(ii) to describe the variation of growth form in such a way as to be able to determine whether there is a general pattern and additionally to be able asses whether the variation can be recognised and

(iii) to compose a series of descriptions for a number of different growth forms in a way that will enable hypotheses about growth form to be tested. Testing hypotheses of growth form are the focus of Chapter 3, but in this chapter an initial interpretation of variation is based on the descriptions so that a positional assessment of structures/features can be determined. Similarly it is important to be able to test whether the features described can be used to recognise a particular growth form i.e. whether sympodial growth can be described by sets of features or whether it is simply a series of processes.

In order to achieve these aims, a very precise approach to the collection of information about growth forms had to be considered. The idea was to consider growth form without any *a priori* recognition of organs/structures, but on the other hand, there is a need to compare equivalent units so that a comparative approach is meaningful. To achieve the aims of a non-typological approach and of a comparative assessment of plant portions, numerous aspects which could severely influence the outcome were carefully considered and these are outlined in detail in the methods section.

In this chapter the morphology of subterranean and aerial axes are examined as well as a few roots with differing position and function. The location of buds and the growth pattern, whether determinate or indeterminate is discussed. The anatomy of the different organ portions sampled as described (see methods), is examined and the pattern recorded so that a comparative basis for anatomical features of different organ portions could be established. Bearing in mind, that to establish the nature of particular structures, the variation in structural features (pattern) are examined. By sampling some plants "completely" (i.e. considering the continuity of the shoot) and investigating seedlings, the process of differentiation as serial homologues can be found. This approach was utilised to ensure that, although the shoot was subdivided, no category was set *a priori* for a particular structure. The question of whether one can "identify" a particular structure and define it by a set of features when it is clearly part of a process is addressed in the next chapter (Chapter 3).

METHODS AND MATERIALS

Sampling Protocol

In order to examine growth forms of monocots, the ideal and most desirable situation would be to sample the entire range of major groups selecting a representative from each one displaying a particular growth form. However, limitations on time and resources have not permitted this. Thus, the sampling protocol had to be carefully considered and refined during the planning phase of the thesis, and the specified protocol adopted needed to be adhered to throughout so that an overall idea of form could be established during the time available for this thesis.

There are two possible major controlling factors of plant form: the first is an historical one, the phylogenetic constraint of a particular group of organisms and the second, is an environmental control, whereby certain forms may respond to specific environmental situations in an adaptational and functional scenario. Thus, in trying to interpret monocot growth form, both possibilities needed to be accounted for in the sampling protocol. For these reasons, the sampling protocol was as follows. Plants were selected in the first instance on a phylogenetic basis, firstly following Dahlgren's (1985) major groups within the monocots and further, using new and additional information from The APG (1998) and Thorne's (1999) updated classification of the major monocot orders (see Reveal 1999). As such, a representative was selected from most of these groups from two or three of the families that are found in Southern Africa, the Western Cape in particular and several Australian taxa found in temperate climates. From these taxonomic groups, plants were selected in the second instance on the basis of growth form, so that the range of variations that are seen e.g. bulbs through to resurrection plants are accounted for. The voucher list of plants sampled and examined for growth form are in Appendix 2.1.

Collection details

Whole plants were collected in the field (see Appendix 2.1 for localities) and planted in pots in a greenhouse in some instances for observation on a seasonal basis. Others were fixed in formalin acetic alcohol (FAA) and set aside for morphological and anatomical interpretation. Seed was also germinated and seedlings harvested at various stages and fixed in FAA. Seeds were initially sown on filter paper using a 0.5% solution of benylate as a fungicide in sterile petri dishes and placed in a germination cabinet with a temperature cycle of 10°C/20°C and a twelve hour daylight cycle, except for the seeds of

Canna indica which were placed in a greenhouse at a constant temperature of 25°C. For certain species, the germination was unsuccessful and alternative methods were employed. For *Thamnochortus spicigerus*, germination percentage was improved when the seeds were germinated on smoke treated filter paper discs (commercially available from Kirstenbosch plant centre). For the *Wachendorfia* seeds, little germination occurred on the smoke treated discs. Seeds were sown into a mixture of washed sand and potting soil (about 50/50) and sown in seedling trays. The seeds appeared to germinate in response to cold evenings and after an initial "resting" period in the soil. Seedlings were harvested at regular intervals (depending on the species and the degree of growth/change) to record their development.

Approach to morphological and anatomical data collection

In order to achieve the aims set out in this chapter a number of important aspects were considered in sampling each plant. The first was the morphological consideration of the internodes, their position on the plant, the associated structures and to a certain extent the various ecological modifications. In each case a simplified approach of dividing up the plant was undertaken as outlined in Figure 2.1(A-C)[1]. Each plant was examined on a morphological basis to determine the mode of growth form, the position of buds, the extent of branching and the various positions of different organs. Following this, internodes, from a wide range of different areas of the plant were identified according to the scheme outlined in Figure 2.1(A-C). Each of the internodes were subsequently anatomically sectioned, without a preconceived recognition of organ structure. Plants were examined and sectioned to include portions from the top of the inflorescence axis to the base, the area where the inflorescence axis and main axis join, and the main axis (stem or rhizome). The area between the underground stem (rhizome) and aerial stem (inflorescence axis) has often been recognised by other authors as being neither rhizome nor inflorescence axis, having features of both, but as it is not really differentiated into a set of distinct features of its own it has been dismissed and ignored as being an important structure (see Burkill 1960 pg. 344; LaFrankie 1986). Roots were also sectioned.

[1] Note that this outline of the sampling protocol for the plants examined is schematic and generalised. Modified internodes/structures are dealt with in detail for each description of the plants examined. Although each area of internodes is labelled, these do not represent preconceived categories for the structures. The labels for the internodes are used for reference purposes throughout Chapters 2 and 3.

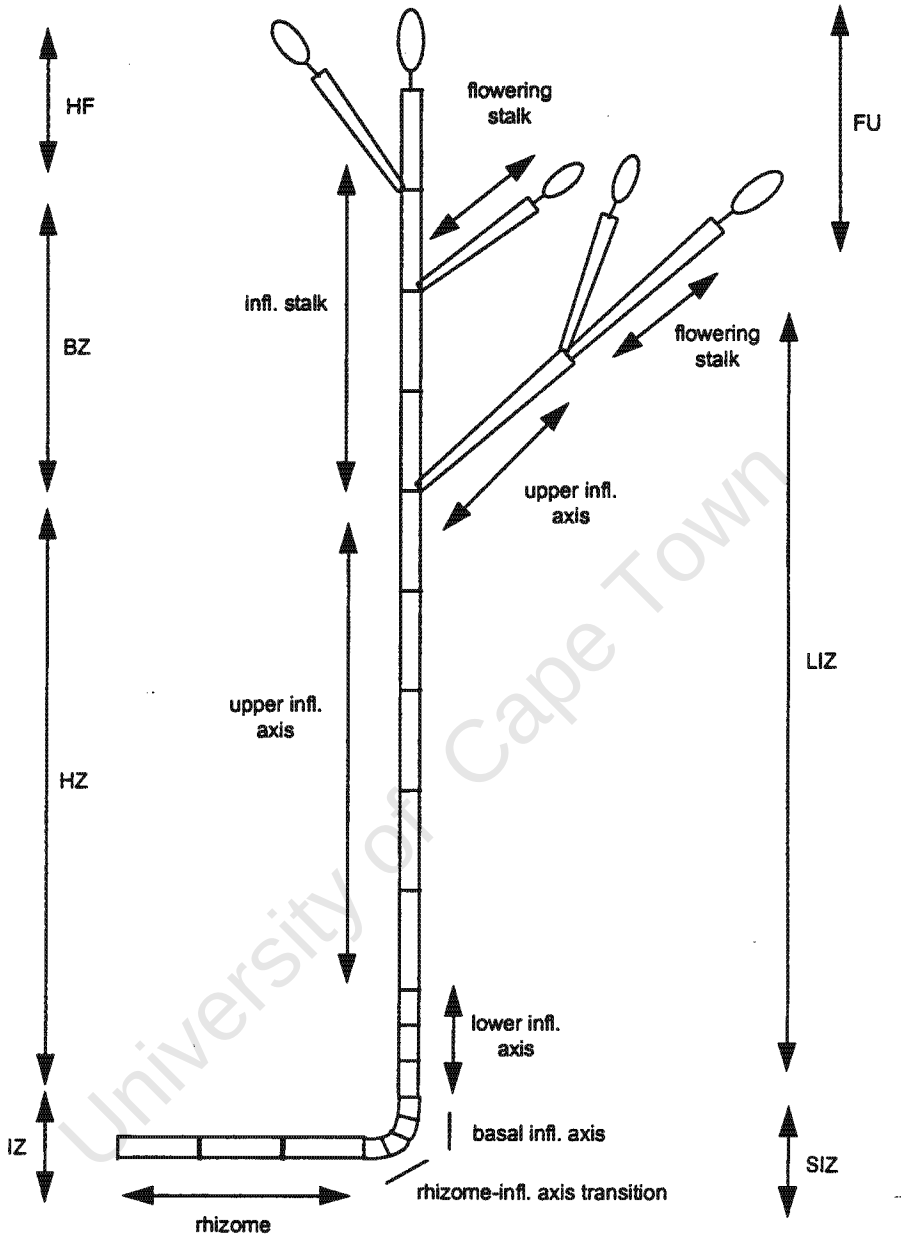


Figure 2.1A. Sampling protocol for internodes applied to the following plants: *Anigozanthos manglesii*; *Aponogeton distachyos*; *Canna indica*; *Chondropetalum deustum*; *Chondropetalum rectum*; *Conostylis prolifera*; *Maxillaria variabilis*; *Merxmuellera cincta*; *Merxmuellera rufa*; *Myrsiphyllum scandens*; *Pentaschistis aristidoides*; *Polystachya ottoniana*; *Pseudopentameris macrantha*; *Smilax anceps*; *Thamnochortus spicigerus*; *Tulbaghia alliaceae*; *Wachendorfia thyrsiflora*; *Zingiber officinale*. Left hand side indicates Troll's (1949, 1951) system, right hand side indicates Rua & Gróttola's (1997) system for comparison. HF = Hauptflorescence (main infl. axis); BZ = Bereicherungszone (paracladial or enrichment zone); HZ = Hemmungszone (inhibition zone); IZ = Innovationszone (innovation zone); FU = flowering unit; LIZ = long-internode zone; SIZ = short internode zone (modified from Rua & Gróttola 1997).

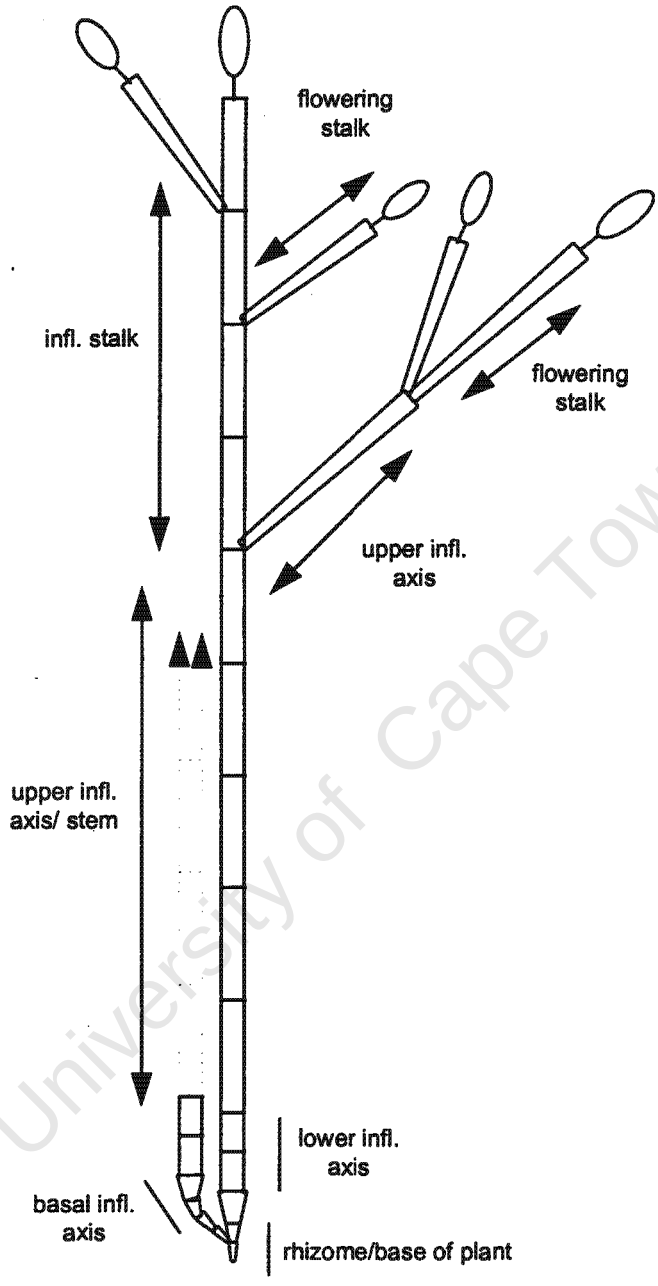


Figure 2.1B. Sampling protocol for internodes applied to the following plants: *Albuca fragrans*, *Arundo donax*; *Borya nitida*; *Calectasia cyanea*; *Chlorophytum comosum*; *Dasypogon bromeliifolius*; *Epidendrum cinnabarinum*; *Holothrix villosus*; *Ischyrolepis cincinnata*; *Johnsonia pubescens*; *Lachenalia klinghardtiana*; *Lachenalia splendida*; *Pentameris thuarii*; *Pentaschistis pallescens*; *Pseudopentameris caespitosa*; *Pseudopentameris obtusifolia*; *Thamnochortus lucens*; *Tribolium obtusifolium*; *Willdenowia glomerata*; *Xerophyta humilis*.

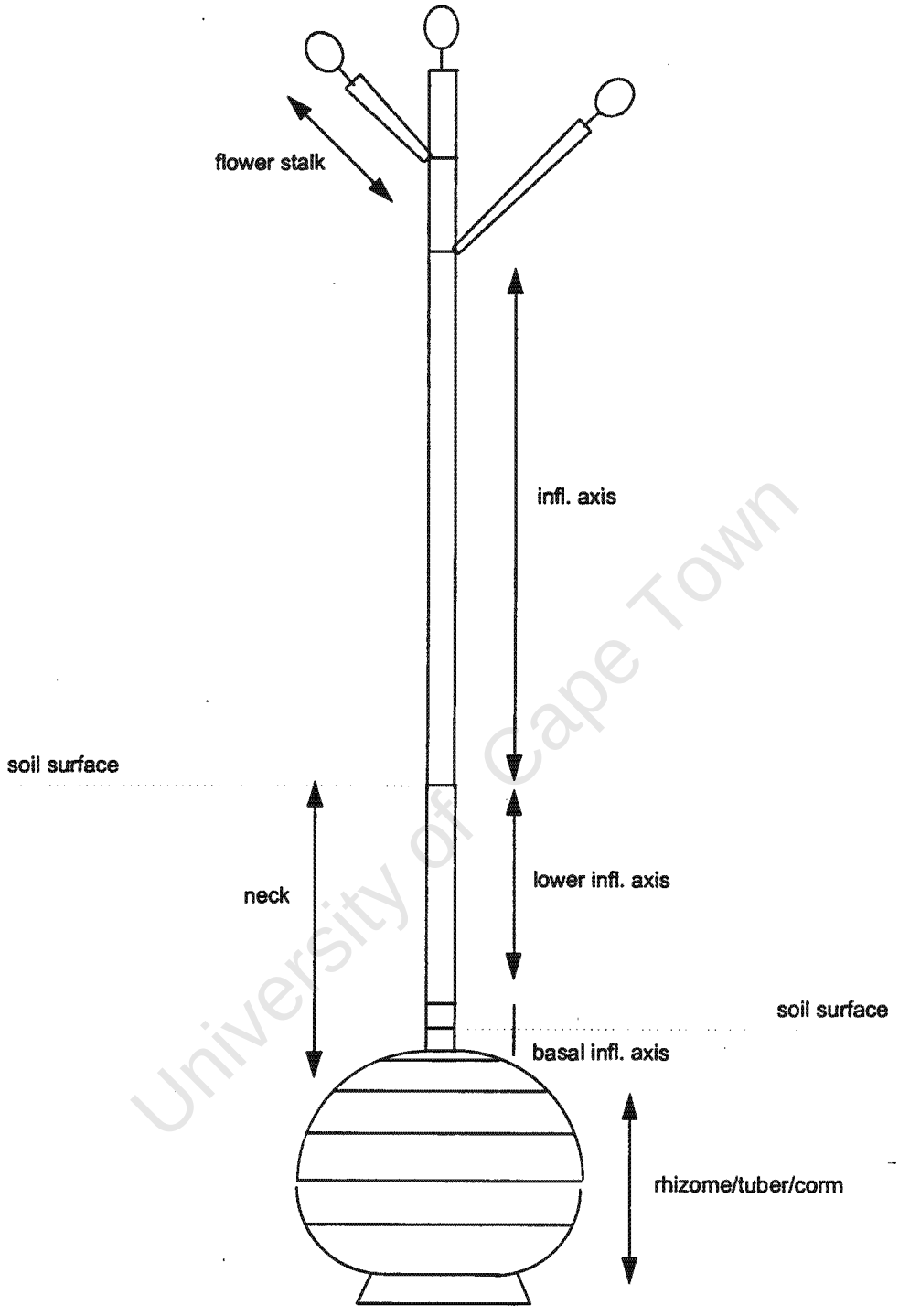


Figure 2.1C. Sampling protocol applied to the following plants: *Baeometra uniflora*; *Cyanella hyacinthoides*; *Eriospermum pumilum*; *Pauridia minuta*; *Spiloxene alba*; *Spiloxene minuta*; *Wurmbea spicata*; *Zantedeschia aethiopica*. Left hand side indicates portions and labels when submerged subterraneanly e.g. *Baeometra uniflora*, *Cyanella hyacinthoides*.

Ideally, it would have been preferable to serially section all of the plants examined from their tips to their bases, but this was not feasible given the time constraints. The approach taken here, while not allowing for serial reconstruction, is adequate in offering "snapshots" of the structure for the organs from the rhizome base through to the flowering stalk right at the apex of the plants, showing how the growth patterns change. In cases where whole plants could be serially sectioned, they were (e.g. seedlings, small cormous and tuberoid plants).

For each of the species sampled, it is of paramount importance that exactly the same portions for each of the demarcated areas was examined and sampled on each occasion. Similarly, when approaching the anatomy of the portions, an equivalent rigour was applied. In anatomical sections, there is a reliance on already defined cell types and features of the roots, rhizomes, inflorescence axes, bulbs, corms etc. For example recognising an endodermis, a vascular bundle etc. The currently defined tissue types (according to the Anatomy of Monocotyledons series) were followed in the anatomical approach, and tissue zones were considered equivalent if they occurred in the same position each time in different taxa and different organs. Where equivalence was questionable or could not be determined, these areas were not "forcibly" classified into the existing zones, but described on a separate basis e.g. additional sclerified band etc. Where modifications occur such as in the inflorescence axes of Restionaceae, where the chlorenchyma band (sensu Cutler 1969) is composed of "palisade" like cells is clearly a specialisation compared to a band of chloroplast containing parenchyma cells of several layers (most aerial axes of monocots), then the Restionaceous terminology of chlorenchyma band was followed for restios and the unspecialised band referred to as an assimilatory band. Additionally, the chlorenchyma band is located in a different position in the restio axis always lying directly beneath the epidermis. In other monoctyledonous aerial axes, the assimilatory band can be located in that position, or below a sclerified layer (such as in grasses) or below parenchyma layers. This example serves to illustrate the difficulty of deciding what the equivalent tissue zones are and the coding of the features according to a positional criterion is taken into consideration in Chapter 3. A further problem which had to be ironed out, was the variation that is seen in the pattern of arrangement of xylem and phloem in the vasculature of the different internodes and the difficulties that it may lead to in interpretation. A system had to be devised to introduce consistency into the recognition of vascular pattern. The system proposed by Cheadle & Uhl (1948) was used as a starting point, and additional arrangements were included in this system, as well as a simplification of some of their types (Figure 2.2).

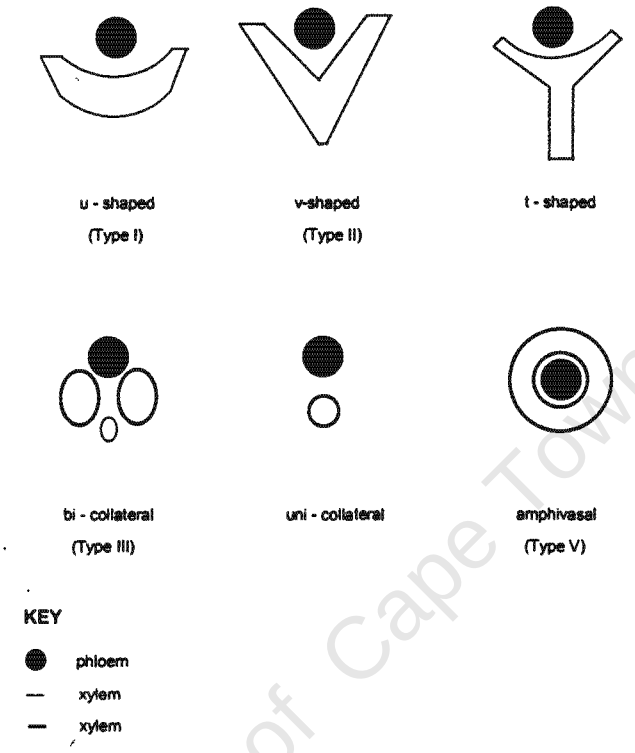


Figure 2.2. Schematic representation of the coding system for the recognition of patterns of xylem construction in vascular bundles. Type labels in brackets refer to the vascular bundle types in Cheadle & Uhl's (1948) system.

Sectioning

Plants fixed in FAA were assessed on the basis of their tissues, plants with soft tissues were processed and sectioned using standard paraffin embedding techniques, while harder, woody tissues were rinsed in 70% EtoH and subjected to sledge microtoming. Dried material from herbarium specimens (mostly the Australian specimens) was reconstituted by boiling in water with a small amount of washing detergent until the specimens dropped to the bottom of the glass beaker. Specimens were removed from the stove and allowed to soak for five minutes in the water. Following this, they were treated to an alcohol soaking process from 50 % EtoH to 70 % EtoH and then either sledge microtomed or paraffin embedded depending on the nature of the tissue.

Paraffin embedding

Internodes were placed in a Sakura tissue processor and subjected to a dehydration process as follows: 70% EtoH; 100% EtoH; Propanol: Butanol: Paraplast. Samples were soaked for eight hours in each of the two baths for each of the treatments. Following the last treatment bath, the samples were placed into a vacuum oven in the paraplast bath for up to 12 hours. This last step in the process was found to improve the quality of soft tissue preparations immeasurably by ensuring complete wax impregnation of the tissue.

After wax penetration, the samples were mounted in metal wax boats in transverse or longitudinal orientation and the wax allowed to harden. The wax blocks containing the mounted specimens were removed from the metal boats after an overnight cooling period in a zero degree refrigerator. The wax blocks were trimmed and mounted on wooden stubs which could be placed in a Leitz-Wetzlar rotary microtome. Thin sections of 15 - 20 μm were cut and wax ribbons (containing the plant sections) were floated in a water bath kept at a constant temperature of 50°C. The wax ribbons were then floated onto glass microscope slides treated with Haupt's adhesive as a sticking agent. The glass slides with the attached wax ribbons (and sections) were allowed to dry in a dust free environment for up to 3 hours (or until they were dry to the touch).

The sections were treated to the safranin-fast green staining procedure (Johansen 1940) in the following process: Two xylene baths (5 mins each); one bath methyl cellusolve (2 mins); one bath 96% EtoH (2 mins); Safranin (30 mins); water rinse; one bath methyl cellusolve (2 mins); Fast Green (2 mins); clove oil rinse (two parts clove oil; one part xylene; one part absolute EtoH); three baths 96% EtoH (rinses); two baths butanol (2 mins each); two baths xylene (5 mins each). The glass slides were then removed from the xylene, Canada Balsam applied to the surface as the mounting agent, and a glass coverslip placed on top. The glass slides were allowed to dry in an oven maintained at 50°C for three months until hard.

Sledge microtoming

Tough material was identified for this process. Plant portions were placed between two pieces of soft cork and mounted in the microtome holder. Sections of 50 μm on average were cut and placed in 50 % EtoH. The sections were subsequently stained in Safranin-Alcian Blue (Tolivia & Tolivia 1987) and transferred into a dehydration sequence performed in watchglasses in the following sequence: water; 50% EtoH; 70% EtoH; 80% EtoH; 90 % EtoH; 96 % EtoH; 100 % EtoH; Xylene. After the xylene treatment, the sections were mounted in Canada Balsam on a glass microscope slide and covered with

a cover slip and allowed to dry for three months in an oven maintained at 50°C. It was generally found that the Safranin-Alcian Blue stain produced better staining results, but the sections were often too thick to achieve good photographs, particularly when detail was required.

Photography and preparation of plates

Sections (produced from both methods) were examined using a Zeiss compound microscope. Photographs of selected anatomical material were taken using a Zeiss Axioskop microscope with fitted camera. Drawings were undertaken with the use of a drawing tube attached to the compound microscope. For the photographs of anatomical sections PanF ASA 50 was found to be most useful, offering good results for a wide range of material. The film was developed using Ilford ID11 developer for 5.5 mins at 20°C. Negatives were scanned digitally into pixel format with a Nikon digitiser, assembled and printed using the Adobe Photoshop 4 graphics package.

Growth form and habit morphology pictures were taken using a light table in a darkroom using PanF ASA 50 film. A blue background was found to give best detail for a range of organ structures, textures and colours. Seedlings were photographed using a Leica dissecting microscope and a blue background with PanF ASA 50 film.

RESULTS AND DISCUSSION

Morphology and anatomy of adults and seedlings

Aranae: Arales: Araceae: Zantedeschia aethiopica

Morphology

Zantedeschia aethiopica produces an underground perennial organ which is generally termed a tuber (see Dahlgren et al. 1985). This tuber produces petiolate leaves at its apex continually and spathe stalks bearing an inflorescence on a seasonal basis, with the basal portion of the tuber withering after each flowering event (Pl. 1, Figs. 1, 3, 4). The spathe stalk bears a single node towards its apex, where the spathe arises and fuses to the lower portion of the inflorescence stalk. This inflorescence stalk is itself without nodes, save the single common node that is shared with the spathe stalk. Many small florets on minute stalks arise in a cylindrical spiral arrangement over its entire surface, with separation in sex maturation of florets. Roots are contractile and arise from the entire surface of the tuber (Pl.1, Fig.1). The roots tend to be bright white in colour and

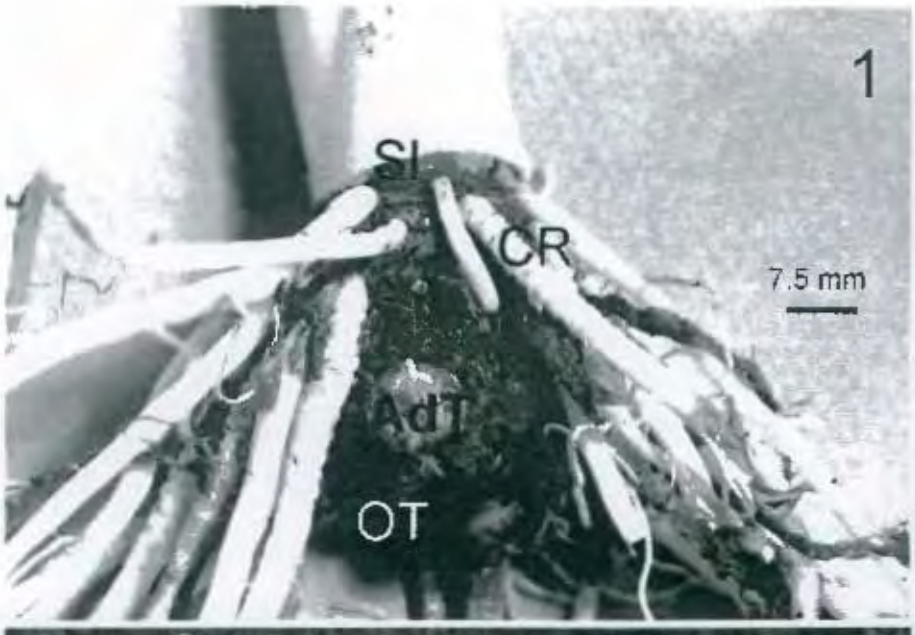
somewhat fleshy in texture, particularly towards their base at the departure from the tuber in their contractile phase.

Germination in *Z.aethiopica* is hypogeal with the cotyledon remaining within the seed coat underground (Pl. 1, Fig. 2). The cotyledonary sheath is distinct, bearing a hypocotyl below it from which the primary root is formed. Later, the hypocotyl expands and T/S examination of the area shows a high degree of starch accumulation attesting to the storage nature of the hypocotyl. The first leaf shoot is produced through a slit in the cotyledonary sheath during the first few days after germination (Pl. 1, Fig. 2; Pl. 2, Fig. 1A, B). Around the same time as the emergence of the plumule, the primary root breaks through the base of the cotyledonary sheath in the hypocotylar region (Pl. 2, Fig. 1A, B). After about two weeks, a second leaf shoot is produced. This is continued until there are at least three leaf shoots, then, the first leaf shoot dies back and at the same time a fourth leaf shoot appears and so on (Pl. 1, Figs. 3, 4). In the first six months of growth there are always up to three leaf shoots on the plant, but never more than this. In *Arum maculatum* the same germination pattern occurs, but there is a dormant phase at first, in which the tuber is pulled by contractile roots to a suitable depth, after which the first above ground organs form (Arber 1925).

Four weeks after germination a swelling at the base of the leaf shoots is clearly visible and is distinct, being separated from aerial shoots apically and from several contractile and adventitious roots basally (Pl. 1, Fig. 5). Thus, tuber initiation is immediate in *Z. aethiopica*. This has also been observed in the geophilous *Arisaema* (Tillich 1995) of which the germination and seedling morphology are identical to that observed in *Z.aethiopica*. The seedling is a smaller replicate of the adult, the leaves showing a "petiolate" leaf base and an expanded lamina in the early phases of growth, much like adult leaves. At this stage the tuber consists of at least four distinct internodes, each expanded and fleshy. The immediate determination of organs in seedlings is not uncommon in monocots that show modification of basic rhizome structure e.g. in *Dioscorea*, the seedlings immediately utilise the hypocotyl for either rhizome elongation or swelling to form tubers (Burkill 1960; Lawton & Lawton 1969; Tillich 1995). Boyd (1932) however, concluded that tuberous plants do not show tuberisation in the seedling phase. She proposes that food storage in the hypocotyl is linked to the condition of an exalbuminous seed and the sole function is nourishment in the very young seedling. The presence of contractile roots in this early stage of development is probably due to the need for the tuber to be "pulled" to a certain depth into the soil substrate in order to assume a favourable position for survival. Movement in the soil in plants with

Plate 1. Morphology of *Zantedeschia aethiopica*

Figure 1. Mature tuber morphology. Swollen internodes forming the basal storage region of the tuber with depleted internodes at the base (ot) and closely spaced, short internodes (si) at the apex. Axillary buds develop into an "adventitious tuber" (Adt) which buds off from the main tuber. Contractile roots (cr) present.
Figure 2. Hypogeal germination in 1 week old seedling. A hypocotyl (hy) is present at the base of the cotyledonary sheath (cs) through which the primary root (pr) has emerged. The plumule (pl) is just starting to erupt through the slit in the cotyledonary sheath.
Figure 3. Seedling 4 weeks after germination. A single petiolate leaf (lf) is present with a leaf bud developing at the base of the plant.
Figure 4. Seedling 8 weeks after germination. Three petiolate leaves (lf) are present with a leaf bud developing at the base of the plant.
Figure 5. Seedling 12 weeks after germination. A swollen region at the base of the plant is present (t) and is the start of tuber formation.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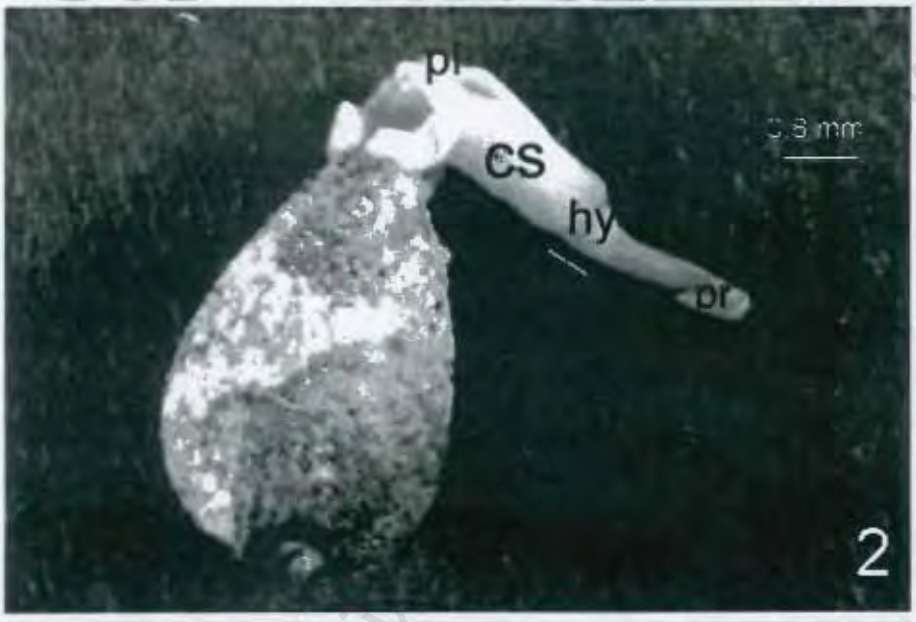
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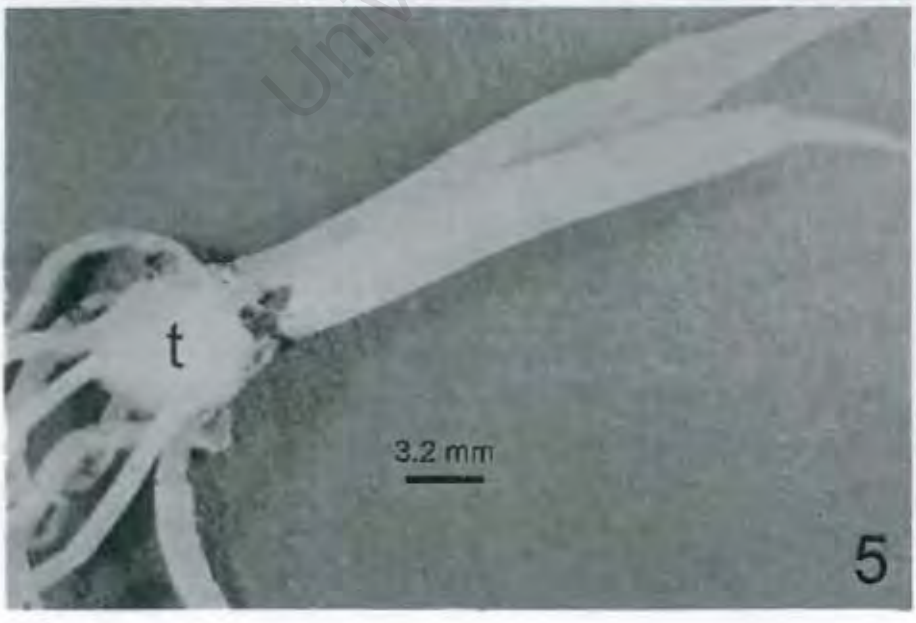
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4

underground elaborated organs in this manner is well documented (Pütz & Froebe 1995; Pütz 1996a; 1996b). Various aspects of the biology of the genus *Zantedeschia* have been examined (e.g. Letty 1973). The diversity in growth forms for the family as a whole has not been studied. Individual studies of shoot construction (e.g. French & Tomlinson 1980; Hay & Mabberley 1991; Murata 1990; Ray 1987; Ritterbusch 1971; Scribailo & Tomlinson 1992) and stomatal apparatus (e.g. Weber 1960) have been examined for selected members of Araceae. The anatomy for particular portions of some members of the family are described in Solereder & Meyer (1928 – 1933). The anatomy and functioning of contractile roots in some members has been examined by Pütz (1996a; 1996b) and Pütz and Froebe (1995). Croat (1997) has revised *Philodendron subgenus Philodendron* and provides descriptions of morphology and anatomy of vegetative portions.

Anatomy

Median longitudinal section of a seedling at the 2 month stage

The tuber is distinct at this stage, containing a diffuse vascular system with a direct supply from the roots to the shoots visible i.e. little branching within the tuber. There are many starch grains in the parenchyma cells of the main region of the tuber. The starch distribution extends to the base of the shoots, but then becomes diffuse into the base of the shoot axis, and, entirely absent from the shoot axis. The shoot meristem is clearly visible and a primary thickening meristem (PTM) is also apparent in this early stage of development. The PTM is responsible for the primary thickening of stems, induction of adventitious roots (Pl. 2, Fig. 2) and for forming links between root and stem vasculature and is present in virtually all monocotyledons (Rudall 1991). The PTM is most obvious in the juvenile stages of the tuber development in *Z.aethiopica*. In later stages it becomes obscured by the expansion of the cortical tissues.

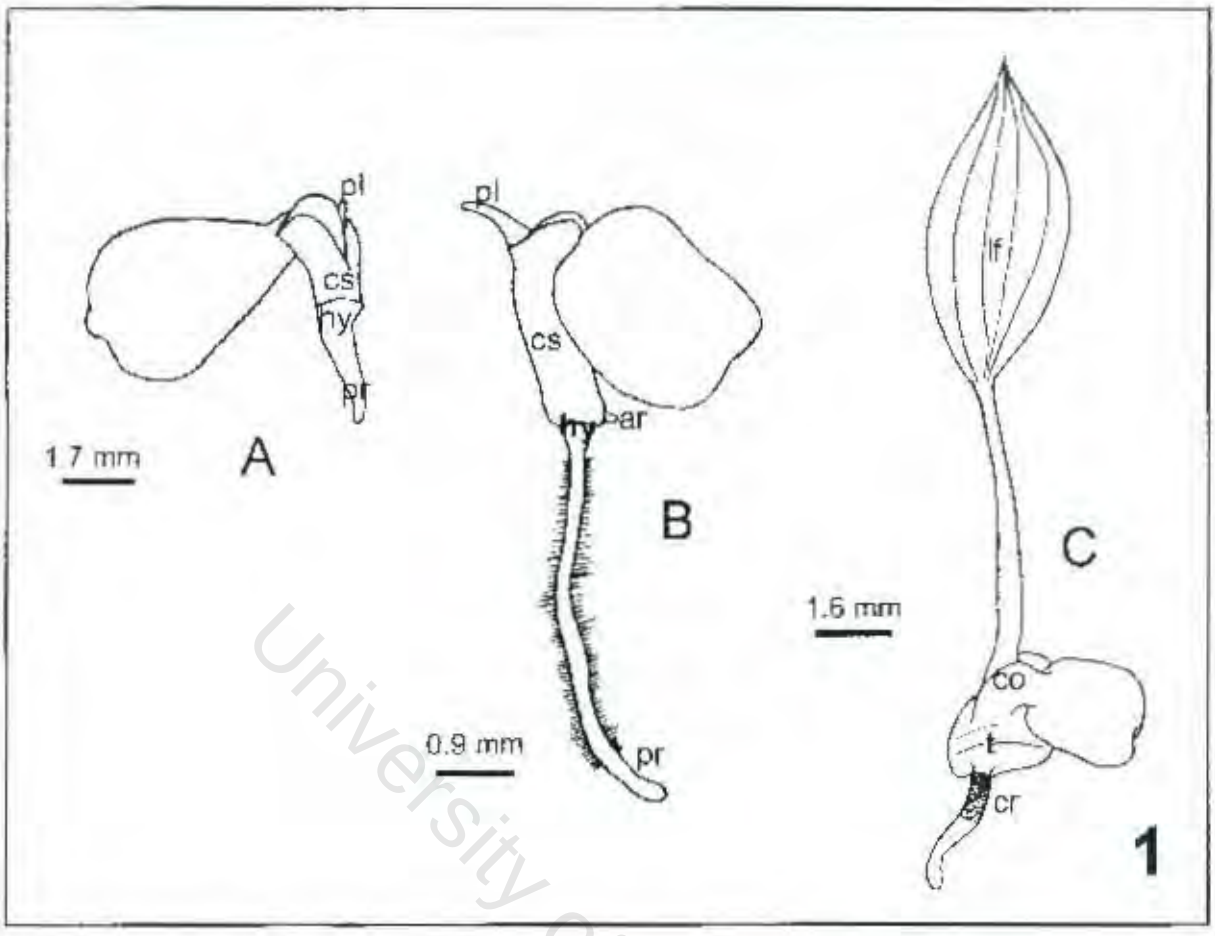
T/S of 2 month old tuber

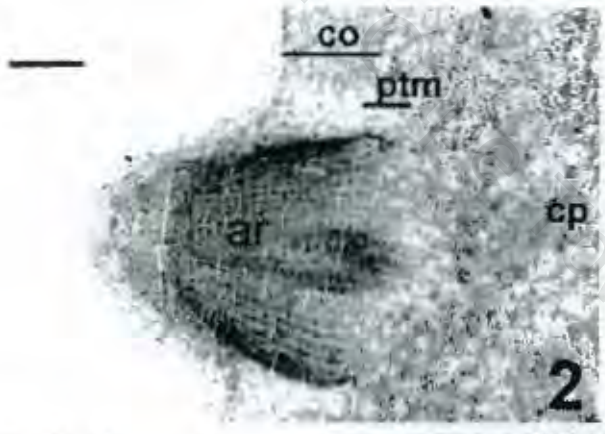
At this stage, it is not easy to distinguish different regions of tuber, except that leaf primordia are clearly distinct surrounding the apical meristem, consisting of three leaves only (Pl. 2, Fig. 3). The vascular tissue in the main central area of the tuber is very diffuse at this stage. Initially, it was thought that such indistinct vascular tissue may have been due to the lack of vessels in stems in Araceae (Cheadle 1953; Macison 1970) but this pattern was generally found throughout the developing organs of seedlings. The vascular tissue and tissue patterning does not appear to established early on in the organ formation, such differentiation seems to occur much later.

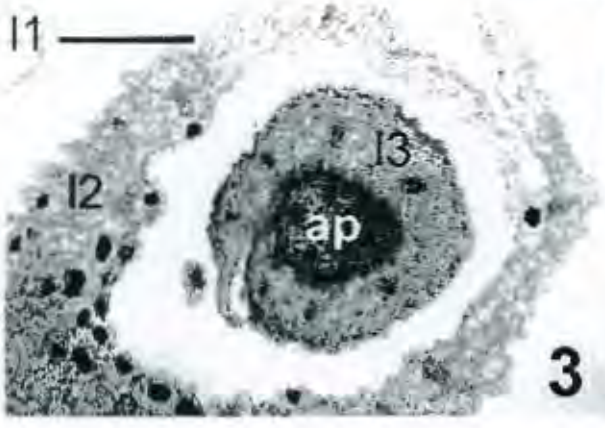
Plate 2. Seedling ontogeny and anatomy of *Zantedeschia aethiopica*

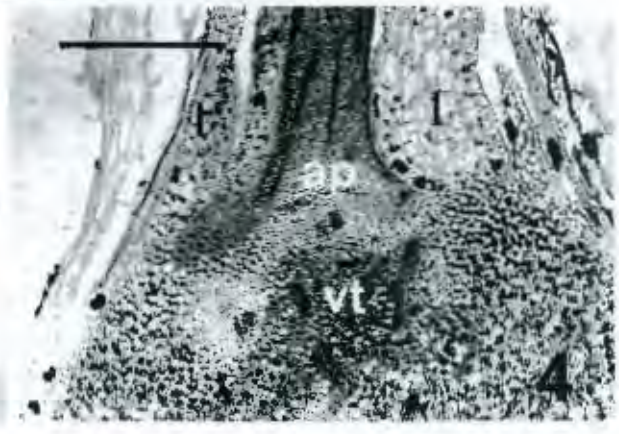
Figure 1. Seedling ontogeny 1 to 4 weeks after germination. **[A]** 1 week after germination, hypocotyl (hy) and primary root (pr) initiates with plumule (pl) starting to emerge through slit in cotyledonary sheath (cs). **[B]** 2 weeks after germination, primary root elongates (pr) and adventitious roots (ar) are initiated in the region of the hypocotyl (hy). The plumule (pl) extends and emerges from the cotyledonary sheath (cs). The plumule continues to expand and forms a laminate leaf. **[C]** 4 weeks after germination. Laminate leaf (lf) and swollen base of plant in hypocotyl region evident (t). Contractile root (cr) developing at this stage. (co) = cotyledon.
Figure 2. L/S through tuber showing initiation of an adventitious root (ar) from the primary thickening meristem (PTM) and emergence through cortex (co) to exterior of tuber tissue.
Figure 3. T/S tuber apex showing three leaves (l1, l2 and l3) surrounding the shoot apex (ap).
Figure 4. L/S through tuber apex. Leaves (l) flank the shoot apex (ap) which is highly meristemmatic. A concentrated region of vascular tissue (vt) is present directly beneath the apex. The cells of the surrounding tuber tissue contain starch granules and a more diffuse arrangement of vascular tissue.

[Bars = 15 μm (Figs. 2-4)].









Median longitudinal section of a 12 month old tuber

There is a distinct regionalisation of the tuber at this stage of the plant's development. There is an apical region which "feeds" the base of the shoot system, this region is very well vascularised with the bundles anastomosing in several directions (Pl. 2, Fig. 4; Pl. 3, Fig. 1). The mid region of the tuber is parenchymatous and contains starch grains in great abundance as well as a few diffuse vascular bundles which can be traced to link up with roots (Pl. 3, Fig. 1). Roots arise in the mid region of the tuber and grow downwards. Roots are not evenly distributed over the tuber, but are tiered. This might indicate that nodes are present in the tubers. There is no other evidence of these suggested nodes. In the younger tuber roots are clearly produced very close to the base. Axillary buds can be seen in axillary positions among the bases of the aerial leaf petioles (Pl. 3, Fig. 1).

The leaf primordia at the apex of the tuber are folded over in the laminar region and the "petiolar" region contains several ducts. These may be raphides which are common in Araceae (French & Tomlinson 1980; Dahlgren et al. 1985). Older "petiolar" leaf regions also contain these ducts. There is a tuber tunic layer which consists of several cell layers or so, and these tend to slough off, much like a corky layer. The origin and nature of this structure cannot be determined, it may be initiated from tuber tissue, or it could be the remains of some sort of ensheathing leaf base.

T/S of 12 month tuber

A transverse section of the tuber at this developmental stage shows that the outermost layers consist of a hypodermis of three to four cell layers, eventually breaking down and sometimes staining brown. The tunic appears to be tuberous and not leaf base in origin. Based on this interpretation, the tuber lacks scaly or ensheathing leaf bases. The majority of the tuber is composed of a cortex. The cortex is largely parenchymatous, the cells are isodiametric, without thickened walls and are loosely packed within the cortex. The vascular tissue is concentrated in the central region of the tuber without any distinct pattern in its arrangement, usually scattered and anastomosing (Pl. 3, Fig. 2). The vascular bundles are probably amphivasal, but the (meta) xylem is not distinct, lacking vessels and showing no secondary thickening. The vascular bundles lack a distinct vascular bundle sheath. The roots are endogenously formed from the central area of the tuber with the vasculature from the central region of the cortex moving towards the exterior to supply the roots. None of the tissues display any degree of sclerification or secondary thickening. There are several crystal inclusions within the ground parenchyma

cells of the cortex of the tuber - these could be raphides. The cortical cells contain scattered starch granules.

T/S inflorescence axis - mid and lower zone

The outermost layer is an epidermis consisting of elongate upright cells with a cuticle apparent. Stomata are present and a substomatal cavity can be distinguished. There is an assimilatory band directly below the epidermis and this is comprised of several layers of chlorophyllous cells with chloroplasts clearly visible in the cells. The central ground parenchyma has a ray-like structure with air spaces between the rays and vascular bundles being supported in the centre of the rays (Pl. 3 Fig. 3), much like the tissue arrangement of the inflorescence stalk. The vascular bundles lack a bundle sheath and are elongate with a single xylem cavity with a phloem cap, or with two xylem cavities. The general tissue structure and arrangement is much like that of the area below where the flowers are formed on the inflorescence stalk.

T/S of the inflorescence axis/inflorescence transition zone

At the base of the inflorescence stalk, where the spathe and inflorescence stalk merge into one, there appears to be no distinction between spathe tissue and the inflorescence stalk tissue. The tissue consists of large air spaces with the parenchyma cells arranged in rays. When the zone is reached where flowers are produced, the air spaces become smaller, but the basic pattern does not change and the arrangement and tissue types remain the same. Aeration in aerial stems has often been interpreted as being for mechanical purposes, rather than simply a direct result of the plants aquatic habitat or ancestry (Tomlinson 1970a). The vascular bundles of the inflorescence stalk consist of a single xylem cavity (probably metaxylem)[2] and are distinct from the vascular bundles of the spathe. These patterns indicate that the spathe and the inflorescence stalk are two distinct structures, but where they fuse, the distinction is fuzzy. In T/S the spathe displays dorsiventrality. The upper surface consists of an epidermis and a mesophyll directly below with a central area of parenchymatous rays which support the vascular bundles. The vascular bundles have a single xylem cavity but differ to the inflorescence stalk in that

[2] The vascular bundles of *Z.aethiopica* have been interpreted here as "uni collatera" (and coded as such in Chapter 3) in nature as the xylem element consists of a single cavity, although not a vessel. The terms that are used to describe vascular bundles (Cheadle 1942; Cheadle & Uhl 1948) are vague in that they apply strictly to the xylem arrangement, whether protoxylem and metaxylem elements or vessels. Terminology here could have been improved to refer to homologous entities, but the situation becomes highly complex in Chapter 3 in binary coding for vascular bundle characters. The use of bundle terms such as *amphivasal* and *collateral* are also used by French & Tomlinson (1980) for Araceae in describing metaxylem.

they are arranged in a row facing a single direction only. The lower surface of the spathe lacks a mesophyll and the epidermis is papillate. In T/S the inflorescence stalk consists of an outermost layer of epidermis with a cuticle clearly apparent. Stomata are present and there is also a substomatal cavity. The layer following this consists of a chlorenchyma band comprising four to six layers with chloroplasts visible. The central ground parenchyma contains large air spaces, the parenchyma cells are arranged to form a series of rays and support vascular bundles in the centre of the rays. The vascular bundles are elongate in shape, they lack a bundle sheath, and comprise a single xylem cavity with a phloem cap.

T/S inflorescence stalk

The basic structure and tissue arrangement of the inflorescence stalk is the same as described for the transition zone, except the vascular bundles are different in their tissue arrangement (Pl. 3, Fig. 4). These vascular bundles have xylem elements arranged in a u-shape and also tending to the bi-collateral arrangement [3]

Growth form affinities and differences

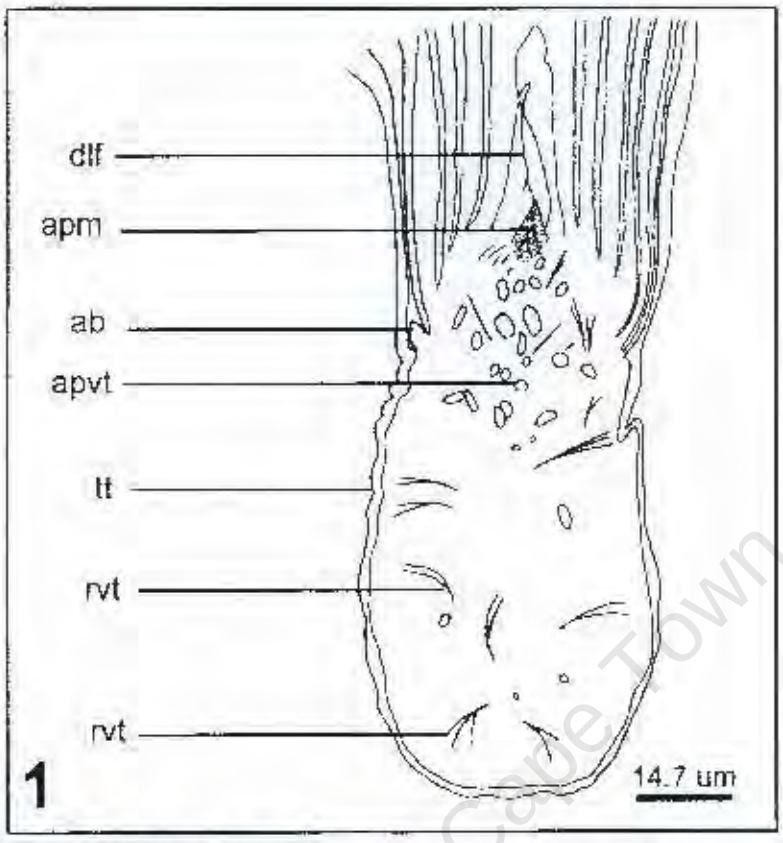
There appears to be conflict in terminology between corms and tubers in Araceae specifically, but this can be extended to monocots as a whole. In true corms the growth is sympodially vertical and the internodes clothed with persistent scale leaves. The apical bud develops into an inflorescence axis which usually bears foliage leaves and the internode associated with this shrivels at the end of the flowering season (Bell 1991). Sympodial growth occurs from one of the axillary buds located on the top of the previous season's corm, which develops into a new corm. Thus, in a sympodial corm there is seasonality in above ground organs, which is not the case in *Z.aethiopica*. Monopodial corms have been described for the corms of Ixioideae (Iridaceae) where the new corm is formed from the apical bud (Rudall 1995). To be more precise, Rudall (1995) describes that the new corm is formed from the short basal internodes of the inflorescence axis. Such branching is clearly not a monopodial form of branching and such corms probably should not be likened to corms formed from rhizome tissue, due to positional as well as

[3] This interpretation is followed for the arrangement into a u-shaped pattern or bi-collateral arrangement regardless of whether the xylem is comprised of protoxylem elements, metaxylem elements, vessels etc.

Plate 3. Anatomy of *Zantedeschia aethiopica* (Figs. 1-4) and of *Aponogeton distachyos* (Fig. 5)

Figure 1. L/S of seedling tuber 1 year after germination of *Zantedeschia aethiopica*. The shoot apex (apm) is meristemmatic giving rise to developing leaves (clf) and ultimately to an inflorescence axis in the following season. Axillary buds (ab) are present in the axils of the leaf bases in the upper internodes of the tuber. The vascular tissue (apvt) is concentrated in the apical region of the tuber supplying the leaves and shoot apex. Root traces (rvt) depart from more central regions of the tuber and form part of a diffuse vascular tissue which supplies roots in the lower, expanded storage internodes of the tuber. (tt) = tuber tunic.
Figure 2. L/S of central portion of tuber of *Zantedeschia aethiopica*. Vascular tissue (vt) diffuse, central parenchyma (cp) cells with starch granules.
Figure 3. T/S mid inflorescence axis of *Zantedeschia aethiopica*. The spathe stalk is composed of parenchyma cells arranged in a ray-like fashion (r) interspersed with air spaces (as). The vascular bundles (vb) are surrounded by parenchyma cells in the central region of the rays. An assimilatory band (ab) occurs between the central parenchyma and the epidermis (ep).
Figure 4. T/S inflorescence stalk of *Zantedeschia aethiopica*, the region above the spathe and consists of an inflorescence axis (ia) surrounded by florets (fl) which branch from the axis. The rays (r) and air spaces (as) comprise the central portion and a parenchyma region (p) separates the central area from the epidermis. The vascular bundles are of two kinds - collateral (vb1) and with u-shaped xylem (vb2).
Figure 5. T/S mid inflorescence axis of *Aponogeton distachyos*. The central parenchyma of the axis is arranged in a ray-like pattern (r), with the rays separated by air spaces (as) and the vascular bundles (vb) are supported in the centre of the parenchyma where the rays meet. An assimilatory band (ab) occurs between the central portion of the axis and the epidermis.

[**Bars** = 150 µm (Figs. 2-5)].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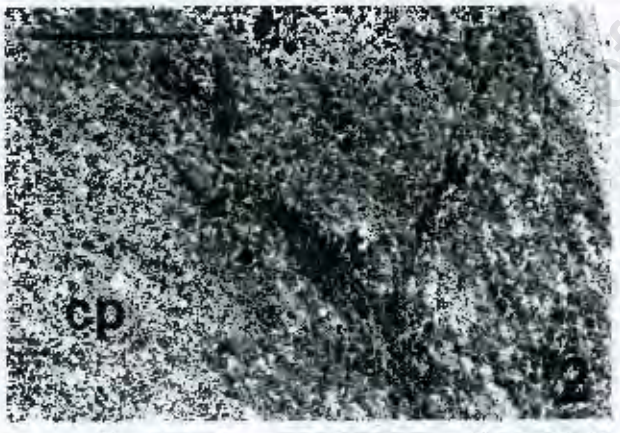
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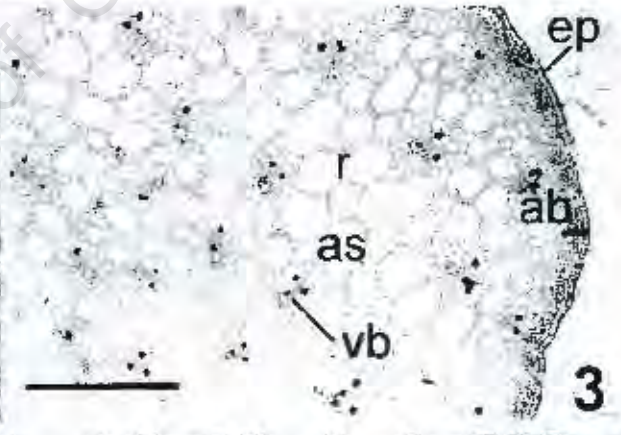
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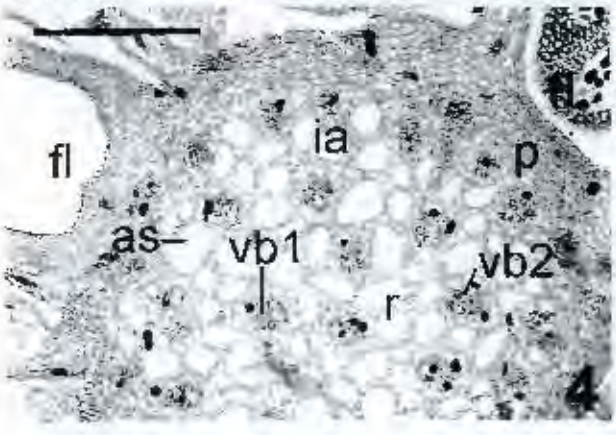
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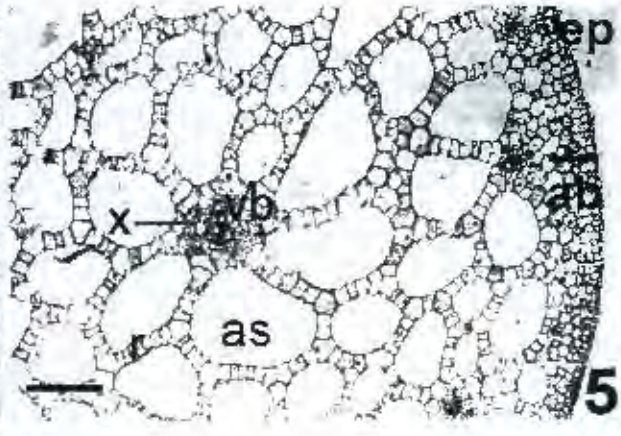
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developmental dissimilarity. Bell (1991) defines a (stem) tuber as an underground shoot usually swollen and bearing scale leaves each subtending one or more buds which give rise to vegetative shoots. It is clear then that this definition of "tuber" is not applicable to the underground organ of *Z.aethiopica*.

This organ may be better described as a vertical rhizome which consists of numerous swollen internodes basally and closely compacted internodes apically, with petiolar leaves being renewed by axillary buds at the apex of the tuber by the shoot meristem. In climbing Araceae, Holttum (1955) describes that the new component of each sympodium arises in the axil of the penultimate leaf and this is often the case in Araceae which have extended internodes (Scribailo & Tomlinson 1992). In the *Z.aethiopica* underground organ, axillary buds are present in the axils of the petioles, but as the internodes are very compact it is difficult to determine the precise process of sympodial renewal (See Pl. 1, Fig. 1). The accretion of tuber internodes by axillary buds in the apical portion of the tuber (Pl. 3, Fig. 1) must occur in a sympodial manner, but the precise fate of the renewal buds and seasonal timing in other tuberous plants such as Dioscoreaceae cannot easily be determined (Holttum 1955; Burkill 1960) and this may be the case for many tuberous plants, some of which may also be complicated by the phenomenon of hysteranthy e.g. *Eriospermum* [Eriospermaceae].

The underground organ of *Z.aethiopica* does not behave in the manner that a corm does, storing food for the following season, bearing an axillary bud which develops into a new corm, and then shrivelling at the end of the flowering season. By contrast, some of the lower internodes of this structure, remain viable and fleshy for the duration of the flowering season and thereafter are restored by the current leaves (the tuber always contains starch granules). Only the basal most internode seems to shrivel and disintegrate. The growth of the aerial axis of the tuber must be the similar to that in corms and bulbs. The inflorescence is produced from the apical bud which in the "tuber" of *Z.aethiopica* is located at the apex at the centre of the leaf primordia (Plate 2, Fig. 4). This is similar to the situation seen in the swollen, fleshy rhizome of *Wachendorfia* [Haemodoraceae] (often interpreted as corms or tubers) in which it is the apical bud that develops into the inflorescence axis (Helme & Linder 1992), thus displaying true sympodial growth and producing a new rhizome from an axillary bud each year. Other members of Araceae that have abbreviated stems seem to be able to produce more than a single inflorescence axis at a time, although the additional axes would appear to arise from subapical positions of buds (see Murata 1990).

It is conceivable that the many subapical axillary buds that are seen at the "tuber" apex in *Z.aethiopica* are capable of continuing the sympodium and are arranged to mature in a sympodially successive manner and develop into vertical, closely compacted internodes at the apex of the tuber. This vertical accretion of new sympodial segments is also described for *Colocasia antiquorum* Schott. [Araceae] in Western Australia (Pate & Dixon 1982). Other subapical axillary buds seem to develop into "bulbils" and must therefore, also have the capacity to form a new "tuber" system. In *Z.aethiopica* this will probably only occur if the main tuber is damaged in some way, or when budding is required and these axillary buds can bud-off to produce new plantlets in certain conditions (Pl. 1, Fig. 1). The buds are predetermined to perform certain functions i.e. a perennial bud (new sympodium - budding); those that will grow if apical dominance is removed (damage) into a new sympodium; those committed to form floral axes (apical bud); and those committed to form leaves. As previously outlined, the position of these buds is important and the function can be deduced on this basis. These key features are patterns which are repeated throughout the monocots and are general, not being specific to certain kinds of growth forms. It is the timing of development through the control of hormones produced in the apical meristem that can change the dominance of the different buds in some monocots (Fisher 1973a) and in addition to this, the orientation of buds on the rhizome can determine whether a leafy shoot or rhizome develops from primary or secondary axillary buds (Cutter 1967; Tomlinson 1970a; Fisher 1973a; Bell & Tomlinson 1980). In *Z.aethiopica* the phenomenon of bulbil formation may arise when the internodes on which dormant axillary buds are positioned, become distally removed from the control of the apical meristem. As such, they will begin to develop, hence, the odd formation of bulbils from axillary buds at lower nodes on the "tuber". The transference in function to formation of plantlet rather than sympodium cannot be determined, but may be under genetic control, much like the organ expression which is controlled by sets of homeotic genes (e. g. Coen & Meyerowitz 1991; Smith & Hake 1994; Albert et al. 1997). The production of axillary shoots in this manner in *Z.aethiopica* is quite different to the formation of adventitious (basal suckering) shoot formation as is seen in many monocots that have a secondary thickening meristem (STM), where the adventitious shoots originate from the STM (Tomlinson 1973; Staff 1970). Meristem (bud) location and release from dormancy is a phenomenon well documented in clonal plants such as white clover (Watson et al. 1997). Axillary meristem potential is determined by the distance from the apical meristem as well as age. Watson et al. (1997) proposed that differences in bud response and development are important in determining overall plant architecture as well

as determining the response that individuals will have to environmental variation giving the plant some degree morphological plasticity.

The interpretation of vascular bundles in Araceae is difficult, and is often complicated by the insertion of adventitious roots at nodes and the additionally complex set of "reserve" buds that can be located in the axils of the leaves (French & Tomlinson 1980). In the tuber of *Z.aethiopica* the course of vascular bundles displays this same complexity, with the bundles diffusing at nodes to where root insertion occurs. French and Tomlinson (1980) found that within Araceae several kinds of vascular bundles occurred, ranging from simple to compound. The compound nature appeared occur via the aggregation of components, which may be developmentally cued and linked to gross morphological features. The fine system of terms and developmental features used by Cheadle (1944) for differentiation into protoxylem, early and late metaxylem in the interpretation of vascular bundles is not generally followed in the literature (e.g. French and Tomlinson 1980) follow the more general set of terms "collateral", "amphivasal" etc. as pertaining to the arrangement of xylem as a whole) and would lead to complexity when applied to the vascular bundles of Araceae.

The lack of distinct xylem tissue in the tuber of *Z.aethiopica* is not unique, as in this study, many other rhizomes that have expanded tissue areas utilised for storage, tend to show a similar lack of distinct xylem tissue. Cheadle (1942) reported in a survey of vessels in monocot organs, that cormous and tuberous plants tended to lack vessels. In fact, the lack of sclerification in any of the tissues of the tuber in *Z.aethiopica* seems to indicate that the rhizome is not structurally important at all. This, in combination with a sparsely arranged and poorly developed vascular system, points to the water transporting function in these kinds of organs as being of secondary importance.

Alismatanae: Potamogetonales: Aponogetonaceae: Aponogeton distachyos

Morphology

Plants with perennial, sympodial, stout, fleshy and horizontal rhizomes which are buried in the mud bottoms of shallow ponds to about three centimetres. Long petiolate leaves with loosely sheathing leaf bases are produced at rhizome nodes on a seasonal basis, and the laminae float on the water surface. A fleshy inflorescence stalk is produced seasonally from the apical bud of the rhizome, bearing a single node towards the apex which branches to form two inflorescence spikes, each subtended by a fleshy bract, which also floats on the surface of the water. Van Bruggen (1973) revised the genus *Aponogeton*

and Solereder & Meyer (1928) and Tomlinson (1982a) has studied the anatomy of the Helobiae as a whole.

Anatomy

T/S rhizome

The rhizome tissues are comprised of an epidermis, which is several cell layers thick and stains brown. This layer very often tends to break down, so there is the possibility that the layer is a periderm, and it is mostly present where the roots arise at the edge of the rhizome. The hypodermis is two to four cell layers thick, the cells are flattened, opaque and stain dark green, suggesting the presence of a mucilaginous substance. The hypodermis of underground stems may often contain a suberised layer (Pate & Dixon 1982), and it is likely that this mucilaginous substance is part of a suberised layer. The cortex, immediately beneath the hypodermis, is expanded and borders an area demarcated by vascular bundles arranged in a ring. These vascular bundles are laterally orientated and therefore are seen in the longitudinal plane in the transverse section. The cortical cells contain starch granules. The area which the central ground parenchyma occupies is expanded and consists of parenchyma cells containing starch granules plus vascular bundles in the transverse plane. The vascular bundles are narrow, and not entirely distinct from the ground parenchyma. They lack a thickened bundle sheath, anastomose frequently throughout the central region, but are generally amphivasal. Most of the vascular bundles are medullary, but a few bundles are scattered in the cortex, outside of the "vascular ring". Vascular rings are generally present in cormous rhizomes which are vertically orientated. However, the axis of *A.distachyos* is definitely horizontal in orientation.

T/S mid inflorescence axis

The inflorescence axis is bounded by an epidermis of rounded cells, the cuticle is not clearly apparent and stomata are not visible. The following layer is an assimilatory band which is one to two cell layers in thickness and could be a chlorenchyma band. The bulk of the axis is comprised of central ground parenchyma tissue, with a lack of sclerifying tissues (possibly because in the aquatic habit structural support is not required). The central ground parenchyma is arranged in rays (usually seven to eight rays) with large air spaces occurring in between the rays. The vascular bundles are held centrally within the parenchyma rays (Pl. 3, Fig. 5), and the parenchyma cells often contain granular bodies, which may be starch. Such a structure may be a result of the aquatic habitat of the genus

and is also present in other species of *Aponogeton* (Arber 1925; Pate & Dixon 1982). There are smaller vascular bundles immediately beneath the assimilatory band (Pl. 3, Fig. 5). The vascular bundles throughout the central ground parenchyma are uni-collateral.

T/S upper inflorescence axis

The tissue patterns are as for the mid inflorescence axis, but with reduced air spaces and as a result the vascular bundles more closely arranged. Thus, the fleshy aerial stem appears to have the same anatomical structure both below and above the node at which the inflorescence is produced.

Growth form affinities and differences

Other members of *Aponogeton* are tuberous or cormous (Pate & Dixon 1982; Dahlgren et al. 1985) rarely rhizomatous or stoloniferous (Tomlinson 1982a). The underground organs are often able to withstand dry seasons in a dormant phase such as the Western Australian *A.hexatepalus* Van Bruggen (Pate & Dixon 1982), but *A.distachyos* tends to occur in ponds which remain damp during the dry season. Related families such as Hydrocharitaceae show a wide variation in growth forms such as free floating rhizomatous plants, bottom-fixed rhizomatous plants and tuberous plants (see Ancibor 1979), all of which are aquatic forms. The family Aponogetonaceae is quite diverse in growth form, albeit that there is habitat convergence. Branching patterns in Hydrocharitaceae are highly variable (see Tomlinson 1970a, 1973, 1982a; Ancibor 1979; Dahlgren et al. 1985) compared to Aponogetonaceae. The vegetative organs are also quite different in anatomy, particularly the "stems" which do not display the ray like arrangement of parenchyma seen in *Aponogeton,* although air cavities are present. Laticifers are meant to be present in Aponogetonaceae (Ancibor 1979; Tomlinson 1982a; Dahlgren et al. 1985) - these were not seen in *A.distachyos.* In tuberous forms of Aponogetonaceae vegetative reproduction occurs by the production of spheroid tuberlets which are terminally presented on thin rhizome outgrowths from the main stem, and are either carried laterally or vertically away from the parent plant Pate & Dixon 1982). These structures are also described for some Hydrocharitaceae (Ancibor 1979).

The seedlings of Alismatales show some variation in basic construction, but those of Alismataceae, Limnocharitaceae and Butomaceae are very similar to each other (Arber 1925; Tillich 1995). Seedlings of Hydrocharitaceae and *Aponogeton* are similar to each other, both having a bi-facial cotyledon (Tillich 1995). In *A.distachyos* the hypocotyl is

highly reduced (Tillich 1995) which may be related to the growth form, that of a sympodial horizontal rhizome.

Lilianae: Liliales: Colchicaceae:(i) Baeometra uniflora

Morphology

Plants with an underground perennial organ, which is buried five to ten centimetres below the soil surface and is generally globose. The structure of this organ resembles a corm, and is composed of more than one vertically orientated internode. The previous season's corm consists of the last few internodes which are degenerate and tend to disintegrate (Pl. 4, Figs. 1, 2). Dahlgren et al. (1985) describe the underground organs of Colchicaceae as starch-rich corms. The roots of *B.uniflora* are produced at the base of the corm (Pl. 4, Fig. 1). The apex of the corm gives rise to an elongated stalk (the neck region), which is ensheathed by leaf bases. The leaves expand into an open lamina on the surface of the soil (Pl. 4, Fig. 2). The corm is clothed in old sheathing leaf bases, which form a tough tunic. The inflorescence axis is produced at the apex of the corm from an apical growth point and grows up through the leaf bases. Thus, the elongated stalk produced at the apex of the corm is probably an inflorescence axis surrounded by leaf bases. At some point above the expanded leaves (a few centimetres although this is variable from plant to plant) the inflorescence axis branches to produce flowers.

Anatomy

T/S mid corm

The corm tissue is surrounded by an epidermis of flattened brick shaped cells, while a cuticle is absent. The cortex is expanded to approximately fifty cell layers in thickness. The cortical cells are packed with starch granules. A few vascular bundles are scattered throughout the cortex. The central region is comprised of isodiametric parenchyma cells, which are slightly smaller than the cortical cells. These are also packed with starch granules. The central region contains a central "core" of vascular tissue in which the vascular bundles are quite closely arranged (Pl. 4, Fig. 3). The vascular bundles have a single layered bundle sheath which is not thickened. The xylem in the vascular bundles is v-shaped (Pl. 4, Fig. 3), but some of the vascular bundles may also be amphivasal.

T/S neck, just above corm

The axis is bound by an epidermis which consists of rounded cells, and a cuticle is present. The following one to two layers consist of parenchyma cells comprising the

parenchyma band. The bulk of the axis is comprised of central ground parenchyma which contains the vascular bundles (Pl. 4, Fig. 4). These are scattered within the central region in no apparent pattern. The vascular bundles are bi-collateral, with a phloem pole external to the xylem, surrounded by a poorly developed unsclerified bundle sheath.

T/S upper neck (still ensheathed by leaf bases)

The tissues of the upper neck are bounded by an epidermis which is comprised of rounded cells. The cuticle is well developed. The parenchyma sheath is expanded (compared to the lower neck region) consisting of four to five cell layers in thickness (Pl. 4, Fig. 5). A sclerenchyma band is present and consists of several layers of sclerified cells and developing vascular bundles towards the periphery of the band. The central ground parenchyma consists of cells with sclerified cell walls (the vascular bundles are found in this strengthened area) and a region of unspecialised parenchyma cells centrally (Pl. 4, Fig. 5). The vascular bundles in the medullary region have a bundle sheath, which is not thickened and are bi-collateral in xylem arrangement, with a phloem pole at the apex.

T/S lower inflorescence axis (portion just emerging from leaf bases)

The lower inflorescence axis is bounded by an epidermis of upright rectangular, elongate cells. A cuticle is present, but stomata are absent. The parenchyma band consists of three to four cell layers in thickness and is composed of unspecialised isodiametric parenchyma cells. A sclerenchyma band is weakly developed with some of the cells in the outer most region, where the vascular bundles are found, appearing slightly thickened. The central region contains the vascular bundles, and the ground parenchyma is composed of unspecialised, isodiametric cells (Pl. 4, Fig. 6). The vascular bundles occur in the medullary region only. There are two kinds of vascular bundles, those with xylem arranged in a u-shaped fashion and those where the xylem is distinctly v-shaped (Figure Pl. 4, Fig. 6). The xylem vessels stain pink and the central vessel elements are prominent. The phloem cap is distinct, while a bundle sheath cannot be defined.

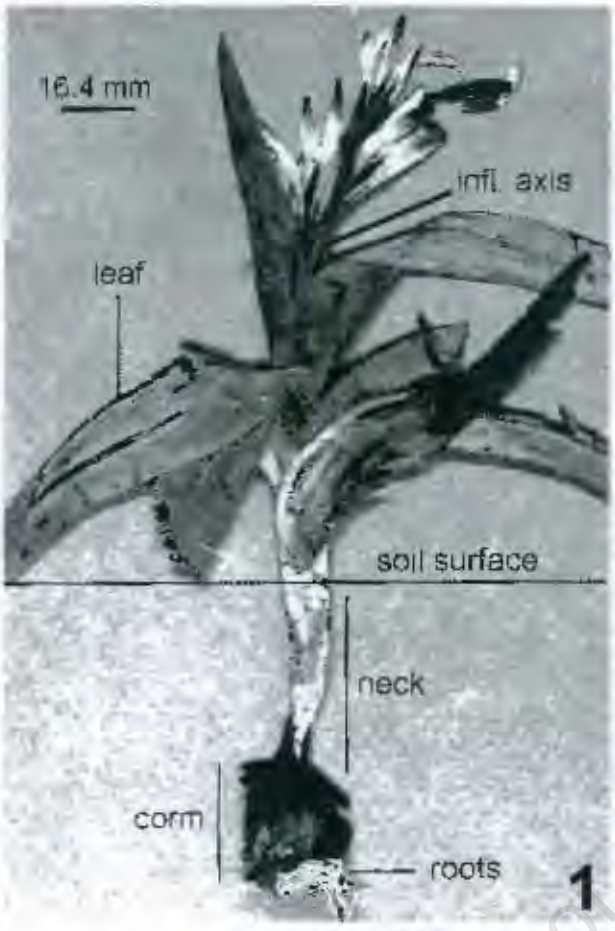
T/S mid and upper inflorescence axis (below inflorescence)

The tissue plan is similar to that for the lower portion of the flowering stalk, the main differences being that a sclerenchyma band is developed in this region and the cells contain tanniniferous substances and fewer vascular bundles are present in the central region.

Plate 4. Morphology and anatomy of *Baeometra uniflora*

Figure 1. Gross morphology showing position of corm and aerial portions relative to the soil surface.
Figure 2. Corm morphology outlining the depleted internode (oc) at the base of the current swollen corm (cc) and the swelling of the renewal corm (rc) above the current corm.
Figure 3. T/S mid corm (c) to show the circular arrangement of the vascular bundles (vb).
Figure 4. T/S neck just above corm. A parenchyma band (pb) separates the epidermis (ep) from the central parenchyma (cp) which contains bi-collateral vascular bundles (vb).
Figure 5. T/S upper neck. A sclerenchyma band (sc) containing the bi-collateral vascular bundles (vb) is present between the central parenchyma (cp) and a parenchyma band (pb) to the exterior beneath the epidermis (ep).
Figure 6. T/S lower inflorescence axis. There is a weakly developed sclerenchyma region (sc) in between the central region (cp) and the parenchyma band (pb). The vascular bundles have a v-shaped xylem (vb1) or a u-shaped xylem (vb2) arrangement and are arranged into a ring. (ep) = epidermis.
Figure 7. T/S inflorescence stalk. An assimilatory band (ab) and a sclerenchyma band (sc) are present between the epidermis (ep) and the central parenchyma (cp). The vascular bundles (vb) are arranged in a ring.

[Bars = 4 μm (Figs 3-7)**]**.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infl. axis
leaf
soil surface
neck
corm
roots
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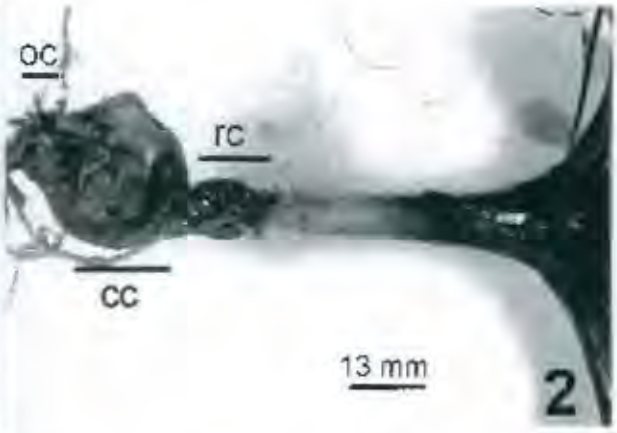
oc
rc
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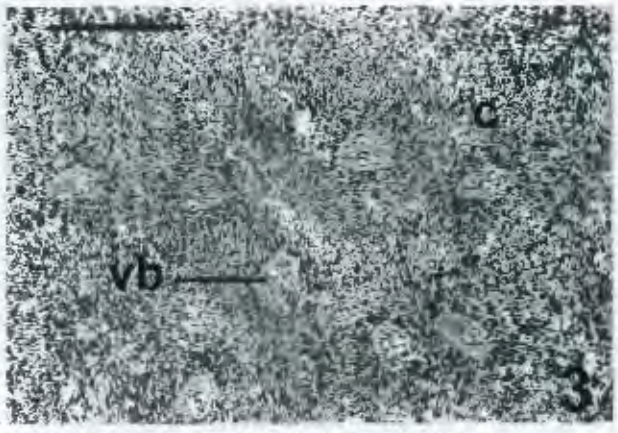
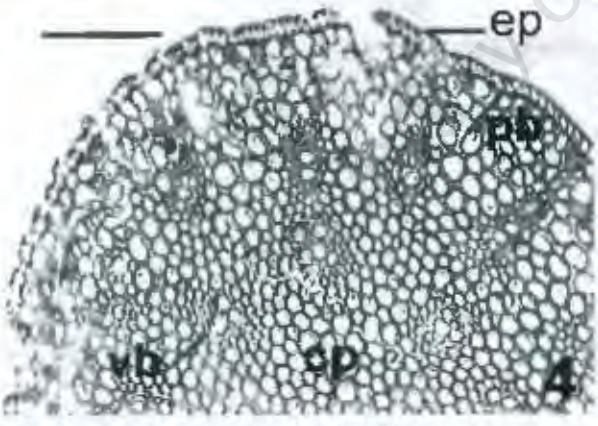

c
vb
3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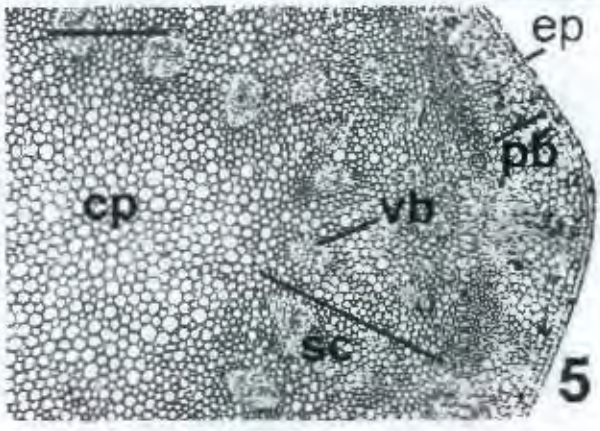
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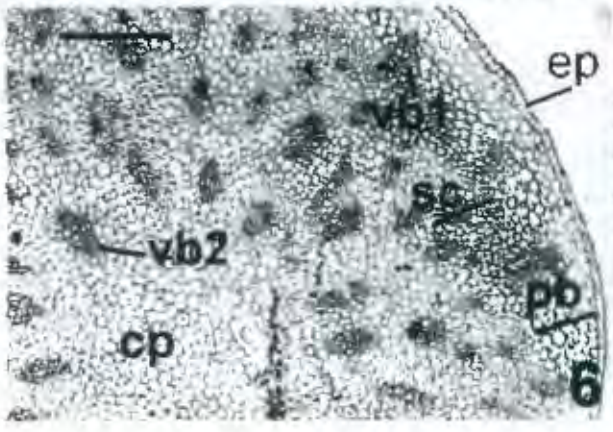
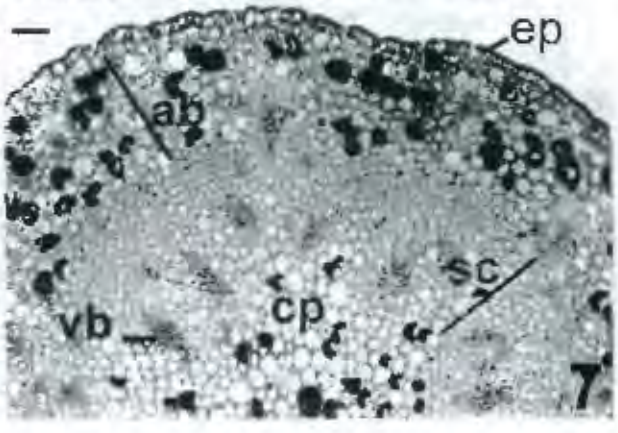
5


ep
vb1
sc
vb2
pb
cp
6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7

T/S inflorescence stalk

The flowering stalk is bounded by an epidermis which is composed of upright rectangular cells. There is a prominent cuticle and stomata are present. The following layers comprise an assimilatory band which is well developed and consists of approximately ten layers of cells (Pl. 4, Fig. 7). The cells of the assimilatory band contain chloroplasts close to upper cell wall and many of the cells are centrally filled with red staining globules, which could be tanniniferous. A sclerenchyma band is present and is well developed comprising approximately twenty cell layers in thickness. There are vascular bundles present towards the periphery of the sclerenchyma band and these sometimes merge into the assimilatory band, so that a few bundles are scattered in the assimilatory band. Vascular bundles are also present on the inner region of the sclerenchyma band. The central region consists of unspecialised parenchyma cells some containing tannin and no starch is visible in this portion of internode. The central region contains vascular bundles arranged into a ring. The vascular bundles in all areas have xylem which is arranged in a u-shape.

T/S flower stalk (upper portion)

The basic tissue plan for this region is the same as for the lower portion, except the diameter of the axis decreases, the T/S being much smaller.

(ii) Wurmbea spicata

Morphology

Plants with a perennating organ, buried three to five centimetres below the soil surface. The organ appears to be composed of more than one rhizome internode, which have a vertical growth orientation, and are thus much like a corm in structure. Pate & Dixon (1982) reported that all Australian *Wurmbea's* are cormous. The roots are produced at the base of the corm. The apex of the corm gives rise to an elongated stalk, which is the inflorescence axis, which is ensheathed by leaf bases which only expand into lamina once they are above the soil surface. The exterior of the corm is covered with modified leaf bases. These are very tough and hardened and are not fibrous in any way. Shortly above the expanded leaves (about one centimetre) the inflorescence is produced. The inflorescence is a spike, with the florets being sessile on the surface of the inflorescence axis, the axis does not branch. The Australian members of the genus have been revised by Mac Farlane (1980), but detailed anatomical studies have not been undertaken.

Anatomy

T/S corm

The corm tissues are surrounded by an epidermis which consists of flattened brick shaped cells. A cuticle is present. There is no further differentiation into tissue bands, the central region of the corm consists of parenchymatous cells, which are rounded and unspecialised. Within each cell there is a proliferation of starch granules. The central region of the corm contains diffuse and anastomosing vascular bundles, with no apparent pattern of arrangement. The vascular bundles are difficult to interpret, due to anastomosing pattern, but appear to have xylem arranged in a u-shaped and are not amphivasal. The phloem cap is difficult to see, and the bundle sheath is not prominent.

T/S neck, just above corm

The neck region is covered with an epidermis composed of rounded cells and consisting of a single layer. A cuticle is not present and stomata are absent. There is no further tissue differentiation, the bulk of the organ is composed of unspecialised parenchyma cells in the central area. This area contains the vascular bundles, which are bi-collateral with larger vessel elements basally. A bundle sheath is not prominent.

T/S mid region of neck

The mid region has an epidermis composed of rounded cells with thickened walls. The innermost and outer walls are suberised or lignified (red-staining). A hypodermis is present and consists of a single layer of rounded cells which are not thickened or specialised in any way. There is a cortex which consists of large, loosely arranged cortical cells which are unspecialised. The cortex contains some vascular bundles which are collateral and are surrounded by thickened bundle sheaths. There is an endodermoid sheath comprised of rounded to upright rectangular cells with the upper wall suberised (green staining, non-transparent). The central region consists of large isodiametric parenchyma cells which are unspecialised. This region contains the majority of the vascular bundles which are scattered throughout. Starch is absent from the cells. The vascular bundles are collateral with prominent thickened bundle sheaths. In some of the bundles, the xylem tends toward a u-shape arrangement.

T/S upper neck/inflorescence axis region just below inflorescence

The region of the axis below the inflorescence has an epidermis composed of rounded to brick shaped cells. Both a cuticle and stomata are present. The epidermis tops an

assimilatory layer, which is comprised of approximately three cell layers of chlorenchyma cells. There is a sclerenchyma band which is composed of five to ten layers of cells with prominently thickened walls containing developing vascular bundles. The central region consists of unspecialised parenchyma cells, without starch granules. The central region contains vascular bundles with variable xylem arrangements, either u-shaped or collateral. The bundle sheath is thickened and prominent.

T/S inflorescence stalk (between flowers)

The tissue plan is the same as for the upper inflorescence axis except that the chlorenchyma layer is sclerified (but still contains chloroplasts).

Growth form affinities and differences

The general morphology of the two species considered here is superficially similar. The corms give rise to axes produced from the apical bud which in the lower portions are subterranean and ensheathed by leaf bases i.e. the neck region. Aerially, the axes are no longer ensheathed by leaf bases, because the leaves are laminate at the soil surface. The axis terminates in an inflorescence. Anatomically there is variation in the corms between the two species.

In *Baeometra uniflora* the corm tissues are relatively unspecialised, being utilised for starch storage, but a distinct cortex and central region can be recognised. The corm differs slightly to that of *W.spicata* in having a central core of vascular tissue i.e. a defined cortex separating a central region. The underground stalk consists of several vertically arranged internodes (the neck region) produced from an apical bud, which at the base shows little tissue differentiation, but towards the apex has numerous features which are similar to the inflorescence axis e.g. the presence of a sclerenchyma band and peripheral and medullary vascular bundles.

In *Wurmbea spicata* the corm itself shows very little differentiation into tissues, while the vascular tissue anastomoses and is quite indistinct, the corm is seemingly utilised for the storage of starch. Such features are similar to the storage tuber of *Z.aethiopica*, with little structural modification and a poorly developed vascular system. The corm gives rise to a series of slender internodes from the apical bud, which are vertically orientated, and are enclosed by sheathing leaf bases (the neck region). At the point of departure from the corm, the internodes show no specialisation, but the following internode has a hypodermis and endodermoid sheath with suberisation present. These features are reminiscent of rhizome structure. The vascular tissue shows some degree of

intermediacy, being comprised of bundles with both u-shaped xylem arrangement and some with collateral arrangement. Cheadle & Uhl (1948) suggest that within a single internode of a monocot the vascular bundle type should be consistent. However, the condition seen in this internode is not uncommon, as many organs in this study contained two kinds of bundles in one plane of section. This could be an indication of an area that is in transition from the slender rhizome internode to the inflorescence axis. Above ground, these slender internodes give way to an inflorescence stalk, which has numerous features associated with inflorescence axis anatomy. The inflorescence axes are anatomically quite similar in the two species.

Differences in corm anatomy, in terms of the tissue differentiation, are also reported in Iridaceae. Rudall (1995) was able to recognise significant differences - some corms have a central vascular cylinder while others don't. This can generally be ascribed as a subfamilial feature in Iridaceae. In Colchicaceae this might also be an historically constrained feature.

The renewal of corms (internodes) in Colchicaceae can be highly variable. In *Colchicum* (Arber 1925) the axillary bud is carried subterraneanly downwards until the new season's growth is initiated, thus not forming the "stacked" arrangement of internodes is commonly observed in cormous plants. In *W. dioica* the axillary buds develop into lateral corms which extend to the side of the corm, rather than forming an internode above the preceding season's corm (Pate & Dixon 1982). Lateral corms are also a feature of some species of *Ornithoglossum* (Nordenstam 1982). In *Gloriosa*, *Littonia* and *Sandersonia* the corm is described as stoloniferous, forming corms at the apex of runners from which buds are developed (Dahlgren et al. 1985). The subterranean organ of *Gloriosa superba* has also been described as a (hyperpodial) tuber by Le Roux and Robbertse (1984). The corms of some species of *Ornithoglossum* are stoloniferous often forcing the corm deeper into the ground upon renewal (Nordenstam 1982). The function of such stoloniferous corms has been likened to that of "droppers" that are often associated with bulbous forms (Nordenstam 1982).

Seedlings of Colchicaceae have a haustorial cotyledon, the cotyledonary sheath is reduced and the plumule can be bi-facial (Tillich 1995). In *Gloriosa* the coleoptile forms an extended encircling structure around the base of the plumule above the primary root. This structure is positionally and functionally reminiscent of the leaf bases which surround the "neck" of adult forms. In some seedlings the hyperphyll forms a squat structure between the plumule and the primary root which appears to be positionally equivalent to the first internode of the corm.

Lilianae: Liliales: Smilacaceae: Smilax anceps

Morphology

Plants with a stout, woody, underground, perennating rhizome (Pl. 5, Fig. 1). Secondary thickening is absent (Dahlgren et al. 1985). Aerial shoots are produced seasonally and consist of laminate leaves with short petioles bearing two opposite tendrils at the base and a sheathing portion (Pl. 5, Fig. 2). The homologues of the tendrils are uncertain. Arber (1925) suggested that the tendrils are the petiole of a compound leaf, which branches to form three equivalent structures: a shortly petiolate leaf with expanded lamina (leaf) and two tendrils (petioles). Dahlgren et al. (1985) suggest that the tendrils are equivalent to the midveins of two lateral leaflets. Martin & Tucker (1985) and Bell (1991) propose that the tendrils are positionally equivalent to stipules. However, Bell (1991) suggests that their paired nature is unusual, as most stipular structures in monocots occur singly. The inflorescences are produced on shorts stalks in the axils of the leaves and branch to produce shortly stalked flowers (Pl. 5, Fig. 2). The aerial stems are covered with prickles on their surface (Pl. 5, Fig. 2) which aid the stems to twine (Dahlgren et al. 1985). The overall morphology is similar to Petermanniaceae (Tomlinson & Ayensu 1969) with which there may be systematic affinities, but, the similarity could equally be the result of a convergence in habit. The morphology of *Smilax* has been treated descriptively in numerous floras (e.g. Cabrera 1968; Jafri & El-Gadi 1978; Koyama 1978). Conover (1983) has examined the vegetative morphology of *Smilax* in relation to reticulate venation.

Anatomy

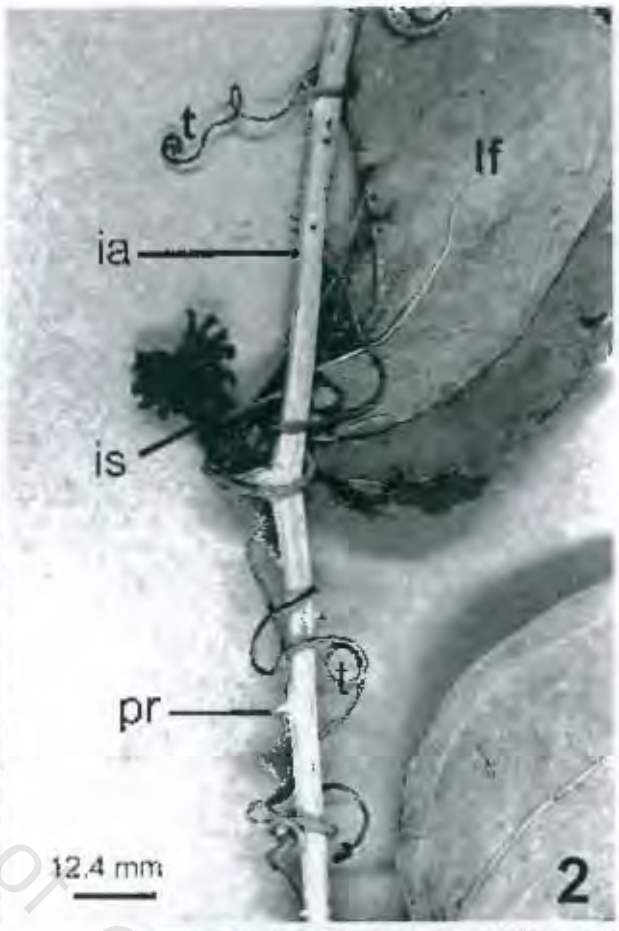
T/S aerial stem

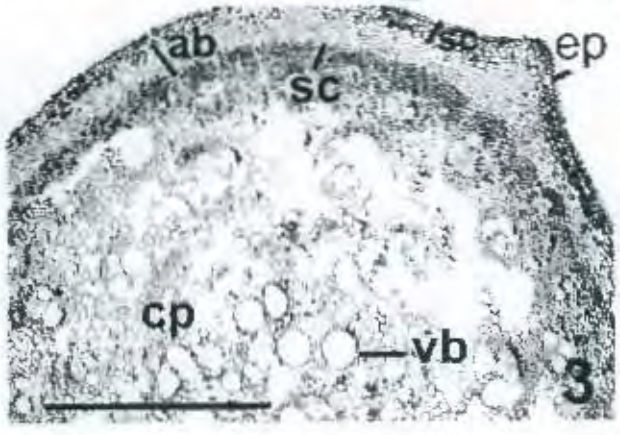
The stem is surrounded by an epidermis which is composed of dome shaped cells. A thick cuticle and stomata are present. Directly beneath the epidermal layer is a single band of cells which are sclerified and the walls tend to stain red (Pl. 5, Fig. 3). This could be a modified parenchyma band to give the stem added strength for the twining habit. There is an assimilatory band which is approximately five cell layers in thickness, the uppermost cells in the band tending to contain the chloroplasts (Pl. 5, Fig. 3). Below the assimilatory band is a sclerenchyma band composed of two to three cell layers and containing cells with very thickened cell walls (Pl. 5, Fig. 3). The central region of the stem is composed of ground parenchyma with thickened cell walls. The central region contains the vascular tissue, which is not arranged in a specific pattern. The vascular bundles are bi-collateral and contain large metaxylem elements (Pl. 5, Fig. 3). There is a single

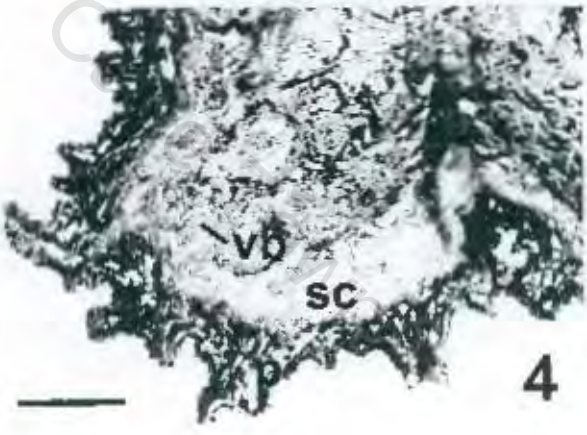
Plate 5. Morphology and anatomy of *Smilax anceps*

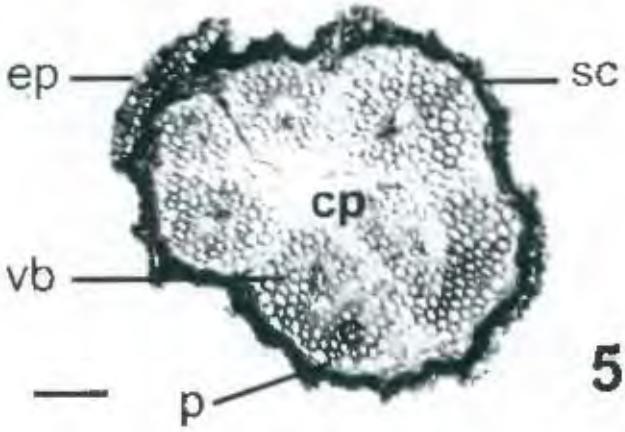
Figure 1. Morphology of plant base showing rhizome (rh), the transition region (tr) between the plagiotropic internodes to the aerial portions and the basal inflorescence axis (bia) or "stem".
Figure 2. Aerial stem morphology (ia) with tendrils (t) and prickles (pr). The inflorescence is lateral in the axil of the leaf (lf) on a short inflorescence stalk (is).
Figure 3. T/S aerial stem. Two sclerenchyma bands (sc) are present, one below the epidermis (ep) and the other beneath the assimilatory band (ab). The central region (cp) contains bi-collateral vascular bundles (vb).
Figure 4. T/S inflorescence stalk. A darkly stained parenchyma band (pb) is present between the epidermis and a sclerenchyma band (sc). The vascular bundles (vb) are contained within the central region.
Figure 5. T/S tendril. The epidermis (ep) breaks down around the sclerified cells (sc). A layer of parenchyma cells (p) separates the vascular bundles from the sclerified region. The vascular bundles are arranged in a ring and each vascular bundle (vb) is surrounded by a bundle sheath which extends into a prominent sclerenchyma cap.

[Bars = 9 μm (Figs. 3-5)].









layered bundle sheath which surrounds the vascular bundle, but at the apex forms a cap-like structure of two to three layers of sclerified cells. The large metaxylem elements and the sclerified cap of the vascular bundle might be common features of climbing plants because the large elements and strength would be needed to transport water from the rhizome to the apex of the twining axis.

T/S inflorescence stalk

The inflorescence stalk has an epidermis which consists of dome shaped cells and a thick cuticle with a wavy appearance is visible. Below the epidermis is a parenchyma band composed of cells with darkly staining cell walls, which may indicate some sort of wall storage substance (Pl. 5, Fig. 4). There is a sclerenchyma band which is composed of slightly flattened cells. The central region is composed of parenchyma cells which have slightly thickened cell walls. The central region contains the vascular tissue, which is scattered throughout and the vascular bundles tend to anastomose. The vascular bundles have xylem arranged in a u-shaped pattern and a bundle sheath is lacking.

T/S tendril

The epidermis of the tendril tends to break down around the tendril, thus losing the detail of the cellular structure (Pl. 5, Fig. 5). Directly below the epidermis is a single layer of sclerified cells (Pl. 5, Fig. 5), followed by a single layer of parenchymatous cells. The middle of the tendril is composed of ground parenchyma cells which have thickened cell walls. The vascular tissue is arranged in a ring within this region. The vascular bundles have a prominent sclerenchyma cap and are surrounded by a bundle sheath (Pl. 5, Fig. 5). The xylem is arranged in a u-shaped pattern and the phloem tends to break down.

The anatomy and arrangement of the vascular tissue is similar to that reported by Arber (1925), although she did not point out the differentiation into tissue layers. The tissue differentiation of the tendril is most similar to the stem, except that a sclerenchyma band (zone) is absent in the tendril and the vascular bundles have u-shaped xylem arrangement as opposed to bi-collateral. In addition, the arrangement of the vasculature differs. In the stem and inflorescence stalk the vascular tissue shows no definite pattern of arrangement, while in the tendril it is arranged in a ring. The interpretation of this structure as a divided petiole or as a leaf midvein or as stipules is difficult to comprehend if the tissue differentiation is considered. The tissue differentiation suggests closer affinities with stem tissue. However, due to the possible connection with the leaf organ system (i.e. the arrangement of the vascular bundles is much like that of the petiole) and the difficulties of

homologising the parameters for another organ system, the tendril of *Smilax* was not included in the analytical aspects of growth form (Chapter 3).

Growth form affinities and differences

Smilax anceps shares with some other reticulate veined Liliiflorae the feature of indeterminate branching of the aerial axis (Conover 1983). The aerial axes of species of *Smilax* range from being evergreen to being produced seasonally from subterranean buds at the apex of the rhizome (Martin & Tucker 1985). The shoot ontogeny of the leaves and axillary branches in the genus as a whole is variable, with some species displaying determinate growth, and others indeterminate growth (Martin & Tucker 1985). Thus, the growth form of *Smilax* is highly complex because the rhizome displays sympodial growth and the aerial axes may be determinate in that they are produced seasonally, while aerial branching occurs from axillary buds such that the inflorescences are in a lateral position. Such a combination of features may well be a result of the twining habit of these plants. Similarly, in *Dioscorea*, the aerial axes are produced seasonally, with some species displaying axillary branching in relation to a climbing habit (Burkill 1960) and lateral inflorescence axes (Pate & Dixon 1982). The morphology (particularly the rhizome and roots) and growth form of Petermanniaceae has been likened to that of *Smilax* (Tomlinson & Ayensu 1969). Tomlinson & Ayensu (1969) reported that the anatomy of the tendril in Petermanniaceae is that of a reduced stem, which may also be the case in *Smilax*. However, the position of the tendrils (leaf opposed) in *Petermannia* is the same as that occupied by inflorescences. Tomlinson & Ayensu (1969) suggest that the tendrils may well be a reduced axillary branch system. A detailed ontogenetic study of the aerial organs and branching in *Smilax* would be desirable before any further organographic analysis can be undertaken.

The seedling of *Smilax* may offer some clues to the growth form of the adults. The seedling consists of a reduced haustorial cotyledon with a short cotyledonary sheath and a short hypocotyl below this. The lower portion displays the seedling morphology often associated with rhizomatous growth forms. The aerial portions of the seedling are strange, the primary shoot internodes are elongated and include the epicotyl, a condition which Tillich (1995) notes is rare in monocots. Elongated internodes above the cotyledon only occur in taxa which have climbing stems (Tillich 1995). The internodes' first leaves are scale leaves and the terminal internode consists of the plumule. This may be a case of precocial development of the aerial portion of the seedling, predisposing the axis to lateral branching and being driven by the twining habit. Burkill (1960) suggests that in

Dioscorea, because the annual climbing axes have to be produced at the start of each season and have to grow to a fair height in the vegetation, the internodes must elongate rapidly. A similar growth pattern may occur in *Smilax*, which is reflected in the seedling morphology.

Conover (1983) in contrast, suggests that the caulescent non-climbing form typical of Liliiflorae is a result of neoteny, being derived from the reticulate veined Liliiflorae, where shoots could become determinate above the scale leaf. Such an interpretation has its grounding in the belief that the original monocot growth habit was a shrubby-like form without a true rhizome (after Hallier). Such an interpretation is problematic, as the "net-veined" Liliiflorae (defined by Conover as Smilacaeae; Philesiaceae; Dioscoreaceae; Stenomeridaceae; Stenomaceae; Trilliaceae; Taccaceae) are not a natural, inclusive group. The phylogeny of Chase et al. (1995) depicts that the previous delimitation of Liliiflorae needs to be redetermined as many of the taxa are no longer included in such a circumscription - Taccaceae; Stemonaceae and Dioscoreaceae are in the order Dioscoreales, while Smilacaceae; Philesiaceae and Trilliaceae are in the order Liliales. The feature of net veins appears to be a case of convergence, as net venation would have been lost far more than gained under a phylogenetic interpretation. In the molecular phylogeny of Rice et al. (1998), a similar situation is apparent with no clear-cut recognition of a "net-veined" group, albeit that the ordinal arrangements and recognitions are slightly different to that of Chase et al. (1995), with no distinction between Liliales and Dioscoreales - Dioscoreales includes Liliales.

Lilianae: Orchidales: Orchidineae: Boryaceae: Borya nitida

Morphology

Borya has resurrection-like qualities, the above ground parts become desiccated in the dry season, but are able to resume metabolic functioning upon rehydration with the next season's rains (Pate & Dixon 1982). Dahlgren & Clifford (1985) describe the growth form of *Borya* as a "graminoid shrublet" with a branched woody stem that is surrounded by stiff spiny leaves. The general morphology of *Borya* is that of an upright stem system. The stem is sheathed and thickly surrounded by tough, fibrous leaf bases (Pl. 6, Fig. 1). Roots are not visible on the exterior of the stem, because they are contained within tightly ensheathing, persistent leaf bases. An inflorescence axis is produced terminally from the stem and this is basally surrounded by the tufts of spiny leaves (Pl. 6, Fig. 1). The axis is displaced into a lateral position after flowering so that the renewal growth of the

sympodium from an axillary bud in the axil of a leaf base can take place in a more or less vertical position. The roots arise along the length of the currently growing portion of the stem at the nodes, but, the roots grow downwards between leaf bases and are covered by the sheathing leaf bases, so that they are only visible when the leaf bases are removed from the stems. There may be a strategy to having the roots forming in such a way. New roots may only be produced on rehydration and new growth (internodal renewal) of the stem may occur when conditions are favourable. In T/S in the rooting region, the stem is surrounded by several roots also in T/S (Pl. 6, Fig. 3). The gross morphology and distribution of *Borya* has been described in the Flora of Australia (Orchard & Thompson 1996).

Anatomy

Root T/S

The exodermis consists of translucent cells, loose in appearance, breaking down in the sectioning process. The cortex is divided into three regions (Pl. 6, Fig. 2, 3). The first region consists of cells with concentrically thickened cell walls which stain blue. This region is approximately three cell layers in thickness. The second region is much the same as the first, but, the cells are sclerified and the walls stain red. In the third region, the cells have slightly thickened cell walls (Pl. 6, Fig. 2). A pericycle is present, consisting of translucent cells which are not specialised. The endodermis is a single layer only and has cells with all walls equally thickened, the walls staining blue and possibly suberised. The stele has an ectophloic arrangement with the xylem tending to be arranged in radial arms (Pl. 6, Fig. 2). The central pith contains parenchyma cells which have thickened walls. The roots of *Borya* are reported to be mychorrizal (Dahlgren et al. 1985). However, there was no evidence of endomychorrizal activity or structure from the root T/S or external morphology.

T/S stem

An exodermis, which is tanniniferous in appearance, is present and is approximately two cell layers in thickness, tending to stain red and often breaking down as a result of the sectioning treatment. The hypodermis is approximately five cell layers in thickness, the cells are flattened, translucent and have slightly thickened cell walls which stain dark red (Pl. 6, Fig. 3, 4). There is an endodermoid sheath which consists of a single layer of cells with all the cell walls equally thickened. The cells are filled with a dense, blue-staining substance, which is solid, not gelatinous or mucilaginous in appearance. This may be

indicative of some sort of suberisation activity or function. The central region is packed with vascular tissue (Pl. 6, Fig. 3, 4, 5), consisting of pith parenchyma cells, which are structurally unspecialised, but are filled with a blue-staining, mucilaginous substance, which may be a storage material. Vascular bundles are present in the central region only. The vascular bundles are all amphivasal. The bundles are very closely arranged and thus the xylem is closely arranged, giving the appearance of a single mass of vascular tissue (Pl. 6, Fig. 3, 4, 5). The xylem is composed of metaxylem elements, surrounding the phloem centrally. The xylem is distinct, the cell walls staining pink to red.

Surrounding the stem are roots which arise as young rootlets within the hypodermis (Pl. 6, Fig. 4, 5). Fully developed roots are external to the stem tissues (i.e. outside the exodermis) and these plus the stem are bounded by the sheathing leaf base (Pl. 6, Fig. 3). Outside of the leaf base are the next level of roots, which would be bounded by the leaf base of the succeeding node.

T/S stem apex

The tissue arrangement and general structure of the stem apex is as for the lower region of the stem, but towards the apex, the stem branches and gives rise to several separate stems, which appear be formed by axillary buds located between the main stem and the leaf bases. The vasculature in the central region of the stem contains collateral vascular bundles, while the stem branches contain amphivasal vascular bundles.

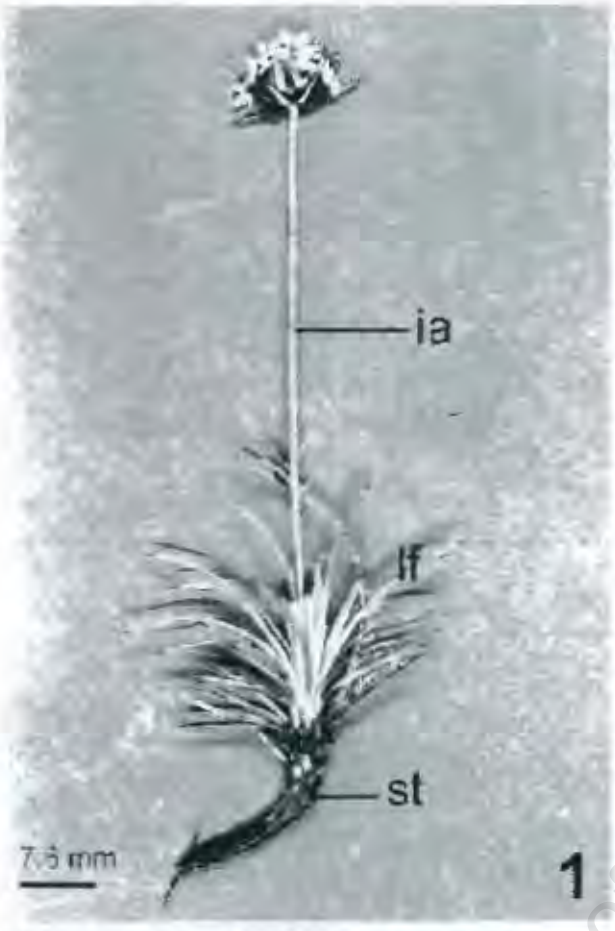
T/S basal inflorescence axis

The epidermis consists of rounded to upright rectangular cells. A cuticle is present and stomata are absent. There is an assimilatory band composed of two to three cell layers in thickness which is chlorenchymatous (Pl. 6, Fig. 6). The parenchyma band is composed of four to five cell layers of unspecialised, isodiametric parenchyma cells (Pl. 6, Fig. 6). The central ground region consists of unspecialised parenchyma cells. The central region contains the vascular bundles which are arranged in a ring. The vascular bundles have a strange tissue arrangement. There is an assimilatory sheath comprised of chlorenchyma cells which is two to three cell layers in thickness with a cap-like portion which is four to five cell layers in thickness (Pl. 6, Fig. 7). The vascular bundles have xylem with a u-shaped arrangement. The xylem elements are red-staining and distinct, as is the phloem.

Plate 6. Morphology and anatomy of *Borya nitida*

Figure 1. Gross morphology showing stem (st), spinescent leaves (lf) and the terminal inflorescence presented on the inflorescence axis (ia).
Figure 2. T/S root. The cortex is divided into a series of deeply stained, thick walled cells to the exterior below the epidermis (i). The following region of the cortex consists of sclerified cells (ii) and the remaining area is composed of slightly thickened cell walls (iii). The stele is bounded by an endodermis (en) and is ectophloic with a central pith (p).
Figure 3. T/S stem. A distinct hypodermis (hy) is separated by an endodermoid sheath from the central region (cp) which contains amphivasal vascular bundles (vb's). Roots (r) are present between sheathing leaves (lf) and the hypodermis.
Figure 4. T/S stem showing detail of outer layers with axillary root trace in the hypodermis (hyp). (es) = endodermoid sheath; (ex) = exodermis; (vb's) = vascular bundles.
Figure 5. T/S stem showing eruption of axillary root in region of hypodermis (hyp). (ex) = exodermis; (es) = endodermoid sheath; (vb's) = vascular bundles; (cp) = central parenchyma.
Figure 6. T/S basal inflorescence axis. An assimilatory band (ab) is separated from the central area by a parenchyma band (pb). The vascular bundles (vb) are arranged in a ring in the central region and have a u-shaped xylem arrangement.
Figure 7. T/S vascular bundle from central region of basal inflorescence axis. The vascular bundles are surrounded by an assimilatory sheath (ash). (x) = xylem, (ph) = phloem.

[Bars = 3.4 μm (Figs. 2, 4 & 7) and 13 μm (Figs. 3, 5 & 6)].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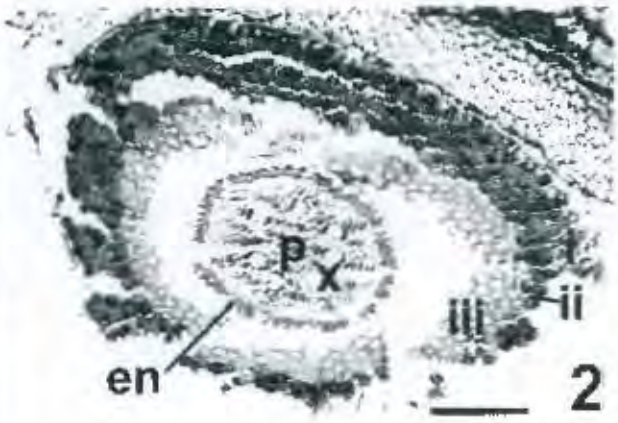
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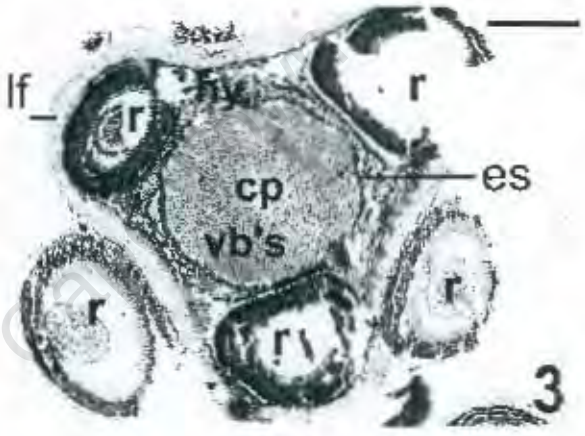
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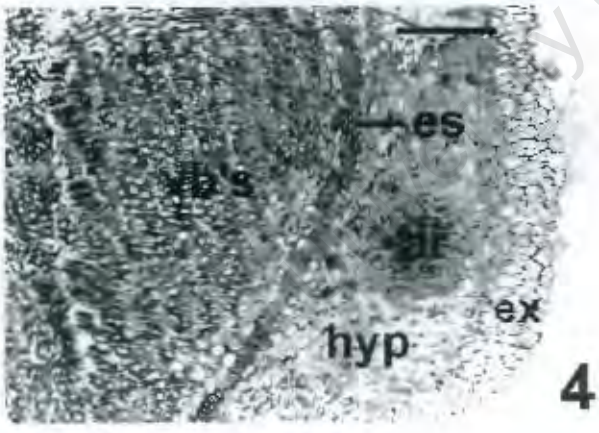
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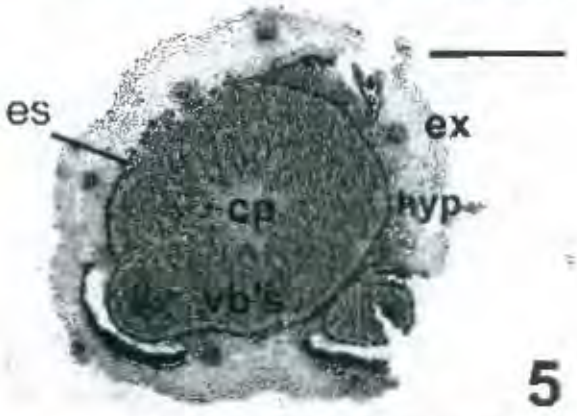
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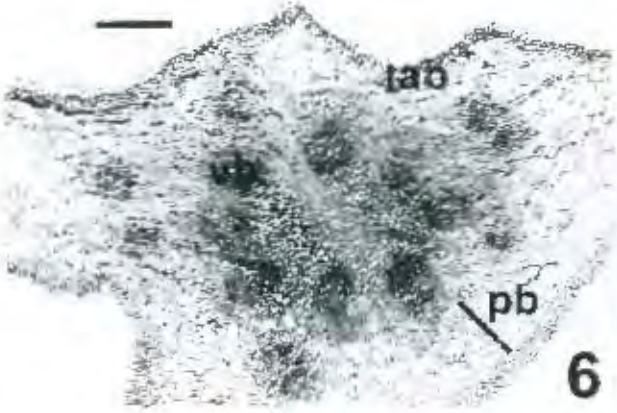
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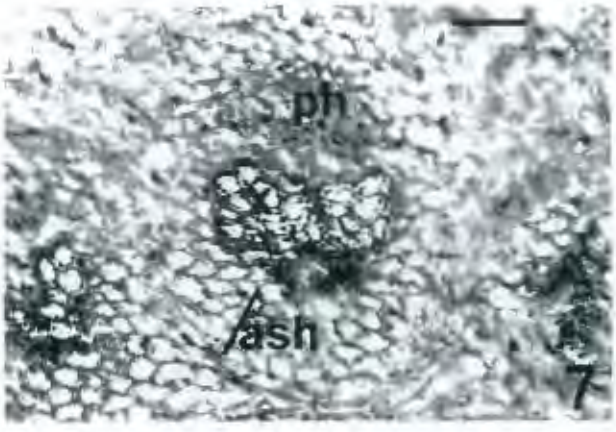
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Plate 7. Anatomy of *Borya nitida* (Figs. 1 & 2) and morphology and anatomy of *Spiloxene minuta* (Figs. 3 & 4)

Figure 1. T/S mid inflorescence axis of *Borya nitida*. Poles of collenchyma (col) are present at intervals between the assimilatory band (ab) and the epidermis (ep). The central region contains the vascular tissue (vt) which is arranged into two regions. The distinct vascular bundles (i) are arranged into a ring. The outer vascular tissue (ii) is not arranged into a distinct bundle.
Figure 2. T/S mid inflorescence axis vascular tissue of *Borya nitida*. The distinct vascular bundle is surrounded by an unsclerified sheath (sh) and the base of the xylem (x) is enclosed by a sclerified sheath (sc). The outer vascular tissue is regionalised into xylem and phloem (ph) components and is bounded by an unsclerified sheath (sh).
Figure 3. Morphology of *Spiloxene minuta*. The corm is divided into a lower region (lc) which is swollen, and an apical portion (ap) with a root initiation zone (ri) at the base. The aerial portions consist of a terminal inflorescence axis (ia) and leaves (lf).
Figure 4. L/S of whole plant of *Spiloxene minuta*. The apex of the corm is the current corm (cc) and is actively growing, supplying roots (rt) and the apex (ap) via a concentrated vascular system (vt). the lower portion of the corm (lc) is a storage region with a sparse vascular system consisting of a few root traces (rvt).

[Bars = 1.4 μm (Figs 1 & 2) and 2 mm (Figs. 3 & 4)].

Growth form affinities and differences

The growth form and corm morphology and anatomy of *Pauridia* and *Spiloxene* are identical. Morphological variation does occur between the two genera, with *Pauridia* having only three stamens (six in remaining Hypoxidaceae) and embryologically, *Pauridia* has nuclear endosperm formation (helobial in other Hypoxidaceae). Dahlgren et al. (1985) suggested that the placement of *Pauridia* within Hypoxidaceae may be dubious, but comparison of growth form does not offer any insight to this testament. This may on the other hand, be a further example of convergence in growth form, *Pauridia minuta* and *Spiloxene minuta* co-occur with individuals growing amongst one another, sharing the same habitat and possibly the same pollinators.

All corms are similar in their anatomical tissue structure, having a proliferation of parenchyma to store starch granules (Rudall 1995). However, differences in the arrangement of the vascular tissue occurs in corms of Iridaceae (Rudall 1995). Some corms of Iridaceae have a distinct cortex, which is expanded and is separated from the central area of the corm by the vascular tissue which often has a core of vascular bundles. Other corms have no distinct cortex and the vascular tissue anastomoses throughout the internode. The corms of *Pauridia* and *Spiloxene* have a distinct cortex and thus, appear to be of the common type. Rudall (1995) suggests that this type is closest to bulbs and rhizomes.

Lilianae: Orchidales: Orchidineae: Orchidaceae*: *Maxillaria variabilis

Morphology

Plants are epiphytic displaying aerial pseudobulbs. The aerial portion of stem consists of a stalked portion (cane-like) which is comprised of several internodes, each ensheathed by scale leaves (Pl. 8, Fig. 1). The basal nodes of the cane-like portion develop roots which lack velamen. The uppermost internode of the cane-like portion is swollen (to form the pseudobulb) and is topped by a single laminate leaf (Pl. 8, Fig. 1). The scale leaf is restricted to the base of the pseudobulb (node). At the apex of the pseudobulb the laminate leaf appears terminal, but the sheathing leaf base of this leaf is adnate to the pseudobulb at the apex and is only two millimetres in length. The cane-like portion (or pseudobulb stalk) has axillary buds, the upper ones possessing the potential to develop into a new sympodium. The upper portion of the pseudobulb stalk therefore branches to form another cane-like stem portion, composed of several internodes and topped by a pseudobulb plus laminate leaf (Pl. 8, Fig. 1). The axillary buds of the cane-like portion also have the potential to develop into inflorescence axes. Hence, the inflorescence is

"tunics". *Spiloxene alba* has the ability to form elongated runners from axillary buds of the current corm internode which contain a miniature corm plus buds at the apex which can develop into a new plant, similar in function to the stoloniferous corms of *Ornithoglossum.* The diversity of underground structures has been described in flora treatments (e.g. Hepper 1968), and a comparative anatomical assessment of the structures of some members of the genus is presented by Thompson (1976).

Anatomy

T/S lower portion of current corm of Pauridia minuta (but also same structure in S.minuta and S.alba)

The corm is bounded by an epidermis which consists of brick shaped cells which are not consistently regular. A hypodermis is present, and is composed of three to four cell layers of translucent cells. The layer below the hypodermis is a cortex, comprised of about ten cell layers of parenchymatous cells. Each of the cortex cells are packed with starch granules. A few vascular bundles are scattered throughout the cortex. The cortex is separated from the central ground parenchyma by a distinctive cell layer, which could be an endodermoid sheath, although it shows no suberisation. The central ground parenchyma region is expanded to form a central core of tissue, probably for storage as the cells contain abundant starch granules. The central ground parenchyma region contains most of the vascular tissue. The vascular bundles tend to anastomose in the central region, they have a poorly developed bundle sheath and the xylem is mostly arranged in a u-shaped fashion.

T/S inflorescence axis of Spiloxene alba

The epidermis consists of brick shaped cells, with the outer walls slightly thickened. The cuticle not distinct and stomata are not present. A few chlorenchymatous cells are present directly below the epidermis, but they are not really united to form a distinct band. The central region of the axis is comprised of parenchyma cells and this area expanded so that most of section is occupied by the central ground parenchyma. The parenchyma cells are unspecialised. The vascular bundles are arranged in the central region into a ring. The vascular bundles have a poorly developed bundle sheath, and are bi-collateral. The same tissue plan and general structure of the axis is present in *Spiloxene minuta*.

Dahlgren et al. 1985). Much of the corm structure and growth form was similar in the three species examined. However, cormous plants are difficult to make successful sections from, and accordingly only details from those sections which showed sufficient information are included. In addition, as the growth form is the same throughout, it was though to be sufficient to examine aerial portions from only one of the species.

The three species collected are dormant in the very dry summer season, and inhabit seasonally inundated marsh areas in winter (the wet season) in the South Western Cape, South Africa. The leaves are produced in mid-winter when the water table rises and floods the sandy flats underlayed with granite rock, on which they grow. Towards the end of winter and the onset of spring, as the day length increases, the inflorescence scape is produced and flowers are formed (Pl. 7, Fig. 3).

An examination of a L/S through the corm plus shoot reveals an interesting structure. The corm can be divided into several regions. The apex of the "corm" consists of a lower region which is slightly swollen and contains most of the vasculature that feeds the leaves and inflorescence axis (Pl. 7, Fig. 4). The upper region of this area is essentially a meristem which produces leaf buds and the terminal inflorescence axis. At some stage in the development, roots will also be produced, but from the lower internodal portion - probably at the basal node of this region. In this precise area, a second "corm" is apparent (second expanded internode). This is a highly swollen area and in L/S has a loose, diffuse vascular system which is generally concentric in nature but towards the base changes direction and supplies numerous roots (Pl. 7, Fig. 4). The roots are also formed in a ring from the last node. Thus, the "corm" is essentially comprised of two distinctly swollen internodes, one consisting of the current growth with shoots and axillary buds, the other of a purely storage growth, which provides the current corm with water and mineral nutrition via its roots. The storage area contains a large proportion of starch granules which are no doubt utilised for the flowering season. Once the axis has flowered, the leaves persist for a while relocating nutrients to the base of the current growth (vasculated internode). Starch is stored in the basal portion of this current internode and it also begins to increase in girth. Roots will be produced from the basal node of this portion in the succeeding season in response to wetting. At this stage the lower internode resources are depleted and the lower internode shrivels and dies, thus new roots form between the shrivelled internode and the swollen internode. The apex area becomes the swollen portion with a renewal bud for the next season's internode (or corm). The swollen corms may also be comprised of several internodes (as is seen in *Spiloxene minuta*). The swollen internodes are enclosed in leaf bases which become rather tough and are called

Acanthocarpus (Dasypogonaceae) and *Xerophyta humilis* (Velloziaceae). All of the non-grass genera with the subshrub habit and scleromorphic leaves are Australian (and southern African), suggesting that the habit is driven by similarity in climatic conditions (Dahlgren et al. 1985).

The location of the roots between the leaf bases of the stem, i.e. effectively produced in an aerial position, is peculiar in monocots, but aerial roots may often be encountered in growth forms where such roots are produced for photosynthesis (epiphytic orchids) or for support of massive stems (pandan stilt roots). Aerial roots were also seen in *Xerophyta humilis* a southern African "resurrection" plant, but the degree of ensheathing by the leaf bases was not nearly as elaborate as that found in *B.nitida*, nor were the roots restricted to developing from only the uppermost nodes. This commonality may point to the root location and development being part of the whole resurrection lifestyle, both plants requiring root growth upon rehydration. In addition to this, the basal portions of the stem of *B.nitida* consist of dead, woody (in the lignified sense) internodes, which along with old roots form a matted connection with mosses and the decomposing debris which overlays the granitic rock slabs on which the plants are growing. The question of firm attachment remains interesting if roots are not permanently subterranean and the whole plant is able to grow in two centimetre thick debris. The form approaches a sort of epiphytic habit, where renewal growth occurs in the upper internodes only.

The peculiar vascular arrangement into two rings and composed of two kinds of arrangement in the inflorescence axis is odd. This sort of arrangement of the vasculature is reminiscent of that seen in Dioscoreales. Ayensu (1972) describes the vascular bundles as being unique and a character by which to distinguish Dioscoreales from all other monocots. Perhaps the similarity in vascular bundle type between Dioscoreales and *Borya* is a simple case of convergence. Perhaps the systematic affinities of *Borya* with Dioscoreales have been clouded by the specialisation's in morphological features in response to the resurrection lifestyle. An alternative explanation may be that the vasculature in the inflorescence axes of *Borya nitida* displays some form of special (secondary?) growth, linked to the resurrection lifestyle.

Lilianae: Orchidales: Orchidineae: Hypoxidaceae: Pauridia minuta, Spiloxene alba, Spiloxene minuta

Morphology

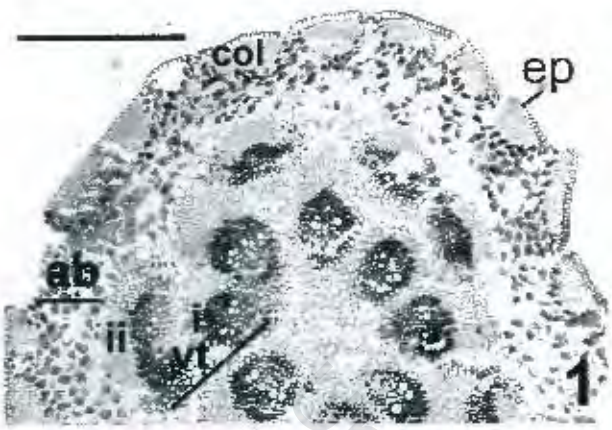
Both *Pauridia* and *Spiloxene* are genera which have a cormous growth form. Members of Hypoxidaceae have either vertical, tuberous rhizomes or corms (Thompson 1976;

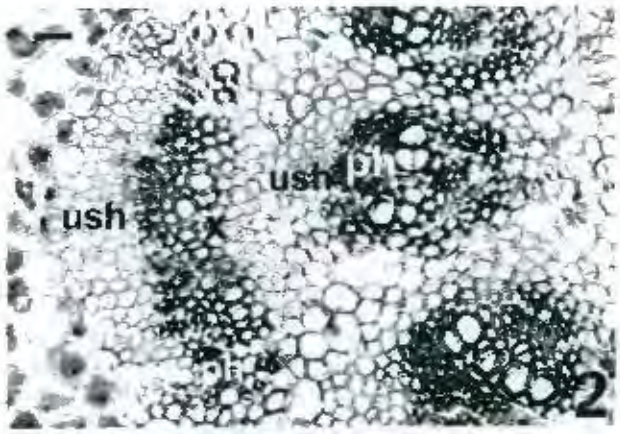
T/S mid inflorescence axis

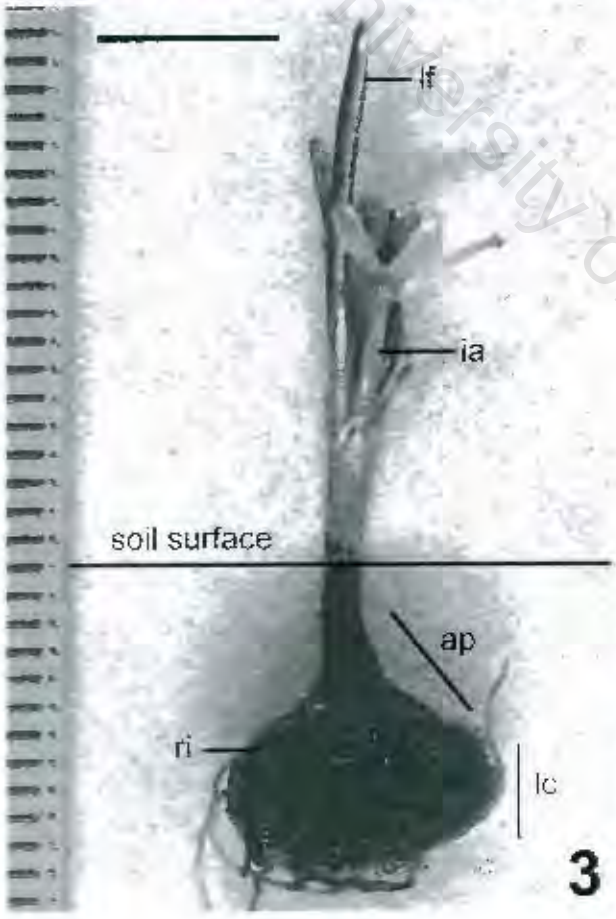
The epidermis is comprised of upright rectangular cells with the upper surface of the cells being dome shaped. A cuticle is present. Stomata are present with a substomatal cavity. Collenchyma is present and is distributed in poles around the stem just below the epidermis, between the epidermis and the assimilatory band (Pl. 7, Fig. 1). The assimilatory band is expanded to comprise eight to ten cell layers in thickness (Pl. 7, Fig. 1). The cell contents are composed of a dense, gelatinous material which stains dark green (this could be broken down chloroplasts and chlorophyll due to reconstitution process). The central region consists of ground parenchyma cells, and is reduced, comprising a few cells with slightly thickened cell walls. The bulk of the central region is taken up by vascular tissue. The vascular tissue is arranged in two rings and essentially is of two kinds (Pl. 7, Figs. 1, 2). The innermost ring (or medullary vascular bundles) consists of a distinct bundle, surrounded by a bundle sheath with bi-collateral xylem, sometimes tending to xylem of the v-shaped arrangement and consisting of metaxylem and protoxylem elements at the base (Pl. 7, Figs. 1, 2). The phloem is arranged in a lateral fashion rather than forming a distinct cap and is topped by a band of unsclerified cells. This whole vascular bundle is surrounded by the unsclerified cells. At the base of the xylem there is a sclerenchyma band, which is in turn bounded by the non-sclerified band (Pl. 7, Fig. 2). The outermost vasculature is not arranged into a distinct bundle, although it is regionalised into xylem and phloem components (Pl. 7, Fig 2). Each vascular collection consists of phloem units (probably primary phloem) which laterally flank a secondary phloem band (which is laterally arranged) and a lateral band of metaxylem (this is positioned below the phloem band). The flanking phloem units also have a number of xylem elements associated with them. The mid region of the vascular collections is bounded on the upper and lower surfaces by unsclerified cells (several layers), the upper being four to five cell layers in thickness, the lower, two to three layers (Pl. 7, Fig. 2).

Growth form affinities and differences

In general habit appearance, *Borya* is similar to *Alania*, both being subshrubs with narrow scleromorphic leaves (Dahlgren et al. 1985). These two genera have previously been included in the tribe Johnsonieae, along with *Johnsonia*; but many of these genera are now recognised at the family level e.g. Johnsoniaceae; Boryaceae (Chase et al. 1997) (see Thorne 1999) and their relationship to Anthericaceae is now very distant, as it is with one another. This growth form is also found in Poaceae; *Calectasia* (Calectasiaceae) and







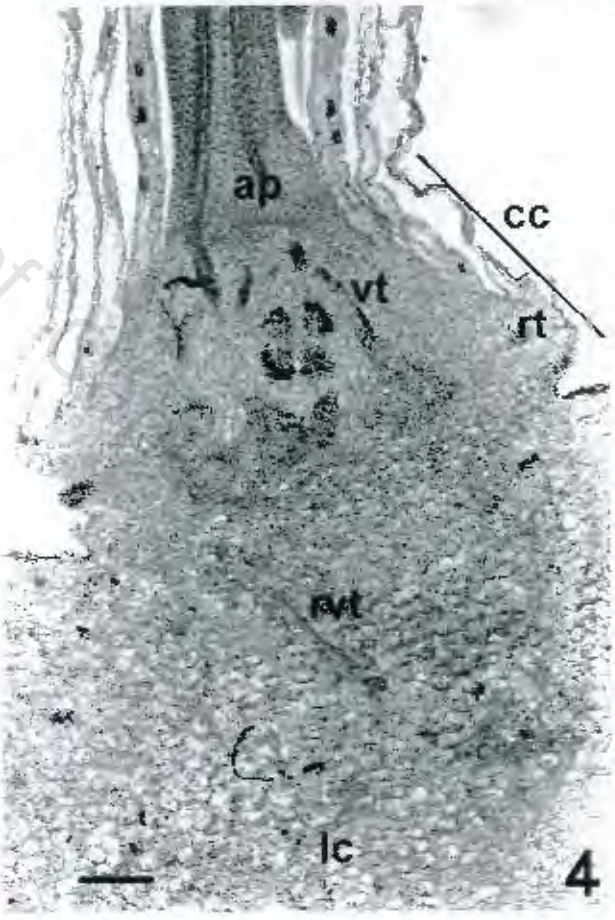


Plate 12. Anatomy of *Holothrix villosus*.

Figure 1. L/S of developing tuber (tub) and shoot meristem at the start of the growing season. At the base of the plant a compact rhizome (rh) is present with vascular tissue (vt) from this region supplying the shoot apex (ap). Lateral root extension (rex) present. (m) = meristem.
Figure 2. L/S of developing tuber (tub) and shoot system at start of growing season showing the adventitious meristem (rexm) of the second lateral root extension at the base of the plant.
Figure 3. T/S of tip of root extension tuber (tub) showing meristemmatic tissue surrounded by tuber tissue (ts) and a developing groove (gr). (tco) = tuber cortex. Also see Plate 10, Fig. 7.
Figure 4. T/S rhizome. The rhizome is composed of a cortex (co), endodermoid sheath (es) and central parenchyma (cp) which contains the vascular bundles (vb) arranged into a ring.
Figure 5. T/S upper inflorescence axis. Am assimilatory band (ab) separates the epidermis (ep) from the central region (cp) which contains the vascular bundles (vb) arranged into a ring.
Figure 6. Detail T/S of upper inflorescence axis outer layers showing a unicellular epidermal hair and detail of assimilatory band (ab) cells containing chloroplasts.

[Bars = 2.1 mm (Figs. 1 & 2); 4.8 μm (Figs. 3 & 6) and 15.6 μm (Figs. 4 & 5)].

There have been many interpretations of the tubers of the Orchideae. The tubers have been interpreted as intermediates between roots and stems (Dressler 1981) because the tuber carries the renewal bud and have thus been termed tuberoids. Others have interpreted the tubers as root tubers (Pate & Dixon 1982; Pridgeon & Chase 1995). The tubers are clearly like root tissue in structure with the independent steles indicating this origin.

The origin of a polystelic tuber is the really interesting question. In the Diseae both monostelic and polystelic tubers are found (Kurzweil et al. 1995). Several have suggested that the stele of the tubers were originally monostelic, the stele then splits up within the tuber to form a polystelic structure (e.g. Arber 1925). Others (e.g. Link; Moreau; van Tieghem) have suggested that polystely is a result of fusion of several roots (concrescence theory) thereby giving rise to a polystelic structure (see Arber 1925; Pridgeon & Chase 1995). A detailed phylogenetic study of the derivation of polystely in Orchidaceae is required to answer this question satisfactorily. Pridgeon & Chase (1995) examined polystely in Diurideae and found that cladistic analyses could not shed light on the problem due to high levels of homoplasy. In their study the problem of tuber origin was confounded by tubers which were polystelic with a common cortex or were a concrescence of steles, each one bounded by a distinct cortex.

In *Holothrix* the tubers are interpreted as polystelic root structures with an additional portion of stem tissue contained in a groove at the apex of the tuber. This interpretation is similar to that of Bell (1991). Pridgeon & Chase (1995) recommend that the term "tuberoid" be discontinued due to its outdated and non-meaningful nature. Instead, they recommend that the terms "root-tuber" or "stem-tuber" be used for tubers which contain shoot buds following Bell's (1991) terminology, and depending on which portion makes up the bulk of the tuber. Thus, in *H.villosus* the tubers would be termed *root tubers* following their recommendations. The droppers which are roots with shoot buds are recommended to be termed *droppers*. In Diurideae they suggest the need for another term - the stolonoid root - which are able to form reproductive tubers and become colonies. Similarly, Kurzweil et. al (1995) suggest the need for the term, which was used to describe tuber formation on the ends of "normal roots". Essentially, on a structural basis, there seems to be little difference between a dropper and a stolonoid root. It seems that the term dropper may be sufficient to describe all roots which are able to produce cauline meristems at their tips.

5, 6). The central region is composed of parenchyma cells which contain sparsely distributed chloroplasts. The central region contains the vascular tissue, the vascular bundles are arranged in a ring in this region (Pl. 12, Fig, 5). The vascular bundles have a v-shaped xylem arrangement, with a phloem cap above the xylem. A bundle sheath is not apparent. Globular inclusions which stain red are scattered throughout the tissues of the axis.

Growth form affinities and differences

The tuberous growth form of the Orchideae is quite unlike the pseudobulbous forms of the Vandoideae and Epidendroideae as well as the monopodial forms of the Epidendroideae. The precise sympodial renewal growth of the tuberous forms is difficult to interpret. The tuber apex has a core of stem structure bounded by a groove and contains an apical bud. The apical bud develops into a new shoot the following season and a new tuber is formed from one of the axillary buds. There are always two tubers present at the base of the plant, the old tuber from the previous season attached to the current aerial growth (also responsible for forming the aerial portion) and a "new" tuber which will over-season with the apical bud and form the new aerial growth the following season. The formation of a new plantlet from the root dropper is a further extension of a sympodial habit. The droppers are functionally equivalent to those seen in tulips and other Liliaceous taxa (e.g. Robertson 1906; Ogura 1952), but structurally different. In the case of *Holothrix* the dropper is a root while in other examples it is a rhizome outgrowth (e.g. Colchicaceae) or is stoloniferous (e.g. *Ornithoglossum*, Nordenstam 1982). In addition the "tuberous" portion at the tip of the dropper can be a true bulb or a cormous structure. In *Holothrix* it seems to be a bud which has the ability to become cauline in nature, turn upright and form a new shoot or become swollen and form a new tuber. The ability of roots to produce shoot meristem at their apices seems to be a phenomenon well established in orchids (Rasmussen 1986), but is probably absent in other monocots and is rare in dicots (see Gray 1879; Arber 1950). The tuber at the base of the stem carries a cauline bud, as does the root dropper. This ensures firstly that sympodial growth continues on a seasonal basis, but also allows the plant to "move" through the substrate to form new clones. The linkage time and mineral dependence of the offshoot plant on the parent plant has not been studied in *H.villosus*. Dry matter partitioning and dependence of the daughter plants on the parent tubers have been explored in Western Australian clonal orchid species (e.g. Dixon 1991).

T/S middle/lower regions of tuber

The tuber is bounded by an exodermis, this is thin and is composed of a single layer of cells only. The cortex region of the tuber appears to be expanded and contains several steles, up to eight steles in total (Pl. 11, Fig. 5). The cells of the cortex contain many starch granules as well as rod-like crystal inclusions (raphides). Each of the eight steles is bounded by an endodermis, which is a single layer of cells with the lateral walls suberised (Pl. 11, Fig. 6). The vascular tissue is composed of a few xylem elements associated with a few phloem cells and, centrally, with a few pith cells (Pl. 11, Fig. 6). The steles are small and indistinct within the tuber as though the steles are fine branches or divisions of a larger stele. The structure of the steles within the tuber is functionally the same as that within a stem where the vascular bundles act as individual entities of the vascular system.

T/S divided stele from tuber

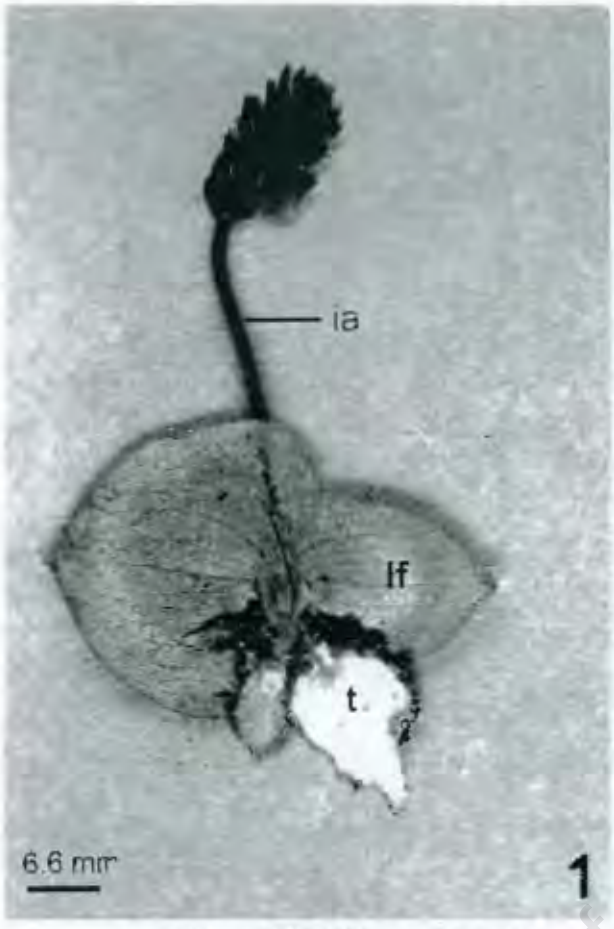
All of the eight steles are each bounded by an endodermis, consisting of a single layer of cells of which the lateral walls are thickened. Each stele consists of a few xylem elements only, none of these are arranged into a vascular bundle. As a result there are a few free groups of phloem cells arranged between the xylem elements in the stele. There are a few pith cells in the central area of the stele. All of the steles have the same basic structure.

T/S rhizome (base of plant)

The epidermis is comprised of flattened brick shaped cells. A cuticle is absent. The cortex consists of two to three cell layers of unspecialised parenchyma cells. There are occasional rod-like crystal inclusions (raphides) in this region. An endodermoid sheath is present which consists of three to four cell layers with sclerified cells with slightly thickened cell walls (Pl. 12, Fig. 4). The central region consists of unspecialised parenchyma cells and contains the vascular tissue. The vascular bundles are quite distinct, with the xylem arranged in a v-shaped manner and the phloem arranged in a cap above the xylem. The bundle sheath is poorly developed. The vascular bundles are arranged in a ring within the central area (Pl. 12, Fig. 4).

T/S upper inflorescence axis

The epidermis consists of rounded cells in a single layer. A cuticle is absent. Unicellular epidermal hairs are present. Stomata appear to be absent. An assimilatory band is present consisting of chlorenchyma cells two to three cell layers in thickness (Pl. 12, Figs.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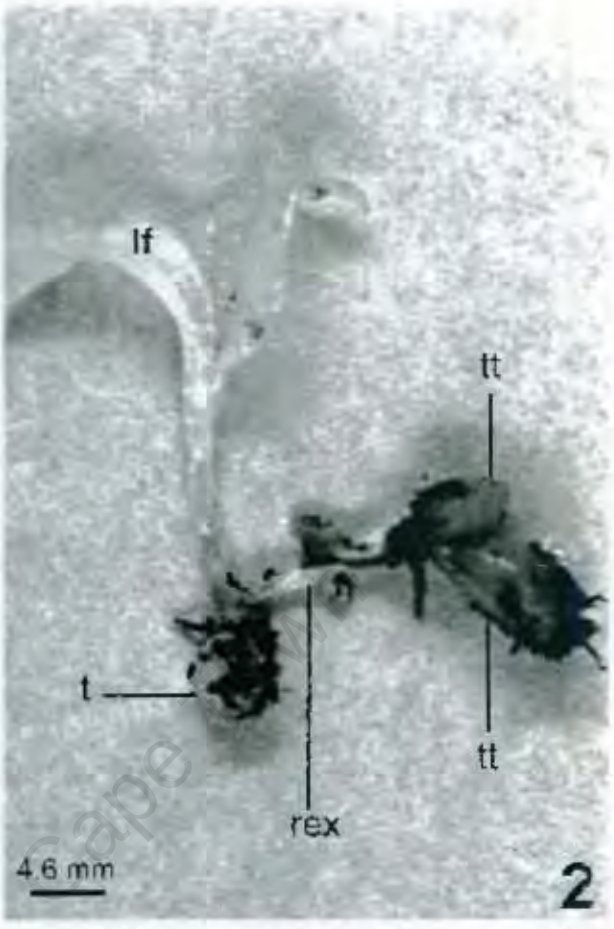
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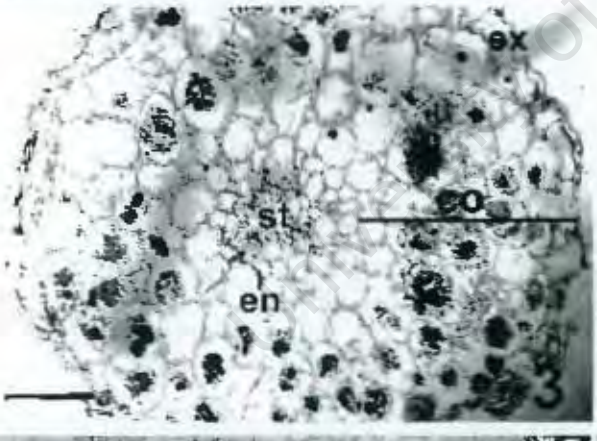
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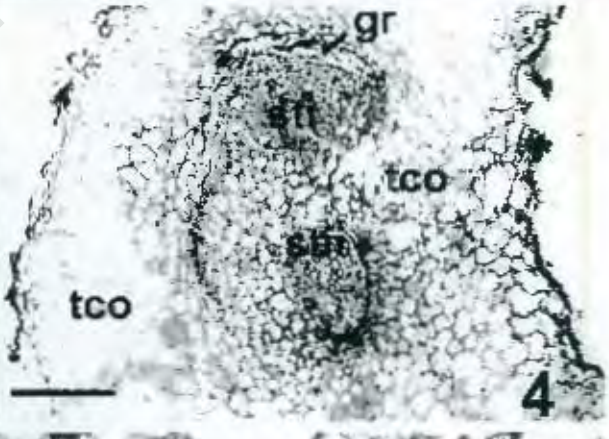
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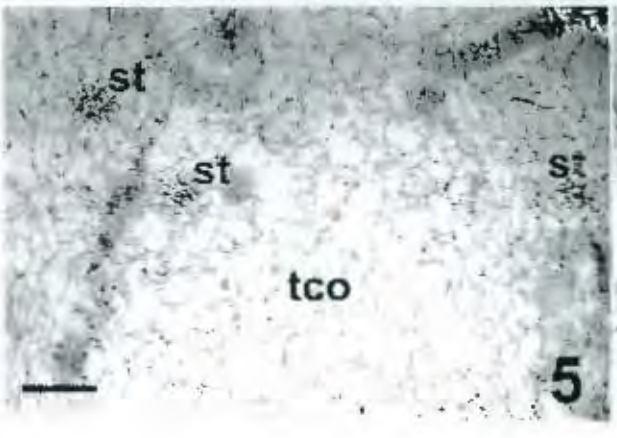
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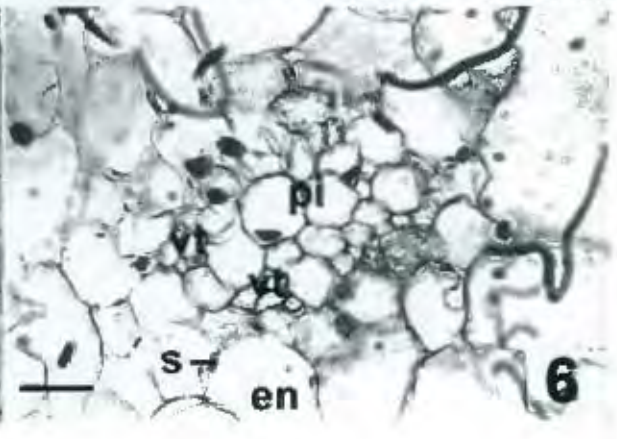
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Plate 11. Morphology and anatomy of *Holothrix villosus*.

Figure 1. Gross morphology showing tubers (t) at the base of the plant and flat, laminate leaves (lf) with the inflorescence axis (ia) in a terminal position.

Figure 2. "Resprouting" tuber morphology (t) at the start of the growth season producing two laminate leaves (lf) and lateral root extensions (rex) which bear tubers at the tip (tt).

Figure 3. T/S root showing expanded cortex (co) with endomychorrizae. (ex) = exodermis, (en) = endodermis, (st) = stele.

Figure 4. T/S tuber apex showing two steles; a shoot stele (sti) and a tuber stele (stii). The shoot stele has a groove (g) associated with it. (tco) = tuber cortex.

Figure 5. T/S middle region of the tuber. the tuber is composed of a cortex (tco) and contains several steles (st), each bounded by an endodermis.

Figure 6. T/S stele from mid region of tuber showing the vascular tissue (vt) arranged into groups of xylem and phloem components, a central pith (p) and the endodermis (en) with suberised lateral walls (s).

[Bars = 2.8 μm (Figs. 3-6)**]**.

multistelic tuber. If this type of structure is correctly interpreted, then the root (lateral outgrowth) functions as a dropper, taking the new shoot bud to a distance some way away from the parent plant. Where the following seasons tuber for the parent plant comes from is not clear, but the L/S shows a bud which is produced from the rhizome above the current tuber. Whether this follows a dropper development is not clear. All plantlets collected showed two lateral outgrowths at the start of the new season (Pl. 12, Fig. 2), both of which in T/S had the same anatomy.

Anatomy

T/S root

The root is bounded on the outside by an exodermis, which is comprised of a single layer of cells. The cortex is composed of large parenchyma cells which contain groups of fungal "balls", indicating endomychorrizae (Pl. 11, Fig. 3). The stele consists of an endodermis which has cells with the lateral walls suberised. The xylem is arranged in radiating arcs with groups of phloem cells in between the arcs, and a region within the central area of the stele contains unspecialised cells which may be a pith.

T/S apical region of tuber

This region is surrounded by an exodermis which is composed of a single layer of cells. The cortex is expanded and is composed of parenchyma cells which contain starch granules and rod-like crystals (raphides). The fungal balls which are present in the cortical cells of the root are absent in the tuber. There are two "steles" which are more or less centrally located and both are surrounded by an endodermis. The endodermis is a single layer of cells with the lateral walls suberised in both steles. One is probably a tuber stele, while the other is a shoot stele as explained previously. The shoot stele is bounded by a groove on one side only (Pl. 11, Fig. 4). Both steles have a siphonostelic structure with the phloem arranged outside the xylem. In the tuber stele, where there is amalgamation of the two steles into the tuber tissue, the xylem is less ring-like in fashion and is more broken up within the stele. There is no distinction between a root tissue and a stem tissue in this area of the tuber. It is undifferentiated cortex.

produced above the tuber region. These are formed from the rhizome and lie on the surface of the substrate. Aerial axes are produced seasonally from the apical bud of the rhizome and bear an inflorescence terminally (Pl. 11, Fig.1). The inflorescence axis has several internodes with small sheathing leaf bases confined to the nodes. The plants reach a height of five to ten centimetres and often grow in loose soil or litter in the crevices of rocks, usually granitic in origin.

A L/S of the tuber shows that the tuber has an apical region where two steles are present. One of these is a "tuber" stele which splits into eight steles in the main tuber and these then unite at the base of the tuber again. The other stele is a "shoot" stele and seems to be involved with supplying the aerial portions of the plant with vasculature. A T/S of the upper region shows that the two steles lie adjacent to each other. The shoot stele is bounded on one side by a hollow "groove" (Pl. 11, Fig. 4).

A longitudinal section of the developing tuber and shoot at the start of the new season shows that the current tuber is positioned below a rhizome (in the central part of the plant) (Pl. 12, Fig. 1). The tuber vasculature is not apparent in L/S, the bulk of the tuber is composed of large parenchyma cells which contain starch granules. At the apex of the tuber two main vascular systems can be identified. The rhizome appears to be the centre of initiation for the lateral outgrowths and for the formation of the aerial shoot portions, as the vasculature runs from the central region of the rhizome to the tuber below, and also to the lateral outgrowths (Pl. 12, Fig. 1). The lateral outgrowths have an anatomy equivalent to roots in T/S. However, at the tip of this lateral outgrowth is a highly meristematic region which appears to contain a bud within it (Pl. 10, Fig. 7; Pl. 12, Fig. 3).

A T/S of the tip of one of these lateral outgrowths reveals root tissue anatomy with a bud zone adjacent to this (Pl. 10, Fig. 7; Pl. 12, Fig. 3). The bud zone tissue is highly meristemmatic and curves upwards and around a central structure, so that a groove is created within the bud tissue directly adjacent to the root. The bud tissue does not, at this young stage, contain any vascular tissue, but some rod-like crystals (raphides) can be distinguished. This offers no clue to the origin of the tissue, as these crystals are found in all three organs viz. tuber, rhizome and inflorescence axis.

This sort of arrangement suggests that the root may carry a bud at the tip which is surrounded by a tissue of different origin to the root. This bud would give rise to a shoot stele and the root carrying the bud would give rise to the tuber stele (as shown in Pl. 11, Fig. 4). As the tuber develops, the shoot stele continues to be surrounded by different tissue plus a groove (as seen in a mature tuber), while the root portion grows and develops into the expanded tuber tissue, the main stele branching into eight to form a

Growth form affinities and differences

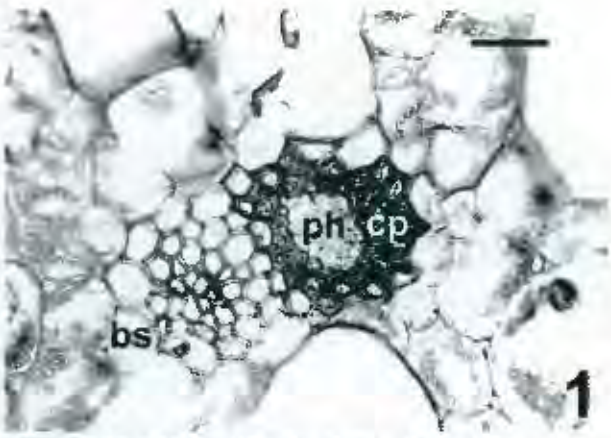
The terminal position of the inflorescences in *P.ottoniana* and the formation of new growth from an axillary renewal bud is indicative of a truly sympodial growth habit. The pseudobulbs are probably rhizomatous in the swollen basal internodal area, turning upward into less succulent internodes and finally terminating in a flowering axis. The anatomy of the internodes changes along with the direction of growth where, at some point, the cortex arrangement of the lower internodes changes to accommodate assimilatory tissues in the upper nodes. Withner (1974), however, suggested that the pseudobulb and rhizome anatomy is the same, without considering the differing structure of homoblastic versus heteroblastic pseudobulbs. The arrangement of this "multinodal pseudobulb" clearly indicates that a pseudobulb (particularly in *P.ottoniana*) is not a distinct organ as was often proposed. This was also pointed out by Dressler (1981) and Rasmussen (1986). The multinodal pseudobulb of *P.ottoniana* appears to be a sympodial unit of a simple rhizomatous growth habit with an erect, leafy stem terminating in an inflorescence axis. The internodes are modified to become succulent for water storage and the many starch grains in the parenchyma cells indicate that the internodes also act as food storage areas.

The vascular bundle anatomy of the pseudobulbs as well as the inflorescence axes indicates that the phloem, with the sclerified structure of the vascular bundle, requires support. These sclerenchymatous regions have also been noted by Withner (1974) and are referred to as crescent shaped sclerenchyma caps by Arditti (1992). The structural support of the phloem may have something to do with the movement of solutes from internode to internode and perhaps with the ultimate translocation of nutrients to the new sympodium each season. The inflorescence axes also have a sclerenchyma cap at the base of the vascular bundle (i.e. supporting the xylem). This suggests that there is some sort of strengthening required for transporting water from succulent areas to the more upright portions of the axes.

Lilianae: Orchidales: Orchidineae: Orchidaceae: Holothrix villosus

Morphology

Plant consisting of a very short vertical stem with contracted internodes from which laminate leaves are produced from apical nodes and lateral roots are produced from nodes towards the base, and with subterranean tubers arising at the base of the plant (Pl. 11, Fig. 1). The roots grow laterally for some way and often bear swellings (small spheroidal tubers) at their apex (Pl. 11, Fig. 2). Only two flat, laminate leaves are



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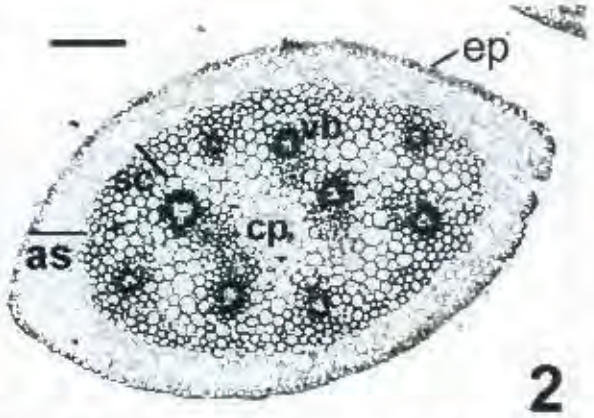

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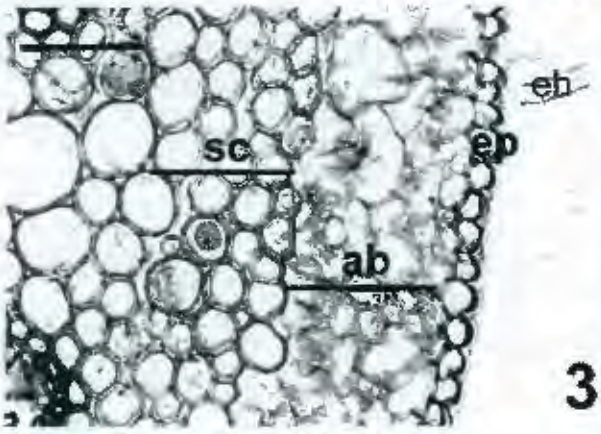

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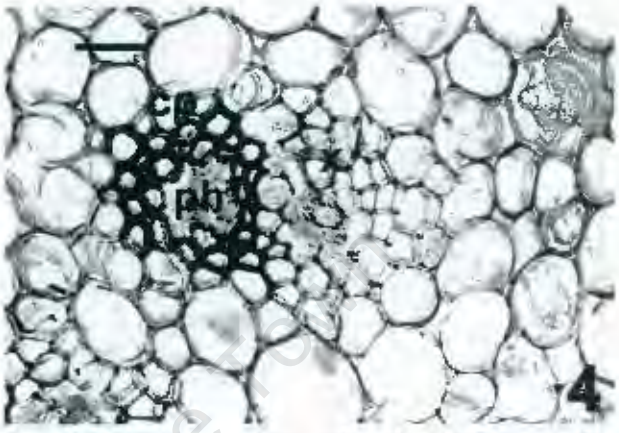

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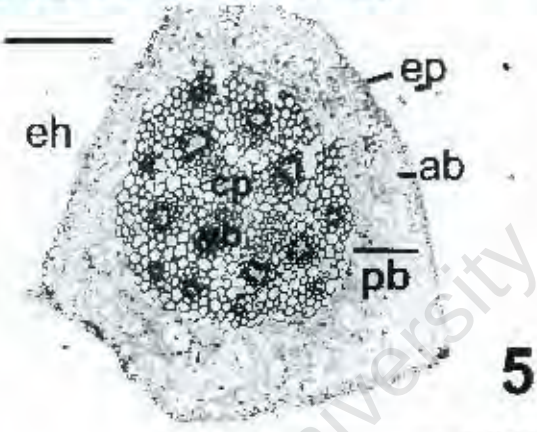

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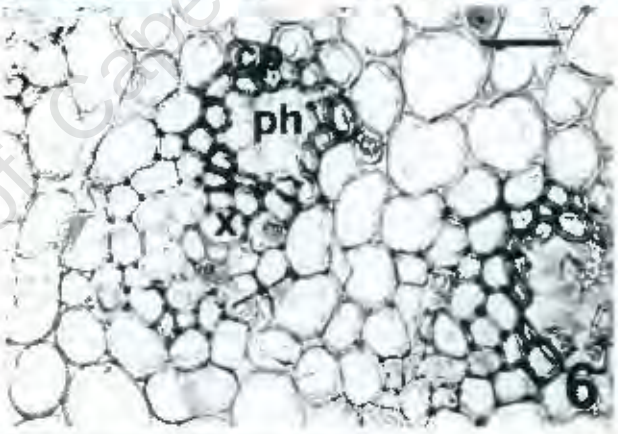

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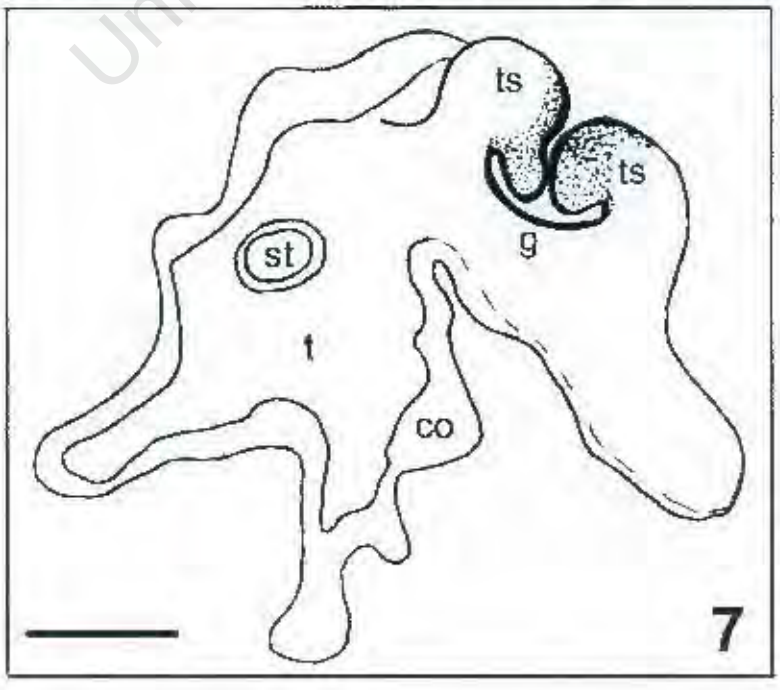

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Plate 10. Anatomy of *Polystachya ottoniana* (Figs. 1-6) and *Holothrix villosus* (Fig. 7).

Figure 1. T/S of vascular bundle from mid pseudobulb of *Polystachya ottoniana*. Each vascular bundle is surrounded by a single layered, non-sclerified sheath (bs) and the phloem (ph) is enclosed by a sclerified cap (cp). (x) = xylem.
Figure 2. T/S mid inflorescence axis of *Polystachya ottoniana*. An assimilatory band (ab) and sclerenchyma band (sc) occur between the central region (cp) and the epidermis (ep).
Figure 3. T/S of mid inflorescence axis of *Polystachya ottoniana* Showing detail of outer tissue layers, the epidermis with epidermal hairs (ep), the assimilatory band (ab) containing chloroplasts and the sclerenchyma band (sc).
Figure 4. T/S vascular bundle from mid inflorescence axis of *Polystachya ottoniana*. The phloem (ph) of each vascular bundle is surrounded by a sclerified cap (cp) and the xylem is bi-collateral (x).
Figure 5. T/S axis between flowers of *Polystachya ottoniana*. A reduced assimilatory band (ab) is present directly beneath the epidermis (ep) and between the parenchyma band (pb). (cp) = central parenchyma, (vb) = vascular bundle.
Figure 6. T/S vascular bundle from axis between flowers of *Polystachya ottoniana* showing a sclerified cap (sc) surrounding the phloem (ph) and the xylem (x) with a t-shaped arrangement.
Figure 7. Stylised plan of T/S of developing root extension tip (tt in Plate 11, Fig. 2) of *Holothrix villosus*. A sheath of tuber tissue (ts) with a meristematic region and associated groove (g) is carried on top of the developing tuber (t) with a prominent stele (st). Stippled areas indicate the meristem region which may play a role is stem tissue initiation and the formation of a second stele at the apex of the tuber. (co) = cortex. Also see Plate 12, Fig. 3.

[Bars = 18 μm (Figs. 2 & 5) and 2.8 μm (Figs. 1, 3, 4, 6 & 7)].

T/S apex of pseudobulb (last internode of pseudobulb)

The tissue arrangement and vascular bundles are similar to that seen for the mid-region of the pseudobulb. There are fewer cells containing the compound sort of starch grain in this region of the pseudobulb and thus, the vascular bundles are more distinct.

T/S pseudobulb apex into first inflorescence axis internode

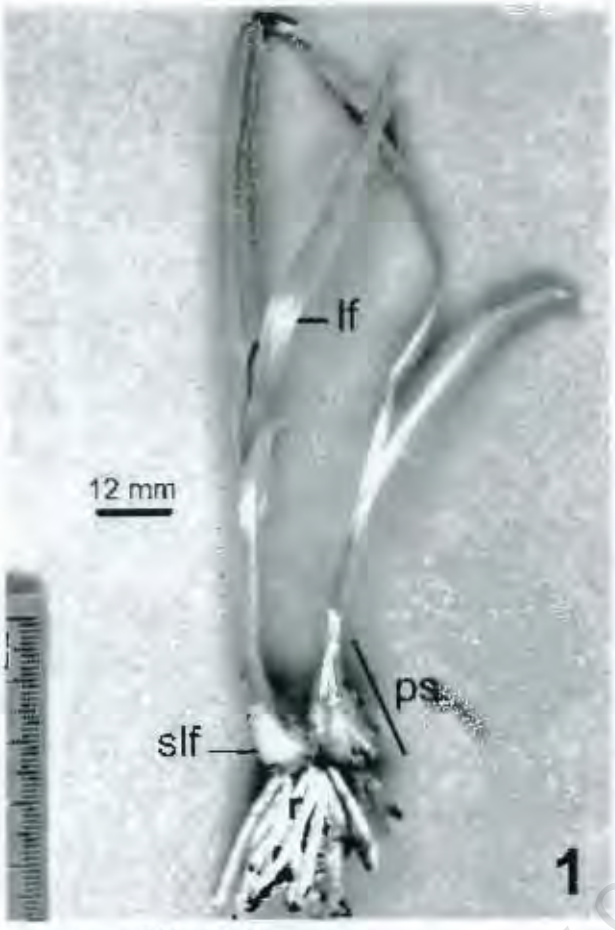
The diameter of this internode is smaller than the apex of the pseudobulb. However, the tissue arrangement and structure is the same as the pseudobulb apex. The only difference is that there is no sclerification present in any of the tissues, as the basal portion of the first inflorescence axis internode appears to be soft tissue during the flowering phase.

T/S mid inflorescence axis

The epidermis consists of rounded cells. A cuticle is present. Unicellular epidermal hairs are present and are also bounded by a cuticle. The following layer is an assimilatory band which is comprised of three cell layers (Pl. 10, Figs 2, 3). There are some large parenchyma cells appearing intermittently in the band which do not contain chloroplasts. A sclerenchyma band is present and is composed of about five cell layers, each of the cells with thickened cell walls. The central region is composed of central ground parenchyma cells which are unspecialised, although the cell walls are slightly thickened. This region contains the vascular tissue (Pl. 10, Fig. 2). The vascular bundles are few in number and are large and conspicuous. The vascular bundles are bi-collateral most commonly (Pl. 10, Fig. 4), but some vascular bundles also have a t-shaped xylem arrangement. The bundle sheath is composed of one to two cell layers of thick walled, deeply red staining cells at the base of the bundle. A sclerenchyma cap is also present and extends to completely surround the phloem cells (Pl. 10, Fig. 4).

T/S axis between flowers

The tissue arrangement and basic cell composition is the same as the mid axis. The shape of the axis differs in this region being rounded as opposed to ovalish, and has an expanded parenchyma region and the vascular bundles often have a t-shaped xylem arrangement (Pl. 10, Figs. 5, 6).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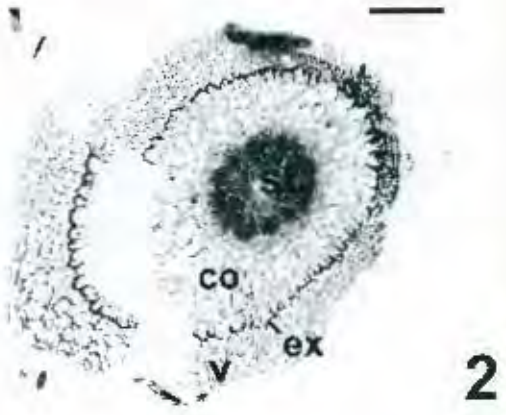
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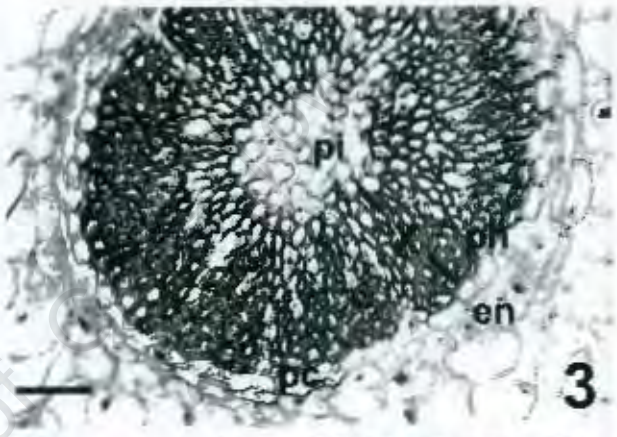
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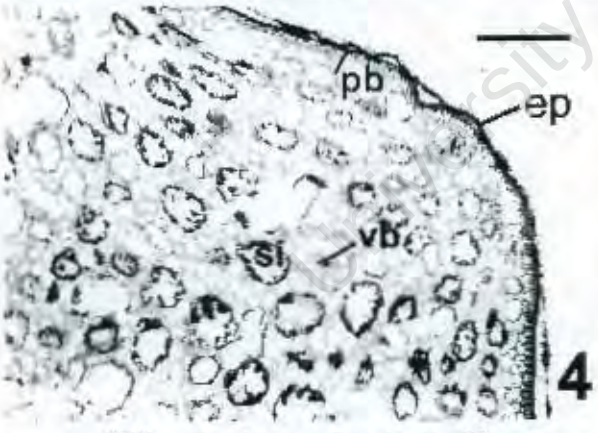
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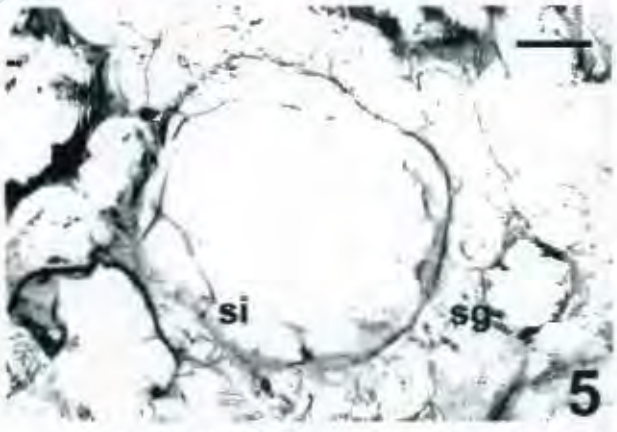
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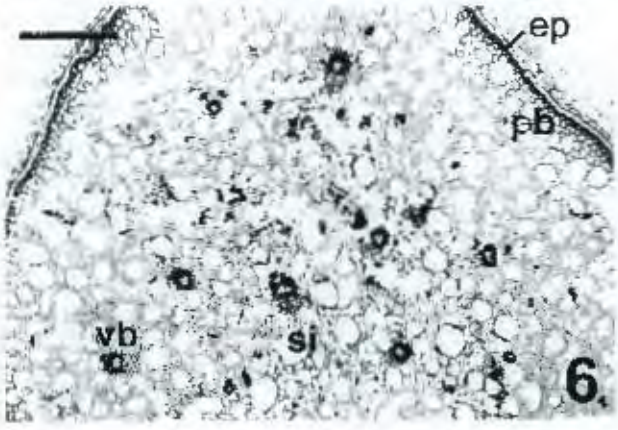
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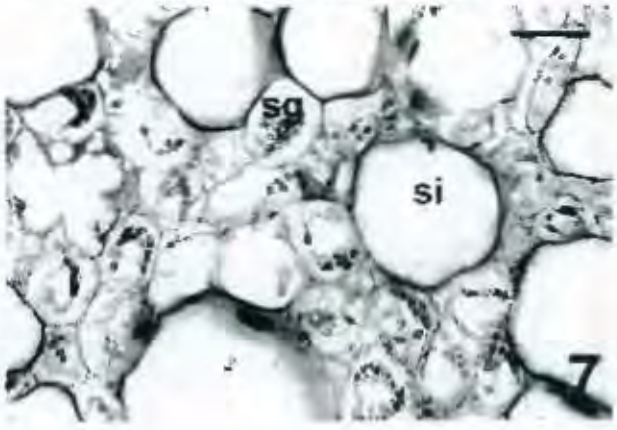
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Plate 9. Morphology an anatomy of *Polystachya ottoniana*

Figure 1. Gross morphology. Pseudobulbs (ps) are composed of several internodes with varying degrees of succulence and are enclosed by sheathing scale leaf bases (slf) of aerial laminate leaves (lf). Roots (r) are covered with velamen.
Figure 2. T/S root. the velamen (v) surrounds the root to the exterior of the exodermis (ex). The cortex (co) contains chloroplasts. (st) = stele.
Figure 3. Detail of stele from root showing endodermis (en), pericycle (pc) and mesarch xylem development (lines) with protoxylem (x) in the centre. (ph) = phloem.
Figure 4. T/S basal internode of axis (first internode of pseudobulb). A parenchyma band (pb) separates the epidermis (ep) from the central region which contains compound starch grains (si) and vascular bundles (vb).
Figure 5. T/S basal internode of pseudobulb showing detail of compound starch grain (si) and starch granules (sg) contained within the central parenchyma cells.
Figure 6. T/S mid region of pseudobulb (2nd internode of axis). A parenchyma band (pb) separates the epidermis (ep) from the central region which contains compound starch grains (si) and vascular bundles (vb).
Figure 7. T/S mid region of pseudobulb showing detail of compound starch granule.

[Bars = 24 μm (Figs. 2, 4 & 6) and 8.6 μm (Figs. 3, 5 & 7)].

T/S basal internode of axis (first internode of pseudobulb)

The basal portion of the pseudobulb has a very thickened cuticle which is the same thickness as the epidermis (Pl. 9, Fig. 4). The epidermal cells are rounded, with thickened outer walls. There is a parenchyma band which is composed of two to three cell layers of unspecialised, isodiametric parenchyma cells (cortex). The central area consists of thin walled ground parenchyma cells which contain striated starch grains that are compound (Pl. 9, Fig. 4). Towards the mid region of the internode of the pseudobulb the starch grains stain grey, but are red staining in the region at the base of the pseudobulb where the roots arise. Some ground parenchyma cells also contain starch granules of the red-staining, crystalline sort (Pl. 9, Fig. 5). The central region contains the vascular tissue, which is sparsely distributed and difficult to distinguish. The vascular bundles have a non-sclerified sheath at the xylem pole which is one layered but becomes two layered below the xylem. Above the phloem pole there is a sclerified cap which extends to completely encircle the phloem cells. The vascular bundles have a uni-collateral xylem arrangement with a single large cavity and a few protoxylem cells below. The vascular bundles are scattered within the central ground parenchyma and xylem pole faces towards centre.

T/S mid region of pseudobulb (second internode of axis)

The cuticle thickness in this region is the same as was seen at the base of the pseudobulb. The epidermis is composed of rounded cells with the outer walls thickened. A parenchyma band is present and is composed of two to three cell layers of unspecialised, isodiametric parenchyma cells. The central area of the pseudobulb is composed of thin-walled parenchyma cells containing red-staining crystalline starch granules, as well as cells which contain the striated, compound sort of starch grains (Pl. 9, Figs. 6, 7). The central area contains the vascular tissue, which is sparsely distributed among the starch grains (Pl. 9, Fig. 6). The vascular bundles are larger than in the first internode of the pseudobulb, while the starch grains tend to decrease in size (Pl. 9, Figs. 5, 7). The vascular bundles are bounded by a single layered non-sclerified sheath around the xylem pole. The sheath is two layered below the xylem, while at the phloem pole there is a sclerified cap which extends to completely enclose the phloem cells (Pl. 10, Fig. 1). The xylem in young vascular bundles tends to have a u-shaped arrangement, but often the vascular bundles are uni-collateral.

Liliianae: Orchidales: Orchidineae: Orchidaceae: Polystachya ottoniana

Morphology

Plants epiphytic with sympodial growth and succulent (pseudobulbous) internodes (Pl. 9, Fig. 1). Inflorescences are produced on terminal inflorescence axes on each sympodial unit at the apex of the pseudobulb. The pseudobulbs are comprised of five to eight internodes, the basal ones most succulent and the aerial internodes with less succulence towards the apex. The internodes are completely ensheathed with papery wax-like scaling leaves, which are the sheathing portions of the leaves and which expand at a constriction zone into a lamina (Pl. 9, Fig. 1). The leaves are therefore not fused to the pseudobulbs in any manner. Each new sympodium is formed at the base of the lowermost pseudobulb node (first node of pseudobulb from the renewal bud in an axillary position), the reserve bud is located right at the base of the pseudobulb. Each new sympodial unit has the same morphology of the previous with the succulence more elaborate in lower internodes of the pseudobulb. The succulent internodes turn upward in true sympodial fashion and taper towards the apex of the axis. Several to many roots are produced at the most basal node of the pseudobulb only and break through the scaling leaf sheath to become exposed to the air. They are green, and fleshy when young and newly produced. Older roots are thickly enveloped in a velaminous sheath (Pl. 9, Figs 1, 2). The roots do not branch.

Anatomy

T/S root

The velamen contains cells with dense spiral thickenings, comprising about four to five cell layers in thickness. The velamen surrounds an exodermis which consists of a single layer and is composed of cells with thickened outer walls (Pl. 9, Fig. 2). The cortex appears to consist of a single region, comprised of six cell layers. The cortical cells contain chloroplasts. An endodermis is present but the walls lack specialisation (Pl. 9, Fig. 3). The pericycle is distinct consisting of clear cells with slightly thickened walls. The central stele is an ectophloic siphonostele, the bottom of the xylem area consisting of a parenchymatous pith region. The xylem is arranged in clusters with protoxylem in the centre (this stains a pale blue) which is surrounded by metaxylem which stains red and has cells with thickened walls (Pl. 9, Fig. 3). The development of the xylem is possibly mesarch. Between the xylem clusters are small groups of phloem cells, with approximately five cells to each group.

is composed of several internodes which bear scale leaves at their nodes. The L/S of the developing shoot with terminal developing pseudobulb may shed light on the peculiar position of the laminate leaf. The apex of the developing pseudobulb is constricted (indicating that the terminal leaf must consist of two parts, the sheath and the lamina, as is normal in orchids) and two buds could be determined adjacent to the apical meristem. The larger is possibly the laminate leaf, while the smaller may be a reserve bud. The nature if this bud cannot be determined and there appears to be no similar structure in other taxa. The constriction points to the location of the sheathing portion of the leaf, which in this case is very reduced.

The nature of lateral inflorescence production has been carefully examined by Andersen et al. (1988) in *Eria*. The degree of lateralness was found to vary substantially from reduced rhizome bearing sympodial units which form terminal pseudobulbs with positionally terminal inflorescence axes (but formed from subapical buds) to inflorescence axes lacking any rhizomatous portion forming in truly lateral positions above nodes on the pseudobulbs. The models proposed showed variation from isomodular to heteromodular architecture. This is important for consideration of monocot growth form models as a whole, as the nature of lateral inflorescence branching has always been difficult to interpret. Andersen et al.'s (1988) models of habits in *Eria* suggest that lateral inflorescence axes are highly reduced modular units. The reduction is evident from rhizome bearing lateral inflorescence axes to reduced modules which develop from lateral buds and lack any rhizomatous portion of the module. Many of the lateral inflorescence axes, which are reduced modular units, lack any reserve buds or axillary buds and hence are unable to branch sympodially. Thus, after flowering, these axes no longer have a function and growth is not continued. In *M. variabilis* the production of lateral inflorescence axes from the cane-like portion of the axis may well represent one of the reduced modular branching types, in which there is little rhizomatous portion of the module remaining. The extreme basal portion of the inflorescence axis in *M. variabilis* displays a slightly different anatomy to the remaining portions of the inflorescence axis. This may be a result of different origins of the portions of the axes (i.e. module separation). Another interesting feature is the lack of specialisation of the inflorescence axis in terms of tissue differentiation, suggesting that the sole function of the axis is to produce flowers, and not actively photosynthesise.

bundles of corms are more commonly amphivasal (but u-shaped xylem bundles also occur). Other pseudobulbs have been found to have no pattern in the arrangement of the vascular tissue (see Withner 1974). There is no general agreement about the derivation of aerial stems in orchids - they may be of axis or rhizome nature and the "stems" of orchids have been difficult to interpret in epiphytic forms particularly. This is also reflected in pseudobulbs which vary positionally. Andersen et al. (1988) have shown in *Eria* that the position of the renewal bud (of the sympodium) is important in determining the nature of the pseudobulb, whether rhizome or aerial stem in nature. The position of the renewal bud should facilitate the distinction between pseudobulbs that arise from the erect part of the shoots versus those that arise from the rhizomatous part. The function of pseudobulbs is largely that of water and nutrient storage. Holttum (1955) proposed that the fleshy internodes developed as a result of the epiphytic habit in orchids. With the roots exposed and velaminous (functionally providing protection against dehydration as well as concentrating absorptive nutrients where possible), and not subterranean in a moist environment, selection favoured the evolution of a new form of water storage - the storage tank of the internodes.

The terms that exist to describe and define orchid stems are very variable and often not correctly determined. The problem of deciding which portions of the sympodium are rhizomatous and which are aerial stem, is steeped in controversy. The term secondary stem has been applied to any non-rhizomatous portion of the sympodium, but, Dressler (1981) rejected this term on the basis that the only primary stem is the seedling stem formed from the protocorm. All other "stems" including the rhizome, are secondary. In line with this sort of terminology, Stern & Pridgeon (1984) proposed that the inflorescence axis-like portion be referred to as a *ramicaul* i.e. branch - stem, which Rasmussen (1985) criticised because the aerial portion of the sympodium is not a branch. Dressler (1981) in fact proposed that the use of aerial stems or vegetative shoots were adequate for describing terrestrial orchids, but in epiphytes were ambiguous as many of the stems are pendant. This problem is an ongoing one in orchid terminology and unfortunately is not restricted to orchids - it is a problem encountered for all monocots and is a central problem which is addressed in this thesis (see Chapter 4).

In *M.variabilis* there is an anatomical distinction between the pseudobulb stalk and the pseudobulb itself which goes beyond the expansion of the tissues to accommodate water and starch storage i.e. tissue differentiation into hypodermis cortex and central region. In addition, morphologically, the pseudobulb is different to the stalk as it bears a foliage leaf terminally and is composed of only one internode. The stalk on the other hand

central region of the upper axis) and the bundle sheath cells have very thickened cell walls. There is a sclerenchyma cap associated with the vascular bundle with cells that have very thickened cell walls. The cap has a peculiar arrangement as it extends entirely around the phloem. Equivalent thickening occurs in the sclerified cap, which also extends completely around the phloem. The xylem of the vascular bundle is arranged in a u-shape.

T/S mid inflorescence axis

The epidermis is composed of rounded cells and a distinct cuticle is present. The axis comprises mostly a central area containing vascular tissue, there is no differentiation into tissue layers. The central region consists of unspecialised parenchyma cells. The vascular bundles are distinct and are enclosed by a sclerified, two layered bundle sheath. The vascular bundles have a u-shaped xylem arrangement, but the xylem tends to be concentrated centrally within the bundle. The phloem is completely surrounded by a sclerified, two layered cap.

T/S upper inflorescence axis

The epidermis consists of rounded cells with the outer cell walls slightly thickened. A cuticle is present and is slightly papillate. There is no further tissue specialisation within the axis, there is only a central parenchymatous region which contains the vascular tissue. The parenchyma cells contain a few granular inclusions, which are probably starch granules. The vascular bundles are surrounded by a two to three layered bundle sheath which consists of cells with thickened walls and a sclerenchyma cap that extends completely around the phloem.

Growth form affinities and differences

The pseudobulbs of orchids have been likened to aerial stems by Holttum (1955) or are interpreted as being equivalent to corms (Dressler 1981; Dahlgren et al. 1985; Bell 1991). It is the more common conclusion, however, that pseudobulbs are modifications of aerial stems. However, the location and composition of orchid pseudobulbs is highly variable (Rasmussen 1986; Andersen et al. 1988). They can be composed of single internodes (homoblastic), which are succulent, or several to very many (heteroblastic) with succulence varying from internode to internode (Dressler 1981; Rasmussen 1986). The anatomical arrangement of tissues within the pseudobulb of *M.variabilis* is reminiscent of corms with a ring-like arrangement of the vascular bundles. However, the vascular

T/S apical region of pseudobulb

The tissue plan and cellular structure is the same as that for the mid portion of the pseudobulb. The pseudobulb in this region is contracted laterally and centrally. The vascular bundles are the same as those which occur in the mid portion. The T/S of this region did not successfully include the sheathing leaf base portion of the foliage leaf.

T/S base of developing shoot (internode)

The developing shoot epidermis is comprised of rounded to slightly flattened cells. A cuticle is present. There is a band of tissue directly below the epidermis which is a parenchyma band consisting of two to three cell layers. The parenchyma cells are unspecialised. The central area of the developing shoot internode consists of parenchyma cells which contain very sparse granular inclusions. This region contains the vascular tissue. The vascular bundles have a thickened bundle sheath and the xylem is arranged in a u-shaped fashion.

T/S mid region of developing pseudobulb

The epidermis of the developing pseudobulb consists of rounded cells and a cuticle is present. Below the epidermis is a parenchyma band, composed of five to ten layers of unspecialised parenchyma cells. The central area is comprised of parenchyma cells which contain globular inclusions. This region contains the vascular tissue. The vascular bundles with have a thickened bundle sheath which is two layered. The vascular bundles have a u-shaped xylem arrangement and the bundles are distinct.

T/S lowest portion of basal inflorescence axis

The epidermis is comprised of rounded and slightly flattened cell and a cuticle is present. Directly below the epidermis is a parenchyma band consisting of two to three cell layers of unspecialised parenchyma cells. There is a central area consisting of parenchyma cells which contain globular inclusions. This region contains the vascular tissue. The vascular bundles have a thickened bundle sheath and the xylem is arranged in a u-shaped fashion.

T/S basal inflorescence axis

The epidermis consists of rounded cells and a cuticle is present, but it is not prominent. There is no further tissue specialisation into layers, there is only a central region which contains the vascular tissue. The parenchyma cells of the central region contain starch granules. The vascular bundles are arranged closely to one another (compared to the

Anatomy

T/S pseudobulb stalk (cane-like portion below pseudobulb)

The pseudobulb stalk has an epidermis composed of rounded cells with a cuticle to the exterior. A parenchyma band occurs directly below the epidermis and is composed of up to five cell layers of unspecialised isodiametric parenchyma cells (hypodermis). A distinct cortex is recognisable and is composed of cells containing globular inclusions (probably starch) and a few vascular bundles are scattered in this area. The central region consists of unspecialised parenchyma cells and vascular bundles which are very closely arranged (Pl. 8, Fig. 4). Each bundle is enclosed by a two layered bundle sheath. The xylem is arranged in a u-shaped pattern within the vascular bundles.

T/S basal portion of pseudobulb

The epidermis consists of rounded to slightly flattened cells. A cuticle is present. The hypodermis consists of five to ten layers of unspecialised parenchyma cells, without inclusions. A cortex is present and consists of parenchyma cells which contain globular inclusions, which may be starch granules. There are also several vascular bundles present in this region. These vascular bundles have a two layered bundle sheath and xylem with a u-shaped arrangement. The central region consists of parenchyma cells with slightly thickened cells walls. The central region contains most of the vascular tissue, which is comprised of very closely arranged vascular bundles. These medullary vascular bundles are also bounded by a two layered bundle sheath and have xylem with a u-shaped arrangement.

T/S mid portion of pseudobulb

The epidermis consists of flattened, elongate cells. A cuticle is present, but stomata are absent. The pseudobulb comprises a central area which is composed of isodiametric parenchyma ground cells, there is no further tissue differentiation (Pl. 8, Fig. 5). The central area contains the vascular tissue which consists of vascular bundles arranged in a ring within the parenchymatous area. The cells of the central area contain globular inclusions which could be starch. In the outer parenchymatous area (outside of the vascular bundle ring) the parenchyma cells do not contain the globular inclusions. This could indicate a weakly developed cortex. The vascular bundles are bounded by a two to three layered bundle sheath which is thickened. The xylem arrangement of the vascular bundles is u-shaped.

produced in a lateral position. As such there is almost a separation between vegetative and reproductive axes. Continued growth does not occur from the apex of the pseudobulb, renewal growth is from the axillary buds (branching) of the cane-like portion. Thus, the growth form must be interpreted as sympodial, albeit that the inflorescences are laterally formed. The growth form of *M.variabilis* has features of both monopodial and sympodial growth which Arditti (1992) has described. Monopodial features include a missing underground rhizome; no new growth from stem bases; lateral inflorescences; branching; and adventitious root production from aerial nodes. The sympodial features are that there is not a single growth axis; renewal growth occurs from axillary buds; and there is the formation of both laminate and scale-like leaves on the "stem".

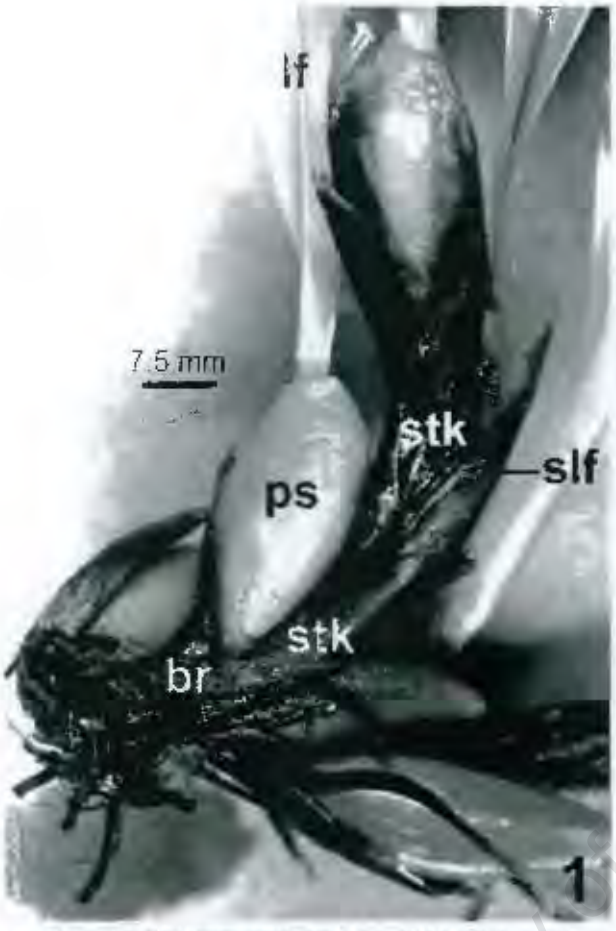
A L/S of a developing side shoot (i.e. produced from axillary bud of cane-like portion) shows that the axis consists of several internodes, the apical portion is covered by several sheathing leaves (Pl. 8, Figs. 2, 3). At the apical growing point, two buds are apparent. There are two possible interpretations. The first is that there could be two leaf buds, of which only one develops, or there is a single leaf bud plus a reserve bud.

The anatomy of selected members of Orchidaceae has been examined by Solereder & Meyer (1930). The morphology and systematics of orchids is presented by Dressler (1981). Arditti (1992) provides a review of orchid biology, taxonomy, anatomy and morphology. The vegetative morphology of selected members of the family have been examined (e.g. Andersen et al. 1988; Rasmussen 1986). The morphology and anatomy of subterranean axes has been described by (Kurzweil et al. 1991, 1995; Pridgeon & Chase 1995). Anatomical adaptations in vegetative and floral structures are described for the family by Pridgeon (1986).

Plate 8. Morphology and anatomy of *Maxillaria variabilis*

Figure 1. Morphology of *Maxillaria variabilis* showing sympodial growth habit (br) with pseudobulbs (ps) terminal on stalk-like portions of stem (stk) ensheathed with scaling leaf bases (slf). A single laminate leaf (lf) tops each pseudobulb.
Figures 2 & 3. Composite of L/S of developing side shoot (branch) showing the apex (ap) with meristem (m) and developing leaves (dlf) as well as sheathing leaves (slf). Below the apex, the internode develops into the pseudobulbous region (dps) with a node below (n) and internodal meristem (m) evident in the internodal region (in).
Figure 4. T/S pseudobulb stalk. A distinct hypodermis (hyp) is present above the cortex (co), the central region (cp) contains closely arranged vascular bundles (vb) which have a two layered bundle sheath.
Figure 5. T/S mid portion of pseudobulb. An epidermis (ep) surrounds the central region (cp) of the pseudobulb which shows little tissue differentiation. The vascular bundles (vb) are arranged into a ring and are sparsely distributed within the central parenchyma.

[Bars = 28 μm].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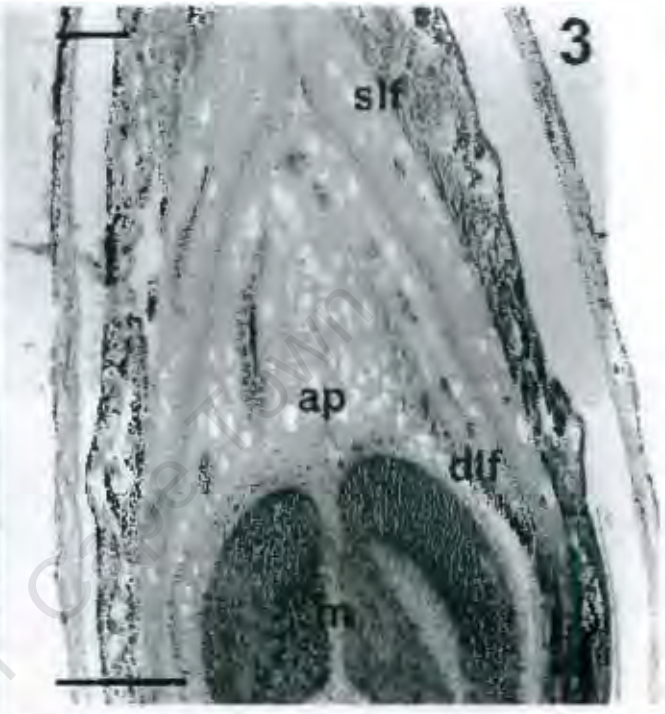
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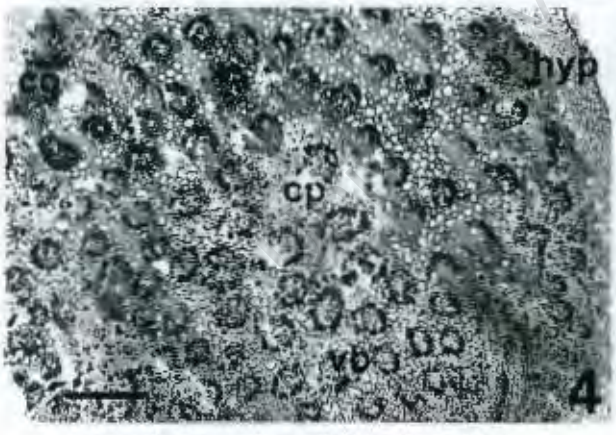
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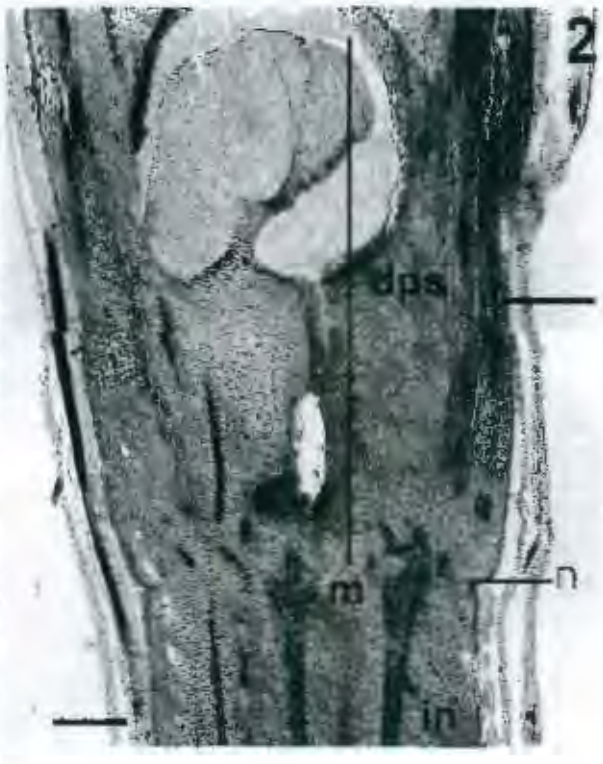
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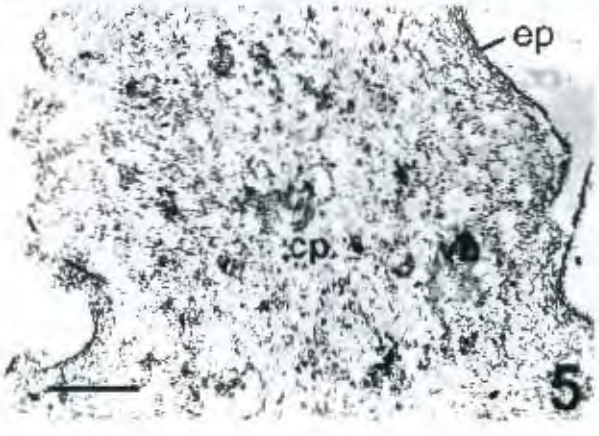
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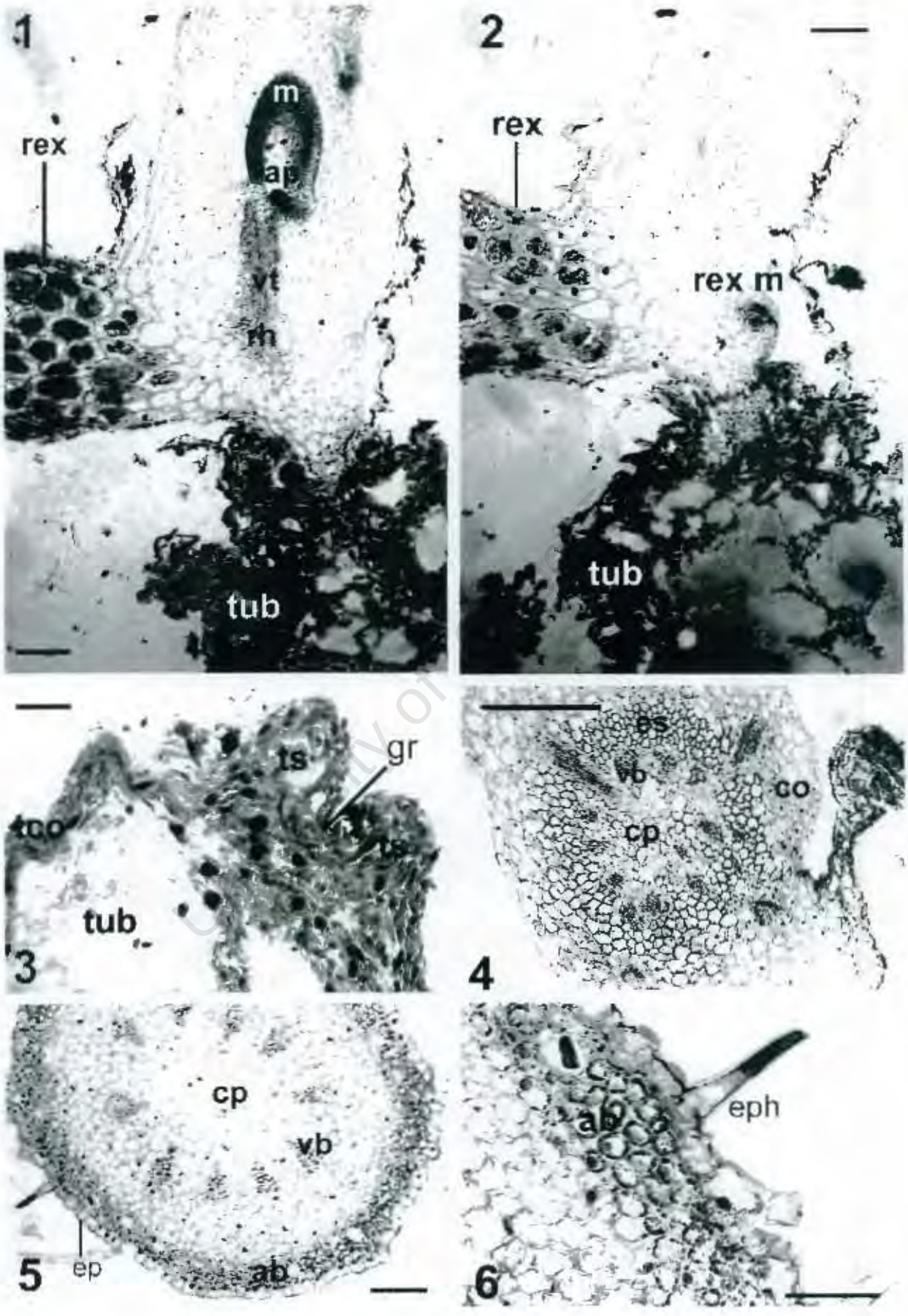
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Lilianae: Orchidales: Orchidineae: Orchidaceae*: *Epidendrum cinnabarinum

Morphology

Plants sympodial with laterally branching axes. There is generally a single leaf per internode, the leaf arrangement appearing alternate. The leaves have a thick, ensheathing leaf base and are thick and leathery in the laminate region. There are axillary buds in the axils of the leaf sheaths which have the potential to develop into lateral branches which can grow continuously. Inflorescence axes are produced both terminally and laterally from axillary buds. With terminal inflorescence axes, new branches arise from one of the axillary buds thus continuing the growth vertically. Clusters of thick velaminous roots are produced around the basal nodes of the plants. Roots can also arise from aerial nodal regions. The lower internodes of the plant as well as older branches tend to become woody and loose their leaves (leaf scars present) or have scale leaves only which are restricted to the nodes. The new branches are soft and green and tend to have fleshy laminate leaves at the nodes. The inflorescence axes often lack laminate leaves, usually bearing scale leaves at the nodes.

Anatomy

T/S root

Velamen without a distinct cuticle, consisting of about six to seven layers, with spirally thickened cell walls. The exodermis consists of cells with slightly thickened upper walls and the cells are very slightly dome shaped. The cortex consists of large parenchymatous cells which possibly contain chloroplasts (these cells were damaged in sectioning). The pericycle appears to contain mucilage. The endodermis is composed of brick-shaped cells with all of their walls slightly thickened. The stele is an amphiphloic siphonostele, with the xylem concentrated in arcs and the phloem situated below the dips of the arcs. The pith is composed of unspecialised parenchyma cells which contain green-staining granular inclusions (chloroplasts?).

T/S aerial axis with leaves

The epidermis consists of small rounded cells. A thick cuticle is present. There is a hypodermis which consists of cells with thickened cell walls. The central region consists of parenchyma cells which contain starch granules and the vascular tissue which is arranged as a series of scattered bundles. The vascular bundles have a sclerenchymatous bundle sheath. This extends to form a cap like structure at the apex of

the bundle, while extending to surround the phloem pole. The xylem is prominent and has a u-shaped arrangement within the bundle.

T/S aerial woody axis

The older axes are somewhat lignified. The hypodermis has thickened cell walls which stain red compared to the young axis. A cortex of parenchyma cells is distinct and a sclerified band is prominent (endodermoid sheath) which contains developing vascular bundles, so that both peripheral and medullary bundles are present. The central region consists of parenchyma cells which contain starch granules and the vascular tissue which is scattered throughout the area. The vascular bundles have a sclerenchymatous bundle sheath. This extends to surround the phloem pole. The xylem is prominent and has a u-shaped arrangement within the bundle.

T/S inflorescence stalk

The epidermis is composed of cells which are rounded and "bead-like" in appearance. A thick cuticle is present which stains pink. The following layer consists of a single layer of parenchyma cells which sometimes contain cellular inclusions. The central region consists of large isodiametric parenchyma cells which are generally unspecialised. The central region contains vascular bundles which are scattered throughout and are distinct. The vascular bundles lack a bundle sheath, and contain xylem which is arranged in a u-shaped fashion. The phloem is arranged in a pole at the apex of the bundle and has a single layer of sclerified cells above the pole forming a very fine sclerenchyma cap.

Growth form affinities and differences

Aerial branching axes are not uncommon in the Orchidaceae with several forms displaying modification into storage structures e.g. pseudobulbs. In *Epidendrum cinnabarinum* the axes become woody, and somewhat cane-like in appearance with age. The interesting feature of the axes of *Epidendrum cinnabarinum* is the production of aerial roots when the base of the plant is subterranean. Furthermore, the base of the plant is weakly developed and most of the proliferation in the stem growth occurs aerially.

Lilianae: Orchidales: Orchidineae: Orchidaceae: Phalaenopsis hybrid (frosty hunter x 'Zuma canyon' amboinensis)

Morphology

Plant epiphytic with monopodial growth. The internodes are closely spaced and new growth is produced toward the apex, while the lower internodes die back. A lateral inflorescence axis is produced from an axillary bud on the main stem, and is green with scale leaves at the nodes. The inflorescence axis grows continuously, producing flowers laterally from the axils of the scale leaves. The leaves are always produced in fours, as are the flowers on the lateral inflorescence axis. The lateral inflorescence axis remains green even after the flowers have been formed, and after flowering when the flowers have dropped off. The roots are green, formed from the more apical nodes of the stem and are covered in a thin layer of velamen.

Anatomy

T/S root

The velamen is approximately two to three cell layers in thickness and is bound by a cuticle to the exterior. The innermost cells of the velamen layer have a thickened base to them (i.e. lower wall thickened). The exodermis consists of a single layer of cells with the upper walls thickened. The cortex consists of large, loosely arranged cells which tend to break down in the sectioning process. Rod-like crystals (raphides) occur occasionally within the cortex. The pericycle is composed of cells with slightly thickened outer walls and contains a cellular mucilage which stains green. The endodermis is composed of cells with all walls thickened and staining red. The stele is probably an ectophloic siphonostele, with phloem clustering in groups exterior to the xylem. The xylem is prominent with thick walls which stain red.

T/S flower stalk

The epidermis consists of flattened brick-shaped cells. A cuticle is present. Cellular inclusions are occasionally scattered throughout the flower stalk. These consist of a collection of red staining globules contained within a blue-staining mass. There is a parenchyma band which is composed of approximately fifteen cell layers of unspecialised parenchyma cells. This region has occasional, scattered globular inclusions and also stacked rod-like crystals (raphides). There is no real distinction between the central region and the parenchyma band area in terms of cell type. The central region is only distinct from the parenchyma band because vascular bundles are scattered within this region.

Globular and crystal inclusions are occasional in this area. The vascular bundles have xylem with a v-shaped xylem arrangement. The bundles are elongate with the phloem arranged as a cap above the xylem pole. The globular inclusions are concentrated within the vascular tissue, particularly the phloem. The bundle sheath is poorly developed.

Growth form affinities and differences

The monopodial growth form of Vandoid orchids and some Epidendroideae as well as *Vanilla* is not common throughout monocotyledons. Some grasses like *Stenotaphrum* and some bamboos have monopodial growth. Otherwise, it is a feature which appears to have evolved in numerous instances within orchids. Holttum (1955) believed that the monopodial form was a way to climb through a canopy and obtain sunny, dry positions, thereby facilitating flowering in some orchids. However, not all monopodial forms require sunny positions for flowering, many prefer cool shady areas. Many monopodial orchids have very short internodes and modifications for climbing are not a consideration. The lower portions of the stem die away in epiphytic monopodial orchids, the renewed growth being able to explore new substrate.

The monopodial epiphytic growth form is a relatively specialised growth form and is restricted to the Vandoid orchids (Holttum 1955). The closely spaced internodes are slow growing and the flowers often large and showy (Dahlgren et al. 1985). There are no specialised storage organs in this growth form. Often, the leaves may act as reservoirs for water (Withner 1974). With the monopodial form of growth, the need for storage organs may be overcome. Lateral branching coupled with continued vertical growth allows for new exploration of an area, and aerial velaminous roots allow for the rapid uptake of minerals when they are periodically available. Without the presence of storage organs, which are often involved in supplementing the process of flowering, it is likely that flowering in *Phalaenopsis* would only take place when minimal nutrient levels are achieved. Very little information is available on flowering in monopodial forms, but, perhaps the continued growth of the inflorescence axis allows for the production and feeding of the large, showy flowers.

Lilianae: Orchidales: Iridineae: Tecophiliaceae: Cyanella hyacynthoides

Morphology

Plants with underground storage organ, referred to as a corm, buried ten to fifteen centimetres below soil surface. The corm appears to be composed of more than one internode, with a vertical growth orientation. The roots are produced at the base of the

corm. The renewal of the swollen internodes occurs by means of an axillary bud located toward the apex, the preceding internodes shrivelling after flowering. The apex of the corm gives rise to an elongated stalk, which appears to lack leaves, but, leaf bases ensheath this structure. The leaves are laminate at the surface of the soil. The corm is clothed in old sheathing leaf bases, which are exceptionally fibrous and tend to come loose with age. The inflorescence stalk is produced at the apex of the corm from an apical growth point and grows up through the leaf bases. At some point above the expanded leaves (a few centimetres – this variable from plant to plant) the inflorescence axis branches and produces flowers. The corm is fleshy and white internally and contains numerous canals with a slightly shiny texture, which are visible to the eye. The corms are well below the soil surface and are difficult to locate and dig out, often breaking at the flimsy neck region. The aerial portions of the plant are only produced seasonally. The swollen corm remains buried during the dry season.

The morphology, chemistry and anatomy of the Tecophiliaceae is not well known. Cheadle (1969) has described the anatomy of vessels from various portions of the plants in the Tecophiliaceae.

Anatomy

T/S neck just above corm

There appears to be no distinct differentiation between the tissue types in the main axial portion of the neck. The axis is surrounded by three layers of sheathing leaves (sheathing leaf bases). The central axial region can be distinguished by being bounded by an epidermis. The epidermis consists of rounded to brick shaped cells. The central area consists of parenchyma cells which have thickened cell walls. This region contains the vasculature which is scattered throughout the central area. The vascular bundles are bounded by a one-layered bundle sheath, the cells of which are not thickened. The xylem consists of large, distinct elements which stain red and are arranged in a wide u-shaped fashion, with the phloem capping the xylem pole.

T/S mid neck

The epidermis consists of flattened, brick shaped cells with a cuticle. The parenchyma band consists of five to six cell layers of unspecialised parenchyma cells. The sclerenchyma band has peripheral vascular bundles associated with it and surrounds the central region. The central area is composed of loosely arranged parenchyma cells, which are slightly sclerified and the vascular bundles are scattered throughout this area. The

vascular bundles have a one layered bundle sheath, which is not thickened. The xylem is arranged in a u-shaped fashion. This mid region of the axis is also surrounded by three sheathing leaf bases.

T/S upper region of neck

The tissue plan and arrangement is the same as for the mid region of the axis. However, indications are that this region is slightly more sclerified than the previous, because the sections tend to break down in the microtoming process. In this region the leaves expand and begin to develop into open leaves, thus the leaf expansion makes the T/S of this region seem much larger than the previous, but the diameter of the axis remains the same.

T/S basal inflorescence axis

The epidermis is composed of flattened cells which are bead-like in appearance. An assimilatory band seems to be absent, but a band of parenchyma cells which is comprised of five to six cell layers, is present. The sclerenchyma band is distinct and has a peripheral vascular system associated with it. The central area is composed of parenchyma cells which do not contain starch granules. The central area contains vascular bundles which are scattered throughout. The vascular bundles are bi-collateral with the phloem arranged like a cap above the xylem.

T/S mid inflorescence axis

The epidermis is composed of flattened, brick shaped cells. A cuticle is present. There is a parenchyma band which is composed of a single layer of isodiametric, unspecialised parenchyma cells. The assimilatory band is composed of two to three cell layers of chlorenchyma cells. The sclerenchyma band is consists of distinct cells with thickened walls and has developing vascular bundles associated on the periphery of the band. The central area is composed of isodiametric parenchyma cells which are unspecialised. The medullary vascular bundles are well developed and more or less arranged in a ring-like fashion within the central area. The vascular bundles are variable in this region being either bi-collateral or uni-collateral, with an undeveloped bundle sheath.

T/S inflorescence stalk

The epidermis consists of rounded to brick shaped cells. A cuticle is present and stomata are absent. There is a parenchyma band which consists of a single layer of unspecialised

isodiametric cells. The assimilatory band consists of chlorenchyma cells arranged in approximately four layers. The following band is composed of a layer of wavy cells, this is possibly a sclerenchyma layer. The cells are flattened and wavy in appearance suggesting that sclerification is lacking. It may well be a suberised layer. The central area is composed of parenchyma cells, which are isodiametric and contain starch granules. The central region contains a few large vascular bundles. The vascular bundles are without a distinct bundle sheath. The xylem in the vascular bundles is in a v-shaped arrangement, with two distinct side flanks and a phloem cap above this.

T/S flower stalk

The epidermis is comprised of flattened, brick shaped cells. A cuticle is present. The parenchyma band is composed of a single layer of isodiametric, unspecialised parenchyma cells. The assimilatory band comprises four to five layers of chlorenchyma cells. The sclerenchyma band is composed of small, rounded cells with thickened walls. This band tends to break down in the sectioning process, but appears well developed where it remains intact in the sections. There are developing vascular bundles present on the periphery of the band. The central area is composed of isodiametric parenchyma cells which contain starch granules. The medullary vascular bundles are well developed and more or less arranged in a ring-like fashion within the central area. The vascular bundles are variable in this region being either of the bi-collateral or the uni-collateral type, lacking a bundle sheath.

Growth form affinities and differences

The corm anatomy of *C.hyacinthoides* displays similarities to other corms examined, and thus was not described here or coded (Chapter 3). The vascular bundles are scattered throughout a parenchymatous central region which comprises the bulk of the corm. A cortex is not distinguishable. The central region is traversed by numerous canals which contain a mucilaginous substance. The chemistry of Tecophiliaceae is not known (Dahlgren et al. 1985). The extended neck region which emerges at the apex of the corm was included in the study because it is desirable to determine whether the structure is a series of unswollen rhizome internodes, or whether they form part of the aerial stem system. In the case of corms, it is difficult to determine this. As the axis is above the renewal bud, following the proposal of Rasmussen (1985) it is likely to belong to the aerial stem system. However, the anatomy of the neck region shows both rhizome and aerial axis anatomical similarities. The tissue differentiation observed could be interpreted as

either parenchyma and sclerified sheath as it is here, or as a cortex and endodermoid sheath. However, the suberisation that is often common in the endodermoid sheath is lacking here. The sclerification of the neck region may be related to a strengthening function, keeping the aerial portions attached to the deeply buried corm. The cormous growth forms often produce contractile roots at the end of the flowering season so that the new swollen internodes can be pulled down to the same level as the previous season's corm (Arber 1925). The plants of *C.hyacynthoides* were collected and examined during the flowering phase and thus, no contractile roots were seen.

The growth and structure of the corm in *C.hyacynthoides* is very similar to that of *Baeometra uniflora* and *Wurmbea spicata* (Colchicaceae; this chapter) and those described for Iridaceae by Rudall (1995). The sheathing leaf bases of the corm (tunic) of *C.hyacynthoides* are extremely fibrous, unlike the brittle tunics of *Baeometra* and *Wurmbea*.

Lilianae: Orchidales: Asphodelineae: Johnsoniaceae: Johnsonia pubescens

Morphology

Plants grass-like in appearance with vertical stems clothed basally with old sheathing leaf bases. Current leaves arising in a spiral arrangement near the apex of the stem, open, green and photosynthetic. The inflorescence axis is produced from the stem apex and gives rise to a compact spicate inflorescence. The morphology and anatomy of members of this family has not been extensively examined.

Anatomy

T/S stem base

The epidermis consists of rounded cells which stain red, lacking any wall thickening. A cuticle is absent. There is a single layer of loosely arranged cells, which stain red and constitute the hypodermis. The hypodermis contains groups of sclerenchyma fibres at intervals. There is a cortex below the hypodermal layer which consists of parenchyma cells with slightly thickened cell walls. The central area consists of parenchyma cells with thickened cell walls and contains the vascular bundles which are scattered throughout. The vascular bundles are amphivasal. Roots are present in this section of the stem, departing from the stem tissues internally.

T/S basal inflorescence axis

The epidermis is comprised of flattened, brick shaped cells. There is no cuticle and stomata are absent. The following tissue band is a parenchyma band, comprising approximately seven cell layers of unspecialised parenchyma cells. The central area is composed of unspecialised parenchyma cells and the vascular bundles are scattered within this region. The vascular bundles are amphivasal with distinct xylem elements which possess red-staining thickened cell walls.

T/S inflorescence axis

The epidermis consists of rounded cells, with the upper cell walls very slightly thickened. The cuticle is absent. Stomata are occasional within the epidermal layer. Unicellular epidermal hairs are present. The assimilatory band is composed of two cell layers (the chloroplasts degenerated in the reconstitution process). The assimilatory band contains groups of sclerenchyma fibres with thickened cell walls, mostly in groups of up to ten cells. The central region consists of parenchyma cells with slightly thickened cell walls and the vascular bundles are scattered within this area. The vascular bundles have a sclerenchyma cap which consists of approximately three cells in thickness. The bundles are bounded by a sclerified bundle sheath which is composed of a single layer of cells. The vascular bundles contain xylem which has a u-shaped arrangement.

Growth form affinities and differences

The growth form of *Johnsonia* is most similar to that of Anthericaceae (within which family it was previously classified (Dahlgren et al. 1985)), the main differences occurring in the inflorescence axis which has a densely compacted spicate inflorescence. The rhizome is very short and compacted in a vertical arrangement, with the inflorescence being formed terminally. The growth form of *J.pubescens* is similar to the tufted form of many grasses. The formation of new axillary sympodia could not be determined from the specimens collected. Arber (1925) examined the leaf anatomy of *J.lupulina* and found the vascular tissue arranged in several associated bundles bound by a sclerified sheath, which she subsequently termed a polystelic leaf. She did not consider the function of such anatomy, but rather discussed the similarity between such an arrangement of structure with the petioles of dicots.

Lilianae: Orchidales: Amaryllidinae: Anthericaceae: Chlorophytum comosum

Morphology

Plants with leaves concentrated in a basal rosette and producing long, slender aerial inflorescence axes. The rhizome is vertically orientated with short, compact internodes which give rise to the spirally arranged rosette of leaves. Leaves with a sheathing leaf base and elongate, laminate fleshy portion. The inflorescence axis is terminal and the internodes expanded with small scale leaves at the nodes giving rise to a panicle. *C.comosum* displays a condition termed 'false vivipary' by Bell (1991). New plantlets develop in the axils of the scale leaves where florets are formed or after flowering has occurred. The plantlets can proliferate on the ends of runners produced from the axil of the flower. They may also form along the length of the old inflorescence axis, which bends towards the substrate, where the new plantlets are able to root and continue to grow. Root tubers are also produced and are generally closer to the root initiation zone and the central portion of the tuber, rather than at the root tip (Pl. 13, Fig. 1).

Germination is hypogeal and occurs after three to four weeks (Pl. 13, Fig. 2A, B). The seed is separated from the cotyledonary sheath by a short middle portion of the cotyledon. There is a short hypocotyl at the base of the cotyledonary sheath from where the primary root arises (Pl. 13, Fig. 2A). The primary root is well developed and has numerous soft root hairs along its length except at the root tip. At the stage where the plumule has expanded, adventitious roots break through the base of the cotyledonary sheath (Pl. 13, Fig. 2B). In the region where the primary root departs from the hypocotyl, the root axis is slightly swollen. When the second leaf is produced, there are several adventitious roots, and the departure area of the primary root continues to swell (Pl. 13, Fig. 2C). This pattern suggests that the swelling of the cortex of the root axis takes place early in the development so that storage reserves can be built up. When the seedling is six months old, there are at least seven leaves on the plant, with the more basal leaves peeling away and dying back (Pl. 13, Fig. 2D). Root buds are still initiated at the base of the seedling (rhizome area). The primary root is still present and at this stage, is swollen predominantly in the central area of the root, and the swelling tapers towards the growing tip (Pl. 13, Fig. 2D). Several adventitious roots show the same pattern of swelling, tapering towards the tip. Other adventitious roots which are more recently formed do not show swelling yet (Pl. 13, Fig. 2D).

Pate & Dixon (1982) have examined the morphology of members of the family with subterranean storage structures. A comparative treatment of the growth form in the family is lacking.

Anatomy

T/S root tuber

The exodermis is arranged in a single layer and is composed of dome shaped cells with an additional layer exterior to this which tends to break down during sectioning. The cortex is enlarged to approximately ten cell layers, of expanded, isodiametric parenchyma cells which also lack inclusions and tend to break down in the sectioning process, compared to the root T/S (Pl. 13, Figs. 3, 4). The stele is bounded by an endodermis and a pericycle. The endodermis lacks thick-walled cells, while the cell walls of the pericycle are thickened on the lateral walls (intercellularly). The stele is an ectophloic siphonostele with the xylem elements arranged in arcs and staining deep red.

T/S rhizome

An exodermis is identifiable, but is not really distinct and is often not consistently present throughout the section. The following layer is the hypodermis which is approximately twenty cell layers in thickness. There is a cortex which is comprised of light staining cells which are isodiametric thin walled parenchyma cells, arranged in approximately ten cell layers. The central area consists of unspecialised ground parenchyma cells and contains the vasculature. The vascular bundles are scattered throughout the central area and tend to anastomose. The vascular bundles are of the amphivasal arrangement.

T/S upper inflorescence axis

The epidermis consists of dome shaped cells covered by a papillate cuticle. Stomata are absent. The assimilatory band is composed of four to five cell layers containing distinct chloroplasts (Pl. 13, Fig. 5). The following layer is a sclerenchyma band and is composed of seven to eight cell layers (Pl. 13, Fig. 5). The cells have thickened cell walls and appear to be highly sclerified. They are deeply red-staining and there are pits present in the walls. The central area is composed of unspecialised ground parenchyma cells and contains the vascular bundles, which are scattered throughout (Pl. 13, Fig. 5). The vascular bundles are either of the bi-collateral type or they may have the xylem arranged in a u-shape, with the phloem arranged in a cap at the apex. The bundle sheath appears to be lacking, but a series of sclerified cells are present above the phloem.

Plate 13. Morphology and anatomy of *Chlorophytum comosum*.

Figure 1. Gross morphology showing compact base of plant and proliferation of adventitious roots which become tuberous (rt).
Figure 2. Seedling ontogeny in *Chlorophytum comosum*, 1 week to 8 weeks after germination. **[A]** Seedling 1 week old showing hypogeal germination with plumule erupting. **[B]** Seedling 2 weeks old showing expansion of plumule and adventitious root formation. **[C]** Seedling 4 weeks old showing two leafed stage. **[D]** Seedling 8 weeks old with root tuberisation in progress. (pl) = plumule; (cs) = cotyledonary sheath; (c) = middle part of cotyledon; (pr) = primary root; (ar) = adventitious root; (lf) = leaf; (rt) = root tuber.
Figures 3 & 4. T/S root and root tuber respectively showing cortex (co) expansion in Fig. 4 due to enlargement of parenchyma cells. (st) = stele.
Figure 5. T/S upper inflorescence axis. An assimilatory band (ab) and sclerenchyma band (sc) are distinct. The vascular bundles (vb) have a u-shaped xylem arrangement and are scattered within the central parenchyma (cp). (ep) = epidermis.
Figure 6. T/S stolon. An assimilatory band (ab) and sclerenchyma band (sc) are distinct. The vascular bundles (vb) are arranged into a ring and the xylem has a v-shaped arrangement.

[Bars = 15 μm (Figs. 3-6) and 7.5 mm (Fig. 2)].

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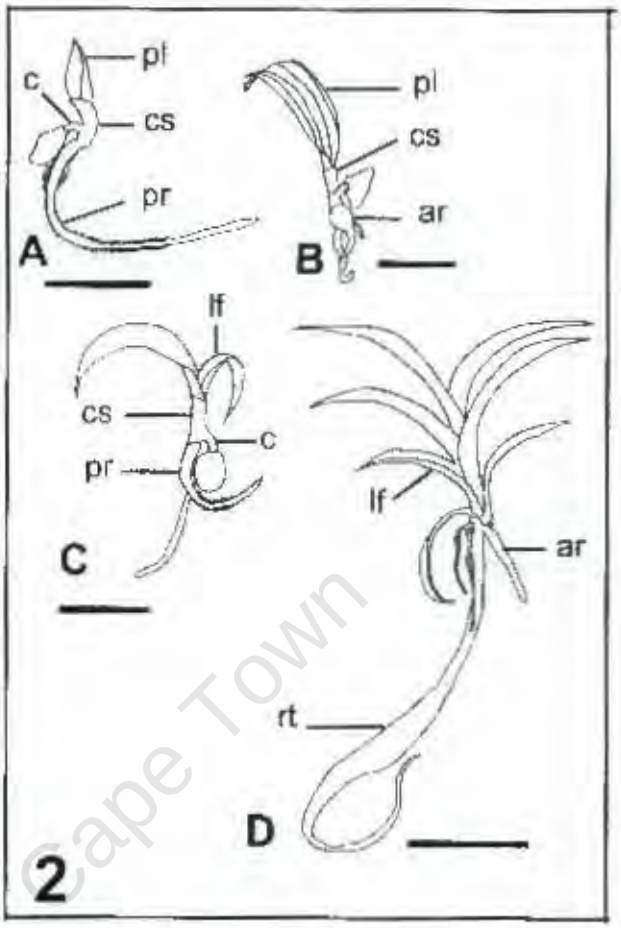

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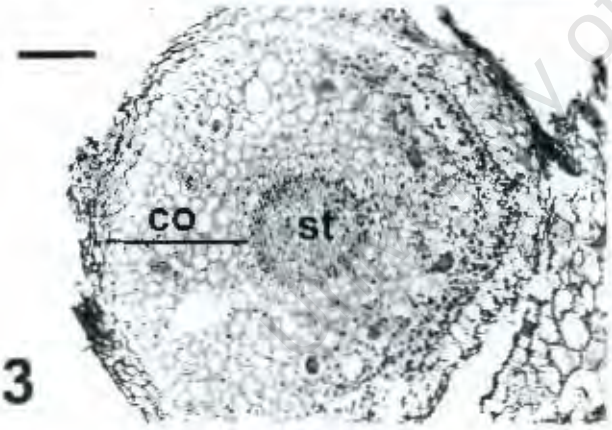

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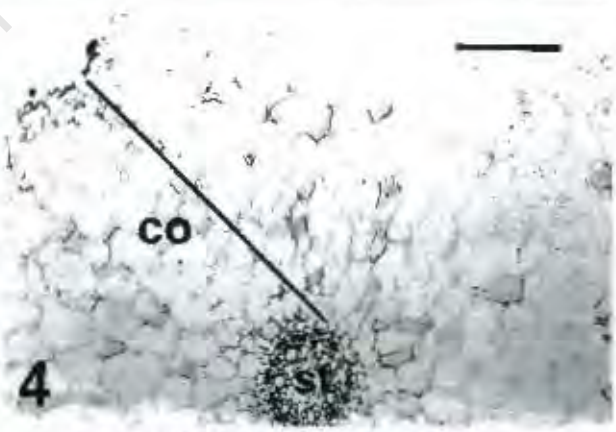

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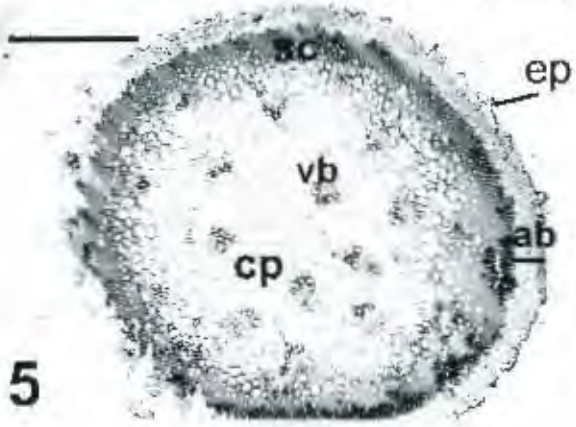

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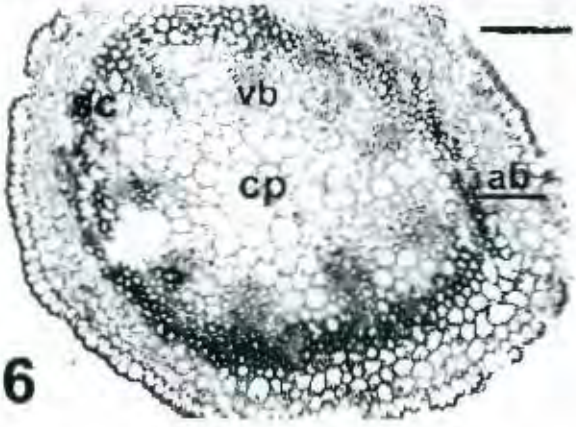

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T/S inflorescence stalk

The axis between the flowers has the same tissue plan as the inflorescence axis, except that the sclerenchyma is reduced to a few cell layers in thickness, and the cells do not appear to be sclerified.

T/S stolon

The epidermis consists of dome shaped cells with a papillate cuticle. Stomata were not seen. The assimilatory band is composed of four to five cell layers in thickness (Pl. 13, Fig. 6), the cells containing distinct chloroplasts. The next layer is a sclerenchyma band which is distinct. The cells have thickened cell walls and appear to be highly sclerified. They are deeply red-staining and there are pits present in the walls. There is a peripheral vascular system associated with the sclerenchyma band and smaller vascular bundles can be seen within the band. The central area is composed of unspecialised ground parenchyma cells and contains vascular bundles. The vascular bundles are distinctly arranged into a ring in this region (Pl. 13, Fig. 6). The vascular bundles have xylem arranged in a v-shaped fashion, with the phloem in a cap at the apex. A bundle sheath is absent.

Growth form affinities and differences

The swollen portion of the root or root tuber of *C.comosum* is a modification of the cortex region of the root. It is expanded to accommodate the area required for storage materials. Other Anthericaceae which posses root tubers have been observed to produce root tubers on an annual basis (Pate & Dixon 1982), serving as storage organs for each season's growth. The root tubers in *C.comosum* clearly serve as storage organs, as the short vertical rhizome is not fleshy and does not contain any storage materials. The propagation of new plantlets in the false viviparity process via the inflorescence dropping down, is an effective mode of cloning. The stolon (dropped inflorescence axis) has an anatomy which is identical to the inflorescence axis, simply displaying sclerification of the tissues. This would serve to strengthen the axis as new plantlets develop, so that the axis can bend without breaking away from the rhizome.

The phenomenon of vegetative development in positions where flowers normally occur (i.e. false viviparity) is a phenomenon often encountered in some grasses (Bell 1991). The apical meristem of the inflorescence (which can develop into a flower or a branched flower bearing structure), in the axil of a modified leaf (bract) develops into a vegetative bud which has adventitious roots associated with it and thus can form an

independent plantlet. The fate of buds, as discussed before, is generally developmentally predetermined. However, changes in certain switch genes can alter the development of the buds (Albert et al. 1998). Similarly, manipulation of internodes in addition to specific hormone controls in certain monocots can also alter bud development (see Fisher 1973a). Clark & Fisher (1986) have suggested that the false viviparity in some grasses is the result of varying environmental factors or teratology, and is commonly observed in forms which lack rhizomes or stolons as a means of vegetative reproduction. In *C.comosum* the flexibility to produce either floral buds or vegetative buds allows for both sexual and vegetative propagation and may be important in areas where water resources are sporadic. Pate & Dixon (1982) found high water contents within root tubers of Anthericaceae and also observed flowering when leaf production was limited by drought conditions. With sporadic water conditions, the onset of the vegetative propagation phase would be desirable, as conditions would not be conducive to seed production or germination. The false viviparity seen in *C.comosum* may therefore, be linked to the growth form and possession of root tubers. However, *C.comosum* is a cultivated plant in Southern Africa and vegetative proliferation seems to be a regular feature of the plants, thus, little link can be made back to the original purpose of such a propagation mechanism. False viviparity has also been observed in the sedge *Isolepis prolifera* which is restricted to shallow pools and slow flowing streams in the South Western Cape and appears to be a means of vegetative propagation by splitting and drifting, as is often the case in aquatic plants. True viviparity (embryo germinating before seed drop) is very rare in monocots but is present in bamboos (e.g. *Melocanna* McClure 1993) and is reported in *Alexgeorgea* (Meney et al. 1990a) which bears geocarpic fruits.

Lilianae: Orchidales: Amaryllidinae: Hyacinthaceae:

(I) Lachenalia splendida

Morphology

The habit is bulbous, the bulb being formed from swollen leaf bases of each season's leaf (Pl. 14, Fig. 1). The juvenile phase lasts for two years. During this period the leaves are cylindrical and only one per year is produced. Contractile roots are formed a few weeks after germination. At the end of each leaf growth period (up to three months), the cylindrical leaf shrivels. The roots also die back at this time. A small, swollen "bulbil" is retained subterraneanly which is formed from the swollen base of the cylindrical leaf. Mature plants produce up to two laminate leaves per year.

Roots are produced first at the start of the new season and this is followed by the production of the leaf. There is no flowering in the first two years. The bulbs have a short compact rhizome, topped by parenchymatous storage leaves. After three years, a single inflorescence axis is formed from an apical bud and the axis grows upwards through the swollen outer leaf bases and displays the flowers which are spicate on the axis.

The seed germinates after approximately three to four weeks. In the first week after germination, the radicle is produced at the base of the hypocotyl which is fringed by a circle of hairs and the seed remains at the apex of the seedling born on a short piece of cotyledon at the apex of the cotyledonary sheath (Pl. 14, Fig. 3; Pl. 15, Fig. 1A). Thus, germination is epigeal. The plumule (first leaf) breaks through the cotyledonary sheath and is cylindrical (Pl. 14, Fig. 3; Pl. 15, Fig. 4). In the second week after germination, the leaf and the radicle extend considerably, but the basic structure does not change except that the fringe of hairs disappears (Pl. 15, Fig. 1B). The leaf extends upwards so that the seed that is attached to the cotyledonary sheath appears to be in a lateral position, and could easily be mistaken as hypogeal germination at this stage (Pl. 14, Fig. 4; Pl. 15, Fig. 1B). When the seedling is three months old, the old cotyledonary leaf sheath decomposes and the seed will detach from the plantlet. At this time, the base of the current leaf is swollen and clearly visible as the "bulb" (Pl. 15, Fig. 1C). Contractile roots are produced at this time and at the end of the three month period (Pl. 14, Fig. 5; Pl. 15, Fig. 1C), the cylindrical leaf dies back and the bulbil over-seasons. The contractile roots pull the bulbil to about one centimetre below the soil surface.

The resting bulbil in L/S has a large proportion of parenchymatous leaf base surrounding the rhizome. This has new leaf shoots at its apex, which are visible but dormant, and a small root at its base, which is non-contractile. At twelve months after germination, the resting bulbil begins to sprout producing roots at the base and then about three to four weeks later, a cylindrical leaf at the apex which is forced out of the swollen portion. At two days after sprouting, the opened one year old plantlet (i.e. with the swollen bulb portion split to reveal the central structure) reveals a growth structure which is exactly the same as the three month old bulb, with a current cylindrical leaf apically, and a swollen leaf base, producing a root at the base (Pl. 15, Fig. 1D).

The bulbous growth form has been examined in other families e.g. Alliaceae (Chouard 1926; Hoffman 1933). Duncan (1988) has described the morphology, taxonomy and propagation of the genus *Lachenalia*.

Anatomy

L/S of sprouting bulb, 1 year after germination

The central most leaf primordium is surrounded by older leaf bases. Only the outermost leaf base is very swollen (Pl. 14, Fig. 2). The shoot apex is distinguishable in the centre of the leaf bases, it has a vascular supply centrally which can be traced down towards the roots. The remaining vasculature throughout the rhizome anastomoses and cannot be distinguish as unidirectional strands. Adult rhizome tissue anatomy is not developed at this stage. The leaf bases seem to contain many rod-like crystals (raphides) and some starch granules in the parenchyma cells.

(ii) Lachenalia klinghardtiana

Anatomy

T/S rhizome

A thin exodermis is present around the rhizome area between the rhizome and the swollen leaf base. A cortex of undifferentiated parenchyma cells comprised of about ten cell layers is present. Root buds traverse this zone and then turn downwards toward the base of the rhizome (bulb). A PTM separates the cortex from a centralised region which contains the vascular tissue. The roots are initiated in the PTM zone and many root buds are thus present in this region. The vascular tissue is arranged into two rings in the central area, the outermost ring is likely to be formed by the PTM and these vascular bundles are amphivasal (Pl. 15, Fig. 2). The central vascular bundle ring anastomoses and the bundle arrangement is difficult to determine. The central region is comprised of parenchyma cells which do not contain any storage material. The swollen leaf bases which surround the rhizome contain starch granules. However. these are absent throughout the rhizome, even in the area where the inflorescence axis is formed.

T/S inflorescence axis

The epidermis is composed of brick shaped cells, which are fragile and tend to break down in the sectioning process. A thick cuticle is present and stomata are absent. A parenchyma band is present comprising two to three cell layers and tending to break down during sectioning. Below the parenchyma band a sclerenchyma band is present which is three cell layers in thickness. The sclerenchyma cells are rounded in appearance and have sparsely thickened cell walls. The central ground parenchyma is not thickened and is comprised of loosely arranged cells which tend to break down. Rod-like crystals (raphides) are present within some of the parenchyma cells. Vascular bundles are both

medullary and peripheral. The peripheral vascular bundles are contained within the sclerenchyma band. The medullary vascular bundles are elongate without a thickened bundle sheath. The xylem is arranged in a t-shape with a phloem cap. There is a tendency for the medullary vascular bundles to be arranged into two rings.

T/S inflorescence stalk, zone immediately below flowers

The epidermis is composed of rounded cells. A cuticle is present. Stomata are absent. The assimilatory band comprises two to three layers of loosely arranged cells which contain chloroplasts. The sclerenchyma band comprises two to three layers of cells which are rounded in appearance and have sparsely thickened cell walls. The central ground parenchyma consists of loosely arranged cells which are not thickened. Vascular bundles are both peripheral and medullary. The medullary vascular bundles are arranged in two distinct rings within the central ground parenchyma. The medullary vascular bundles are elongate with the xylem arranged in a t-shape and a phloem cap at the apex of the vascular bundle.

T/S inflorescence stalk (between flowers)

The epidermis consists of rounded to brick shaped cells. A cuticle is present. Stomata are present and level with the epidermal cells. The assimilatory band consists of loosely arranged cells, with the chloroplasts scattered throughout the cells and comprises about five cell layers. The central ground region consists of large loosely arranged parenchyma cells without thickened cell walls. The vascular bundles are both medullary and peripheral, and a sclerenchyma band is absent (or undifferentiated). The vascular bundles are elongate, with the xylem tending to be arranged in a t-shape and the phloem arranged in a cap above the xylem. The bundle sheath is visible but the cell walls are not thickened.

(iii) Albuca fragrans

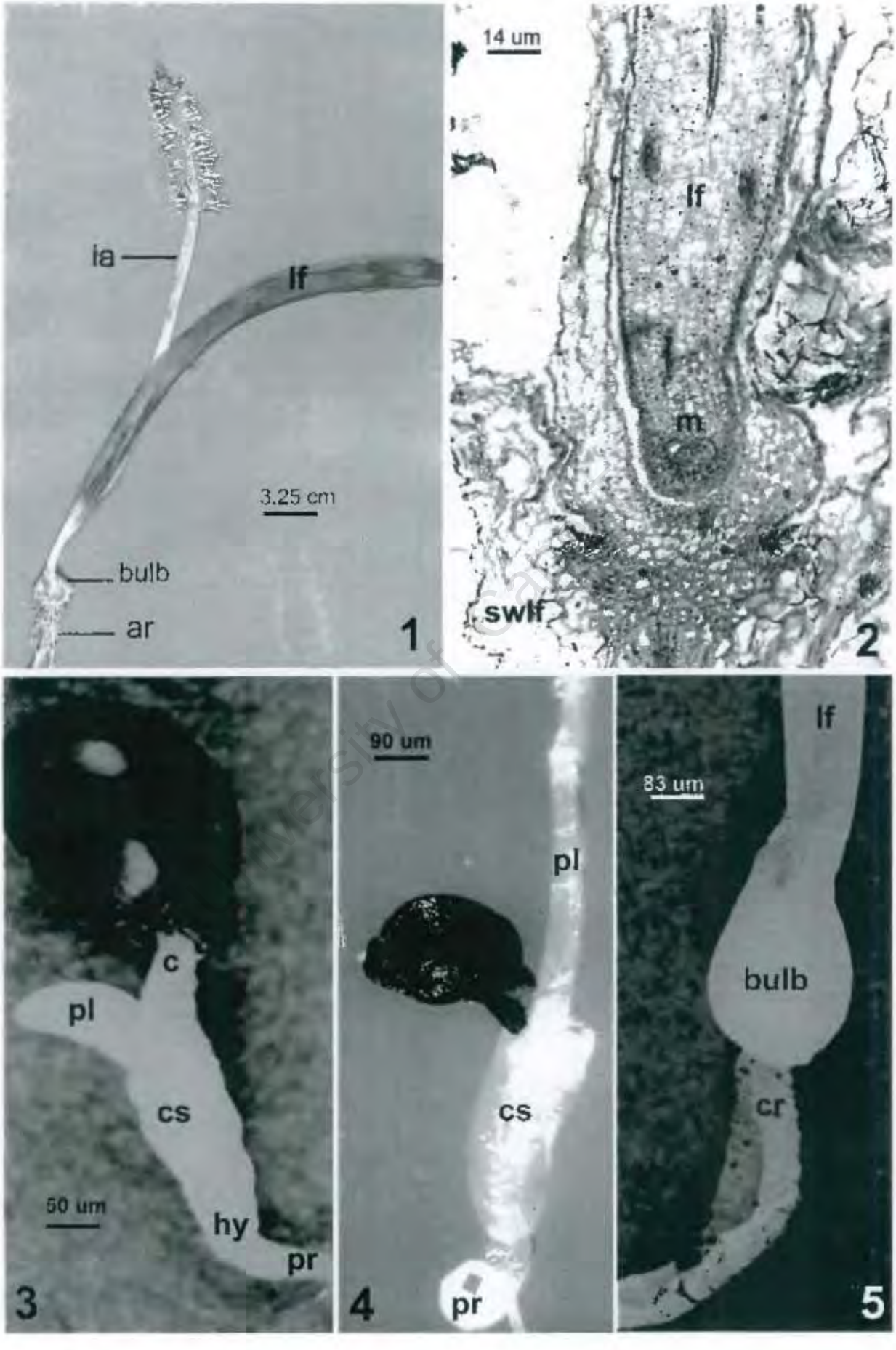
Anatomy

T/S contractile root

The root structure comprises all regular root tissue types with an exodermis, cortex, endodermis, pericycle and stele (Pl. 15, Fig. 3). The xylem is arranged in radiating arcs within the stele and the phloem occurs between the arms, outside of the xylem (ectophloic arrangement). The contractile root structure differs little to the ordinary root structure, excepting that the exodermis forms a slightly thicker cell layer and the surface becomes wavy after the sectioning process.

Plate 14. Morphology and anatomy of *Lachenalia*.

Figure 1. Gross morphology of *Lachenalia klinghardtiana* showing bulbous habit; adventitious roots (ar) are at the base of the plant and a terminally positioned inflorescence axis (ia) and a single laminate leaf (lf) occur aerially.
Figure 2. L/S of sprouting bulb of *Lachenalia splendida* 1 year after germination showing position of swollen leaf bases (swlf), aerial leaf (lf) and meristemmatic region (m) of shoot system.
Figure 3. Seedling of *Lachenalia splendida* 1 week after germination showing epigeal germination. (c) = cotyledon; (cs) = cotyledonary sheath (cs); (pl) = plumule; (hy) = hypocotyl; (pr) = primary root.
Figure 4. Seedling of *Lachenalia splendida* 2 weeks after germination showing cylindrical plumule (pl). (cs) = cotyledonary sheath; (pr) = primary root.
Figure 5. Seedling of *Lachenalia splendida* 3 months old with swollen leaf base of cylindrical leaf (lf) forming the bulb. Contractile roots (cr) present.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T/S inflorescence axis

The epidermis consists of brick shaped cells with the outer wall thickened. Stomata are absent. A parenchyma band is present and is composed of approximately ten layers of unspecialised cells. The following band is composed of a single layer of sclerenchyma cells with thickened walls which stain dark green. A peripheral ring of vascular bundles is associated with this band. The central area is composed of parenchyma cells which are unspecialised and contain three to four vascular bundles. The medullary vascular bundles have xylem arranged in a t-shape with a phloem cap on the adaxial surface and a distinct one-layered bundle sheath.

T/S flower stalk

The epidermis is composed of upright rectangular, elongate cells, topped by a thick cuticle. Stomata are absent. The following layer comprises closely packed parenchyma cells without thickened cell walls which is expanded into approximately ten cell layers. The layer directly below this consists of five layers of sclerenchyma cells with thickened walls (also staining dark green, as in the inflorescence axis region) and peripheral vascular bundles on the exterior of the band. The central area is composed of parenchyma cells which are unspecialised. There are three to four medullary vascular bundles. The xylem of the medullary vascular bundles is arranged in a u-shape with the phloem arranged adaxially to this. The bundle sheath tends to break down.

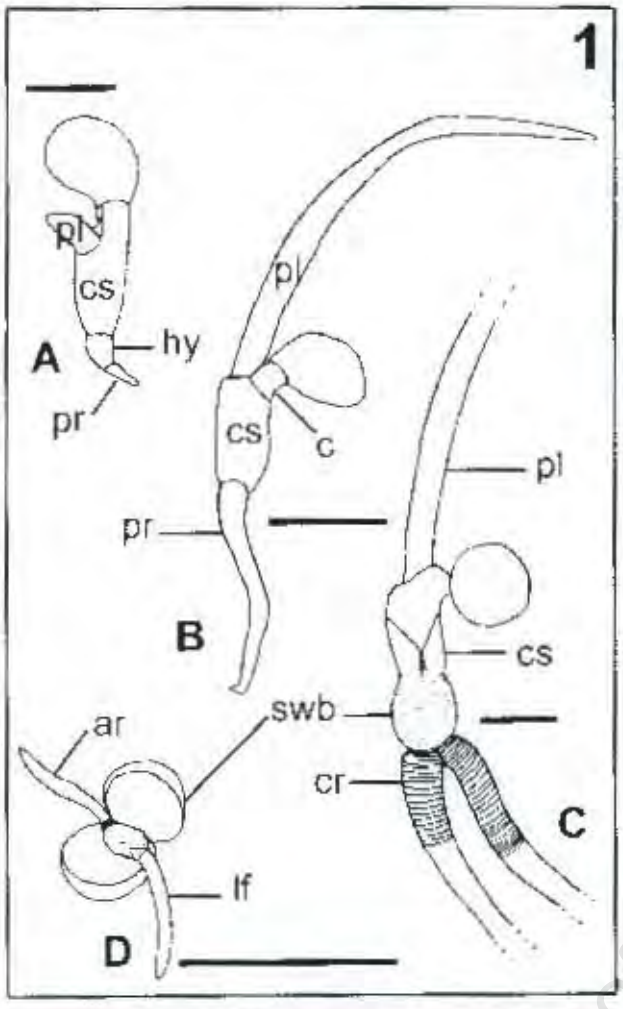
Growth form affinities and differences

Bulbs are restricted to the Liliiflorae and are found most commonly in the orders Asparagales and Liliales. The anatomy of bulbs has been studied in detail in Iridaceae by Rudall (1989) who established that the PTM is responsible for stem thickening growth (maintaining leaf separation at the apex) as well as primary vascular bundle development and root initiation. These patterns are also seen in the bulbs of Hyacinthaceae. The precise initiation of the different buds constituting the bulbous growth form have been examined and established in *Endymion*, *Scilla* and *Narcissus* (Chouard 1926). There seems to be little variation in the positioning of the inflorescence axis in bulbous forms, the flowering axis always tends to be formed from the apical bud (with two reserve buds in subapical positions). The renewal of the bulbous growth is entirely sympodial (Holttum 1955). Rhizome internodes are renewed by an axillary bud located toward the apex of the bulb often in the axil of one of the leaf bases, much like in corms. However, the rhizome internodes are compact and do not contain storage materials and the leaf bases take on

Plate 15. Morphology and anatomy of Hyacinthaceae (Figs. 1-3), *Myrsiphyllum scandens* (Figs. 4-6) and anatomy of *Eriospermum pumilum* (Fig. 7).

Figure 1. Seedling and bulb ontogeny in *Lachenalia splendida* 1 week to 3 months after germination. **[A]** Seedling 1 week after germination showing epigeal germination and plumule emerging through cotyledonary sheath. **[B]** Seedling 2 weeks after germination the plumule extends and displaces the cotyledon plus seed into a lateral position. **[C]** Seedling 3 months after germination, the seed begins to shrivel and the cotyledonary sheath decomposes. The base of the plumule is swollen and contractile roots are developed. **[D]** Sprouting "resting bulb" in 1st year after germination, second day split open to show new swelling of cylindrical leaf base within previous growth season's swollen leaf base. (pl) = plumule; (cs) = cotyledonary sheath; (hy) = hypocotyl; (pr) = primary root; (c) = cotyledon; (swb) = swollen leaf base; (cr) = contractile roots.
Figure 2. T/S rhizome of *Lachenalia klinghardtiana* showing the arrangement of vascular tissue into two rings; the outer ring (or) consisting of amphivasal bundles and the inner ring (ir) as a series of traces.
Figure 3. T/S contractile root of *Albuca fragrans* (co) = cortex; (st) = stele; (ex) = exodermis.
Figure 4. Morphology of *Myrsiphyllum scandens* seedling showing compact plagiotropic rhizome giving rise to tuberous roots (rt) basally and to axes (ax) aerially which bear scale leaves and phylloclades (ph).
Figure 5. T/S phylloclade of *Myrsiphyllum scandens* showing a single layered epiderm's (ep) surrounding an assimilatory layer (al) and a central parenchyma (co) region. A single vascular bundle (vb) is present which is not orientated towards the abaxial surface.
Figure 6. L/S of side branch of *Myrsiphyllum scandens* showing shoot apex (ap) with lateral phylloclade primordia (pp) in the axils of scale leaves (sl).
Figure 7. L/S of apex of tuber of *Eriospermum pumilum* showing current growth region of tuber (cg) with a concentrated vascular system (vt) above the storage region (st) of the tuber. (ap) = shoot apex.

[Bars = 2.03 mm (Fig. 1); 8 µm (Figs 5-7) and 13 µm (Figs. 2 & 3)].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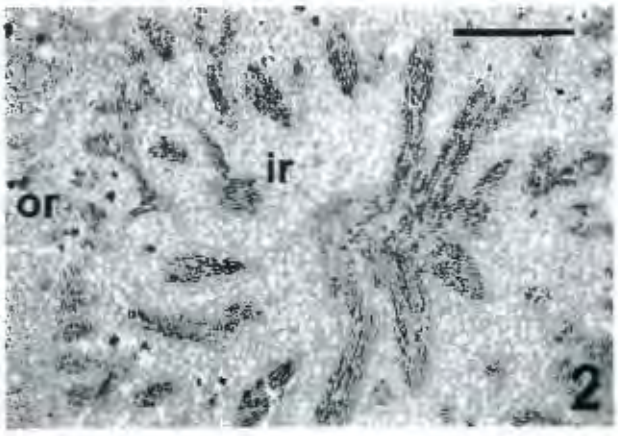
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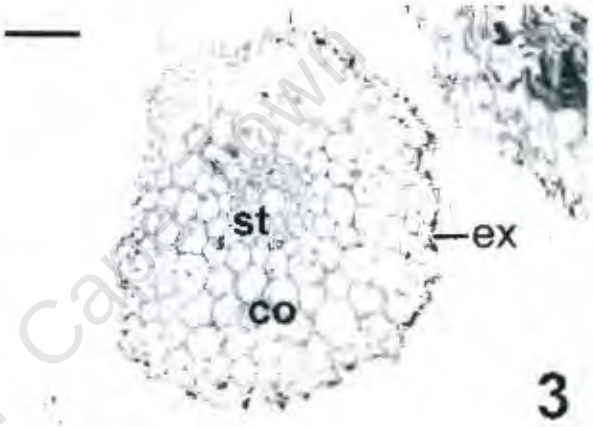
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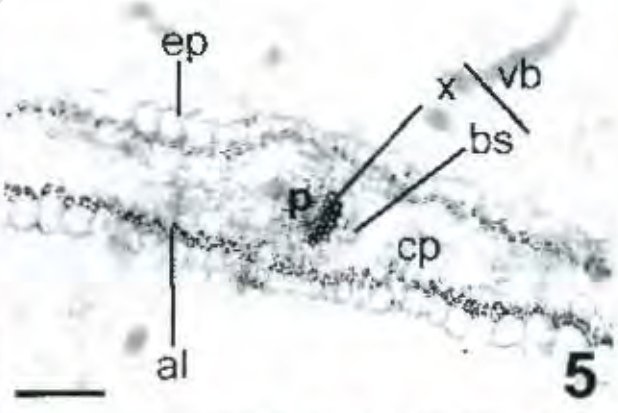
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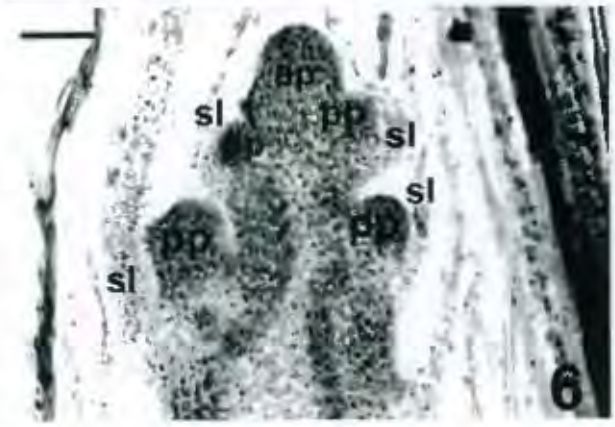
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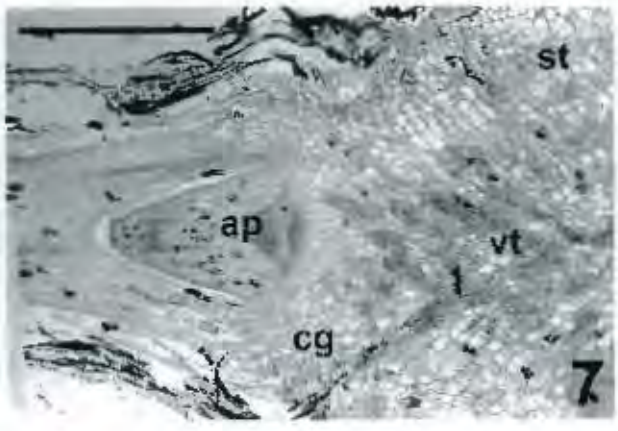
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this role instead and become expanded, storing starch and water in Hyacinthaceae. This may be the case for other bulbous forms too, except in *Allium cepa* (possibly other genera too) in which storage materials are carbohydrates in the form of fructans rather than starch (Pate & Dixon 1982; Dahlgren et al. 1985). The degree of swelling, compactness and storage quantities of leaf bases is what varies amongst the bulbous forms (see Pate & Dixon 1982), the rhizome shows no modifications, except the presence and location of the PTM which ultimately controls the leaf arrangement as well as the ring-like pattern of root initiation. Branching in the bulbous growth form is not uncommon with axillary buds towards the base of the compact rhizome or at the base of the last season's leafy shoot developing into new bulbils (Holttum 1955).

The developmental anatomy of the bulb has also been examined in some detail in *Allium cepa* from the embryo through the germination process and into the adult stage (see Hoffman 1933). The development of the bulb in *L.splendida* is similar to that described for *A.cepa* (see Hoffman 1933; Tillich 1995). The germination and subsequent formation of the cotyledon and first leaf in *L.splendida* is of the "*Scilla* type" described and illustrated by Chouard (1926). The cotyledon is photosynthetic and grows above the soil surface and the first leaf bud is formed just below the soil surface. The first leaf (plumule) then grows through the cotyledonary sheath through a small opening. This is a feature of Alliaceae and Hyacinthaceae seedlings (Tillich 1995). The seedlings of Amaryllidaceae, Alliaceae and Hyacinthaceae are similar in that the axis is short, so that the hypocotyl is very compacted and as a result the primary root appears to be linked directly to the base of the cotyledon (Tillich 1995). This may be related to the bulbous growth form and thus, the hypocotyl being responsible for the formation of the rhizome, is compact early in the ontogeny so that the leaf bases can be modified both positionally and functionally.

Contractile roots seem to be present in most bulbous growth forms, but may only be produced at certain times of the year as was observed in *L.splendida*. The anatomy of the contractile roots did not differ to that of adventitious roots, which is in contrast to the findings of Pütz and Froebe (1995) who measured cell sizes in macerated roots. The external morphological features of the contractile roots of *L.splendida* such as expansion of the diameter and wrinkling of the surface with a concomitant increase in the parenchyma of the cortex are commonly reported (e.g. Arber 1925; Chouard 1926; Hoffman 1933; Ruzin 1979; Pütz 1996b).

Lilianae: Orchidales: Amaryllidinae: Alliaceae: Tulbaghia alliaceae

Morphology

Plant approximating a hysteranthous condition, producing aerial flowering axes in late autumn. After flowering, the axes die back and leaf shoots are produced, usually coinciding with moist conditions i.e. early rainfall events in field populations. The plant has an almost succulent condition with the rhizome internodes appearing fleshy and the leaves somewhat succulent. The plant is rhizomatous and composed of several sympodial units, producing thick fleshy internodes which may be easily mistaken for bulbs in dried herbarium material. What appears to be a bulb is simply the swollen flowering shoot base, leaves are "fleshy" (rather succulent) but are not organised in a true bulbous manner. Within the Alliaceae, only two of the genera are rhizomatous *Agapanthus* and *Tulbaghia*, the remaining genera are bulbous (Dahlgren et al. 1985). When the tissues of *T.alliaceae* are damaged, strong onion smelling compounds are released which are the sulphur compounds in the essential oils which are typical of the family (Dahlgren et al. 1985). The anatomy and morphology *Tulbaghia* are not well documented. A cytotaxonomical analysis of the genus has been undertaken (see Vosa 1975).

Anatomy

T/S rhizome

The epidermis consists of flattened, brick shaped cells. A hypodermis is present and is composed of two to three cell layers of flattened cells which are closely stacked one upon the other. The cortex is expanded to approximately twenty cell layers in thickness. The cells of the cortex contain red staining globular inclusions (starch granules). The cortex lacks vascular tissue. The central area consists of parenchyma cells which contain starch granules and this area contains the vascular tissue. The vascular tissue anastomoses. The vascular bundles are generally amphivasal, but are not always distinct due to the anastomosing. Root buds are evident in T/S, and are endogenously formed, possibly from a PTM which is present between the cortex and the central vascular area.

T/S basal inflorescence axis

The epidermis is composed of cells which are upright rectangular in shape, with their outer walls thickened. The assimilatory band consists of two to three cell layers of rounded parenchyma cells containing chloroplasts. A sclerenchyma band is present directly below the assimilatory band and peripheral vascular bundles are present towards the exterior of the band. The sclerenchyma cells have thickened walls. The central region

is composed of a ground parenchyma cells with slightly thickened walls. The medullary vascular bundles are arranged in a ring within the central ground parenchyma and have xylem which is t-shaped in arrangement.

T/S mid inflorescence axis

The epidermis is composed of cells which are upright rectangular in shape with thickened outer walls. An assimilatory band consisting of two to three cell layers is present and is composed of rounded parenchyma cells containing chloroplasts. A sclerenchyma band is present directly below the assimilatory band and peripheral vascular bundles are present on the exterior of the band. The sclerenchyma cells have thickened cells walls. The central area is composed of parenchyma cells with slightly thickened cell walls which are wavy in appearance and contains vascular tissue. The medullary vascular bundles are arranged in a ring within the central ground parenchyma. The medullary vascular bundles have a u-shaped xylem arrangement and a poorly developed bundle sheath.

T/S inflorescence stalk

The epidermis consists of upright rectangular shaped cells and a thick cuticle is present. Stomata are possibly present - stomates were not actually seen, but some substomatal cavities were visible as tears in the tissue. An assimilatory region composed of two cell layers is present, not a distinct band, and consisting of rounded cells which contain chloroplasts. The central area consists of unspecialised parenchyma and contains the vascular bundles which are concentrically arranged, with none in the centre. The vascular bundles have a poorly developed bundle sheath, but are distinct. The xylem is arranged in a u-shaped fashion in the T/S of the bundle.

T/S flowering stalk

The tissue arrangement is the same as was observed in the inflorescence stalk, but the shape of the axis as well as the arrangement of the vascular tissue differs. The shape of the inflorescence axis is triangular and this has affected the distribution of the various components of the inflorescence axis. There are only three vascular bundles contained within the vascular bundle ring of the central ground parenchyma. The vascular bundles are medullary only, with a poorly developed bundle sheath, and the xylem is arranged in a u-shaped fashion.

Growth form affinities and differences

The growth form and life history features of *T.alliaceae* are somewhat similar in function to the forest gingers described by Holttum (1955) in which the leafy aerial portions are produced during the wet season, while fleshy rhizomatous internodal addition may occur prior to leafy axial generation. The whole rhizome remains as a fleshy underground resting organ during the dry season in these gingers. The almost hysteranthous condition of *T.alliaceae* is interesting as this is usually only a feature of bulbous, tuberous or cormous monocots which are able to store substantial reserves for the unseasonal flowering event. The presence of storage materials and the fleshy nature of the rhizome of *T.alliaceae* points to the possibility that the formation of flowering axes prior to leaves in at the onset of the wet season is a result of storage materials from the previous season's leafy growth. Thus, the rhizome does behave as a resting organ and is responsible for both floral and leafy initiation at the start of the wet season.

Lilianae: Orchidales: Asparagineae: Asparagaceae: Myrsiphyllum scandens

Morphology

Plants with a compact rhizome producing vegetative shoots aerially (often climbing or twining), with the leaves on these axes tending to be reduced to scales (Pl. 15, Fig. 4). The precise nature of the flattened structures that are borne in the axils of the scale leaves is uncertain, superficially resembling leaves but more often interpreted as cauline structures. Roots are produced from nodes along the rhizome and bear swellings which are often close to the departure from the rhizome rather than at root apex (Pl. 15, Fig. 4), although swellings can be present midway along roots.

The swellings on the roots lack nodes, and they produce adventitious branches, which can be interpreted as a normal branching root. The rhizome is always horizontal and subterranean, comprising several nodes, with the apex of the rhizome having a new shoot bud. Thus, there is directionality in the growth of the rhizome, with the rhizome renewal bud apical on the last formed rhizome internode. The older portions of the rhizome show abscission scars where the previous season's aerial shoots have died back. The aerial axis is composed of nodes and internodes with lateral inflorescences. The aerial axes bear axillary buds in the axil of the scale leaves, so innovation occurs both basally (i.e. sympodially) and aerially (with axillary buds) and thus, the aerial shoots can branch too, a condition which may be related to the twining habit.

The cotyledon is haustorial and the cotyledonary sheath is short and reduced, and ensheaths an axial portion in which the first leaf organs are scale leaves. The hypocotyl is

short and compact and after the first growth increment becomes slightly laterally expanded and bears the renewal bud of the following shoot. At the base of the hypocotyl is well developed single primary root, which expands laterally to form a root tuber. The plant displays sympodial renewal with each new sympodium developing from an axillary bud of the rhizome. The rhizome is ensheathed with scale leaves and the bases of the aerial axes are covered with short protrubances, spine like in nature.

The morphology and anatomy of the phylloclades of Asparagaceae are well studied (e.g. Cooney Sovetts & Sattler 1986; Hirsch 1976; Sattler 1988; Schlittler 1953; Troll 1937) and Arber (1925) examined the anatomy and morphology of the phylloclades of *Myrsiphyllum* in detail.

Anatomy

L/S seedling (field collected, age unknown)

The seedling in L/S shows several aerial axes arising from the rhizome region. The current aerial shoot can be determined by the presence of a shoot meristem which is located above a region, which can be identified as the rhizome. Below the rhizome portion, the root system can be identified and the vasculature can be followed into each root. The roots in this early developmental stage are swollen in the cortex region and therefore, already show tuberisation. In this juvenile phase, the rhizome is already strongly developed and each rhizome unit turns upright to form an aerial axis.

T/S root tuber

The root is surrounded by an outer layer which is probably epidermal in origin and which also has unicellular epidermal hairs at regular intervals along the surface. Directly below this is an exodermis which comprises three layers of cells which have thickened walls. The cortex consists of loosely arranged parenchyma cells and is expanded to about twenty cell layers in thickness (compared to five cell layers in the non-swollen region). The cortex is probably the storage area, but is highly sclerified and tends to break down in the sectioning process. Accordingly, starch granules are difficult to detect. The cortex surrounds the stele, which in turn is bounded by an endodermis composed of cells with only the inner walls thickened. The pericycle is external to the vascular tissue. The xylem is arranged in a concentric ring, with the phloem external to that. The stele contains a central pith region, comprised of parenchyma cells which show no thickening.

T/S rhizome

The rhizome is surrounded by a several layered epidermal area composed of flattened cells which stain pink (possibly an exodermis). There is a distinct hypodermis of green staining cells and the inner material of the cells has a fine granular appearance. This may be some kind of suberisation. The cortex consists of four to five cell layers of isodiametric parenchyma cells. Rod-shaped crystals (oxalate raphides) and red staining inclusions (probably tannins) are present in abundance in this region. The central region contains the vascular tissue and is a distinct "core" separate from the other tissue layers. The central region is composed of unspecialised parenchyma cells, which lack storage materials, and the area is packed with vascular bundles. The vascular bundles are not arranged in any specific pattern, they anastomose and are scattered throughout the central region. The vascular bundles are amphivasal with the xylem elements staining distinctly.

T/S aerial axis

The epidermis is composed of vertically rectangular, elongate cells, with the outer walls thickened. A cuticle is present as are stomata. The following layer is a parenchyma band comprising two to three cell layers of unspecialised parenchyma cells. The parenchyma band is external to a sclerenchyma sheath which is composed of two to three cell layers of cells which have thickened walls. Smaller/developing vascular bundles are present close to the inner surface of sclerenchyma sheath. The central area is composed of parenchyma cells which are unspecialised and the area contains most of the vascular bundles. The vascular bundles have the xylem arranged in a u-shape with the flanking elements larger than the central elements. The bundle sheath is one layered and the cell walls are not thickened.

T/S flowering stalk

The epidermis is composed of vertical rectangular shaped cells with dome shaped outer walls and a cuticle. The assimilatory band is composed of a single layer of parenchyma cells which contain chloroplasts. There is a parenchyma band which consists of two to three cell layers of unspecialised parenchyma cells. The sclerenchyma band is two to three cell layers in thickness and the cells have concentrically thickened cell walls. The central area is highly reduced and is composed of a few unspecialised parenchyma cells. This region contains the vascular tissue which is reduced to three vascular bundles which

are surrounded by highly sclerified bundle sheaths and are arranged in a ring. The xylem in the vascular bundles is u-shaped in arrangement with the phloem located above this.

T/S phylloclade

The phylloclade appears initially to be dorsiventrally flattened with lateral expansion to form a spindle shaped structure (Pl. 15, Fig. 5). The phylloclade is surrounded by a single layered epidermis which is composed of regular, brick shaped cells. There is an assimilatory layer comprised of two to three layers of cells which contain chloroplasts (Pl. 15, Fig. 5). There is also another parenchyma layer which comprises the central area, and does not contain chloroplasts. Within this area is a single vascular bundle (Pl. 15, Fig. 5). The bundle is surrounded by a bundle sheath, has xylem arranged in a u-shape manner with the phloem in a cap above this. The peculiar feature of the vascular bundle is its orientation. The xylem is oriented towards the lateral axis of one side rather than to the abaxial surface (as is the usual arrangement in a leaf). Thus, the phylloclade expansion appears to have taken place across an adaxial/abaxial axis rather than being dorsiventrally flattened. In a T/S of the shoot apex, this xylem orientation was found to be towards the axis from which the phylloclades branch.

L/S side branch and shoot apices

If an L/S of a main axis plus a lateral branch bud is examined, the subtending scale leaf is evident below the branch bud and is attached to the main axis, with the vasculature of the main axis following into the leaf scale. Between the branch bud and the main axis is a small insignificant structure, which is likely to be the prophyll of the branch bud. From there, the bud and axial relationship becomes complex as the scale leaves are large compared to the bud meristems. However, if just a branch bud is considered, the prophyll is distinct between the bud primordium and the main axis, with the scale leaf subtending the whole unit (Pl. 15, Fig. 6). There is a possibility that a second subtending scale leaf ensheaths the whole unit, as this pattern is repeated consistently upwards towards the shoot apex of a branch. At this stage, the number of vascular traces cannot be used as a measure of how many structures there are, as the trace tends to end at the primordial region. At the apex of the branch, a shoot primordium is present, with a pattern that develops downwards where a small primordium is directly below the shoot apex, and a leafy structure below this (this is repeated twice). It is likely that the primordium is the undeveloped phylloclade and that the leafy portion is the scale leaf. It is difficult to see where a prophyll interpretation fits in here, as no prophyllar primordia can be identified. A

T/S of the shoot apex did not clarify the situation as there are possibly prophylls present between the main axis and the phylloclades.

Growth form affinities and differences

The seedling structure in *M.scandens* is similar to the seedlings described by Tillich (1995) for the basal taxa of Asparagales. The extension of an aerial axial region covered with scale leaves is as previously discussed, likely to be a result of the twining habit of the plants. The epidermis which surrounds the roots is possibly a velamen, as velamen is sometimes present in members of Asparagaceae (see Dahlgren et al. 1985). The formation of swellings of the root (tubers) is common in the family (Dahlgren et al. 1985) and Pate & Dixon (1982) observed that the tubers of *Asparagus racemosus* survived for two or more seasons with annual recruitment of new tubers. Similar swellings of the root organ were observed and examined in *Chlorophytum comosum* with little difference occurring between the structures in the two taxa. The tubers are likely to be used as storage organs and may supply the vigorously growing new aerial shoots with sufficient nutrients required for the rapid increment in size that is often seen. The aerial shoot tissues approximate the arrangement of other aerial inflorescence bearing axes of monocots and the sclerification is likely to be present as a structural support mechanism.

The interpretation of the "leafy" structures which are born on the aerial axes is very complex. Dahlgren et al. (1985) refer to these structures as "branchlets transformed into flat, leaf-like cladodes" i.e. short shoots, while the long shoots have reduced scale-like leaves. These are not equivalent structures to the needles of *Asparagus* which are filiform stems and they themselves bear small scale-like leaves (Arber 1925; Dahlgren et al. 1985). A problem has been the tendency to recognise Asparagaceae and Ruscaceae within Asparagaceae, when they are considerably different in both floral morphology and also vegetative morphology (Dahlgren et al. 1985). The "phylloclades" of Ruscaceae are also complex structures and Arber (1925) interpreted those of *Danaë* as being most similar in structure to the "leafy" appendages of *Myrsiphyllum*, as the prophylls of short shoots. Others (e.g. Troll 1937; Hirsch 1976) interpreted these as flattened stems on the basis of the axillary position in the scale leaf - all organs which are axillary are by position cauline in nature. The problem with both of these interpretations relates to the position of the flowers in Ruscaceae - on either the adaxial or abaxial surface in the mid vein region of the structure. The interpretation which is currently held is one of homeosis where developmental studies have elucidated that these organs within Asparagaceae are a continuum in the expression of leaf and stem features i.e. intermediate between both

(Cooney-Sovetts and Sattler 1986; Sattler 1988). In fact, Arber (1925) strongly held the belief that in Rusceae, the lateral shoot axis is completely adnate to its prophyll explaining the adaxial appearance of flowers. She did not however uphold the view of the phylloclade being an intermediate organ. She preferred to refer to it as a leafy organ, as the dominant component of the phylloclade was the prophyllar portion. The prophyll interpretation of Arber (1925) rests on the observation that the xylem pole of the vascular bundles of the phylloclades are orientated towards the main axis and thus she interprets them as prophylls of short shoots arising in the axils of scale leaves and thus representing "true leaves". The link between the short shoots and the formation of long shoots in association with these prophyllar structures in *Myrsiphyllum* is not clear, as indicated by Arber (1925). Not even rudimentary structures of short shoots could be located in my examination of both axillary shoot buds and phylloclade structure. Cooney-Sovetts and Sattler (1986) suggested that the absence of any short shoot primordia was the result of changes in plastochron sequences in primordial initiation. In *Danaë*, however, shoot primordia are rudimentarily developed on lower order branches, but towards the apex of the vegetative meristem, there is a switch to phylloclade primordial formation in the axils of the scale leaves.

The short coming of the prophyll interpretation of Arber (1925) for the phylloclade, lies with the peculiar adaxial/abaxial expansion of the structure, which is not like a prophyll or a leaf at all. The phenomenon of inverted vascular bundle arrangement in phylloclades in Asparagaceae is accounted for by Cooney-Sovetts and Sattler (1986) who suggest that the fusion of prophyll and cauline portion result in the reorientation of the vascular bundles. In addition, the development of the phylloclade takes place by periclinal divisions much like leaves, and therefore results in the dorsiventrality observed in the phylloclades. These authors also suggested that the development of the vascular bundles and the subsequent venation patterns in phylloclades follows that of monocotyledonous leaves. However, the presence of only a single vascular bundle in the phylloclade of *M.scandens* appears to be a peculiar feature and this combined with the inversion of the bundle and peculiar adaxial/abaxial direction of expansion is not easily reconciled with the "leafy" features described by Cooney-Sovetts and Sattler (1986). Due to the intermediate nature of this organ, i.e. composed of both "stem" and "leaf" characteristics and therefore requiring some sort of foliar interpretation, this structure is not coded for organ analysis in Chapter 3. This is simply, as explained before, due to time constraints and that the organs of interest in this thesis are of the axial system and leaves are not examined. Hence, the phylloclade is not considered further in this thesis.

Lilianae: Orchidales: Asparagineae: Eriospermaceae: Eriospermum pumilum

Morphology

Eriospermum pumilum forms an underground storage organ which is globose in shape and produces aerial portions from an apical growing point. The organ is described as a hypercotyledonary tuber which is the common storage organ for the genus (Perry 1994). *Eriospermum pumilum* is hysteranthous with the inflorescence axes produced first in the sequence, in late autumn and the leaves produced in early winter following rain. The number of leaves varies, usually being one, but greenhouse specimens often produced two leaves concurrently during each season. The leaves are lanceolate with an extensive "petiolate" portion to them. The base of the lamina lacks the presence of an appendage which has been observed in other species (see Dahlgren et. al 1985; Perry 1994). The basal internode of the tuber shrivels towards the end of spring just as the leaf is ending its growth period. By contrast, the mid and upper internodes of the tuber are fleshy and expanded at this stage. The seeds are covered with hairs, probably a dispersal feature, but in the field the seeds fall close to the parent plants. The seeds germinate readily, taking up to ten days to germinate after wetting.

The morphology of the tuber plus inflorescence axis is difficult to interpret. However, a close examination of the tuber apex where the current flowering inflorescence axis base occurs, reveals that the basal portion of the axis and lower inflorescence axis are ensheathed by a sheathing leaf which has a small rudimentary laminate tip at its apex. This structure is termed a peduncular bract by Perry (1994). If the sheathing portion is removed, the basal portion of the axis can be shown to have two nodes (i.e. it should consist of three internodes). When a L/S of the current shoot system is examined, three sheathing structures surround the basal portion of the inflorescence axis suggesting that each node produces a reduced sheathing leaf. In fact this is the case, the lower two internodal sheathing leaves seem to decompose and flake away at the apex of the tuber, while only one remains to surround the softer portions of the growing aerial axis. The second inflorescence axis node contains a bud, which is possibly a replacement bud for the current axis if it gets damaged.

Roots are produced from the top third of the tuber only. This leads to the interpretation that only the apex of the tuber is involved in current growth, the base of the tuber acts as the storage zone only, not producing roots or buds for new shoots. This is possibly a vertical rhizome system with laterally expanded internodes. Nodes along the tuber are very difficult to locate macromorphologically, and can only be recognised where roots arise. The sympodium is like that of a cormous system, where current growth relies

on storage material from the previous season's growth, except a new "storage" organ is not produced every season. There must be a source-sink pump active in this kind of tuber.

In a L/S of the apex of the tuber, the inflorescence axis appears to be flanked by two axillary buds on either side. One of these may be the leaf bud which will mature when the inflorescence axis has finished flowering. The other bud may be a renewal bud for the sympodial continuation of the tuber. There is almost a distinct vasculature at the base of the inflorescence axis, which is in a different plane with that of the main tuber region, this may be related to the current growth sector of the tuber (Pl. 15, Fig. 7). The previous season's storage area contains very diffuse indistinct vascular bundles. This suggests a maintenance role rather than a growth support role. Perry (1994) has provided a revision of the family and examines the morphology, ecology and flowering times in some detail.

Anatomy

T/S tuber mid region

The outermost layer of the tuber consists of an exodermis of several layers of loosely packed cells which tend to break down. A hypodermis is present which consists of flattened cells closely arranged and wavy in appearance. The cells are not sclerified and do not show any wall modifications. The cortex appears to be undeveloped and the bulk of the tuber is composed of unspecialised isodiametric parenchyma cells which make up the central region of the tuber. Thus, the central region is much expanded in this organ. The parenchyma cells contain a dense mucilage which stains an emerald green, and does not wash out of the cells. The parenchyma cells also contain rod-like crystal inclusions (raphides). Starch granules are absent from the parenchyma cells. This poses an interesting consideration of what the storage material is likely to be in this organ. Furthermore, the vascular tissue is diffusely scattered and poorly developed throughout the organ. The vascular bundles sometimes anastomose within the tuber, some tend to be amphivasal, while others have the xylem arranged in a u-shape.

T/S lower inflorescence axis

The epidermis consists of flattened brick shaped cells with the outer wall thickened. A chlorenchyma band is absent, as is a parenchyma band (compared to the upper inflorescence axis region) and the bulk of the inflorescence axis is comprised of unspecialised parenchyma cells. The vascular bundles are arranged in a ring in the central area. The vascular bundles have a t-shaped xylem tissue arrangement. The most

apparent difference between the lower and upper inflorescence axis regions is that the lower portion is ensheathed by a leaf which is separate from the tissue of the axis. This sheathing leaf is not easily visible when examining the inflorescence axis, but is in the transverse section. The sheathing leaf structure is determinably a "leaf" structure due to the epidermal tissue layers on both the dorsal and ventral surfaces as well as a more "linear" arrangement of the vascular bundles.

T/S upper inflorescence axis

This area corresponds to the upper portion just below the flowering region. The epidermis consists of flattened brick shaped cells with the outer wall thickened. A cuticle is present. Stomata are absent. An assimilatory band comprising two to three cell layers of rounded parenchyma cells which contain chloroplasts is present. There is possibly a parenchyma layer, but the cells are not distinctly different to the central ground parenchyma cells other than their mucilaginous contents which stain green. The mucilage layer is absent in the central ground parenchyma cells, which are isodiametric and unspecialised. The central area contains the vascular tissue. The vascular bundles are arranged in a ring within the central ground region and the xylem is arranged in a t-shape. The bundle sheath is poorly developed.

Growth form affinities and differences

The tuber morphology, anatomy and sympodial renewal is similar to the storage organ described for *Z.aethiopica*. Several differences are apparent though, such as the seasonality of leaf production and the mucilaginous storage material, as opposed to starch. Mucilage has been found as a concurrent feature of organs which store a high percentage of water, most of these were corms which occur close to the soil surface and often experience severe water stress in the summer (Pate & Dixon 1982). A similar mucilaginous substance was noted in the corms of *Cyanella* that were examined and in the staining process, the mucilage also stained blue-green. The tuber is also without sheathing leaf bases at the nodes, which are difficult to identify, except for the presence of the roots. The subapical position of the leaves is similar to the leaf position in *Z.aethiopica* and the terminal formation of the inflorescence axis is the same position that is seen in bulbs and corms. Thus, the tuber of *E.pumilum* while being similar to a corm, is more similar to the tuber of *Z.aethiopica* as it behaves as a resting organ, remaining fleshy and viable in the mid portions (internodes).

Not all species of *Eriospermum* have globose tubers with apical renewal. Many have lateral renewal of the leafy portions and the tubers can be either swollen rhizomatous or globose and can produce lateral appendages with each one forming an aerial portion (Perry 1994). In addition, stoloniferous outgrowths have been observed, each one having the ability to turn upwards and form an aerial leafy portion (Perry 1994). The diversity in tuber structure in *Eriospermum* is indicative of a rhizomatous organ system which has the ability to modify the growth orientation to suit certain conditions. Such variation within a single genus has been attributed to variations in habitat conditions by Perry (1994). Irregularly shaped tubers with a lateral growing points occur frequently in arid areas and Perry (1994) proposes that this form is a development which aids to protect the perennating bud. The phenomenon of hysteranthy is also thought to be a response to arid conditions and is also a common feature in arid zone Amaryllidaceae.

Similarities were observed in the germination sequence in *E.pumilum* with that already described for *E.bowieanum* by Perry (1994). The germination in *E.pumilum* is epigeal and the cotyledon is cylindrical and the seed remains at the tip of the cotyledon for up to four weeks. The cotyledonary sheath extends downwards into the soil so that the hypocotyl and plumule primordium are below the soil surface. A single primary root is formed below the hypocotyl. The hypocotyl swells slightly to form a small spheroidal tuber and the aerial portion of the cotyledon dies back at the end of the first season. Further development of the tuber plus aerial portions was not observed in *E.pumilum* (the second season tubers did not form any aerial portions), but Perry (1994) described that in *E.boweianum* during the second season the first foliage leaf is produced which is broad, ovate and prostrate. In species with lanceolate leaves, the juvenile phases (up to the fourth season) also produce ovate prostrate leaves. After the fourth season the lanceolate forms are produced (Perry 1994).

Pandananae: Velloziales: Velloziaceae: Xerophyta humilis

Morphology

Plants inhabiting hollowed out rocky crevices which are filled with a shallow soil layer and decomposing plants material. Plants having a diminutive shrublet growth form with a branched woody base and stiffly arranged leathery leaves. Physiologically, *X.humilis* is a resurrection plant, producing new leaves when moist conditions are present, otherwise the leaves dry down to a metabolically inactive state. The stems are clothed with the fibrous remains of leaf bases and new leaves are produced towards the apex of the stem in a spiral rosette-like fashion. The roots arise along stem nodes, and seem to be

confined to the basal nodes and grow downwards towards the substrate. This is in contrast to the pattern of root formation observed in *Borya*, with a similar habit and resurrection life style. Inflorescence axes were not present on the plants at the time of collection. The biology, morphology and leaf anatomy of *Xerophyta* has been well documented (e.g. Ayensu 1973; Ayensu 1974; Smith 1962; Smith & Ayensu 1974).

Anatomy

T/S root

The root has an exodermis which consists of a single layer of cells. Unicellular hairs are produced by the exodermis. The cortex is divided into two regions. The first is a sclerified region of about ten cell layers in thickness. The second region also comprises ten cell layers in thickness, but the cell walls are not thickened. An endodermis and pericycle are present, the endodermis not showing any wall specialisations or suberisation. The stele is an ectophloic siphonostele, with the xylem arranged in discrete poles in a circular fashion and the phloem alternating with the poles to the exterior. The central pith is sclerified.

T/S base of stem

This portion of the stem is close to the substrate. In this part of the stem, there does not appear to be a tissue plan. The stem is bounded by an epidermis which consists of flattened brick-shaped cells. Centrally, the stem consists of unspecialised parenchyma cells. The vascular tissue arrangement and pattern is the same as that found at the stem apex - consisting of elongate bundles, with the sclerenchyma cap below the xylem. Roots are present at the nodes in this region of the stem.

T/S stem apex

The epidermis consists of flattened brick shaped cells with all walls equally thickened and staining pink. A hypodermis is well developed and comprises five cell layers consisting of loosely arranged cells, these with a wavy appearance. The following zone is an endodermoid sheath and consists of fifteen to twenty cell layers of small cells, with highly thickened cell walls which stain red. The central region consists of large, isodiametric parenchyma cells with thin cell walls. The central area tissue is reduced as most of the area is taken up by vascular tissue. The vascular tissue consists of bundles which have elongate xylem which is sometimes t-shaped, but generally is just grouped together in a u-shaped arrangement and topped by a phloem pole. There is no bundle sheath. A sclerenchyma cap is present, but this is positioned at the base of the xylem pole. It is

composed of eight cell layers and the cells have very thickened cell walls which stain deep pink. There are no roots in this area.

Growth form affinities and differences

The vascular bundles of the stem apex are similar to those observed in *Borya* with a sclerenchyma cap at the base of the bundle. The tissue arrangement of the stem suggests that the organ is most suited to water transport with prolific numbers of vascular bundles, and no storage tissues. The growth form, that of a woody upright stem which is clothed by persistent, tough leaf bases is similar to the Australian resurrection plant *Borya nitida,* except that *X.humilis* is often described as mat forming, low growing with prostrate branches (Smith & Ayensu 1975). Dahlgren et al. (1985) report that *X.humilis* has an underground stem portion which they term a rhizome. There appeared to be no distinct rhizome versus upright stem in the material that was collected and examined. The upright portion of the stem appeared to continue directly from the basal portion. The anatomy of the upper stem was however, different to that of the lower portion which lacked tissue differentiation.

Arecanae: Dasypogonales: Dasypogonaceae: Dasypogon bromeliifolius

Morphology

Plant a branched, upright, tufted graminoid shrub-form with older portions of the stem becoming woody by lignification (secondary thickening is absent) (Pl. 16, Fig. 1). The stem bears an inflorescence axis in the terminal position, which is multinodal and bears small scale-like ensheathing leaf bases at the nodes (Pl. 16, Fig. 2). Branching of the upright axes occurs in the basal internodes of the stem. The woody bases of the stems are clothed in tough leaf bases. Towards the apex new leaves are formed. These are tough and stiff, but tend to roll towards the base of the plant. Root production is limited to the basal nodes of the stems and are not formed by any aerial nodes. The whole plant is covered with stiff hairs, but these are most notable on the naked internodes of the inflorescence axis. The biology and morphology of the family has been described by Staff & Waterhouse (1981) - when *Dasypogon* was included within Xanthorrhoeaceae. Fahn (1954) has examined the anatomy of *Dasypogon* (also when included within Xanthorrhoeaceae).

Anatomy

T/S root

The exodermis is corky in textural appearance and the cells are brown staining. The cortex consists of two regions - a sclerified outer region and an unsclerified inner region which tends to break down during sectioning (Pl. 16, Fig. 3). The sclerified portion of the cortex consists of approximately five cell layers, while the unsclerified portion is slightly expanded, consisting of up to ten cell layers. The stele is bounded by an endodermis only, a pericycle is absent (Pl. 16, Fig. 3). The endodermis is comprised of cells which have a thickened inner cell wall. The stele is an ectophloic siphonostele, with the phloem in poles outside the xylem elements which display sclerification. The pith is unspecialised.

T/S base of stem

There is little tissue specialisation in the stem of *D.bromeliifolius*. The stem is bounded by an epidermis which consists of small rounded cells. There is a hypodermis, which is two to three cell layers in thickness and the cells are sclerified. The central area is packed with vascular bundles so that the central ground tissue is much reduced and does not occupy much area (Pl. 16, Fig. 4). The central ground tissue consists of parenchyma cells with slightly thickened cell walls. The vascular bundles are slightly elongate in shape and have xylem which is arranged in a u-shaped pattern. The phloem pole is topped by a small sclerenchyma cap. Each vascular bundle is surrounded by a three-layered bundle sheath which is highly sclerified. The bundle sheaths are closely arranged next to one another so that there is little space between the bundles (Pl. 16, Fig. 4).

T/S green stem

The tissue plan and arrangement of the green stem differs little from that of the inflorescence axis internode. The degree of sclerification is greater, so that the xylem vessels are very distinct (Pl. 16, Fig. 5) and the sclerenchyma band stains deep pink.

T/S inflorescence axis internode

The epidermis consists of small, rounded cells. Epidermal hairs are present which are multicellular and club-shaped (Pl. 16, Fig. 6). Stomata are present. The assimilatory band consists of two cell layers and the cells contain a green-staining substance (which is probably broken down chloroplasts as a result of the reconstitution process). The parenchyma band is approximately four cell layers in thickness and is composed of isodiametric parenchyma cells (Pl. 16, Fig. 6). The sclerenchyma band is approximately

five cell layers in thickness. The cells have very thickened cell walls and are slightly sclerified. Developing vascular bundles are present in this zone. The central region is composed of isodiametric parenchyma cells which have slightly thickened cell walls. The central region contains the bulk of the vascular tissue. The vascular bundles have xylem which is arranged in a u-shaped fashion, but is not deeply staining and thus, is not distinct. Above the phloem pole, there is a small sclerified area, probably comprising a sclerenchyma cap.

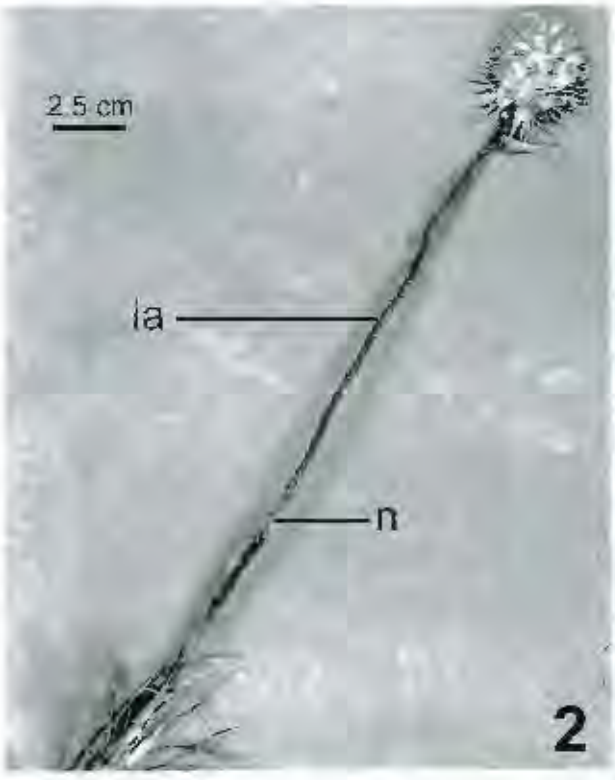
Growth form affinities and differences

The genus *Dasypogon* includes two species. *Dasypogon hookeri* is arborescent and forms a single unbranched woody trunk which has no secondary thickening (Staff & Waterhouse 1981; Dahlgren et al. 1985). In *D.hookeri* the inflorescence axes (peduncles) are produced in an axillary position on "top" of the trunk flanking the shoot apex, while the apical meristem is used exclusively for shoot regeneration (Staff & Waterhouse 1981). The growth form is in contrast to that of *D.bromeliifolius* in several ways. The inflorescence axes in *D.bromeliifolius* are terminal; the stem although woody, is not pachycaul and in addition, branches at basal nodes; and the roots are formed at basal nodes and not aerially as is often found in *D.hookeri* (growing much like the roots of *Borya* and Velloziaceae, ramifying through leaf bases). The stiff leaves and graminoid shrub appearance of *D.bromeliifolius* is similar to that of some grasses, *Borya* and *Calectasia* and possibly represent cases of convergence. The similarity may simply be a result of the plants inhabiting very dry areas with only seasonal (temporary) wetness and thus, a short growth period. In such instances, the production of soft, green aerial portions is restricted to the wet, short growth season, while a persistent, lignified "stem" is a possible solution for the long, dry season. The transition from lignified stem to aerial inflorescence axis is not a clearly demarcated area, although the area where new leaves are produced seems to be part of the upright stem system, while the naked green axes which bear inflorescence terminally are fully photosynthetic and display anatomical differences to the main stem system.

Plate 16. Morphology and anatomy of *Dasypogon bromeliifolius* (Figs. 1-6) and *Calectasia cyanea* anatomy (Figs. 7-8).

Figures 1 & 2. Gross morphology of *Dasypogon bromeliifolius* showing basal branching (br) of stem and the terminal inflorescence axis (ia). (ar) = adventitious root; (lf) = leaf; (n) = node.
Figure 3. T/S root of *Dasypogon bromeliifolius* with a cortex comprising two regions - an outer sclerified region (oc) and an inner unsclerified region (ic). An endodermis (en) encloses the stele (st).
Figure 4. T/S stem base of *Dasypogon bromeliifolius*. The stem tissue is composed of a hypodermis (hyp) and a central area which contains the vascular bundles (vb) which are surrounded by a highly sclerified, three layered bundle sheath.
Figure 5. T/S green stem of *Dasypogon bromeliifolius* showing the sclerenchyma band (sc) and distinct vascular bundles (vb).
Figure 6. T/S inflorescence axis of *Dasypogon bromeliifolius* showing multicellular epidermal hairs (meh), an assimilatory band (ab) with a parenchyma band (pb) directly below followed by a sclerenchyma band (scl). Vascular bundles (vb) are located in the central parenchyma region.
Figure 7. T/S stem of *Calectasia cyanea*. A parenchyma band (pb) separates the epidermis from a sclerenchyma region (sc). The vascular bundles (vb) are located in the central region (cp).
Figure 8. T/S inflorescence axis. An assimilatory band (ab) is present above a sclerenchyma band (sc) and the central region contains distinct vascular bundles (vb) with a u-shaped xylem arrangement.

[Bars = 16 μm**]**.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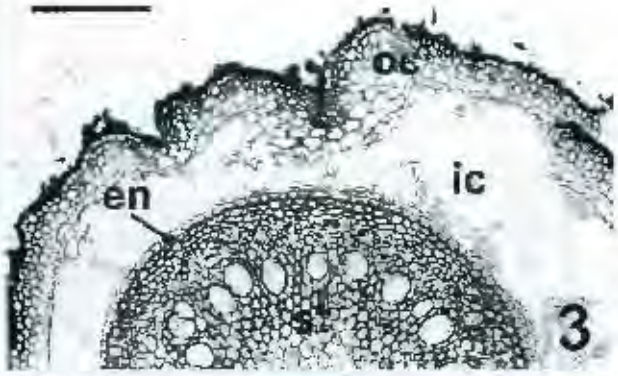
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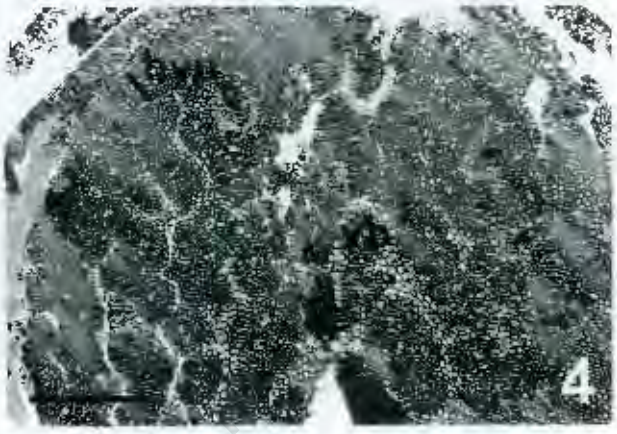
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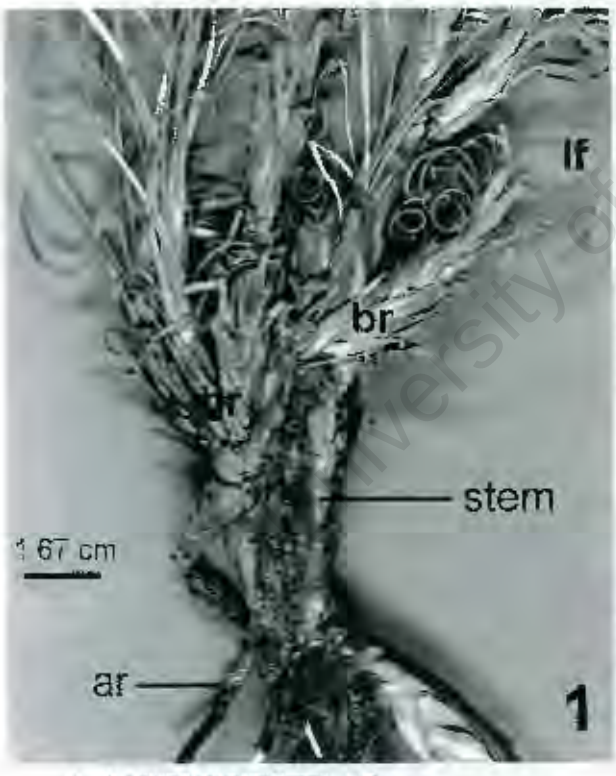
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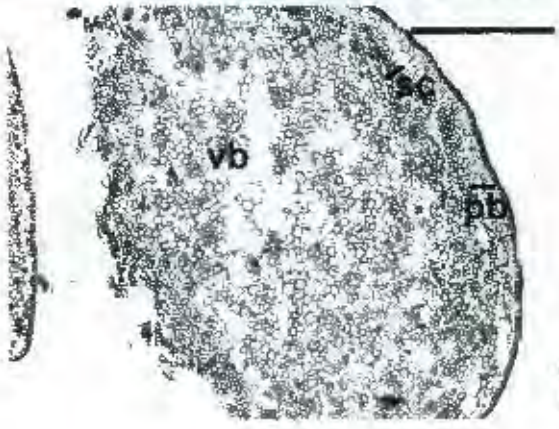
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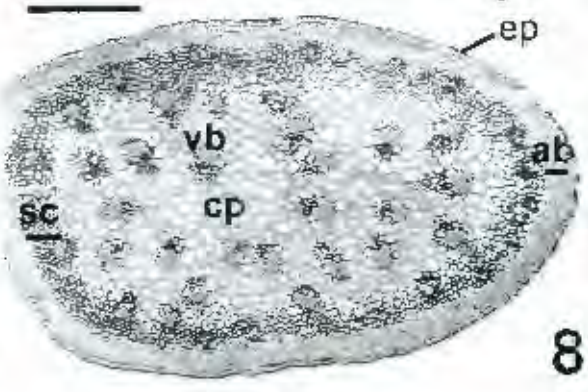
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Arecanae: Dasypogonales: Calectasiaceae: Calectasia cyanea

Morphology

Plants rhizomatous, bearing branched aerial stems which become lignified in the lower portions. The leaves tend to be produced by most of the stem axis at nodes, only the lower portions are covered by old leaf sheaths. The leaves are very flat-laminate and are leathery, but not stiff or spinescent. The growth form is superficially reminiscent of the woody Iridaceous genus *Nivenia,* but the leaves are not opposite in *C.cyanea*, they tend to be spirally arranged. The woodiness is by lignification, not by secondary thickening which is the case in *Nivenia* (see Rudall 1995). The habit of *C.cyanea* is similar to that of *Acanthocarpus* (probably of Lomandraceae - circumscription of previously defined Dasypogonaceae not finalised). Detailed studies of the anatomy and morphology of *Calectasia* are lacking.

Anatomy

T/S stem

The epidermis consists of rounded cells with very thickened outer walls which stain deep red. Stomata are present and are sunken below the thickened walls. A parenchyma band is present, consisting of two cell layers in thickness and comprised of unspecialised isodiametric parenchyma cells (Pl. 16, Fig. 7). The sclerenchyma band is four to five cell layers in thickness (Pl. 16, Fig. 7). The central region is composed of parenchyma cells with slightly thickened cell walls and contains the vascular tissue. The vascular bundles are thus, medullary only and generally scattered within the area. The xylem of the medullary vascular bundles has a u-shaped arrangement with the phloem arranged in a pole above this. The bundle sheath is one layered with slightly thickened cell walls.

T/S inflorescence axis internode

The epidermis consists of rounded cells. Stomata are present and are sunken below the upper walls of the epidermis. An assimilatory band is present (Pl. 16, Fig. 8), the cells are filled with dense, green-staining material (which may be broken down chloroplasts resulting from the reconstitution process). A sclerenchyma band is present (Pl. 16, Fig. 8), but the cell walls are not heavily sclerified as they do not stain red. The central region is comprised of unspecialised parenchyma cells and contains the vascular tissue. The vascular bundles are surrounded by a one layered bundle sheath. The xylem is arranged in a u-shaped pattern within the bundle.

T/S flowering stalk

The epidermis consists of upright rectangular cells which have a dome shaped outer wall. An assimilatory band is present and consists of two to three cell layers and contains broken down chloroplasts. The central region is composed of unspecialised parenchyma cells and contains the vascular tissue. The vascular bundles are arranged in a ring in the central region. The xylem within each bundle is arranged in a u-shaped pattern.

Growth form affinities and differences

The aerial stem of *C.cyanea* is difficult to interpret - the parenchyma band could also be a cortex and the sclerified band an endodermoid sheath and thus interpreted as a rhizomatous system. The problem occurs because the stem has stomata, which are not usually observed in underground rhizomatous systems at least. For this study, the parenchyma band and sclerenchyma band are interpreted and coded as such for the analysis of growth form in Chapter 3. Unfortunately, rhizome material of *C.cyanea* could not be examined so that comparisons could be made. The woody graminoid shrub form, as previously discussed is likely to be similar to that seen in some grasses, *Borya* and *Dasypogon* and might be related to the long dry season of the habitat. Other features suggestive of xeromorphic adaptation are the sunken stomata.

Commelinanae: Commelinales: Haemodoraceae

(i) Wachendorfia thyrsiflora

Morphology

Plants consisting of a several noded, fleshy underground organ which often forms irregular or subglobose shapes, the growth direction is difficult to determine without the seasonally produced aerial axes (Pl. 17, Fig. 1). Runners may also be produced from axillary buds from any of the nodes (Pl. 17, Fig. 3). The pattern of growth increment is such that the older internodes dry out and the newer internodes are fleshy and often give rise to runners and terminally to an inflorescence axis. Renewal of successive fleshy internodes is from an axillary bud located in the axil of a sheathing "rhizome" leaf (Pl. 17, Fig. 2). A L/S of the apical region of the rhizome shows clearly the arrangement of the shoot apex with the apical meristem which will ultimately develop into the inflorescence axis. The duration of the fleshy internodes may last for a whole "resting" season, with the renewal growth being initiated with the onset of moist conditions. Runners (formed from axillary buds on the main fleshy organ) extend new plantlets some distance from the main organ (in some instances the runner consisted of fourteen nodes before it turned upright,

produced foliage leaves and a new plantlet (Pl. 17, Fig. 4)). A new plantlet develops from an axillary bud on a runner and the first internode of the new plantlet becomes fleshy with roots developing from the first node (Pl. 17, Fig. 4). Removal of aerial portions by fire results in prolific "resprouting" the following season with the onset of moist conditions. This resprouting and ramet formation is due to the formation of a large number of runners i.e. mobilisation of reserve buds at the nodes of the parent fleshy portions, which occurs naturally but seems to be enhanced by fire.

Germination of *W.thyrsiflora* seeds are sporadic, there appears to be no pattern to the germination and a distinct cue could not be determined. Seeds were initially sown on filter paper with a smoke water treatment, as smoke is believed to enhance the germination of the seeds, and placed in a temperature controlled seed germination cabinet on a 10°C - 20°C cycle. No germination was forthcoming under these conditions, the seeds became mouldy and the treatment was terminated. Following this seeds were sown in a seedling tray in potting soil and placed in a greenhouse under natural conditions. Two factors seemed to benefit germination potential. These were cold nights, with temperatures below 6°C and a year long soil resting period for the seed. Seeds that had germinated only did so in the second year after sowing and seemed to have lost a large amount of the "hairiness" of the seed coat. It is possible that the seeds require a long imbibition time before germinating and successfully developing into seedlings.

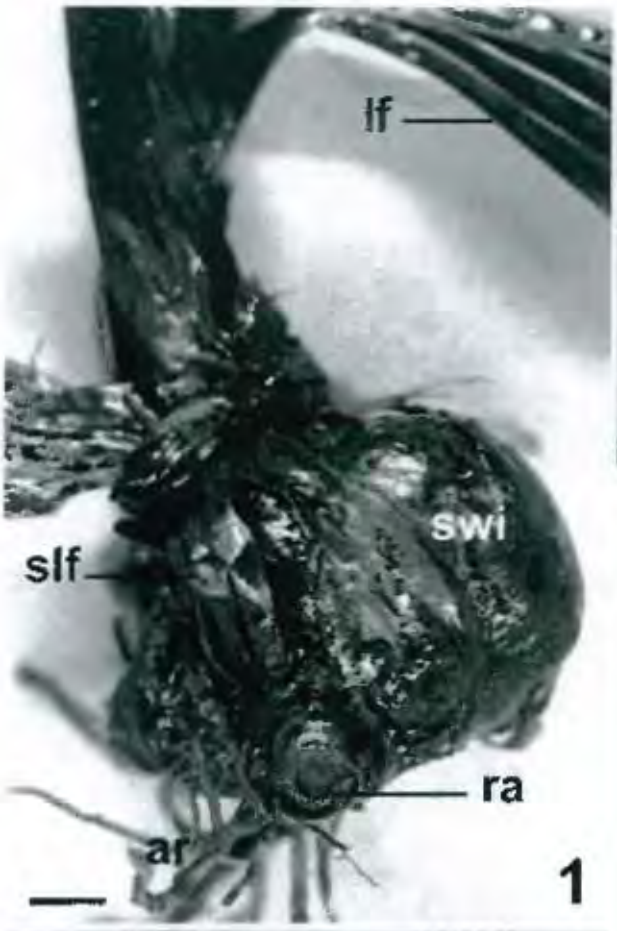
Germination in *W.thysriflora* is hypogeal with the cotyledon forming a partial haustorium (Pl. 18, Fig. 1; Pl. 19, Fig. 1A). The middle part of the cotyledon extends out of the seed coat for some way before fusing into the cotyledonary sheath, which encircles the base of the plumule (Pl. 19, Fig. 1A). In a three week old seedling a short hypocotylar region can be distinguished and roots are developed from the base of this area (Pl. 19, Fig. 1A). There is a single primary leaf at this stage which breaks through the cotyledonary sheath (Pl. 18, Fig. 1; Pl. 19, Fig. 1A). Very few seeds germinated and those that did, died within the first few weeks of germination, so further developmental stages could not be recorded. Seedlings of *W.paniculata* were examined instead, hoping that the developmental sequence of the rhizome morphology could be established (see under *W.paniculata*).

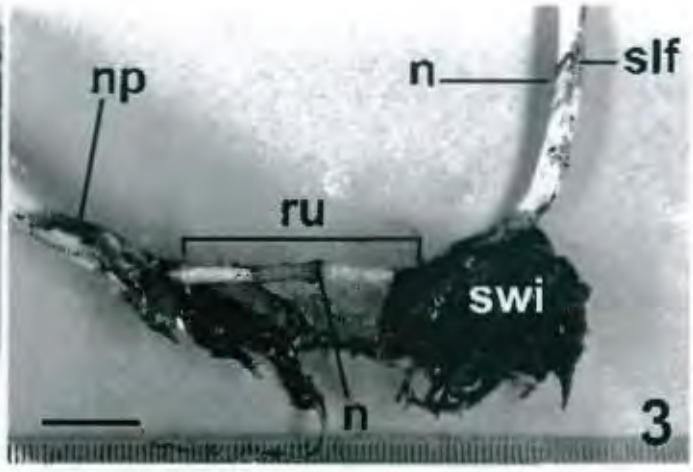
The taxonomy and morphology of the genus *Wachendorfia* has been examined (e.g. Dellert 1933; Helme & Linder 1992). The underground storage structures of *Tribonanthes* have been examined by Pate and Dixon (1982). Cheadle (1968) has documented vessel characteristics in the order Haemodorales.

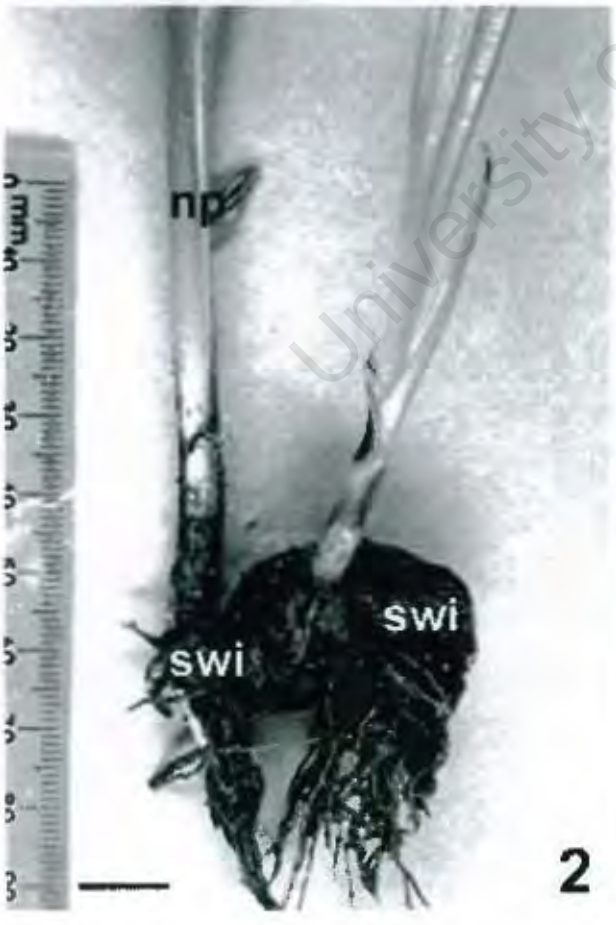
Plate 17. Morphology of *Wachendorfia thyrsiflora*.

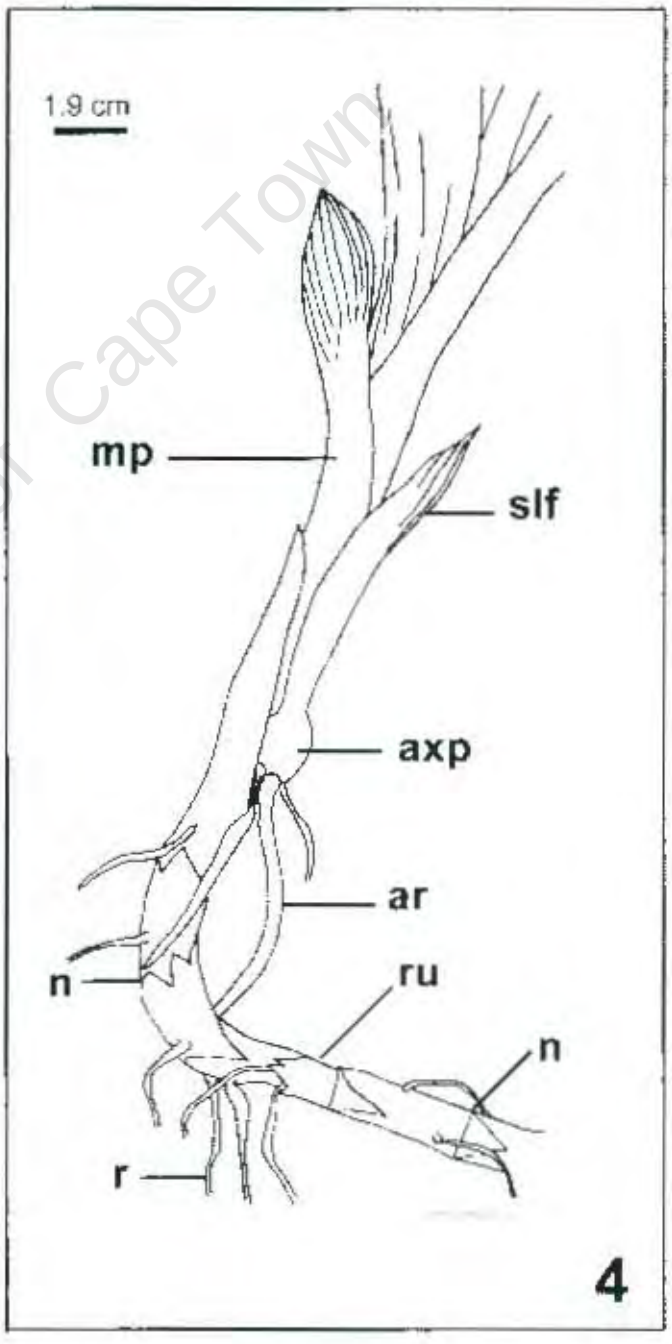
Figure 1. Gross morphology of fleshy underground rhizome consisting of several, swollen internodes (swi) each with a sheathing leaf base (slf). Rhizome giving rise to leaves aerially (lf); and adventitious roots (ar) basally. Axillary buds develop into runners (ra = runner attachment area).
Figure 2. Rhizome with swollen internodes (swi) showing sympodial renewal of swollen internode from axillary bud. (np) = new aerial portion.
Figure 3. Detail of runner morphology showing runner initiation (ru) from axillary bud on swollen rhizome portion (swi). (n) = node; (slf) = sheathing leaf; (np) = new aerial portion.
Figure 4. Plan drawing showing position of axillary bud on runner which ultimately develops into a new plant with swollen rhizome internodes. (mp) = main aerial portion; (axp) = axillary plant; (ar) = adventitious root; (n) = node; (ru) = runner; (r) = root on runner.

[Bars = 9mm (Figs 1-3)**]**.









Anatomy

T/S rhizome

The epidermis consists of brick shaped cells. A cortex is present and is expanded to comprise approximately fifteen cell layers and starch granules are present in the unspecialised parenchyma cells (Pl. 18, Figs. 2. 3). An endodermoid sheath is distinct staining slightly red, but without suberisation (Pl. 18, Figs. 2, 3). The central area is composed of unspecialised parenchyma cells which contain starch granules. The central area contains the vascular tissue which is scattered throughout the area. The vascular bundles have a poorly developed bundle sheath with the xylem arranged predominantly in a u-shaped pattern, but amphivasal vascular bundles are also present.

T/S runner

The runner anatomy and tissue arrangement is essentially the same as that described for the rhizome but with several differences. These occur in the cortex, which is approximately five cell layers in thickness and in the central region in which the vasculature is arranged into distinct regions (Pl. 19, Fig. 2). The outermost ring of the vascular bundles are amphivasal in the central region, while the innermost bundles are of mixed arrangements with the xylem predominantly arranged in a u-shaped pattern with some bundles displaying bi-collateral arrangement too (Pl. 19, Fig. 2). Otherwise all other tissues are similar to those of the rhizome.

T/S inflorescence axis internode

The epidermis is composed of rounded to brick shaped cells as well as unicellular hairs. The epidermal hairs are flanked by four special cells which are adjacent to and surround the hairs. A cuticle is absent. An assimilatory band of a single layer of cells containing chloroplasts is present but tends to merge into a parenchyma band which is composed of two to three layers. The parenchyma band has vascular bundles associated with it on its inner surface. A sclerenchyma band is present and composed of approximately eight cell layers with a few associated vascular bundles. The central area consists of unspecialised parenchyma cells and contains the vascular bundles. The vascular bundles are scattered within the region and the xylem is arranged in a u-shaped pattern.

Plate 18. Morphology of *Wachendorfia* seedlings and rhizome anatomy.

Figure 1. *Wachendorfia thyrsiflora* seedling 4 weeks after germination showing hypogeal germination with middle portion of cotyledon fusing (fr) onto the cotyledonary sheath (s). (p) = plumule; (ar) = adventitious root.

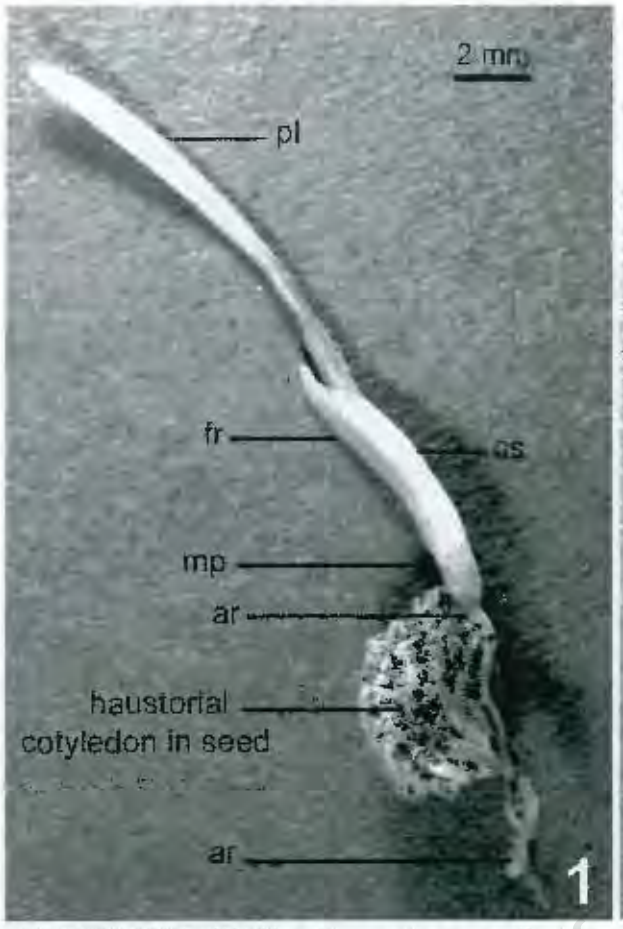
Figure 2. T/S rhizome of *Wachendorfia thyrsiflora* view of mid area. Rhizome layers consist of a cortex (co) and a central parenchyma region (cp) which contains the vascular tissue. The vascular bundles are of two kinds; the outer bundles being amphivasal (a) while the more central bundles have xylem arranged in a u-shape (u).

Figure 3. T/S rhizome view of cortex (co) to show expansion in this region. (es = endodermoid sheath).

Figure 4. *Wachendorfia paniculata* seedling 3 months after germination with extended middle part (mp) of cotyledon trailing from seed and fusing (fr) onto the cotyledonary sheath (cs). A three noded (ni-nili) dropper (dr) has formed which shows slight swelling of the internode. (pl) = plumule; (aep) = aerial portion; (ar) = adventitious roots which form at nodes.

Figure 5. Axillary plantlet of *Wachendorfia thyrsiflora* showing initiation from "resting" swollen internode (swi) of previous season. A swollen internode is developing at the base of the new plant (swi np). (ar) = adventitious root; (lf) = leaf.

[Bars = 31 µm (Figs. 2 & 3)]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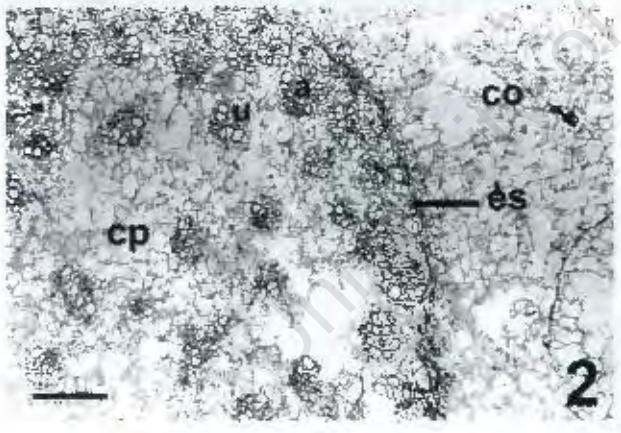
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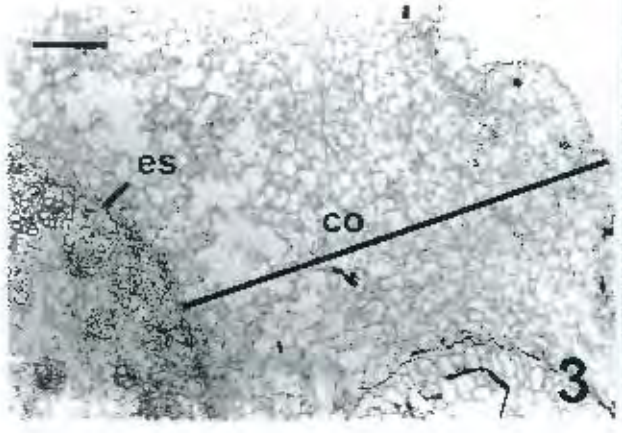
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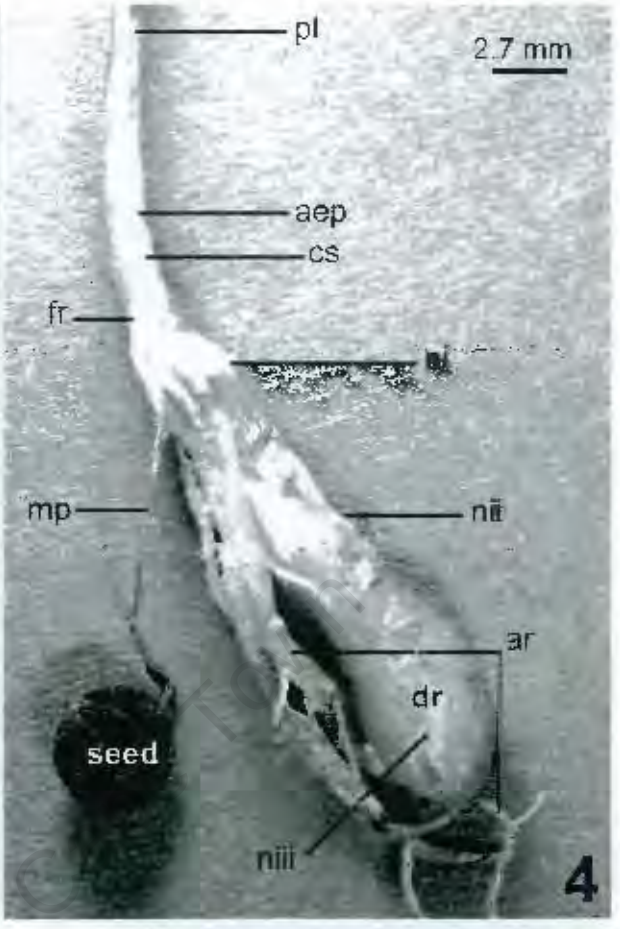
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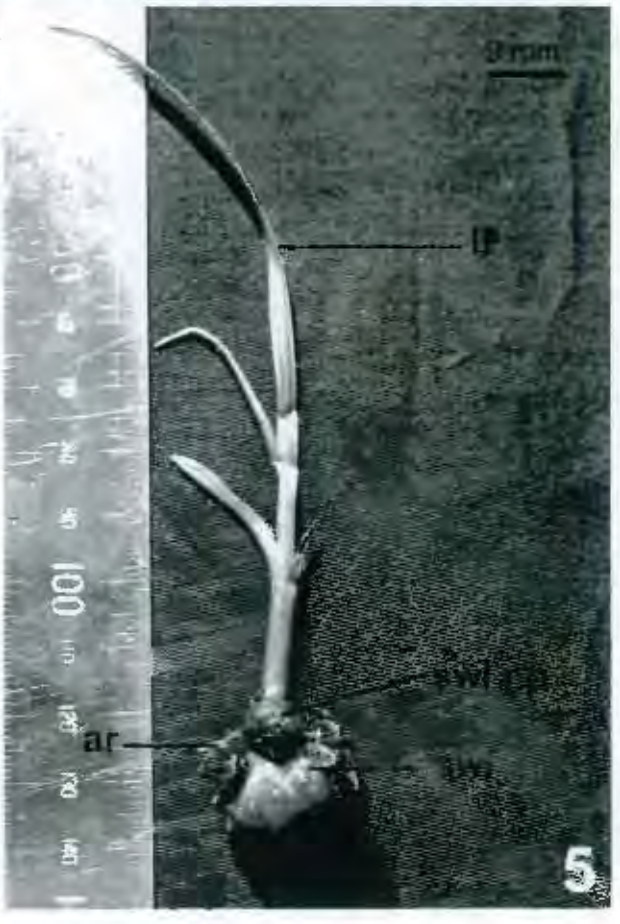
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T/S inflorescence stalk node

The epidermis is composed of brick shaped cells with the outer walls thickened. A cuticle is absent. The parenchyma band is comprised of five cell layers of loosely packed, unspecialised parenchyma cells. The assimilatory band is not present in the nodal area. The sclerenchyma band is composed of cells with thickened walls with pits between the cell walls. The central area is composed of isodiametric parenchyma cells and contains the vascular tissue. The vascular bundles are bi-collateral, but some bundles are elongate with a single, large xylem element and two reduced cavities alongside it. There is a well developed sclerenchyma cap above the phloem pole, otherwise a bundle sheath is lacking and little other sclerification is present.

(Ii) Wachendorfia paniculata

Germination and seedling morphology

Germination of the seeds of *W.paniculata* seemed to require the same stimuli as described for those of *W.thyrsiflora*, only germinating in the second season after sowing. Germination is also hypogeal in *W.paniculata* and in the very early stages of germination the cotyledon is short and is fused to the side of the cotyledonary sheath with the seed displaced laterally and slightly to the base of the seedling (Pl. 19, Fig. 1B). The primary root is produced at the base of a short hypocotylar region and adventitious root primordia develop from this zone too (Pl. 19, Fig. 1B). In the single leaf stage the middle part (sensu Tillich 1995) of the cotyledon is long, very delicate and trailing. This middle part is part of the cotyledon and seems to have a sheath structure around it where it extends up towards the cotyledonary sheath (Pl. 18, Fig. 4; Pl. 19, Fig. 1C, D). The cotyledonary sheath surrounds the seedling and primary leaves break through the sheath. The base of the seedling is a slightly swollen hypocotylar region which gives rise to two to three roots. In this same region is an axillary bud (at the base of the first leaf) which is initiated at the same level as the cotyledon, but is laterally positioned (Pl. 19, Fig. 1D). From here, the development and the seedling morphology of *W.paniculata* is quite different to that described for *W.thyrsiflora* and it is possible that this is due to the slight differences in the subterranean organ morphology between the two species.

Helme & Linder (1992) reported that "new rhizomes" could be produced below the "parent rhizome" in *W.paniculata* and in their Figure 8A of the gross morphology of the subterranean organ, the downward growth of successive internodes of the subterranean organ are clearly visible, before, in the currently growing internode the apex turns upwards and starts growing towards the soil surface. This exact growth pattern is

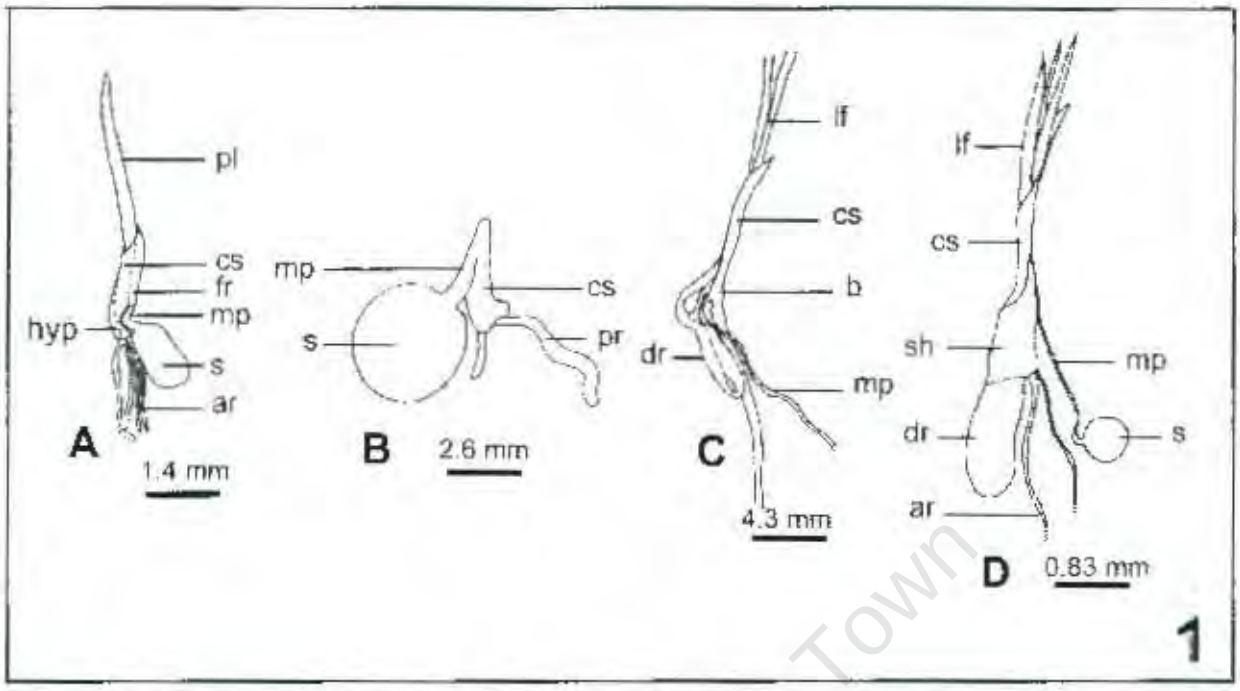
Plate 19. Seedling ontogeny in *Wachendorfia* (Fig. 1); runner anatomy in *Wachendorfia thyrsiflora* (Fig. 2) and morphology and anatomy of *Conostylis prolifera* (Figs. 3& 4).

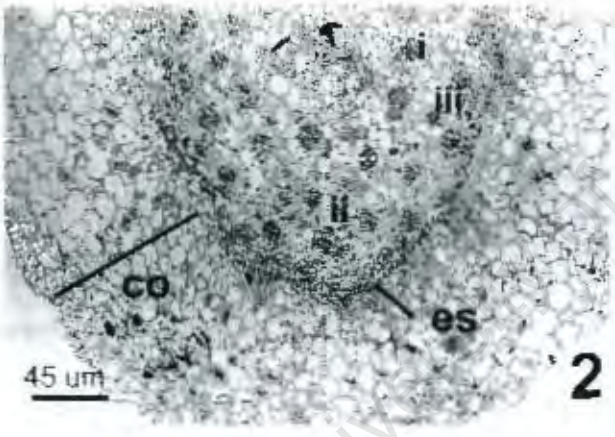
Figure 1. Seedling ontogeny in *Wachendorfia thyrsiflora* (A) and *Wachendorfia paniculata* (B-D). **[A]** 4 week old seedling of *Wachendorfia thyrsiflora* showing middle portion fusing to cotyledonary sheath. **[B]** 2 week old seedling of *Wachendorfia paniculata* showing hypogeal germination and middle portion of cotyledon fused to cotyledonary sheath. **[C]** 4 week old seedling of *Wachendorfia paniculata* showing where the dropper outgrowth occurs from the base of the seedling. **[D]** 3 month old seedling of *Wachendorfia paniculata* with well developed dropper enclosed in sheath at the three leafed stage. (pl) = plumule; (cs) = cotyledonary sheath; (fr) = fusion region; (mp) = middle portion of cotyledon; (s) = seed; (ar) = adventitious root; (pr) = primary root; (dr) = dropper; (sh) = sheath; (lf) = leaf.

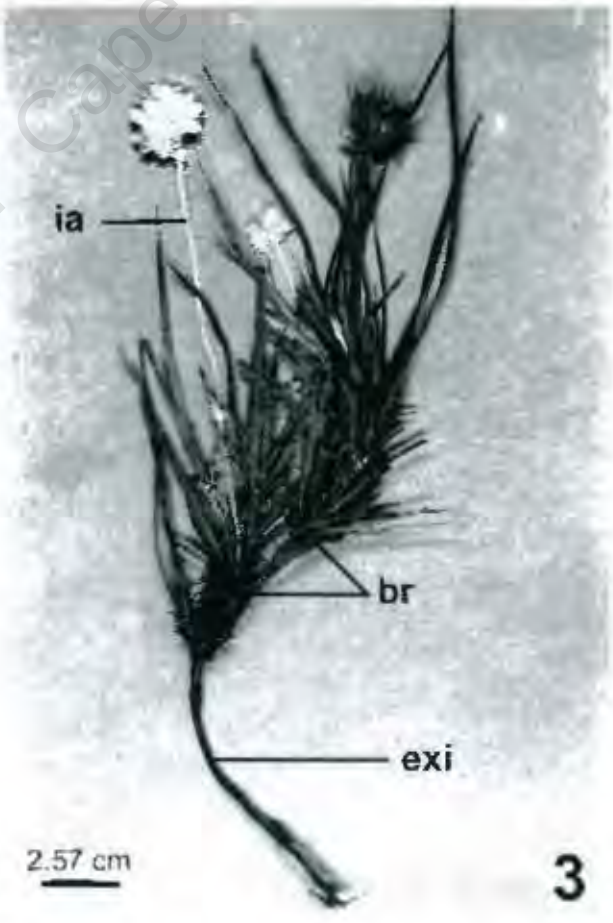
Figure 2. T/S runner of *Wachendorfia thyrsiflora* comprised of a cortex (co); endodermoid sheath (es) and central area which contains the vascular tissue with three kinds of vascular bundles - bi-collateral (i); u-shaped xylem arrangement (ii) and amphivasal (iii).

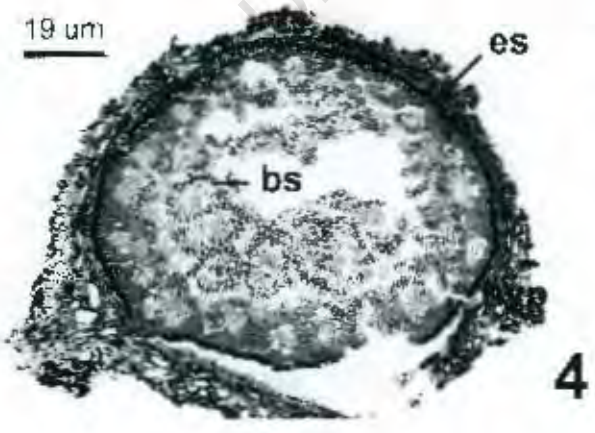
Figure 3. Morphology of *Conostylis prolifera* showing extended rhizome internodes (exi) which branch (br) along their length to form aerial portions with a terminal inflorescence axis (ia).

Figure 4. T/S rhizome/runner of *Conostylis prolifera* showing the several layered hypodermis (hyp), the endodermoid sheath and the vascular bundle distribution in the central area, each vascular bundle being surrounded by a two layered, sclerified bundle sheath.









developed and initiated in the seedling of *W.paniculata*. Each of three internodes is formed by an initial downward growth which is initiated by the development of the laterally placed bud at the base of the plumule. Each time the growth apex is taken to develop slightly deeper in the substrate (Pl. 19, Fig. 1D), until the third internode, where the apical bud turns upwards and grows towards the soil surface where three foliage leaves are visible (Pl. 19, Fig. 1C). All of the downwardly growing internodes in the seedling produce two to three roots at their nodes and the whole "dropper" structure is enclosed by a sheath (Pl. 18, Fig. 4; Pl. 19, Fig. 1D). This formation of three internodes and three leaves is as described for the adult of *W.paniculata* by Helme & Linder (1992) and is thus a fixed pattern which is repeated throughout the life of the plant, each season three internodes develop, produce three leaves and an inflorescence axis terminally, these die back and the fleshy underground internodes are replaced from an axillary bud on the last formed internode, in true sympodial fashion. In *W.thyrsiflora* the elaborate three-noded system is not precisely defined and if the rhizome of a runner offset is examined (Pl. 18, Fig. 5), the swelling at the base of the offset plant would more or less correspond to the hypocotylar region of the seedling and the two (offset and seedling) are almost identical in their morphology.

(iii) Conostylis prolifera

Morphology

Plant rhizomatous, rhizome becoming lignified with age. Internodes of the rhizome are short and ensheathed with scaling rhizome leaves, and the internodes are not fleshy or expanded. The rhizome branches from axillary buds in the axils of the scale leaves along its length and tends to grow upwards as well as laterally towards the soil surface rather than in a strict horizontal fashion (Pl. 19, Fig. 3). Proliferation occurs by the extension of the internodes of the rhizome, which then turn upward at their apex and develop aerial portions. Continuation of growth can be through the development of axillary buds at the basal node of the upright portion of the plant or by the development of the axillary bud of the last formed rhizome portion of the plant. The inflorescences are produced terminally on axes which have elongated internodes, are highly pubescent and have small sheathing scale leaves at the nodes.

Anatomy

T/S rhizome/runner

The exodermis is lignified and becomes bark-like with age consisting of several layers of loosely arranged cells with densely red-staining walls. The hypodermis consists of approximately four cell layers of flattened cells which are stacked closely together. The endodermoid sheath is composed of a single layer of cells only. These cells have concentrically thickened walls which indicate a certain amount of suberisation (staining deep orange) (Pl. 19, Fig. 4). The central area is composed of parenchyma cells with sclerified cell walls and also contains the vascular tissue, which is prolific and the vascular bundles are tightly packed together (Pl. 19, Fig. 4). The vascular bundles are surrounded by a two layered, sclerified bundle sheath. The vascular bundles are amphivasal, but the xylem is arranged in two layers, the outermost layer sclerified.

T/S inflorescence axis internode

The epidermis consists of flattened to brick shaped cells with the outer walls slightly thickened. A thin cuticle is present. Stomata are present and are level with the epidermal cells. A substomatal cavity is also present. Multicellular epidermal hairs are present with small cells closely arranged at the base, and larger elongated cells towards the apex. An assimilatory band is present and is composed of two to three cell layers in which the chloroplasts are densely concentrated and four to five layers in which the chloroplasts are sparsely scattered (possibly equivalent to a parenchyma band). The central region contains the vascular bundles which are arranged in a ring and a central pith area of unspecialised parenchyma cells. The vascular bundles have the xylem arranged in a u-shaped pattern and a slightly sclerified cap above the phloem pole.

T/S inflorescence stalk

The epidermis consists of upright rectangular cells with the upper walls slightly thickened. A thin cuticle is present and stomata are absent. A parenchyma band consisting of four to five cell layers of loosely arranged parenchyma cells is present. Rod-shaped crystals (raphides) are occasional in this area. A sclerenchyma band is present with associated peripheral vascular bundles on the lower region of the band. The cell walls are very thickened and pits are visible between the cells. The central region is composed of parenchyma cells which are of two types, large isodiametric cells and smaller rounded cells concentrated around the former. This region also contains vascular bundles, which

are arranged in a ring. The vascular bundles have the xylem arranged in a v-shaped pattern and are topped by a two layered sclerenchyma cap.

(iv) Anigozanthos manglesii

Morphology

Plants with a subterranean rhizome which displays regular rhizomatous growth and branching, giving rise to an upright inflorescence axis which is formed from the apical bud. Continuation of the rhizome is from an axillary bud just below the basal most internode of the curved portion of the inflorescence axis. The rhizome is ensheathed with scaly leaves and does not appear to be fleshy or swollen in any of the internodal regions. Roots are produced from the nodes of the rhizome.

Anatomy

T/S rhizome

The rhizome is bound by an exodermis which is comprised of loosely arranged cells which are lignified, becoming corky with age and the cellular structure tending to break down. The cortex is expanded and is comprised of approximately fifteen cell layers which are unspecialised and lack any cellular inclusions. The central area contains the vascular tissue which is comprised of two to three layers of bundles arranged in a ring, with a central pith of unspecialised parenchyma cells. The vascular bundles are amphivasal.

T/S inflorescence axis

The epidermis consists of rounded cells arranged together like a string of beads. A cuticle is present. The parenchyma band is approximately two to three cell layers in thickness and is composed of unspecialised parenchyma cells. A sclerenchyma band comprising at least eight cell layers is present with associated peripheral vascular bundles on the inner region of the band. The central region is composed of loosely arranged parenchyma cells which are unspecialised and contains the vasculature which is scattered throughout the region. The vascular bundles have the xylem arranged in a u-shaped pattern and are enclosed by a single layered, unsclerified bundle sheath.

Growth form affinities and differences

Dahlgren et. al (1985) describe the subterranean organs of *Wachendorfia* as tubers. The organs are very similar in morphology and anatomy to the tubers that are described for *Z.aethiopica* and *E.pumilum* (this chapter) except for the growth orientation of the organs

which may be lateral or downward and not upward. The number of internodes involved in organ formation in the previous two taxa cannot always be clearly determined which is often the case in *Wachendorfia*. Anatomically the organs are very similar, with diffuse vasculature in the storage areas of the internodes and more concentrated and distinct vasculature in the current growth areas. Little strengthening tissue differentiation is evident and the main role of the organ is clearly storage and not water transport. The accretion of seasonal fleshy internodes is similar to the renewal of tubers described in *Tribonanthes* by Pate & Dixon (1982), where new tubers form above or laterally to the parent tuber, which then dries out.

The seedling structure of Haemodoraceae is distinct between the two subfamilies (Tillich 1995). The seedlings of Conostyloideae have a long photosynthetic cotyledon, the hypocotyl is either well developed or absent and the roots are white (Tillich 1995). Seedlings of the Haemodoroideae have a haustorial cotyledon and the cotyledonary sheath bears a pair of sheath lobes or one median sheath lobe and the roots are pigmented, red, orange, violet or yellow (Tillich 1995). The latter stages of seedling development i.e. after four to six weeks and up to three months is where the deviations from the basic seedling morphology pattern as described by Tillich (1995), take place in *Wachendorfia* and is likely to be related to the slight differences in the structure of the perennating organs.

The inflorescence axis anatomy in *W.thyrsiflora* is somewhat strange in that the sclerenchyma band is well developed (up to eight cell layers) and that the peripheral vascular system consists of bundles in both the parenchyma band and also associated with the sclerenchyma band. This basic arrangement differs at the nodes, where bundles are collateral and medullary only with a sclerenchyma cap indicating the need for extra strengthening in this region.

The delimitation of Haemodoraceae remains unclear with numerous genera such as *Lanaria* sometimes included in the family. There is also a diversity of growth forms within the family, only the Haemodoreae displaying red pigments in either the roots or underground organs (these can be tubers, rhizomes or bulbs) while the Conostyloideae seem to lack pigment and are often rhizomatous (*Anigozanthos, Conostylis*) or tuberous (*Tribonanthes*). Simpson & Dickison (1981) suggested that the inclusion of *Lophiola* in Haemodoraceae was not compatible with the differences that were observed in the anatomy of organs between *Lachnanthes* and *Lophiola*, particularly in the rhizomes and the leaves.

The scaly sheaths of the rhizomes and the rhizome anatomy of *Conostylis prolifera* are reminiscent of the subterranean rhizomes of Restionaceae and this is possibly related sandy, summer dry habitats. The rhizome appears to be highly strengthened and contains many vascular bundles, suggesting a water transporting role for the rhizome. The suberisation present in the endodermoid sheath may be present to prevent drying out from within the rhizome to the exterior. The aerial portions of *C.prolifera*, such as the leathery bi-facial leaves and the pubescence, are possibly also related to the summer dry condition.

The rhizome anatomy of *Anigozanthos* is more like that of *Wachendorfia* with an expanded cortex. However, the vascular bundles are amphivasal and highly sclerified, which is different to the vascular bundles seen in *W.thyrsiflora* which are not sclerified. The expanded cortex may allow for some storage function in *A.manglesii* but no starch was present in either the cortex or the central pith area of the rhizome. This may be a seasonal feature i.e. starch used for flowering, or may be a general feature of the rhizomes of *A.manglesii*.

Commelinanae: Cannales: Cannaceae: Canna indica

Morphology

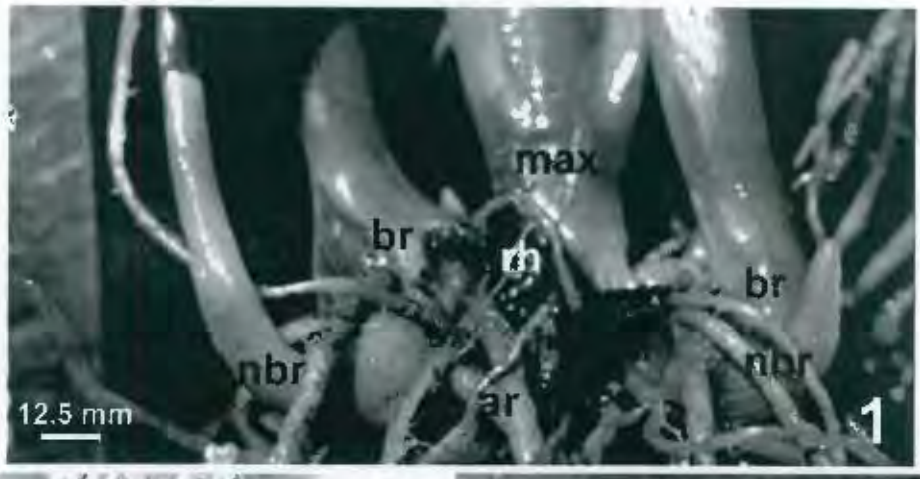
Plants with subterranean rhizome, somewhat fleshy, branching, with the apical portions of each rhizome unit turning upright to form aerial portions (Pl. 20, Fig. 1). Rhizome units developing from axillary buds in the axils of the leaf bases which ensheath the subterranean portions (Pl. 20, Fig. 2). Aerial axes are slender and have elongated internodes which remain ensheathed by the leaf bases in the lower portions, while aerially, the sheathing portion is restricted to the nodes and the lamina is absent. The aerial axes terminate in an inflorescence.

Germination is hypogeal and the seed germinates after four to six weeks and a radicle emerges from the seed coat, initially lateral, but then turning downwards (Pl. 20, Fig. 3). A few days after germination the seedling, has a short middle part of the cotyledon, a cotyledonary sheath with a short hypocotyl at its base and a primary root which is covered in fine root hairs (Pl. 20, Fig., 4A). At one week after germination, the radicle is divided into a collar area plus a lower region (extending radicle) (Pl. 20, Fig. 4A, B). The collar region produces collar roots which grow laterally for several weeks. Towards the apex of the collar there is an short cotyledonary sheath from where the primary leaf erupts, breaking through a small slit (Pl. 20, Fig. 4B). Above the primary root (radicle) and between the cotyledonary sheath a very short hypocotyl can be identified. In

Plate 20. Morphology and anatomy of *Canna indica*.

Figure 1. Morphology of base of plant showing rhizome (rh) with main axis of aerial portions (max) and axillary branches (br) of rhizome with renewal buds developing into new branches (nbr).
Figure 2. L/S through whole plant to show the development of rhizome units from axillary buds (ab) on main rhizome (rh) internode. (n) = node; (max) = main axis of aerial portion.
Figure 3. Seedling a few days after germination showing hypogeal germination. Seedlings have a collar region which produces collar roots (cor) initially. (pr) = primary root; (cs) = cotyledonary sheath; (c) = cotyledon; (ez) = eruption zone where plumule emerges.
Figure 4. Seedling ontogeny in *Canna indica*. **[A]** Seedling a few days after germination showing plumule eruption and collar root formation. **[B]** Seedling one week after germination showing loss of primary root/collar root division. **[C]** Seedling 3 weeks after germination with loss of collar roots and adventitious root and leaf formation. (mp) = middle part of cotyledon; (pl) = plumule; (cs) = cotyledonary sheath; (hyp) = hypocotyl; (pr) = primary root; (ez) = eruption zone; (cor) = collar root; (col) = collar; (lf) = leaf; (ar) = adventitious root.

[Bars = 4.3 mm (Fig. 4)].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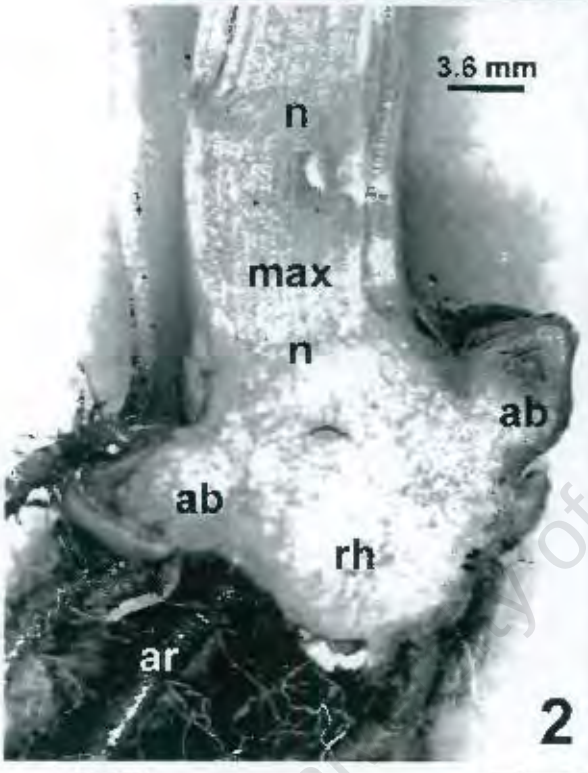
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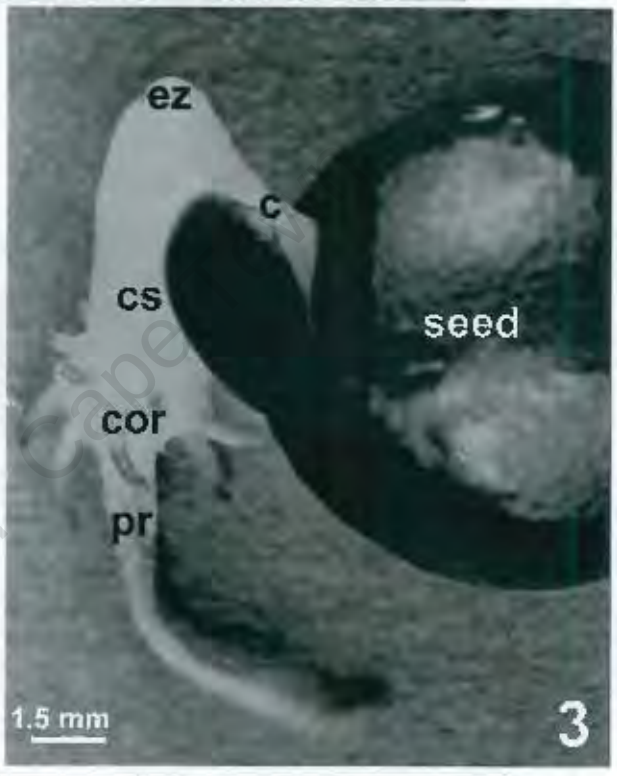
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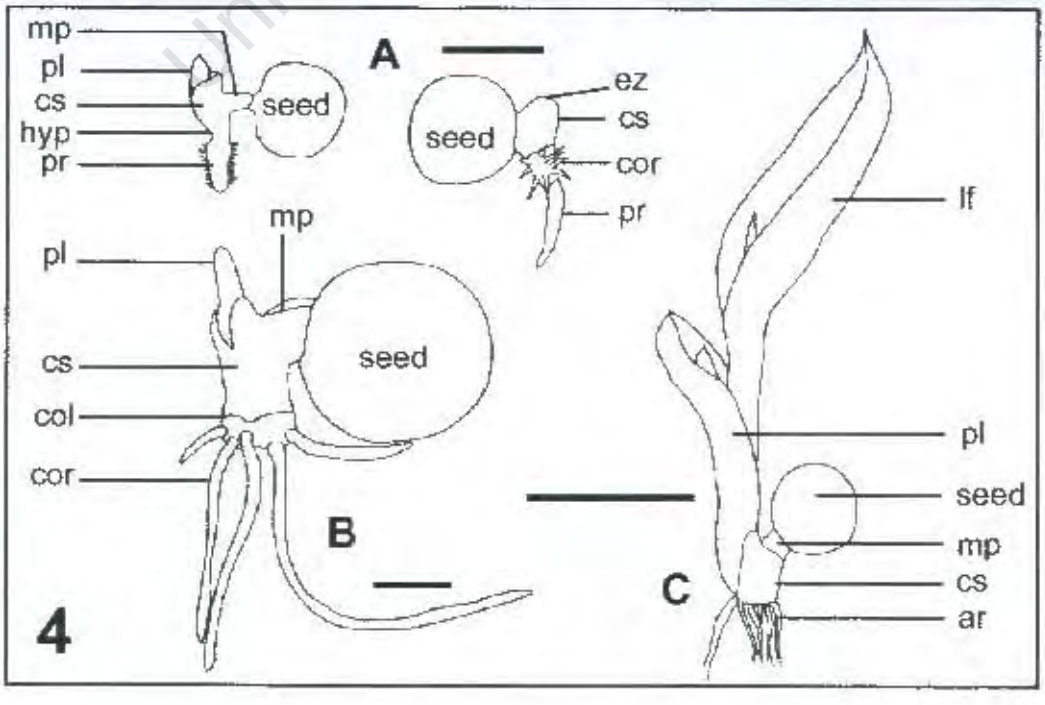
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the second week another leaf is formed and when the seedling is three weeks old, four leaves have already developed and the collar region at the base of the plant has disappeared (Pl. 20, Fig. 4C). Many adventitious roots develop from the base of the plant and the cotyledonary sheath has split and is disintegrating. The seed is still retained at this stage.

The seedling takes approximately three months to produce a rhizome and additional aerial portions. The basal portion of the seedling bears two axillary buds which are located in the axils of the sheathing leaf bases (Pl. 20, Fig. 2). The axillary buds develop into an underground rhizome portion (internode) which grows horizontally for some portion before turning upright and forming an additional aerial portion. Several roots are produced at the base of the current aerial shoot - this suggests that the three month old rhizome consists of several nodes. After six months the aerial shoots terminate in inflorescences which are presented on inflorescence axes. The anatomy of some members of Cannaceae has been described for rhizome and aerial axes (e.g. Solereder & Meyer 1933; Tomlinson 1961b; 1969).

Anatomy

T/S central rhizome

The rhizome bounded by an epidermis with irregularly shaped cells followed by a second layer of slightly dark staining cells which is flimsy and, tends to break down (possibly a hypodermis?). A cortex is present and is composed of approximately ten layers of parenchyma cells which are loosely arranged and contain starch grains. The cortex also contains vascular bundles. The cortex is separated from the central ground parenchyma by a band of cells with thickened cell walls, approximately one to two layers in thickness, but not sclerified. This is described as an indistinct endodermoid layer by Tomlinson (1969). The central ground parenchyma cells are not thickened and are loosely arranged together and tend to break down in the sectioning process. They contain starch granules. The vascular tissue is very poorly developed and only slightly thickened. Each vascular bundle comprises a single xylem cavity with a small phloem cap and lacks a thickened bundle sheath. Some vascular bundles tend to have xylem arranged on the outside - perhaps becoming amphivasal, but this is not clear as the bundles are so poorly developed. Thus, the rhizome would seem to contain a mixture of collateral and amphivasal bundles. Mucilaginous canals are also present in this region.

T/S aerial axis (inflorescence axis)

The epidermis comprises cells which are rounded to brick shaped with the outer walls thickened. There are no tissue specialised regions between the epidermis and the central area which contains the vascular tissue. The central region comprises unspecialised parenchymatous cells. There appear to be developing vascular bundles close to the periphery of the inflorescence axis. These vascular bundles are distinctly collateral, being elongate in shape with a small sclerenchyma cap apically. The central vascular bundles are also collateral in arrangement, but they lack a sclerenchyma cap, and consequently have a small phloem cap at the apex.

T/S inflorescence axis

The tissue plan of the inflorescence stalk is similar to that for the inflorescence axis, but there is a distinct band that separates the epidermis from the central ground parenchyma region. The cell walls are not thickened, but they contain granular inclusions which could possibly be chloroplasts and thus would represent a narrow assimilatory band. The vascular bundle tissue arrangement and distribution pattern is the same as is present in the aerial axis.

T/S inflorescence stalk node

The epidermis consists of brick shaped cells with the outer walls thickened. The following layer comprises a parenchymatous band which is composed of approximately two cell layers of unspecialised parenchyma cells. An assimilatory band is present and comprises rounded cells which contain abundant chloroplasts. The central area is composed of unspecialised parenchyma cells and is generally expanded to occupy most of the inflorescence axis T/S area. The vascular bundles are contained within this area. All of the vascular bundles are collateral with a large sclerenchyma cap which does not stain red. The vascular bundles are scattered throughout the central region.

Growth form affinities and differences

The seedlings of *Canna* are most similar to those of *Strelitzia* where they commonly develop a distinct collar region, which bears collar roots with a single primary root below and a short hypocotyl above before the cotyledonary sheath is borne (Tillich 1995). However, the adult morphology of these two families is vastly different with *Strelitziaceae* displaying dichotomous branching and pleionanthic shoots (Tomlinson 1970a; Fisher

1976). The seedlings of Cannaceae are distinct from the seedlings of Zingiberaceae which do not develop the collar region (Tillich 1995).

The presence of either hapaxanthic or pleonanthic shoots results in a diversity of growth forms as described by Tomlinson (1970a) in the Scitamineae (includes most of the families in Dahlgren et al.'s (1985) Zingiberales). The presence of terminal inflorescences on each vegetative axis is considered by Holttum (1955) to be the primitive condition in Zingiberaceae and appears to be the general condition for Cannaceae. Tomlinson (1973) considered that in the order Scitamineae, the tree like form of *Phenakospermum* with hapaxanthic shoots and production of stoloniferous offsets is possibly the ancestral form in Scitamineae. The basic sympodial rhizomatous growth, often herbaceous, that is present in most of the Scitamineae is derived from this basic arborescent form. Tomlinson suggests that the stoloniferous offset portion of *Phenakospermum* is equivalent to the rhizomatous, fleshy portion of Cannaceae and Zingiberaceae. Pleonanthic shoots, he suggests, are precocious flowering axes e.g. *Strelitzia*. This is a different interpretation to that of Rasmussen (1986) and Anderson et al. (1988) in Orchidaceae where separate flowering axes are interpreted as highly reduced and modified vegetative branches. These two occurrences of pleonanthic shoots may well have different origins if the example of form described by Holttum (1955) for *Hornstedtia grandis* (Zingiberaceae) is considered. In *H.grandis* the rhizome which bears very short pleionanthic shoots, is raised "two to three feet above the ground by stilt roots" seemingly to elevate the inflorescence. Holttum proposed that the stilt roots were a way of raising the inflorescence because the peduncles could not elongate which would be the case if the flowering shoot was precociously developed. Tomlinson's (1970a) proposal is important to consider as Holttum (1955) in his proposal of the sympodial habit, never considered where arborescent forms (except for *Pandanus*) were placed in the variations of the basic theme. However, the idea of an arborescent woody form in ancestral monocots is not supported by current thought in which sister relationships of the monocots are Piperalean, thereby proposing an herbaceous origin. Tomlinson (1970a) proposes that the thickset basal cormous axis, leaf opposed renewal buds and the specialised (false) aerial axis of *Musa* is a specialisation of the sympodial rhizomatous form being quite different to the arborescent form of *Phenakospermum*. Skutch (1932) has suggested that the leaf opposed position is a result of the apical meristem displacing the renewal bud, so that lateral branches are in fact displaced terminal units. With the axillary nature of many vegetative renewal buds in monocots, the displacement to a leaf opposed position in such a manner is difficult to understand. In other monocots which have leaf opposed branches

e.g. *Thalassia* the position is due to a precocial branching process of the apex of the rhizome and subsequent unequal development of the two portions (see Tomlinson 1980).

The poor development of mechanical tissues in the anatomy of Cannaceae is also noted by Tomlinson (1969). The only area where strengthening was apparent is at the nodes in the inflorescence axis. There may be several reasons for this, but possibly the most important one being the rapid growth from seedling to flowering and the short replacement time for each sympodial unit, which leaves little time for strengthening tissues to be laid down and additionally negates the need for such tissues.

Commelinanae: Zingiberales: Zingiberaceae: Zingiber officinale

Morphology

Plant with a subterranean fleshy rhizome with a more or less linear branching pattern. Aerial axes of two kinds, vegetative (hapaxanthic) and reproductive (pleionanthic). Vegetative shoots are closely ensheathed by the distichous leaf bases of laminate leaves and do not terminate in an inflorescence. The reproductive shoots on the other hand are ensheathed by small scaling leaves which arise at the nodes, the internodes are extended and the axis terminates in the inflorescence. Both kinds of shoots die back, but the sympodium with which they are associated remains fleshy and viable. New sympodia are formed from the development of the renewal bud at the subapex of the current rhizome internode.

The morphology of leaf sheaths has been examined in Zingiberaceae (Spearing 1977) and Burtt (1972) provides a review of the information available for Zingiberaceae. Tomlinson (1969) has described the anatomy of the vegetative portion of Zingiberaceae. Bell and Tomlinson (1980) and have examined the architecture in Zingiberaceae rhizomes and Bell (1980a; 1980b) describes the vascular construction of the axial system in some members of Zingiberaceae.

Anatomy

T/S vegetative axis

The basic tissue construction of the axis is very simple. It is bound by an epidermis which is composed of brick-shaped cells. There is no further tissue differentiation, the central region being composed of unspecialised parenchyma cells and also containing the vascular tissue. The vascular bundles are scattered in the central area, they are uni-collateral with a small phloem cap. There is no sclerification of any of the tissues in the axis.

T/S reproductive axis

The diameter of the axis is greater in the reproductive shoot system compared to the vegetative axis, but the tissue arrangement and histology does not vary between the two.

Growth form affinities and differences

The branching pattern in Zingiberaceae is generally either hexagonal or linear and can be attributed to the renewal bud position (paired on lower node of inflorescence axis in hexagonal; single on lower rhizome scale nodes in linear) (Bell & Tomlinson 1980). Bell (1980a; 1980b) has also demonstrated how the vasculature in aerial axes and rhizomes in these branching systems are related and interconnected which in some instances may also be related to the phyllotactic pattern (Bell & Tomlinson 1980). This is important in determining the vegetative survival of the clones within the rhizome system because although aerial shoots can abscise seasonally, or after some years, the sympodial unit can remain healthy and may be viable for up to twelve years and thus, is important in the translocation of substances to the growing portions of the sympodium (Bell 1980b). The rhizomes of Zingiberaceae generally contain abundant starch as the storage substance (Tomlinson 1969). A similar system of continued viability in rhizome sympodia which flowered ten years ago or more, is present in *Maianthemum* (*Smilacina racemosa)* (LaFrankie 1984; 1985; 1986) and some bamboos (McClure 1993).

The puzzling lack of strengthening tissues is again observed in both the vegetative and reproductive axes of *Z.officinale*. In addition to this, the possible support role that the sheathing distichous leaves may serve is purely a physical role, as the leaves and leaf axes do not contain any additional strengthening tissues (see leaf anatomy in Tomlinson 1969). This may also be related to the rapid growth of both axes and the short lived nature of the aerial portions as is the situation in *C.indica*.

Commelinanae: Bromeliales: Bromeliaceae: Billbergia nutans

Morphology

Plants with short vertical rhizomes giving rise to a dense rosette of stiff leaves which are sheathing at their bases. Inflorescences are produced terminally on lax inflorescence axes. Runners are formed from axillary buds on the upper nodes of the rhizome. Runners extend laterally from the parent plant and then turn upright to form new plants. Several runners can be produced from a single parent plant resulting in a cluster of clones. Roots can develop from the nodes of the runner and may also develop from the upper nodes of the rhizome. A L/S of the rhizome shows that the rhizome is divided into a series of

closely spaced internodes at the apex with a vascular system that supplies the dense leaf bases in the region (Pl. 21, Fig. 1). Away from the apex of the rhizome the formation of the axillary root trace system occurs.

The anatomy of Bromeliaceae has been described by Tomlinson (1969). The anatomy of the organs of *Ananas* has been examined in detail by Krauss (1948). Cheadle (1955) has reported on the conducting elements in the xylem of Bromeliaceae. The ecological role of the epidermis in the Tillandsiodeae is discussed by Benzing et al. (1978).

Anatomy

T/S rhizome

The epidermis consists of flattened to brick shaped cells with some sort of suberisation present in the cell walls. The epidermis is lignified, thereby resembling a periderm structurally, rather than a simple epidermis. A hypodermis is present and consists of flattened, brick shaped cells of several layers stacked on top of each other which appear to be suberised. There is no real distinction between a cortex and the central area which contains the vascular tissue. A thin layer of cells forms a ring outside the vascular tissue which is possibly the PTM. Root traces depart from the central area and move towards the exterior through the band which does not contain vascular tissue (cortex). Root bud primordia consistent with an adventitious root system were not observed. The "cortex" band is comprised of approximately ten cell layers of unspecialised parenchyma cells. The central area is composed of large parenchyma cells which lack starch, but are filled with rod-shaped crystals (raphides). The central vascular bundles are enclosed by a two layered bundle sheath and are mostly bi-collateral but several bundles with the xylem arranged in a u-shape are also present.

T/S runner

The epidermis is composed of rounded cells with the inner cell walls thicker than the outer cell walls. A cuticle is absent. The hypodermis is well developed and is composed of several layers of the same flattened cells seen in the rhizome (Pl. 21, Fig. 2). The cortex is composed of loosely arranged unspecialised parenchyma cells (Pl. 21, Fig. 2). Root primordia and vascular tissue are absent from the cortex. An endodermoid sheath is present and is composed of thick-walled cells and also contains vascular bundles. The central area is composed of unspecialised parenchyma cells and contains the bulk of the vascular tissue. The vascular bundles are surrounded by a highly sclerified bundle sheath

of a single layer of cells and are predominantly bi-collateral, but some bundles with the xylem arranged in a u-shape.

T/S basal inflorescence axis

The epidermis is composed of rounded cells which are bead-like in appearance. A cuticle is present. The outer layers of the basal inflorescence axis display tissue infoldings which are v-shaped and appear to be grooves. No associated ducts were evident in the region. A series of sclerenchyma poles are present arranged in a ring in the position of a sclerenchyma band and are associated with a peripheral vascular system, each vascular bundle positioned below a sclerenchyma pole. The central area is composed of unspecialised parenchyma cells and contains the vascular tissue which is scattered throughout. The vascular bundles are enclosed by a two to three layered sclerified bundle sheath. The vascular bundles have the xylem arranged in a v-shape topped by a phloem pole.

T/S lower inflorescence axis

The epidermis is composed of flattened, brick shaped cells. A cuticle is present. A parenchyma band of one to two cell layers is present and is composed of small, rounded cells. The central region is not distinct from the parenchyma band except that the area contains the vascular tissue and the cells are larger and isodiametric. The vascular bundles are enclosed by a two layered bundle sheath and are bi-collateral towards the centre, while towards the exterior they have a u-shaped xylem arrangement.

T/S inflorescence axis

The epidermis is comprised of rounded cells. A cuticle is present. An expanded parenchyma band composed of about eight cell layers of large, isodiametric parenchyma cells is present. A sclerenchyma region of groups of sclerenchyma cells can be distinguished and the area has peripheral vascular bundles. The central area is composed of unspecialised parenchyma cells and contains the vascular tissue. The vascular bundles are of two kinds, they are bi-collateral and also have a v-shaped xylem arrangement and are enclosed by a two layered, sclerified bundle sheath.

T/S inflorescence stalk

The epidermis is composed of flattened, brick shaped cells with a papillate cuticle. Stomata are absent. A parenchyma band is present and contains large parenchyma cells

which are intermittently interspersed between smaller cells. The central area contains the vascular tissue and is composed of parenchyma cells which contain rod-like crystals (raphides) and the bundles are generally arranged in a ring. The vascular bundles have xylem arranged in a u-shaped pattern and are enclosed by a two to three layered bundle sheath.

Growth form affinities and differences

The growth forms observed in the family are diverse, ranging from rosette trees through to moss-like epiphytes (Tomlinson 1969; Dahlgren et al. 1985). *Billbergia* is a terrestrial, medium sized herb and does not display many of the specialised ecological adaptations to water storage that many of the epiphytes do and which have altered their habit (see Tomlinson 1969; Tomlinson 1970a). The vertical arrangement of the rhizome internodes and the orientation of growth is reminiscent of a squat tree-like growth form that is able to produce basal offsets from axillary buds. The morphology of the seedlings of *Prionium* are similar to this growth form (Munro 1995, Munro & Linder 1997).

The development of an inner adventitious root system as described in the axis of the pineapple (Krauss 1948) and for Bromeliaceae in general (Tomlinson 1969) was not observed in the anatomical sections of the rhizome or the runner. This may simply have been the location in the rhizome at which the anatomical sections were observed, or perhaps, the system is not as clearly developed in *Billbergia nutans*. In *Billbergia nutans* a system of vascular traces could be observed supplying the roots of the rhizome in more upper portions of the stem. The formation of intracauline roots also occur in the Velloziaceae (Tomlinson 1969), but were not observed in the stem sections of *Xerophyta*. Functionally, they are probably similar to the roots observed in *Borya nitida* but, are positionally different. The roots in *Borya* seemed to break through the stem tissues and grow through the leaf bases rather than through the stem cortex.

The grooves that were observed in the epidermis of the basal inflorescence axis may be related to an absorption-expansion function. The rounded, thin walled cells that comprise the groove area are similar in their basic structure and arrangement to bulliform cells that occur in the leaves of the Poaceae and Cyperaceae. The poorly developed sclerotic tissues throughout the flowering axis is reported for some members of Bromeliaceae (Tomlinson 1969), but the reduction into small groups of sclerenchyma cells as opposed to the formation of a sclerenchyma band was not observed in any of the other inflorescence axes examined for the sample of monocots in this study.

Commelinanae: Restionales: Restionaceae:

(i) Thamnochortus spicigerus

Morphology

The growth form of *Thamnochortus spicigerus* is rhizomatous. The rhizomes are horizontal, growing underground and interweave with one another, so that the aerial inflorescence axes appear clumped together. Each rhizome gives rise to many inflorescence axes, but only the first four or so inflorescence axes are photosynthetic i.e. green. The remaining inflorescence axes are brown. This suggests that more than a single season's growth is maintained. The internodes on the rhizomes are generally closely spaced, with roots arising from the nodes. The inflorescence axes are formed when the apical bud turns upright and elongates to become aerial (Pl. 21, Fig. 5). The rhizome is able to branch from axillary buds, which in turn, give rise to aerial inflorescence axes from their apical buds. Rhizome branches generally have several buds along their length positioned at the nodes and arising in the axils of the scale leaves. These buds must have the potential to develop into further rhizome branches as they lie in a horizontal direction. This is not the case for the two or three buds which are positioned on the upwardly turning portion between the rhizome axis and aerial inflorescence axis which are orientated aerially (or perpendicular to the rhizome). The very basal area of the inflorescence axes are curved. It is important to note that the rhizome scales (which completely ensheath the rhizome) are very similar in appearance to those which cover the basal portion of the inflorescence axis (i.e. keeled with pitted surface etc.). At the first node of the aerial portion of the inflorescence axis, the node base is slightly constricted, forming a neck-like structure, which gradually widens aerially, until the following node occurs. This neck constriction seems to be repetitive along the inflorescence axis region, right up until the inflorescence. The growth of the inflorescence axis appears to involve successive increase in internode length, until the inflorescence is reached, where internode length decreases again. Aerial buds are lacking on mature vegetative aerial axes.

There is no clear distinction between where rhizome ends and inflorescence axis begins, particularly when the scale leaves are still retained. Obviously the aerial internodes of the inflorescence axis are different, being green and photosynthetic and the scale leaves do not completely ensheath the entire internode, being restricted to the nodal area. The internodes show successive elongation into the aerial portions, which is a result of the internodal meristem. The basal inflorescence axis region consists of very closely spaced internodes and for this reason is difficult to distinguish from the rhizome

(Pl. 21, Fig. 5). It is also curved and is generally not upright (i.e. perpendicular to the rhizome) and is non-photosynthetic. The number of nodes on the basal inflorescence axis varies generally being two to five. The first two nodes of the basal inflorescence axes often have buds. Replacement inflorescence axes may be initiated from these basal inflorescence axis buds if the current inflorescence axes were destroyed. At the growing tip there is a single larger more prominent bud positioned on a node that is probably on the rhizome portion of the plant. This is the renewal bud for the following sympodium (Pl. 21, Fig. 5). It appears as though roots are restricted to developing only from the nodes on the horizontal portion of the rhizome in this species. Root growth from basal inflorescence axis nodes was not observed. In addition, root growth from aerial inflorescence axis nodes never occurs.

The germination in *T.spicigerus* is of type A where the green cotyledon is aerial and the seed is pushed up on this green cotyledon above the soil surface. After three to four weeks the primary leaf is formed and then several others (up to four) are formed in the following two months. When the plant is eight to ten centimetres high a rhizome seems to be present (has scale leaves) and it turns upright to produce the juvenile foliage. The scale leaves are sheathing at the nodes for a while and the new branches form from the basal aggregation of the rhizome base. The growth form does however still seems to be superficially caespitose i.e. the rhizome has not elongated horizontally. The scales in the seedling (i.e. basal scales as well as the leaf scales) are very similar. They differ slightly to the adult scales in that a papery scale is associated with each leaf at each node. Branching of the seedling axis occurs from within this papery scale at the nodes. Thus each new branch is associated with a filmy scale, so, if there are two leaves, there are two filmy scales, one on the outside and the other on the inside. There is also a papery scale in the basal rhizome area, but branching juvenile foliage is produced from these, and they seem to enclose the aerial portions at the base. The pointed apical outgrowth of the seedling leaf has papillae which are evident in very young newly formed leaves. In the older leaves these papillae seem to die back and leave pits (i.e. the surface is pitted). In the rhizome scales, the surface is pitted only in the same apex region. This pitting seems to be followed through to the adult scale leaves and rhizome scales.

Several axes with juvenile foliage are formed in the first year of growth (after six months growth a second aerial shoot is produced). The axes are thin and the internode distance of the basal portions of the plant are short. The first year's growth is retained. In the following season, two to three upright axes are formed. These have a large diameter and also show a greater degree of elongation of the aerial internodes. The axes still retain

juvenile foliage. The internodal distance of the basal portions of the plant is greater so that the aerial axes arise some distance apart from each other. Both the first and second season's growth are retained. In the third year of growth, two to three axes are formed again (Pl. 21, Figs. 3, 4). The upright axes are developed by a considerable increase of internodal distance of the basal portions. The axes are stout, compared to the previous season's growth accumulation and the internodes elongate so that the juvenile foliage is restricted to the nodes of the axis. The aerial axes after three years of growth are equivalent to the inflorescence axes seen in mature plants.

The anatomy of the inflorescence axes in Restionaceae have been extensively described by Cutler (1969). Tomlinson (1973) examined bud positions in some members of Restionaceae. The morphology of *Alexgeorgea* is described by Carlquist (1976) and Meney et al. 1990a.

Anatomy

T/S main axis of seedling

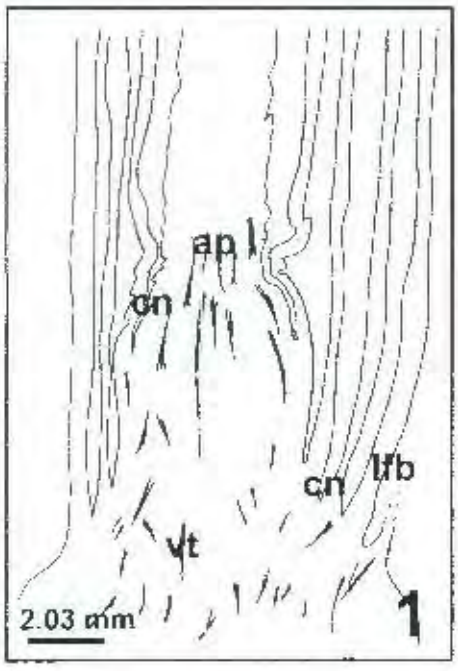
The epidermis consists of a single layer of rectangular cells with a thickened outer wall. A very thick cuticle is present. Stomata with an associated substomatal cavity are present. The chlorenchyma consists of elongate cells and is composed of two cell layers (Pl. 22, Fig. 1). The parenchyma sheath consists of one to two cell layers and is composed of large isodiametric parenchyma. The central region is comprised of unspecialised parenchyma cells and contains the vascular tissue which is arranged in a ring (Pl. 22, Fig. 1). The vascular bundles have the xylem arranged in a u-shape. Tannin is present in the parenchyma band and the epidermis.

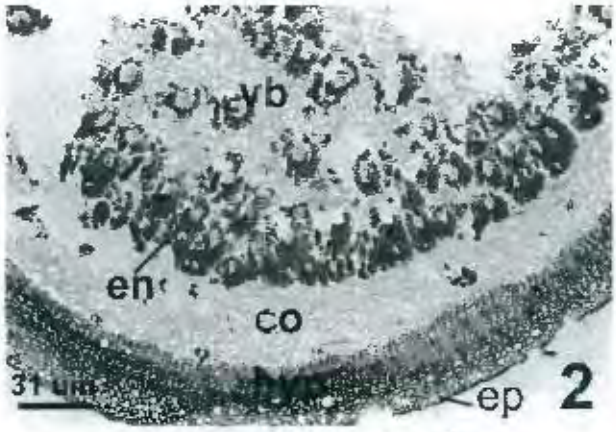
T/S rhizome (internodal area between two upright axes)

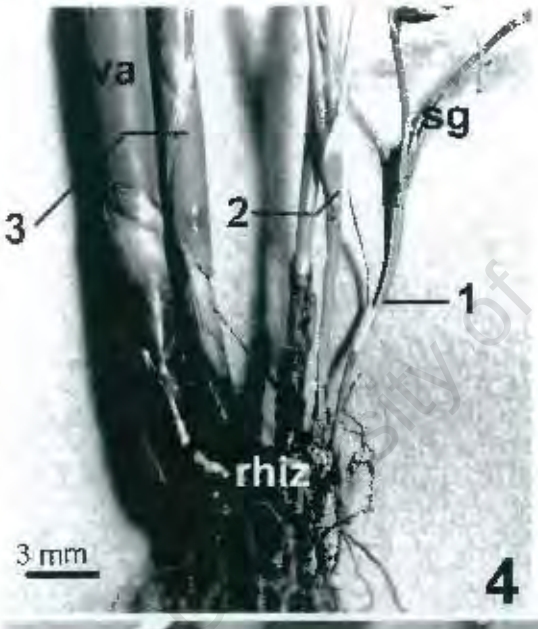
The epidermis consists of one to two layers of loosely arranged cells. The hypodermis is comprised of approximately ten cell layers of cells which have evenly and extensively thickened walls which stain a russet-orange in colour indicating the suberised nature of the walls. The cortex can be divided up into three regions. The upper area consists of two layers of small, closely arranged cells. The middle region is composed of large, isodiametric, loosely arranged cells and is two cell layers in thickness. The lower region is composed of small, blue staining cells approximately two cell layers in thickness and is possibly a PTM. The endodermoid sheath is bound to the exterior by a layer of suberised cells (staining orange). The sheath consists of four to six layers of cells with very thickened cell walls which are thickened in a concentric layering. Small vascular bundles

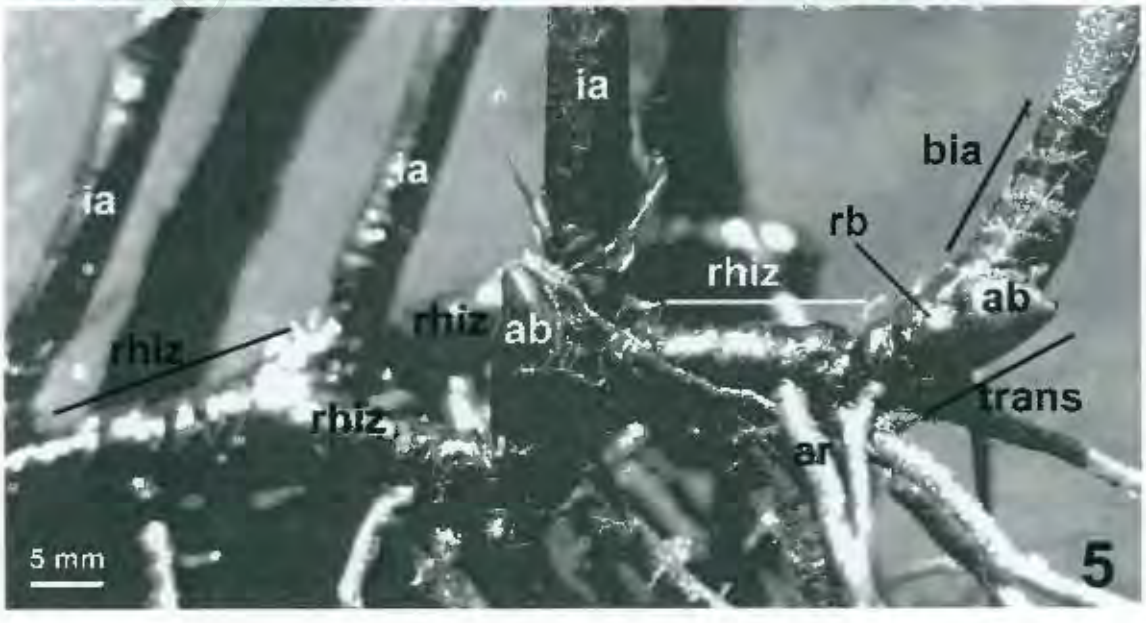
Plate 21. Anatomy of *Billbergia nutans* (Figs. 1 & 2) and morphology of *Thamnochortus spicigerus* (Figs. 3-5).

Figure 1. L/S rhizome apex of *Billbergia nutans* showing several, closely spaced nodes at the apex and the vascular system (vt) which supplies the leaf bases (lfb) associated with the apex (ap).
Figure 2. T/S runner of *Billbergia nutans* showing a well developed hypodermis (hyp) with a cortex (co) beneath and an endodermoid sheath (es) with associated vascular bundles surrounding the central area. The vascular bundles (vb) are surrounded by a sclerified sheath.
Figure 3. Morphology of *Thamnochortus spicigerus* 3 years after germination showing the underground rhizome (rhiz) which produces "seedling growth" aerially in the first two years (sg; 1 & 2) and elongated internodes comprising axes in the third year of growth (va; 3). (ar) = adventitious roots.
Figure 4. Detail of base morphology of 3 year old plant of *Thamnochortus spicigerus* showing rhizome (rhiz), three years of growth (1-3) and the difference in seedling (sg) versus mature, vertical growth (va).
Figure 5. Rhizome morphology of *Thamnochortus spicigerus* showing axillary bud position (ab), reserve bud position (rb) and detail of the transition (trans) from rhizome to basal inflorescence axis (bia). (ar) = adventitious roots; (ia) = inflorescence axis.









develop in the endodermoid sheath. The central area contains the vascular tissue which is distributed in a negligible amount of ground parenchyma tissue (Pl. 22, Fig. 2). The vascular bundles are surrounded by thick bundle sheaths which are so closely spaced, that the ground parenchyma is greatly reduced. The larger vascular bundles are found towards centre and smaller vascular bundles towards exterior. There are two kinds of vascular bundles in the central area of the rhizome. The first are amphivasal, where the xylem vessels are all approximately the same size and they completely surround the phloem. The others have the xylem arranged in a u-shaped xylem arc where the vessels are of unequal size and the xylem does not entirely surround the phloem. The vascular bundle sheaths are two to three layers in thickness (Pl. 22, Fig. 2).

T/S rhizome (nodal area where roots arise)

The same basic plan with all layers between two axes (internode) approximately the same as for the rhizome region, except that the central ground tissue is slightly more expansive, but still appearing strand-like. The roots are formed in the PTM just outside the endodermoid sheath which surrounds the central area. The PTM is also continuous around the root, as is the endodermis, until the root breaks through the cortex and outer layers of the rhizome. The endodermoid sheath and PTM merge into the endodermis and the cortex of the root. The roots also break through the rhizome scale leaves to reach the exterior.

T/S rhizome/inflorescence axis base turning upright, no roots, scale leaves removed for sectioning

The general tissue plan is as for the rhizome internode region but with several differences (Pl. 22, Fig. 3). This area differs in having several different types of vascular bundles in the central area. The vascular bundles vary from amphivasal, to xylem arranged in a u-shaped arc and also with the xylem arranged in a v-shaped arc (weakly). In addition, the vascular bundles anastomose to a great extent in this particular organ portion. The vascular bundles appear to be in several different planes and extend outwards in different directions.

T/S constricted region of inflorescence axis base where it grows out of rhizome (base of inflorescence axis)

The overall tissue plan changes in this region, most of the cells having some sort of thickening. The sclerenchyma in the sections from this area stains dark orange. The diameter of the sections have decreased, because the inflorescence axis is very narrow (neck region). The epidermis is composed of a single layer, but the layer immediately below this is similar in structure too. Both layers have cells with very thickened cell walls (this could be an epidermis with a merging hypodermis). The following region is composed of two to three cell layers of loosely arranged parenchyma cells, which are thin walled and tend to break down (probably a cortex). The following layer is composed of two to three layers of small, rounded cells which stain bright blue (possibly a PTM). A greatly expanded sclerified sheath greater than ten cell layers in thickness surrounds the central area. The sheath contains developing vascular bundles which are found in the outer layer only and are arranged in a ring. The sheath also lacks suberisation. The parenchyma tissue of the central area is reduced in the area that it occupies, most of the central area is taken up by the vascular bundles. The vascular bundles in the central area are bi-collateral and are enclosed by a two to three layered bundle sheath.

T/S lower inflorescence axis internode (aerial portion)

The epidermis is composed of a single layer. Stomata are present. A chlorenchyma band consisting of two layers is present with associated substomatal spaces. A parenchyma sheath composed of two to three cell layers of unspecialised parenchyma cells is present. The sclerenchyma sheath consists of approximately seven cell layers and contains one row of developing vascular bundles. The central area consists of loosely arranged, isodiametric parenchyma cells and contains the vascular tissue which is "scattered" throughout the area. The vascular bundles in the central area are bi-collateral and are enclosed by a one to two layered bundle sheath.

T/S lower region of aerial inflorescence axis (node)

The epidermis consists of a single layer of brick-shaped cells. Stomata are present. The assimilatory band is composed of elongated cells with thickened walls and a number of air spaces between groups of cells (possibly the remains of the substomatal cavities). The sclerenchyma sheath is composed of two to three cell layers and contains regularly spaced, developing vascular bundles. The central area is composed of a small amount of parenchyma tissue, the area being predominantly occupied by the vascular tissue as the

bundle sheaths of the vascular bundles are very closely arranged together. The vascular bundles also anastomose in this region with many vascular traces moving from the centre towards the exterior. The vascular bundles are of three kinds in the central area. The majority of the vascular bundles are bi-collateral, a few have u-shaped xylem, while some are amphivasal. The vascular bundles are enclosed by a single layered bundle sheath which contains red staining material (tannin) which is concentrically and regularly arranged within the cells.

T/S aerial inflorescence axis (internode)

The epidermis comprises a single layer of upright rectangular cells with the outer walls thickened and the lateral walls convoluted. Stomata are present, the guard cells staining pink, while the subsidiary cells stain blue. The substomatal cavity continues from the epidermis externally through to the first layer of the chlorenchyma, the cells below which stain pink and lack chloroplasts. The assimilatory band is composed of two cell layers of vertically elongated cells which are stacked on top of one another, both layers containing densely concentrated chloroplasts (Pl. 22, Fig. 4). The parenchyma sheath is composed of approximately three cell layers of large rounded cells, which contain red-staining globular inclusions visible with DIC only (Pl. 22, Fig. 4). The sclerenchyma sheath is composed of six to ten layers of cells with thickened cell walls and contains developing vascular bundles toward the exterior. The central region is composed of loosely arranged, isodiametric parenchyma cells, many of which contain tannin and some sparse globular inclusions. The vascular tissue is "scattered" within the central area (Pl. 22, Fig. 4). The vascular bundles in the central region are bi-collateral, with a single layered, thickened bundle sheath.

T/S aerial inflorescence axis (node)

The epidermis is composed of a single layer of brick shaped cells with the inner walls slightly convoluted. Stomata are present, but substomatal cavities are absent. The following layer is a parenchyma sheath consisting of two to three cell layers and composed of cells with concentrically thickened cell walls (Pl. 22, Fig. 5). The sclerenchyma sheath is comprised of approximately ten layers of cells with concentrically thickened cell walls. Air spaces are present in the sheath and alternate with developing vascular bundles (which occur at a slightly lower level than the air spaces) which are enclosed by a two-layered bundle sheath (Pl. 22, Fig. 5). The central region contains very little parenchyma tissue, most of the area is composed of vascular bundles which have

thickened bundle sheaths. The central zone of the region contains vascular bundles which are transverse in outline. The bundles change their orientation to longitudinal toward the exterior, so that approximately twenty traces move outwards to the node. The vascular bundles are bi-collateral with metaxylem vessels well developed. The protoxylem is grouped below the metaxylem, but lacunae are not developed. The vascular bundles are enclosed by a bundle sheath composed of cells with concentrically thickened cell walls.

T/S inflorescence axis (second last internode before inflorescence stalk)

The epidermis comprises a single layer of upright rectangular cells with the outer walls thickened and the lateral walls convoluted. Substomatal cavities are present and extend into the second layer of the chlorenchyma band. The chlorenchyma band is composed of two cell layers. The parenchyma sheath is composed of two to four cell layers of rounded cells which contain tannin. The sclerenchyma sheath comprises approximately six cell layers of cells with thickened walls and contains developing vascular bundles in the upper part of the sheath. Tannin is present in the sclerenchyma cells. The central region consists of isodiametric, closely arranged parenchyma cells which contain a large amount of tannin. The vascular bundles are spread out within the central area and are bi-collateral.

T/S inflorescence stalk

The epidermis consists of one layer of cells with all walls equally thickened. The assimilatory band appears to be broken down, consisting of loosely arranged isodiametric cells about two cell layers in thickness (Pl. 22, Fig. 6). The parenchyma sheath is composed of two layers of cells with thickened walls. The sclerenchyma sheath comprises ten to twelve layers of cells with concentrically thickened cell walls and contains developing vascular bundles which are arranged into two rings and are enclosed by a two-layered bundle sheath. Between each of these vascular bundles is a clump of cells which contain tannin and have more thickened walls than the other sclerenchyma cells. The central region consists of closely arranged vascular bundles with parenchyma tissue in between (Pl. 22, Fig. 6). The parenchyma cells of the central area have slightly thickened cell walls with pits evident and contain tannin. The vascular bundles are bi-collateral and are enclosed by a two to three layered bundle sheath.

T/S inflorescence stalk node

The epidermis of the inflorescence stalk is the same as that for the internode, except that the substomatal cavities are shallow, only touching the upper cells of the first layer of chlorenchyma. The chlorenchyma stains deep red-purple and consists of two cell layers. The chloroplasts are still visible, but the second layer tends to break down and forms large air spaces, which are more apparent closer to the branching zone. The parenchyma sheath is composed of three cell layers of cells with thickened walls and which are filled with tannin. The sclerenchyma sheath consists of cells with concentrically thickened cell walls with pits visible and contains developing vascular bundles which are arranged in both an upper and an inner ring. The cells contain abundant tannin. The central area consists of large parenchyma cells which contain a large amount of tannin and are generally red staining. The vascular bundles are evenly distributed throughout the central area but tend to anastomose. The vascular bundles are bi-collateral, with the xylem arranged in a u-shaped arc and are enclosed by a two layered bundle sheath of tannin filled cells with concentrically thickened walls.

T/S flower stalk

The epidermis consists of vertical, rectangular cells with a thickened outer wall. A cuticle is present. Stomata are present with a small substomatal cavity which extends to the first layer of cells beneath the epidermis. The parenchyma sheath is composed of five to six cell layers and contains air spaces (Pl. 22, Fig. 7). The sclerenchyma sheath consists of five to six cell layers which contains a ring of smaller vascular bundles in the outer layer (Pl. 22, Fig. 7). The central area is composed of large, isodiametric cells and contains the vascular bundles, which are dispersed throughout the tissue (Pl. 22, Fig. 7). The vascular bundles in the central region are bi-collateral and are enclosed by a two layered bundle sheath. Tannin is present in the cells of the parenchyma sheath, the sclerenchyma sheath and the central ground tissue.

Growth form affinities and differences

The gross morphology of *Thamnochortus spicigerus* is characteristic of the basic plan of Restionaceae. Plants are often (subterranean) rhizomatous, sympodially branching and producing aerial, photosynthetic inflorescence axes (which may or may not branch) that are terminated by an inflorescence. The location of buds is variable in Restionaceae as a whole, with some being restricted to the basal portions of the aerial axes and generally suppressed, while others are aerial and can proliferate to produce many branched axes

either vegetative or reproductive (e.g. *Elegia capensis)*. These buds are always axillary. The rhizomes generally have a renewal bud located just below the upwardly turning portion of the most recent aerial inflorescence axis, as well as axillary buds along the rhizome nodes, which results in rhizome branching. Tomlinson (1973) and Fisher (1978) reported that the rhizomes of some Restionaceae (e.g. *Leptocarpus*) have leaf opposed buds, similar in position to the buds of the Musaceae and *Thalassia*. Leaf opposed buds may be a specialised feature of certain kinds of rhizomes in Restionaceae (see later), with the more general condition being the presence of axillary buds. The inflorescence axis anatomy varies extensively among species and genera, and is used as a taxonomic delimiter. However, the basic tissue plan is thought to be a response to xeric conditions (Cutler 1969). The formation of a juvenile phase following germination seems to be a general feature in Restionaceae, with most taxa displaying the juvenile foliage in the first three years of life before stout aerial inflorescence axes and rhizome axes are further developed.

The similarity in rhizomatous growth form is superficial to other regular rhizomatous growth forms in monocots i.e. sympodially branching and renewed subterranean rhizome which turns upright and produces aerial axes which terminate in an inflorescence. But the similarity ends there. The growth form of Restionaceae plants may reflect an adaptation to xeric summer conditions. Features associated with these possible adaptations can be observed in the growth form of *T.spicigerus* and others (see later).

Firstly, the juvenile phase persists for the first three years of life before any axes undertake the function of flowering. This developmental phase needs to be carefully evaluated on a physiological basis, but the branched and "leafy" axes may be a way of maximising photosynthate gain in the juvenile years. Similarly, an ecological competition assessment may also be important. Following germination, at least for the first two years of growth, the degree of competition between other plants is limited and the need for tallness is not required until the surrounding Fynbos vegetation starts to dominate, this is when the aerial single (in this case) inflorescence axis phase is initiated. In the juvenile phase, all the growth seems to be focused at the level of the rhizome. This may be to increase the size of the rhizome diameter and the length of the internodes so that following juvenile development, stout aerial inflorescence axes can be produced. If this situation is compared to the rhizomatous form of *Canna* in which the germination to flowering phase is a short six months, the extended juvenile phase in *T.spicigerus* is emphasised. The growth forms are not ostensibly different on the basis of the rhizome branching system (bearing in mind the specialised inflorescence axes of Restionaceae vs.

the supporting leaf sheaths of the *Canna* form). However, in the juvenile phase of the seedlings of *T.spicigerus* there must be time to accumulate strengthening tissue. This is noticeable in all organ portions of the plant as well as in the vascular system, seen as elaborate bundle sheaths. The slow growth in the juvenile phase is undoubtedly related to the nutrient status and environmental conditions of the habitat with pronounced seasonality, but the need for a structural rhizome to inflorescence axis system is also important for water transport and height in order for the plants to compete successfully in the Fynbos vegetation. Following this establishment phase, growth seems to accelerate with the axes elongating substantially and ultimately forming inflorescences. The need for an establishment phase is highlighted in the woody growth forms of monocots described by Tomlinson (1961a; 1970a; 1990) and Tomlinson & Esler (1973) and seems to be related to the structural constraints of the particular growth forms in the adult phase.

Secondly, the inflorescence axes are highly specialised. These aerial axes are the sole photosynthetic organs, as no laminate leaves or green scale leaves are formed, as is found in other monocots which produce upright axes that terminate in an inflorescence. The inflorescence axes also vary in morphology and anatomy from the base to tip, which is possibly related to different functions. The growth form of *T.spicigerus* is related to the life cycle and habitat of the plant and possibly to mechanical and/or physical constraints. The presence of basal cauline innovation buds suggests the possibility that, in addition to the subterranean reserve/renewal buds on the rhizome, that the plant is able to resprout. The inflorescence axes are retained on the plant for several seasons, and actively photosynthesise (Van der Heyden & Lewis 1989). This is a slightly different situation to that found in *Maianthemum* and some bamboos, where the inflorescence axes are retained for several years (McClure 1993; LaFrankie 1984; 1985; 1986) in relation to tropical habitats. The retention of inflorescence axes in Restionaceae is thought to be due to the low nutrient status of the soil (Stock et al. 1987; Meney et al. 1990b). Thus, the physiological functioning of the inflorescence axes of *T.spicigerus* precludes the inclusion of this kind of growth form into the regular rhizomatous model, where inflorescence axes are produced and live for a single season only (sensu Holttum 1955). In addition to the physiological constraints, the effect of fire influences the production of aerial axes too. Resprouting after fire in *Thamnochortus* usually results in juvenile foliage being produced again, with single, stout inflorescence axes produced in the season following fire. The formation of juvenile foliage has also been observed to develop from the nodes in the year after flowering in *Thamnochortus* (Linder 1991).

Thirdly, the rhizomes are specialised for water transport and structural support. The central cylinder of rhizome seems to be structured for water transport only as there are no storage materials and all available space is filled with vascular bundles. Linked to this is a seasonal photosynthetic rate, and high transpiration rates in some species with rapid use of available water and uptake of nutrients in the moist winter season (Stock et al. 1987; Van der Heyden & Lewis 1989). The rhizome also has a large amount of strengthening tissue. This would suggest that the main roles of the rhizome are water transport (in large quantities) and structural support for the aerial portions of the plant. This phenomenon may be related to wet winters and very dry summers where, the growth season occurs towards the end of winter when water is available. In *Alexgeorgea* rhizome extension and the production of new inflorescence axes is initiated with the onset of rain, growth rate of these parts is slow in winter, peaks in spring and then tapers off in the hot summer period (Meney et al. 1990b). The presence of globular substances which may be proteinaceous in aerial axes suggests an aerial accumulation of storage materials. It is thought that nutrients (Nitrogen in particular) are translocated from older inflorescence axes with onset of growth season to the actively growing zones (Stock et al. 1987; Meney et al. 1990b).

There are small variations in tissue arrangement/modification, the degree of sclerification and in the kinds of vascular bundles from the base (rhizome) to the tip (inflorescence stalk) of a single plant e.g. *Thamnochortus spicigerus*. There is a large amount of variation in orientation, bud location and function of differing plant portions. The areas which show peculiar anatomical features are the upward turning area between the rhizome and the aerial inflorescence axes. In this region several different kinds of vascular bundles are found. This may be interpreted as a transition between one organ and another (if each can be recognised by a certain kind of vascular bundle), or it may be a situation where vascular bundle ontogeny is taking place and new directions in the vascular components result in a change in the orientation of the xylem and phloem poles. Little examination of the changes that occur in the kinds of vascular bundles has taken place in monocots, although Skutch (1932) and Cheadle & Uhl (1948) have noted that there are intermediate stages between amphivasal and collateral bundles at different levels of the plant. Most of the focus has been related to the vascular construction of monocot stems in terms of a continuous axis and how branching is effected (Bell 1980a, 1980b; French & Tomlinson 1980; Krauss 1948; Kumazawa 1961; LaFrankie 1985; Tomlinson 1970a, 1984b, 1990; Tomlinson & Zimmermann 1969; Zimmermann & Tomlinson 1968, 1972). Exactly why the pattern of xylem and phloem construction

changes through the course of vascularisation is not clearly understood, but must be related to the developmental pattern of vascular bundles (see Tomlinson & Vincent 1984), their orientation and branching of the vascular system from the central cylinder to other organs. Although the control of primary vascular differentiation by the apical meristem release of auxin is well described in plants in general, the precise pattern-forming role of this system and stelar architecture is not well understood (Stern 1993). The change of stelar architecture from root to aerial portions within single plants has been documented over the years and while these changes remain enigmatic, so too does the change in structure of the vascular bundles from organ to organ in higher plants.

*(ii) **Thamnochortus lucens***

Morphology

The plants form a closely arranged tuft. They are rhizomatous and produce aerial photosynthetic inflorescence axes which terminate in an inflorescence. Roots are produced from the lower portions of the rhizome nodes. The rhizomes are upright, aerial and short (composed of up to five internodes) and the internodes are ensheathed by brown scale leaves. Axillary buds are present in the axils of the scale leaves on the nodes of the upright internodes (Pl. 23, Fig. 1). The basal area of the inflorescence axes extends directly from the upright rhizome area. These internodes are extended, lack axillary buds and have scale leaves confined to the nodes. The rhizome renewal bud is found on the third or fourth highest node of the upright rhizome portion and when initiated, grows slightly laterally for two short internodes and then commences vertical growth, finally terminating in the aerial axial portion (Pl. 23, Fig. 1).

Anatomy

T/S base (upright rhizome portion)

The epidermis is composed of brick shaped cells with the outer wall thickened. A hypodermis is present and is composed of two to three layers of brown staining cells which are loosely arranged. The cortex is reduced and consists of two cell layers of rounded blue staining cells. One of the layers could be a PTM. The endodermoid sheath consists of approximately four cell layers and surrounds the central area which is functionally a vascular cylinder. The central area ground tissue consists of a few unspecialised parenchyma cells and is predominantly occupied by the vascular bundles (Pl. 22, Fig. 8), which have u-shaped xylem or are amphivasal and anastomose throughout the area, connecting with root traces. Roots develop from an area just outside

the endodermoid sheath (probably in a PTM). A two layered, sclerified bundle sheath encloses the vascular bundles.

T/S rhizome/inflorescence axis transition area

The epidermis consists of a single layer of brick shaped cells with the outer wall thickened. The hypodermis is reduced to a single layer of cells which have concentrically thickened cell walls. The cortex is composed of three cell layers which stain red. The endodermoid sheath contains vascular bundles and consists of two cell layers. The central area contains two kinds of vascular bundles. In an outer ring of vascular bundles, the arrangement is amphivasal, while in an inner ring bi-collateral vascular bundles are present. Both kinds of vascular bundles are surrounded by a sclerified two layered bundle sheath. The central area parenchyma is sparse within the vascular cylinder and has slightly thickened cell walls.

T/S inflorescence axis

The epidermis is composed of brick shaped cells with thickened outer walls. A cuticle is present. Stomata are present at the same level as the epidermal cells. The chlorenchyma sheath is composed of two cell layers and is followed below by a thin parenchyma sheath consisting of a single layer of cells (Pl. 23, Fig. 2). The sclerenchyma sheath is composed of several layers and contains cells with concentrically thickened cell walls and also has an associated ring of peripheral vascular bundles. The central area is composed of unspecialised parenchyma cells which contain the bulk of the vascular tissue (Pl. 23, Fig. 2). The vascular bundles are evenly spread throughout the area, they are bi-collateral and are enclosed by a single layered bundle sheath.

Growth form affinities and differences

The growth form of *T.lucens* is superficially similar to the tufted, caespitose form of grasses with a few differences. The basal cauline buds are suppressed in *T.lucens* and therefore do not develop into basal intravaginal tillers as is the case in grasses. In addition, the single stem aerial inflorescence axes differ greatly from the leafy axes seen in grasses. The presence of basal cauline buds suggests the possibility that resprouting after injury (fire) may be possible. The renewal growth and position of the rhizome renewal bud is consistent with a regular sympodial growth habit. The main difference being that the rhizome internodes are laterally compressed in *T.lucens* and tend to

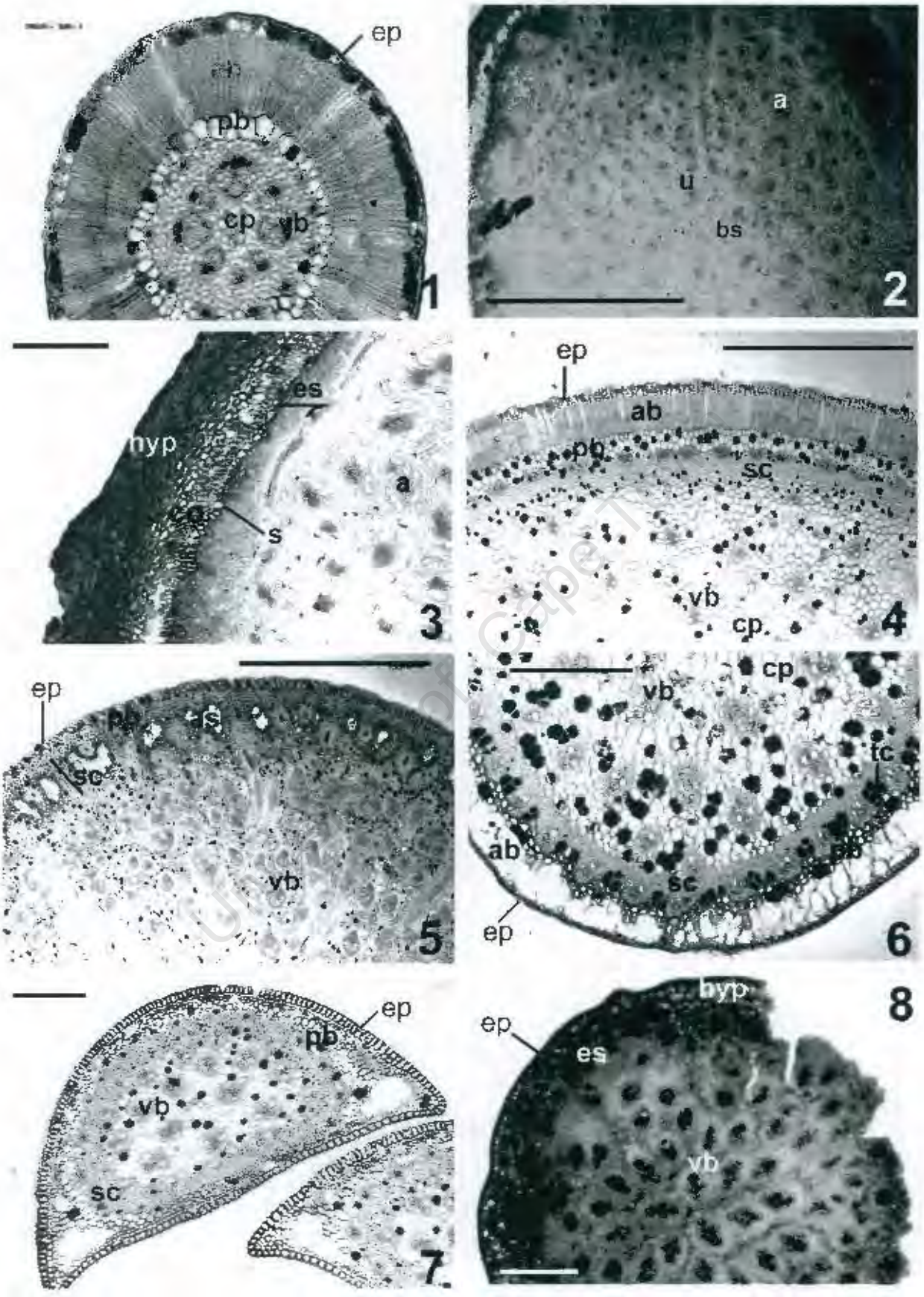
elaborate in the vertical position as the rhizome turns upwards to form the aerial axial portion.

The difference between rhizome internodes and inflorescence axis internodes is somewhat easier to identify than in many other monocots examined in this study (assuming that the two structures can be differentiated and this follows the current interpretation of the structures in Restionaceae in the literature). The rhizome internodes are short, closely spaced and possess axillary buds located in the axils of the entirely ensheathing scale leaves. One internode between the rhizome and aerial axis is elongated, lacks axillary buds, but retains the scale-like rhizome leaf. This corresponds to the anatomical description for the transition between the rhizome and the inflorescence axis (above). The inflorescence axis internodes are green, elongated and are not completely enclosed by a sheathing scale leaf. When the anatomy of this transition internode region is considered, the arrangement of the vasculature in the central area indicates the changeover from rhizome to inflorescence axis. If the inflorescence axis is produced from an apical bud, consistent with the interpretation of the growth form, then the inner region which contains the collateral vascular bundles may well be the area where the internode changes over to the inflorescence axis. Aerial axes in many Restionaceae have collateral vascular bundles and are thought not to contain amphivasal vascular bundles (Linder 1991). LaFrankie (1986) describes a similar elongated internode above the rhizome internodes which commences the aerial portion, noting that the area indicates a discrete transition from rhizome to leafy stem in *Maianthemum* (Liliaceae). LaFrankie (1986) proposed the idea that in *Maianthemum* there is a single shoot consisting of three discrete portions rhizome, leafy stem and terminal inflorescence which represent different developmental stages of the shoot, and not distinct organs. The transitional nature of areas between the discrete portions seem to have been discounted in the single shoot idea which ultimately proposes a continuum. LaFrankie did not report on the anatomy of this region, only that of the rhizome which could be defined by the presence of amphivasal vascular bundles, and the aerial leafy stem which had collateral vascular bundles. The two concepts within this single shoot idea are contradictory i.e. if it is a single shoot system is it possible to have discrete portions? This highlights the interpretation that needs to be considered for the transitional internode area of the rhizome and inflorescence axis in *T.lucens* (see Chapter 3).

Plate 22. Anatomy of *Thamnochortus spicigerus* (Figs 1-7) and of *Thamnochortus lucens* (Fig. 8).

Figure 1. T/S main axis of seedling of *Thamnochortus spicigerus* showing assimilatory band (ab) below epidermis (ep) and parenchyma band (pb) binding the central area (cp) and vascular bundles arranged into a ring (vb).
Figure 2. T/S rhizome of *Thamnochortus spicigerus*. Mid area showing closely arranged vascular bundles which are amphivasal (a) or with u-shaped xylem arrangement (u) and enclosed by a two to three layered bundle sheath (bs).
Figure 3. T/S detail of outer layers of rhizome of *Thamnochortus spicigerus* showing several layered hypodermis (hyp); a cortex (co) and endodermoid sheath (es) bounded by an outer layer of suberised cells (s). (a) = amphivasal vascular bundle.
Figure 4. T/S inflorescence axis of *Thamnochortus spicigerus* showing assimilatory band (ab) beneath the epidermis (ep) ; a parenchyma band (pb) and sclerenchyma bands (sc) and the central region (cp) which contains bi-collateral vascular bundles (vb).
Figure 5. T/S inflorescence axis node of *Thamnochortus spicigerus*. The epidermis binds a parenchyma sheath (pb) with thickened cell walls and a sclerenchyma band (sc) which contains air spaces (as) and the central region contains vascular bundles (vb) which traverse the nodal region toward the exterior and into the leaf base.
Figure 6. T/S inflorescence stalk of *Thamnochortus spicigerus*. The assimilatory band (ab) tends to break down while the parenchyma band (pb) and sclerenchyma band (sc) remain intact. The region contains tannin deposits in clumps (tc). (cp) = central region; (vb) = vascular bundle.
Figure 7. T/S flower stalk of *Thamnochortus spicigerus*. The epidermis (ep) binds a parenchyma band (pb) with a sclerenchyma band (sc) below. The central area contains bi-collateral vascular bundles (vb). Note shape of T/S compared with other sections from the inflorescence axis.
Figure 8. T/S base of *Thamnochortus lucens* showing a highly sclerified region with a hypodermis (hyp) and prominent endodermoid sheath (es). The central area contains vascular bundles (vb) with a sclerified, two layered bundle sheath.

[Bars = 9 μm**]**.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(iii) Chondropetalum deustum and (iv) Chondropetalum rectum

Morphology

Plants long rhizomatous, giving rise to aerial inflorescence axes at intervals along the length of the rhizome (Pl. 23, Fig. 5). The rhizomes are composed of several to many internodes which are entirely ensheathed by brown, scaly leaves. The aerial inflorescence axes are formed from the apical bud of a long rhizome which turns upright to form the aerial portion (L/S of apex of rhizome Pl. 24, Fig. 1). Sometimes two or three aerial inflorescence axes are formed at this time. These appear to develop from axillary buds which are located on the basal portion of the aerial inflorescence axis. A close examination shows that the axillary bud develops two to three closely spaced internodes, ensheathed by scale leaves (compacted rhizome) before turning upright to form the inflorescence axis. The renewal of long rhizomes takes place from an axillary bud on the node of the rhizome portion that initially turns upright to form the inflorescence axis (basal portion of the inflorescence axis). Thus, two or three new long rhizomes can develop from a "tufted inflorescence axis" region along the length of the plant (Pl. 23, Fig. 5). The branching pattern is consistent with a sympodial growth model. The aerial portions of the inflorescence axes lack axillary buds. Roots develop from the basal nodes of the rhizome that gives rise to inflorescence axes and may also develop along the length of the long rhizome, although this is very infrequent. Usually, the long rhizome consists of up to twenty centimetres of scale-leaf sheathed axis, lacking roots or aerial axes with pronounced growing tips enclosed in a sheathing scale leaf. The plants are usually found in seasonally moist hollows that occur on sandy flats

Anatomy

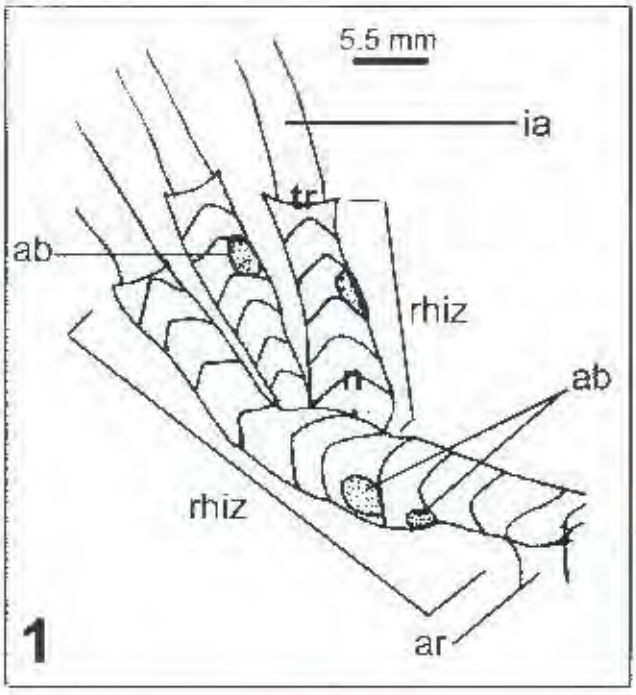
The anatomy of the organ portions examined in both *C. deustum* and *C. rectum* are essentially identical, and accordingly the descriptions are based on the material of *C. deustum*.

T/S base of portion giving rise to aerial axes

A periderm-like layer is present, but tends to break down in sectioning and also, lacks clear detail of cellular shape and structure. The following layer is composed of two to three layers of large, loosely arranged parenchyma cells and is positionally consistent with a cortex. An endodermoid sheath with an associated suberised layer is present and contains developing vascular bundles. The central area is composed of unspecialised

Plate 23. Morphology and anatomy of *Thamnochortus lucens* (Figs. 1 & 2) and morphology and anatomy of *Chondropetalum deustum* (Figs 3 & 4) and *Chondropetalum rectum* morphology (Fig. 5).

Figure 1. Morphology of *Thamnochortus lucens* showing vertical rhizome orientation (rhiz) and position of axillary buds (ab). (tr) = transition and (ia) = inflorescence axis.
Figure 2. T/S inflorescence axis of *Thamnochortus lucens* showing assimilatory band (ab); parenchyma band (pb) and sclerenchyma sheath (sc) surrounding the central region which contains the bi-collateral vascular bundles (vb).
Figure 3. T/S long rhizome of *Chondropetalum deustum* showing parenchyma band (pb) and a layer of sclerified cells constituting an endodermoid sheath (es). Outer layers not shown in detail in this T/S. The central area contains bi-collateral vascular bundles (vb).
Figure 4. T/S basal inflorescence axis of *Chondropetalum deustum*. The outer layers below the epidermis not shown in detail. Loose cells constituting the parenchyma band (pb) and the suberised cells (es) demarcating the start of the central area are shown. The central area is sclerified and contains bi-collateral vascular bundles (vb).
Figure 5. Morphology of base of *Chondropetalum rectum* showing the runners (run) enclosed by scale leaves and with distinct nodes (n). The formation of new runners occurs from the base of the inflorescence axis (bia) and note the position of the axillary bud (ab). (br) = branching region of inflorescence axis (ia), (slf) = scale leaf.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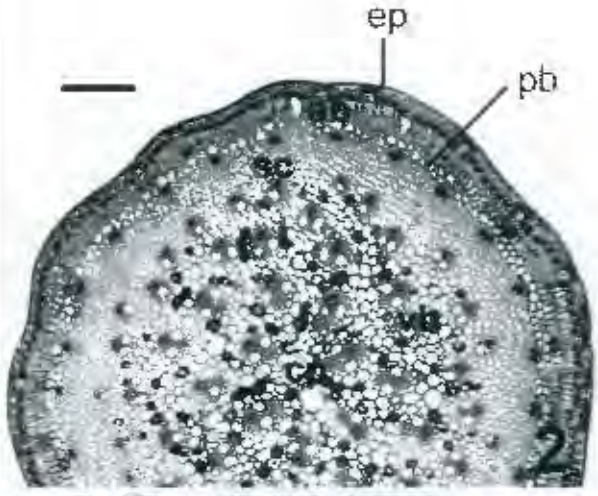
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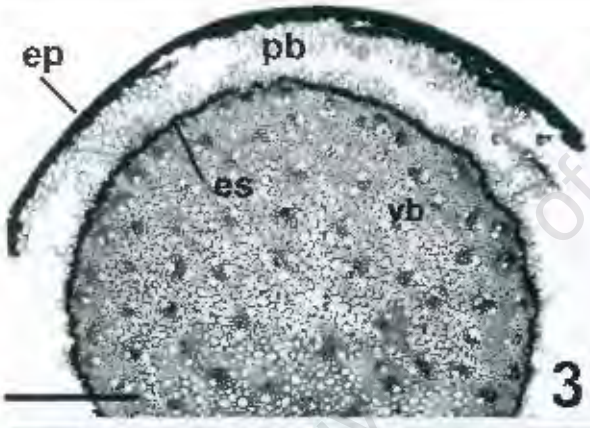
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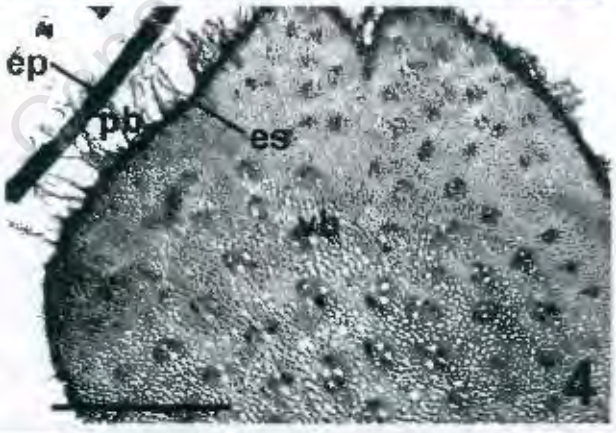
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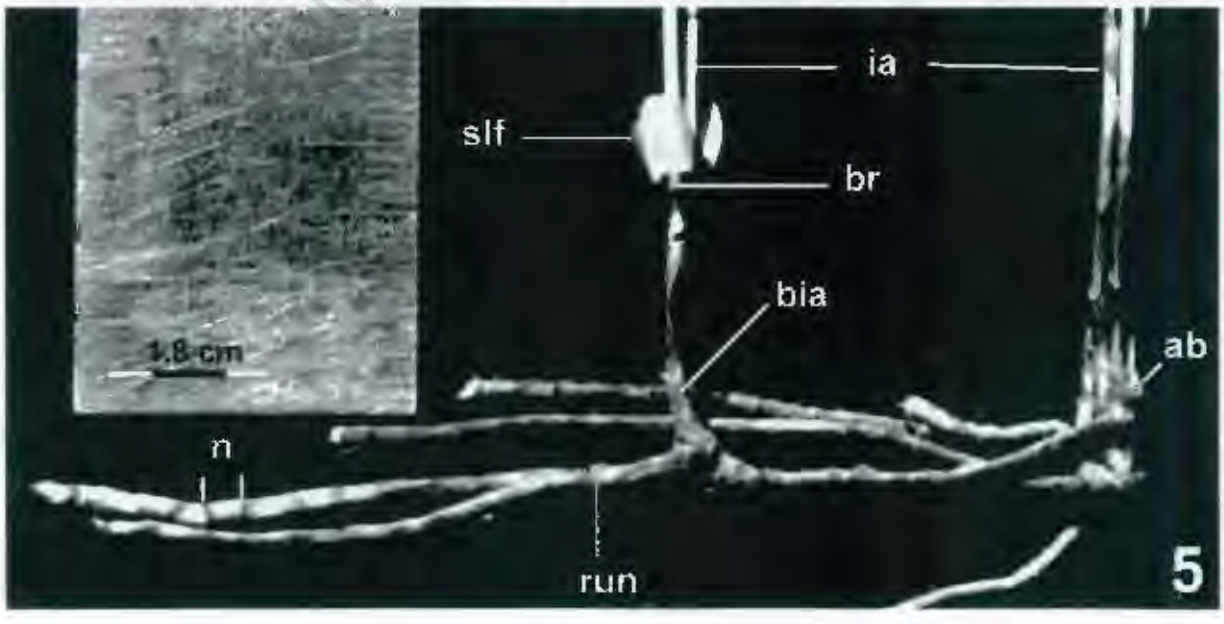
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parenchyma cells and contains amphivasal vascular bundles, which are evenly distributed within the area.

T/S long rhizome

The epidermis consists of flattened, brick shaped cells. A thick cuticle is present. There are two to three cell layers directly below the epidermis which are composed of parenchyma cells with slightly thickened cell walls (Pl. 23, Fig. 3). Following this is a single layer of sclerified cells which have concentrically thickened cell walls (making a continuous sheath). A parenchyma band of approximately seven cell layers is present and consists of thin walled, loosely arranged parenchyma cells. A suberised layer, with lower cell walls thickened and staining orange separates the parenchyma band from the central area, probably constituting an endodermoid sheath. The central area is composed of unspecialised parenchyma cells and contains the vascular bundles which are scattered within the area (Pl. 23, Fig. 3). The vascular bundles are bi- collateral and lack a well defined bundle sheath.

T/S basal inflorescence axis

The epidermis consists of a single layer of brick shaped cells. Directly below the epidermis is an area composed of two to three layers of small parenchyma cells, followed by a layer of sclerified cells. A parenchyma band consisting of four to five layers of loosely arranged parenchyma cells is present (Pl. 23, Fig. 4). A layer of suberised cells demarcates the central region from the outer layers (Pl. 23, Fig. 4). The central region is composed of sclerified parenchyma cells and contains bi-collateral vascular bundles which are evenly distributed.

T/S aerial inflorescence axis

The epidermis consists of two cell layers, the outermost layer is composed of brick shaped cells and the inner of vertically elongated cells. There is a thick cuticle on the outside of the epidermis. The stomata are sunken so that they coincide with the base of the first epidermal layer. The chlorenchyma is composed of two cell layers and contains substomatal cavities which extend to the base of the first layer. A single layered parenchyma sheath is present. The sclerenchyma sheath contains peripheral vascular bundles. The central area is composed of unspecialised parenchyma cells and bi-collateral vascular bundles.

Growth form affinities and differences

A morphology and anatomical structure similar to that of *C.deustum* and *C.rectum* was observed in the long rhizomes of *Elegia extensa*. In *Thamnochortus obtusus* morphologically similar long rhizomes also occur. The anatomy and morphological features of the long rhizomes in *C.deustum* and *C.rectum* are difficult to interpret as some of the features are "rhizome-like", while others are "inflorescence axis-like" and some e.g. suberised layer without an associated sclerenchyma sheath are peculiar. The lack of sclerification in the more central regions of the rhizome are perplexing. Possible explanations for this lie in the consideration of habitat and life history. The moist hollows are seasonal and therefore, there is a short window of growth opportunity for the rhizomes. They must therefore extend and elongate rapidly to cover new ground in the moist season, when nutrient uptake is also most favourable. Thus, the time period for laying down sclerified tissues is reduced. The very tightly sheathing scale leaves may take on the role of supporting tissue. The presence of a suberised layer would be a necessary feature in the long, dry summer to prevent water loss from the central tissues. The presence of exclusively bi-collateral vascular bundles cannot be explained in this horizontal rhizome system. A more extensive study is required to examine the growth increments, bud initiation intervals and physiology of these interesting rhizomes. With such a different set of morphological and anatomical features, I have referred to these as "runners" in preference to rhizomes, as they also differ anatomically from the main "rhizome" portions of the upright axes. Their anatomy is similar to the basal inflorescence axis area and if the point of initiation of the runner (long rhizome) is considered, they actually arise from an axillary bud located in this region.

The anatomy of the long rhizomes of *Alexgeorgea* described by Meney et al. (1990a) is very similar to the anatomy of the long rhizomes of the species described in this study, although in *Alexgeorgea* rhizomes there is a greater degree of sclerification. Meney et al. (1990a) also examined the basal inflorescence axis anatomy of *Alexgeorgea* species and this anatomy is similar to the basal inflorescence axes of *C.deustum* and *C.rectum*. The similarity between these taxa is likely to be the result of similar habitats, *Alexgeorgea* is found in sandplain habitats which are seasonally waterlogged. In addition, both of these taxa display some degree of clonality, where much of the nutrient cycling and retention of aerial inflorescence axes may be related to this particular lifestyle (see Meney et al. 1990b).

(v) Ischyrolepis cincinnata

Morphology

Plants forming densely tangled caespitose tufts up to 50 cm in height and growing in sandy areas on mountain slopes. The aerial inflorescence axes are fine in appearance and form axillary branches. The axillary branches on lower portions of the plant tend to be suppressed, so that aerially there is a fan like expansive tuft of branches, each often terminating in an inflorescence. At the base of the plants, runners are produced with elongated internodes and the scale leaves are confined to the nodes, not extending to ensheath the internode entirely (Pl. 24, Fig. 2). These are usually superficial on top of the soil surface. At intervals aerial plantlets develop and these produce roots from their bases which anchor both the runner and the new plantlet into the soil. The runners bear axillary (non-terminal) buds at the nodes at intervals along their length, which ultimately give rise to new plantlets (Pl. 24, Fig. 2). It is difficult to determine precisely where the end of the runner is as many plantlets arise in the tangled mass and thus, it is uncertain whether the apex continues to grow laterally, or turns upward and develops into aerial axes.

Anatomy

T/S base of plant

The epidermis is composed of small, rounded cells. A thick cuticle is present. The following layer is composed of rounded translucent cells (probably a hypodermis). The cortex is composed of two cell layers. The endodermoid sheath has an associated suberised layer with the lower cell walls thickened and staining orange-red. The central area is composed of unspecialised parenchyma cells and contains amphivasal vascular bundles which are evenly distributed within the area. The vascular bundles are enclosed by a three layered bundle sheath.

T/S runner

The epidermis consists of a single layer of flattened, brick-shaped cells. Stomata are not apparent, but there are areas along the epidermis which appear to be vestigial/broken down substomatal cavities. The following band consists of large elongated cells arranged approximately into two cell layers, stacked one on top of the other, in a semi "palisade" arrangement (Pl. 24, Fig. 3). The cells tend to be loosely arranged and break down at intervals. The parenchyma band consists of two cell layers of small rounded cells. The sclerenchyma band consists of cells with suberised cell walls and contains associated vascular bundles. The central region is composed of unspecialised parenchyma cells and

contains the vascular tissue which is scattered throughout (Pl. 24, Fig. 3). The vascular bundles are bi-collateral and are surrounded by a single layered bundle sheath.

T/S single stem region

The epidermis consists of brick shaped cells with a thick cuticle outside the upper surface of the cells. Stomata are present and are more or less at the same level as the epidermal cells, but occasionally are slightly raised above the upper surface of the cells. The chlorenchyma band consists two cell layers in which the cells tend to break down and create air spaces within the area. The chlorenchyma cells tend to stain purple. A parenchyma sheath is present and is composed of small, rounded parenchyma cells. The sclerenchyma sheath contains cells with concentrically thickened cell walls and the cell walls tend to stain orange, suggesting the presence of suberisation. The central region consists of unspecialised parenchyma cells and contains the vascular tissue, which is scattered throughout. The vascular bundles are bi-collateral and are enclosed by a single layered bundle sheath.

T/S branching inflorescence axis

The epidermis is composed of rounded cells. A thick cuticle is present. The stomata are raised above the level of the epidermal cells. The chlorenchyma band consists of vertically elongated cells arranged in two layers in a "palisade" type of arrangement (Pl. 24, Fig. 4). A single layered parenchyma sheath is present and is composed of rounded cells. The sclerenchyma sheath contains cells with concentrically thickened cell walls and contains associated vascular bundles. The central region consists of parenchyma cells with thickened cell walls and contains the vascular bundles which are arranged in a single ring (Pl. 24, Fig. 4). The vascular bundles are bi-collateral and are enclosed by a single layered bundle sheath.

Growth form affinities and differences

The morphology and anatomy of the base of the plant, the aerial inflorescence axis and the runner is the same for the organ portions examined of *Restio harveyii*. In *Restio harveyii*, the central area of the runner is sclerified. The precise growth form of *Ischyrolepis cincinnata* is difficult to interpret when the runner is considered. The runner produces upright plant portions from buds located at nodes on the extended internode. From the material examined, it appears as though vegetative proliferation occurs by the production of these runners and they produce axillary (non-terminal) plantlets. From the

basic structure of the aerial portion, it seems as though the base of the plant is essentially rhizomatous (the first to third internodes of the upright portion). The single stemmed area and branching aerial axes tend to be most like photosynthetic inflorescence axes. These inflorescence axes are branching. The anatomy of the aerial inflorescence axes and the runner tend to be quite similar, with the runner having some modifications in basic tissue differentiation. In both organ portions, the positioning of the buds is interesting. They are not located directly in the axil of the scale leaf sheath. Instead, they are somewhat laterally displaced so that they are located more closely to the opening of the leaf sheath. In the aerial axes, this tends to result in a "curvy" branching pattern. In the runner, the buds are similarly placed.

(vi) Willdenowia glomerata

Morphology

The overall growth form of *W.glomerata* is short rhizomatous with branching aerial inflorescence axes. The rhizomes are similar in morphology to those of *Thamnochortus lucens* and *Staberoha aemula* and hence, the anatomy was not examined. The aerial inflorescence axes branch at the nodes, but usually only once at each node and therefore the branching is sparse. In addition, underground runners which are long, usually complex and often rambling are produced. These runners consist of elongated internodes with scale leaves which do not entirely ensheath the length of the internode. The runners have the ability to branch, forming either new branches of runner or forming a runner which goes underground for some distance but then turns upright and becomes aerial and photosynthetic. The runners also have numerous buds in varying stages of development along their length. These buds are located slightly laterally on the axes, not directly in the axil of the leaf (Pl. 24, Fig. 7). The open side of the leaf scales are arranged almost in an alternate manner as one moves along the runner (Pl. 24, Fig. 7). The runners are also able to produce roots of two sorts, both fine roots and single large roots. Single large roots arise at a node in a region where the internodes have become very closely spaced (four to five nodes) and tend to be coated with a sandy sheath. *W.glomerata* forms very untidy bushes which are generally tufted in appearance. The bushes usually grow up to one metre in height.

Anatomy

T/S root

The epidermis is composed of a single layer with unicellular, epidermal hairs. The exodermis consists of one layer made up of rectangular cells. The cortex is composed of two to three cell layers of parenchyma cells with slightly thickened cell walls. The endodermis is a single layer composed of cells with the lower walls thickened. A pericycle is present. The vascular tissue consists of metaxylem with protoxylem alongside and groups of phloem cells above. The central area is composed of parenchyma cells, making up a solid pith.

T/S underground runner

The epidermis consists of a single cell layer. Stomata are present. Directly below the epidermis is a region containing rounded parenchyma cells. Another, more distinct layer of larger, loose parenchyma cells is present below this region (Pl. 24, Fig. 5). The sclerenchyma band is composed of two distinct regions. The outer region contains smaller vascular bundles and is a single layer in thickness (Pl. 24, Fig. 5). The vascular bundles have the xylem arranged in a u-shaped arc. The second region consists of approximately ten cell layers and contains vascular bundles. The vascular bundles in this area are bi-collateral. The central area is unsclerified and as a result breaks up in the section in the cutting process. A maceration of this area showed a number of parenchyma cells and a few xylem elements.

T/S aerial inflorescence axis node

The epidermis is composed of a single layer of brick shaped cells with their outer walls thickened. Stomata are present. The region below the epidermis consists of three layers of rounded cells and not elongated chlorenchyma cells. A parenchyma sheath is not clearly distinct from the previous layer, but comprises two cell layers of rounded parenchyma cells. The sclerenchyma band consists of approximately ten cell layers and contains developing vascular bundles. The central region consists of vascular bundles which are very closely packed together and there are thin strands of parenchyma cells between the vascular bundles. The vascular bundles are enclosed by a two to three layered bundle sheath and have the xylem arranged in u-shaped arc with a phloem cap above. The vascular bundles are arranged in several planes suggesting that the vascular bundles move outwards towards the edges of the inflorescence axis at the nodal region

and that several peripheral vascular bundles are formed by branching of the main vascular bundle system with some degree of anastomosing.

T/S aerial inflorescence axis internode

The epidermis is composed of a single layer of brick shaped cells and stains pink. Stomata are present. The chlorenchyma band is composed of two cell layers one on top of the other and the cells are elongated, vertically rectangular in a palisade-like arrangement. Substomatal spaces are present extending to the first layer of chlorenchyma cells. The sclerenchyma sheath is composed of approximately five cell layers and contains developing vascular bundles with xylem and phloem differentiating. The central area consists of unspecialised parenchyma cells with the vascular bundles scattered throughout. The vascular bundles are enclosed by a single layered bundle sheath and most of the vascular bundles bi-collateral

T/S of aerial inflorescence axis branching zone (serial sledge microtome sections)

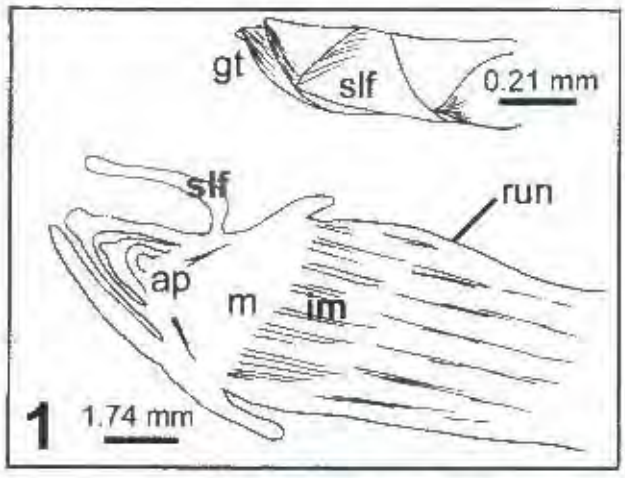
(The sections begin in the internode area of the aerial inflorescence axis zone just below a node, and then are taken through the node and into the branching zone).

The chlorenchyma band narrows and changes from staining blue to red, then the cell walls are thickened and stain orange/brown. The cell shapes change from elongate to round. The sclerenchyma band also changes, the cells lose the thickened walls and the tissue seems to blend into the chlorenchyma, almost as a continuous tissue. A separation region (probably bud of new branch) develops and is marked by the new formation of blue parenchyma strands. In addition, the whole area (both the main zone and separation zone) has a thicker epidermis than in normal inflorescence axis internode sections. The central region contains nearly all amphivasal vascular bundles. The separation zone has smaller vascular bundles (not able to distinguish vascular tissue arrangement). The central and main area is probably the node and the separation zone is probably the bud of the new branch. The morphological position of buds corresponds to the anatomical position of this separation zone, where the bud is slightly laterally positioned relative to the base of the scaling leaf sheath (Pl. 24, Fig. 6). The bud eventually obtains a distinct epidermis and becomes separated off from the central area, which also develops its own epidermis and reforms the inflorescence axis outer layers. These then form two separate "cylinders" and the shape of the main inflorescence axis T/S changes from circular to half semi-circle. Two separate axes are obtained and the branching event has taken place. The vascular tissue remains u-shaped and amphivasal throughout the branching event.

Plate 24. Morphology and anatomy of the runner of *Chondropetalum rectum* (Fig. 1); morphology and anatomy of *Ischyrolepis cincinnata* (Figs. 2-4) and of *Willdenowia glomerata*.

Figure 1. L/S of tip of runner of *Chondropetalum rectum*. Growing tip (gt) of runner with scale leaves shown above for growth direction orientation. L/S showing upright turning of apical bud (ap), scale leaves (slf) and internodal meristem (im). (run = runner).
Figure 2. Morphology of *Ischyrolepis cincinnata* runner showing position of aerial portion of plant and development of roots (ar) from the base of the plant (ba). Axillary buds (ab) occur along the length of the runner at nodes (ab). Scale leaves on runner removed.
Figure 3. T/S runner of *Ischyrolepis cincinnata* showing broken down assimilatory band (ab); parenchyma band (pb) and sclerenchyma band (sc). The central area tends to break down in the middle and also contains the vascular bundles (vb).
Figure 4. T/S inflorescence axis showing epidermis and raised stomata (st); assimilatory band (ab); parenchyma band (pb); sclerenchyma band (sc) and bi-collateral vascular bundles (vb) arranged into a ring in the central area (cp).
Figure 5. T/S runner of *Willdenowia glomerata* showing second parenchyma band (pb) below epidermis; sclerenchyma band (sc) and sclerified parenchyma (sp) of central area which contains bi-collateral vascular bundles.
Figure 6. T/s inflorescence axis plus branch showing slightly lateral position relative to scale leaf. (max) = main axis; (bz) = branching zone; (slf) = scale leaf; (egd) = expected growth direction; (cgd) = current growth direction.
Figure 7. Morphology of *Willdenowia glomerata* runner showing bud location. Stippled axillary buds (ab) occur within the sheathing leaf (slf) but are drawn darkly so that location can be compared to opening of the scale leaf. Buds are slightly lateral so that they occur just inside to one side of the opening of the sheathing scale leaf and appear to have a spiral arrangement on the runner (run). (rb) = reserve bud; (n) = node and (ar) = adventitious root.

[Bars = 24 μm (Figs. 3; 5 & 6) and 5 μm (Fig. 4)].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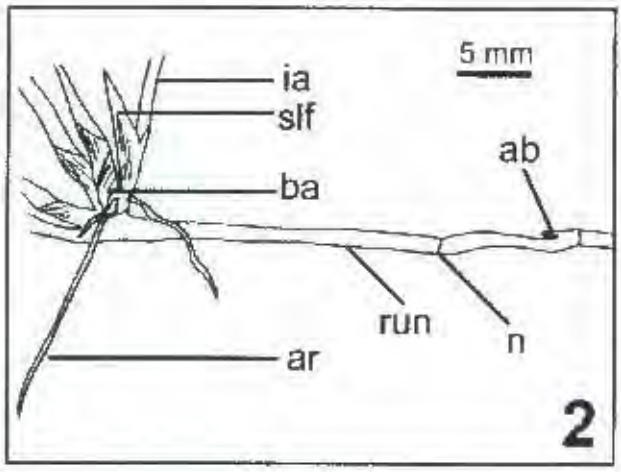
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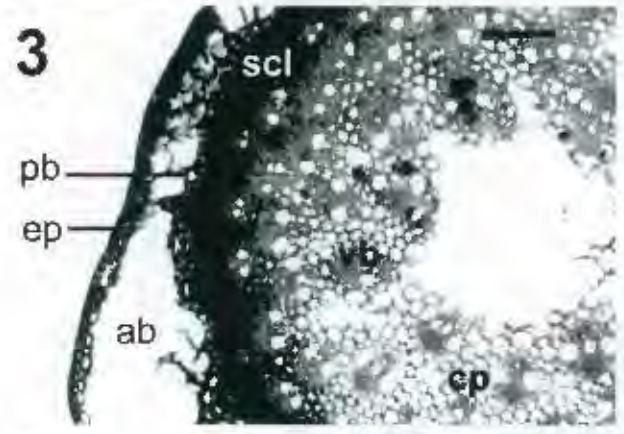
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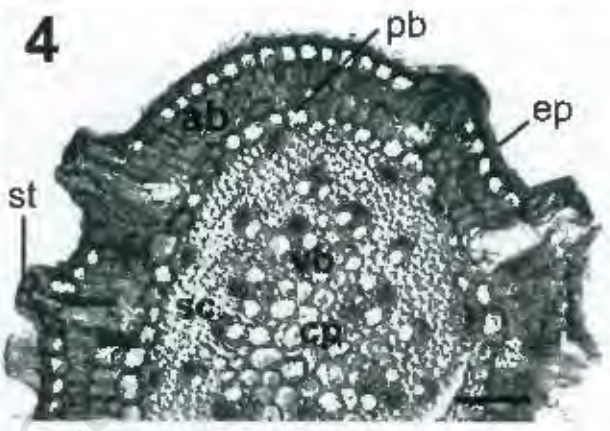
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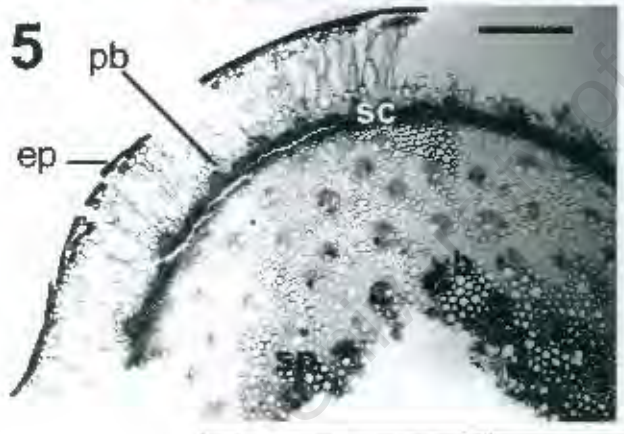
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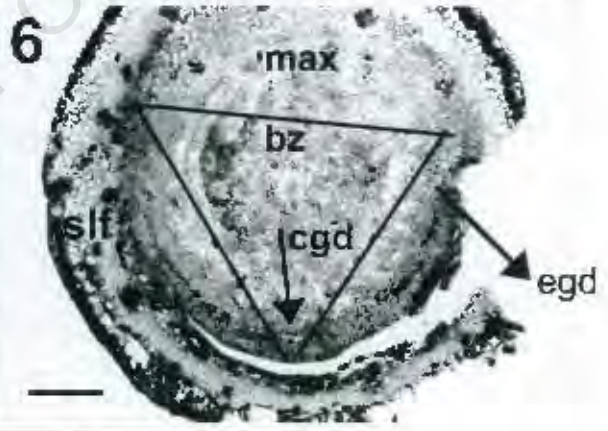
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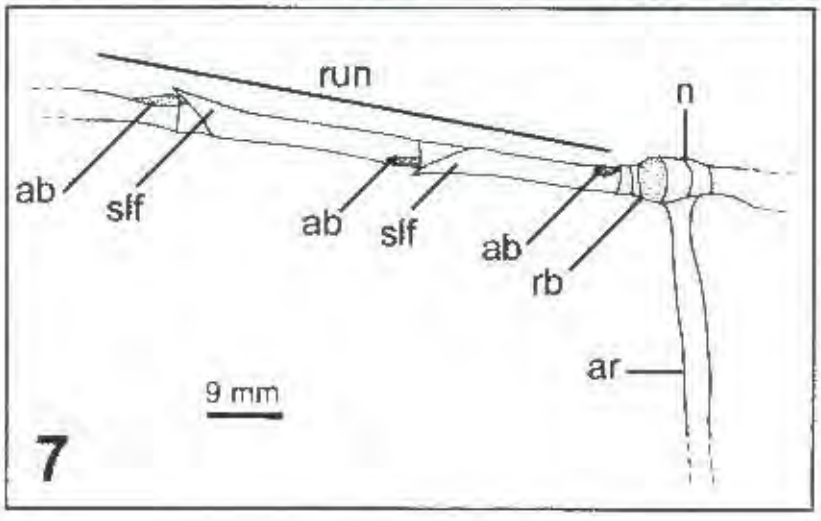
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Growth form affinities and differences

The runner anatomy of *W.glomerata* is difficult to interpret due to the occurrence of stomata and additional layers of sclerification. The location and positioning of the buds are somewhat different to the usual axillary position of buds at nodes. The runner does however turn upright apically to form the aerial axes, similar to the way in which the runners of *Chondropetalum deustum* and *Chondropetalum rectum* do. The slight lateral displacement of the buds on both the aerial axis and the underground runner in *W.glomerata* is similar to the slightly lateral buds of *Ischyrolepis cincinnata*. These buds are essentially axillary buds, but through their developmental sequence, they seem to be shifted slightly laterally. This situation is different to the leaf opposed position of rhizome buds that Tomlinson (1973) describes for some Restionaceae. This slightly lateral position of the buds is unusual in Restionaceae and monocots as a whole where most branching occurs through the initiation of axillary buds. However, leaf opposed branching (e.g. *Musa* (see Tomlinson 1970a; Fisher 1978), some Restionaceae (see Tomlinson 1973) and dichotomous branching (e.g. *Flagellaria indica* (see Tomlinson 1970b) and *Strelitzia* (see Fisher 1976)) may occasionally occur in monocots. In *W.glomerata* and *I.cincinnata*, the bud position may be linked to the leaf arrangement pattern and may be affected by their initiation. The slightly lateral position of the buds on the runners may be advantageous in allowing the runner a certain amount of plasticity and several options at different nodal positions and orientations to develop axial portions. The lateral movement of the bud may be due to the activity of an intercalary meristem after the branch meristem has been initiated in the normal axillary position as occurs in *Zostera marina* (Tomlinson 1973).

Commelinanae: Restionales: Poaceae

(i) Pentameris thuarii

Morphology

Plants up to two metres in height, often single stemmed, erect, but also decumbent forms (probably related to the age of the plant, older plants single stemmed and erect). The single stem has short, closely spaced internodes at the base, which successively and progressively increase in length towards the apex (Pl. 25, Fig. 1). There are cauline innovation buds basally, giving the stem the potential to branch from the base, as well as cauline buds aerially. Roots and root buds arise in a circular fashion from the nodes at the lower portion of the stem only (Pl. 25, Fig. 1). These roots behave as stilt roots, mechanically supporting the stem. They are thick and somewhat tough at the nodal innovation area, becoming thinner and branching when they grow into the soil surface.

Leaves arising from the lower nodes are deciduous and a tough fibrous leaf sheath is all that remains, often not ensheathing the entire internode. Towards the apex of the stem, the terminal inflorescence axis is present, the inflorescence is a branched panicle. Aerial cauline buds are not often visible in the axils of the leaf sheaths, but aerial branching does occur (Pl. 25, 2, 3, 5). The leaf sheath ensheaths the entire internode only opening and expanding at the node above it. Plants often form dense stands in riverine habitats. They appear to be killed by fire and mass death has been observed after a certain time period. This is hypothesised to be a result of the considerable size that is attained after up to five years of growth, which cannot be supplied by the small number of roots that are formed and the water transporting constraints of the fixed number of vascular bundles.

Seed set in *P.thuarii* is poor, with many of the spikelets showing aborted ovules, and proceeds to deteriorate with the number of years after fire, the first year usually yielding most fruit. Many of the seeds collected and used for germination were infested with insect larvae and in addition, the dry, late winters that were encountered over the study period seemed to contribute to a low seed set. The seeds germinate after about four weeks on moist filter paper treated with smoke water. The seedlings do not establish well in greenhouse and pot conditions dying after about three months of growth. Field collected seedlings in the first year after fire were used for further observations.

The seedlings do not display the same growth form as the adults. They are of the basic tufted habit with at least three stem branches (usually up to five) which arise intravaginally from basal cauline buds of the short vertical rhizome. All of the rhizome and branching regions are entirely ensheathed by the leaf bases. Roots are produced from the basal nodes of the very short rhizome, often breaking through the leaf sheaths.

The morphology of grass plants are described by Clark & Fisher (1986). The leaf epidermal anatomy of members of Poaceae has been extensively examined by Metcalfe (1960), with less detailed descriptions of the axial system. Detailed observations of the growth form and morphology of bamboos are available (e.g. McClure 1993).

Anatomy

T/S base of vertical stem

The epidermis is composed of flattened brick shaped cells. A cortex comprised of approximately ten cell layers of rounded parenchyma cells is present (Pl. 26, Fig. 1, 2), sometimes containing vascular bundles. An endodermoid sheath is present and the innermost area has associated vascular bundles (Pl. 26, Fig. 1). The central area is composed of unspecialised parenchyma cells and also contains vascular bundles. The

vascular bundles are amphivasal and are surrounded by a sclerified bundle sheath (Pl. 26, Fig. 4). Roots are formed endogenously from the endodermoid layer in this region(Pl. 25, Fig. 4).

T/S aerial internode (stem)

The epidermis is composed of flattened, brick-shaped cells with all the walls equally thickened. A sclerenchyma region consisting of five cell layers in thickness is present directly beneath the epidermis. The parenchyma band contains vascular bundles and is approximately ten cell layers in thickness. Another sclerenchyma band is present which separates the central area and vasculature from the outer parenchyma band. The central area is composed of isodiametric parenchyma cells and contains the vast majority of vascular bundles (Pl. 26, Fig. 3). A hollow pith is present in the centre of the section. The vascular bundles are larger towards the centre and are enclosed by a single layered bundle sheath. The vascular bundles are bi-collateral in this area (Pl. 26, Fig. 3).

T/S node of vertical stem

The leaf base at the node tends to merge into the stem tissues, so that two distinct regions of vasculature are evident. The whole node is surrounded by an epidermis of flattened, brick shaped cells. The central region is composed of sclerified parenchyma cells and is solid (Pl. 26, Fig. 4). The vascular bundles are elongated in the outer ring and tend to merge into the central area vascular tissue. The vascular bundles are bi-collateral and are surrounded by a three layered, sclerified bundle sheath. Some transverse bundles anastomose through the nodal area and would appear to move from the centre towards the periphery as though feeding into leaf traces.

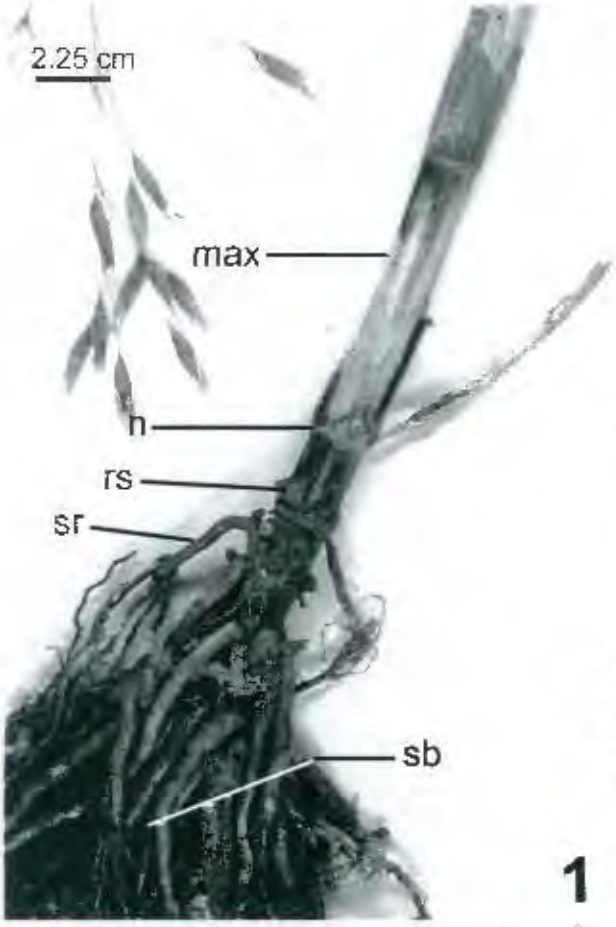
T/S inflorescence stalk

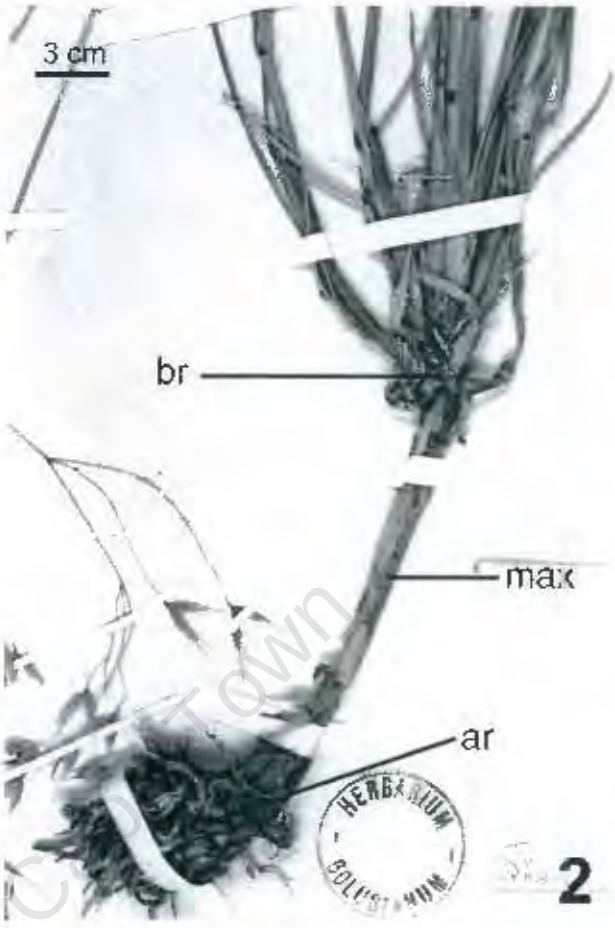
The anatomy of this region is similar to that of the main stem internode, with a sclerenchyma region directly below the epidermis. The central area is composed of parenchyma cells and contains bi-collateral vascular bundles. A hollow pith forms in the centre of the stalk. The second sclerenchyma band which is present in the main stem is absent in this region.

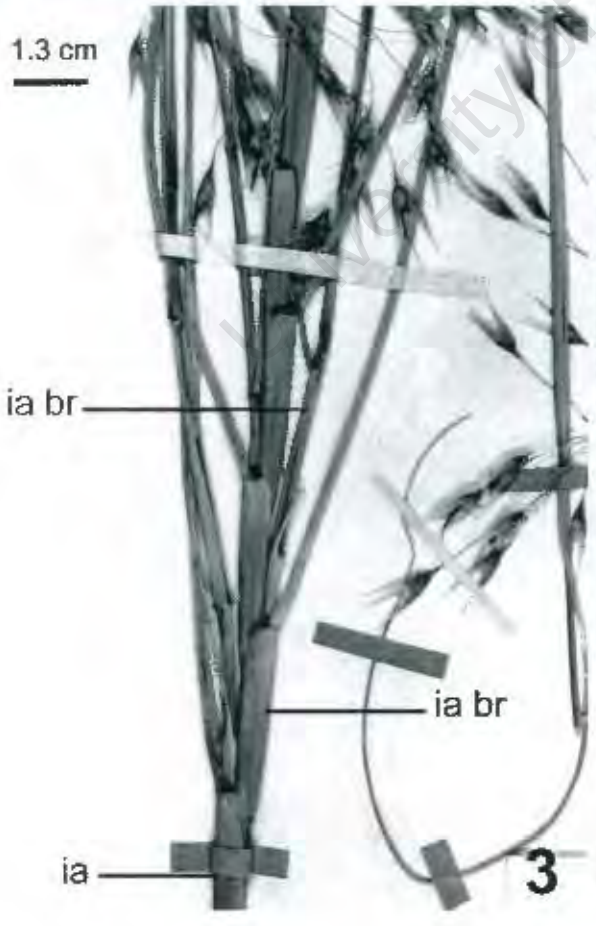
Plate 25. Morphology and anatomy of *Pentameris thuarii.*

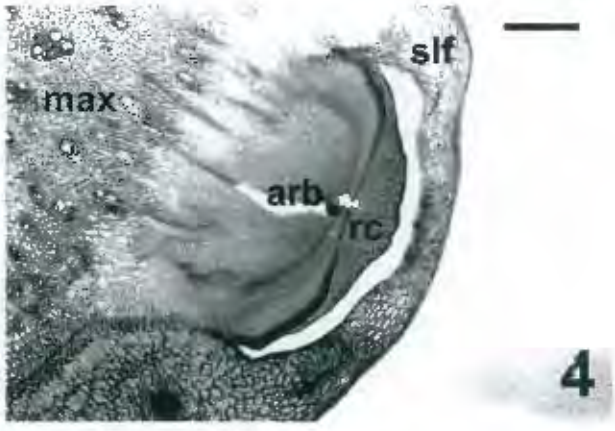
Figure 1. Morphology of mature stem base showing root scars (rs); stilt roots (sr) and nodes (n). (sb) = stem base; (max) = main axis.
Figure 2. Morphology of mature stem showing suppression of basal branching at lower nodes, while branching at higher nodes is evident (br). (max) = main axis; (ar) = adventitious roots.
Figure 3. Morphology of aerial portion of stem showing aerial branching of the main axis (ia). Branches = ia br.
Figure 4. T/S of base of stem showing root bud initiation (arb). (slf) = sheathing leaf; (max) = main axis; (rc) = root cap.
Figure 5. T/S of aerial portion of stem (max) showing axillary bud detail (ab). (slf) = sheathing leaves.

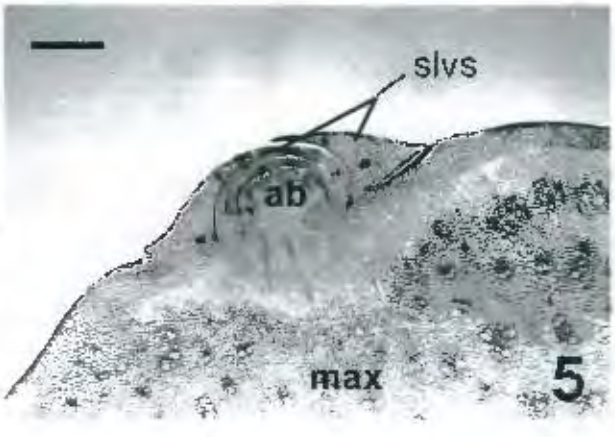
[Bars = 34 µm (Figs. 4 & 5)].











Growth form affinities and differences

The vascular pattern and arrangement is of the two circular system described by Esau (1953) for grass stems. This description is for the aerial stem and possibly for the assimilatory portion and thus the inflorescence bearing portion. Rhizome anatomy and tissue arrangement is not often considered for grasses. The basal region of the vertical stem of *P.thuarii* has a different tissue arrangement and vascular anatomy to the more aerial portion. The precise transition between the basal stem and the aerial stem cannot be determined, but may well be indicated by the suppression (loss) of cauline axillary buds (either with root or branch fate). Barker (1993) considered that the aerial branching portions were equivalent to inflorescence axes, but that they differed anatomically from the basic grass inflorescence axis anatomy, having the anatomy of a rhizome. This study indicates that the aerial branching axes have many features which are more often found in grass inflorescence axes. The nodal anatomy differs from the internodal areas and is consistent with the observations of Sharman (1942) and Esau (1953). The transverse arrangement of the some of the vascular bundles in the central region of the node is described by Kumazawa (1961) as a plexus for maize and the pattern is thought to be as a result of the bundles changing direction to link with the leaf traces of the leaf sheath which is intimately united with the node.

The formation of prop/stilt roots is also found in *Zea mays* and *Sorghum* (Clark & Fisher 1986). In these taxa the roots are used both for structural as well as absorptive purposes and are also thicker than adventitious roots, but are anatomically similar (Clark & Fisher 1986). While the growth forms of maize and *P.thuarii* are very similar, maize does, however, differ in its anatomy to that of *P.thuarii* in that the stem is solid as opposed to hollow (Metcalfe 1960). Furthermore, the life history of the two forms is different, with *P.thuarii* considered to be perennial. However, in its life characteristics, *P.*thuarii does behave very much like an annual - being killed by fire and dying after a certain size has been reached. Similarly, the seedling phase in the first three months of growth seems to be sensitive to extrinsic factors and thus, requires the very specialised habitat of riverine (mesic) areas for successful recruitment. It has to be considered that *P.thuarii* exhibits an extended annual life habit, rather than true perennial and sympodial renewal growth. Few field specimens were observed to display sympodial renewal growth from the basal innovation buds that are present, once the single stem stage is achieved i.e. after three years of growth. Linder & Ellis (1990) classified *P.thuarii* as a competitor grass within the Fynbos region, having a weakly developed base and cauline innovation buds. The tall growth form (resulting from aerial bud growth) is postulated as a strategy to allow the

grass to compete with the mesic Fynbos components in the first few years after fire (Linder & Ellis 1990; Barker 1993).

The presence of solid nodes in the aerial portions of the stem is a surprising feature in *P.thuarii*, particularly when the potential height of the plants is considered. The hollow nodes of bamboos have been postulated as a mechanism for providing maximum strength for a particular amount of tissue and may be related to the rapid growth of the inflorescence axis (Holttum 1955). Such a mechanism would be expected in a growth form like *P.thuarii*, the erect aerial shoots requiring maximum support. The absence of this feature may offer an additional explanation for the sudden death that is observed once a particular size has been achieved.

(ii) Merxmuellera rufa

Morphology

Plants often referred to as bulbous, the base of the plant swollen and ensheathed by woolly leaf bases which are subterranean. Removal of the leaf bases reveals a series of closely connected internodes which are swollen forming a bead-like structure (Plate 26, Figs. 5, 6). The subterranean organ gives rise to elongate runners with long internodes from axillary buds and to swollen internodes (effectively branching from another axillary bud). At intervals, where the last internode of the organ turns upright, a swollen base to the inflorescence axis is evident, this ultimately is terminated by the inflorescence (Pl. 26, Figs. 5, 6). Runners bear axillary buds (Pl. 26, Fig. 6), but also along their length the internodes can be compacted and swollen forming the "bulbous" structure again. The outermost leaf bases of the internodes are thin and tend to be very hairy. However, some leaf bases, particularly those intimately enclosing the compacted internodes (mid region of rhizome) tend to be somewhat fleshy.

Anatomy

T/S rhizome

Epidermis consisting of flattened, brick shaped cells. A hypodermis is present and is composed of a single layer of cells which have concentrically thickened cell walls. The cortex is very expanded (often up to 30 cell layers) and consists of thin-walled, isodiametric parenchyma cells (Pl. 26, Fig. 7). The cells contain globular inclusions, but these did not stain positive in an iodine starch test. The cortex contains vascular bundles which are arranged in a ring and are amphivasal, but some of these anastomose, appearing longitudinal in the transverse sections (Pl. 26, Fig. 7). The cortex surrounds a

central vascular core which is bounded by an endodermoid sheath comprising several layers of cells (Pl. 26, Fig. 7). The central area is composed of unspecialised parenchyma cells and contains amphivasal vascular bundles which are arranged quite closely, some of which anastomose throughout the region.

T/S runner

The runner is bounded by an epidermis of brick shaped cells. A single layered hypodermis is present as is found in the rhizome, with concentrically thickened cell walls. The cortex is expanded to approximately ten cell layers in thickness and contains vascular bundles arranged in a ring (Pl. 26, Fig. 8). The endodermoid sheath is reduced to a single layer and the central vascular core is composed of sclerified parenchyma cells, constituting a sclerenchyma band which contains the bulk of the vascular tissue (Pl. 26, Fig. 8). A region of unsclerified cells is present in the central area of the vascular cylinder.

T/S basal inflorescence axis

The epidermis is composed of rounded to brick shaped cells, with the outer wall thickened. A cuticle is absent. A cortex of approximately eight to ten cell layers is present and is composed of parenchyma cells and contains vascular bundles which are arranged in a ring. An endodermoid sheath composed of two to three cell layers is present and surrounds the central area. The central area is composed of unspecialised parenchyma cells and contains the bulk of the vascular tissue. The vascular bundles consist of larger, elongate bundles which are clearly arranged in a ring-like manner and additionally with smaller bundles scattered between them and throughout the central area. The vascular bundles are either amphivasal with a sclerified xylem and a single layered bundle sheath, or with the xylem arranged in a u-shaped pattern and also with a single layered bundle sheath.

Growth form affinities and differences

Swollen internodes/bases are generally uncommon in grasses, but have been observed in a few species e.g. *Poa drummondiana*, *Panicum bulbosum*, *Arrhenatherum elatius* var. *bulbosum*. In the Cape grasses swollen bases are found in *Merxmuellera decora*, *M. lupulina*, *Erharta capensis*, *E. longifolia*, *E. dura*, *Pentaschistis aristidoides*, *P. viscidula*, *P. argentea* and *P. velutina* as well as in *Festuca scabra* (Linder & Ellis 1990). These structures have been termed stem tubers (Pate & Dixon 1982; Bell 1991). Pate & Dixon (1982) suggested that these structures were distinguishable from rhizomes because of

their jointed nature. Linder and Ellis (1990) reported that the bulb-like structures of *Pentaschistis viscidula, P. argentea* and *Merxmuellera rufa* were formed from swollen leaf bases. The examination of *M.rufa* and also *M.lupulina* in this study revealed that most of the "bulbous" structure was a result of swollen internodes of the underground organ as discussed above.

The geophytic habit of many of the Cape grasses has been suggested as a fire survival strategy and the behaviour of the plants closely mirrors that of geophytes, with profuse flowering in the first season after fire and subterranean survival once they are overshaded by the post fire Fynbos communities (Linder & Ellis 1990). In populations of *M.rufa* profuse flowering was observed in an area which had recently been cleared of pine plantation. Thus, shading would appear to be an important factor in preventing yearly flowering in *M.rufa*. The storage reserves in the underground organs are proposed to allow the plants to flower freely in the first year following fire (Linder & Ellis 1990), but the precise translocation of photosynthates is not clearly understood. In *M.rufa* the storage substance was clearly not in the carbohydrate class, the globule structure suggests a protein body storage material in the swollen rhizome internode, while in the runner starch was present. This may be related to the runner requiring rapid moments of elongation to explore new soil. Runners also have the ability to turn upright and develop aerial plant portions and thus would require an easily mobilised storage material.

(iii) Pentaschistis aristidoides

Morphology

Plants with a subterranean rhizome with closely arranged, swollen internodes which are ensheathed by hairy, swollen leaf bases. Renewal growth is from an axillary bud at the apex of the current internode of the rhizome. The rhizome turns upright and the apical portion grows into the aerial axis, which is slightly swollen at the base and terminated by an inflorescence. The lower swollen inflorescence axis base has buds in the axils of the leaf sheaths at the lower nodes only and there are also buds in the axils of the sheaths along the rhizome.

Anatomy

T/S rhizome

The internode is laterally expanded and the outline of the cross section is oval. The epidermis is composed of brick shaped cells. The following region becomes corky in appearance staining brown, which could be the hypodermis and is expanded to

approximately three cell layers in thickness. The cortex is approximately four to five cell layers in thickness and the thin-walled parenchyma cells contain starch granules. An endodermoid sheath of two to three cell layers in thickness binds the central region which contains the vascular tissue. The sheath is not continuous where traces move out of the central region to the root buds, which are present on the exterior portion of the cortex. The central region is expanded and occupies a large proportion of the rhizome. The parenchyma cells of the central region are packed with starch granules. The vascular bundles are arranged in a ring and are amphivasal.

T/S rhizome/inflorescence axis transition

The cross section of the internode in this region is approximately circular. An epidermis composed of brick shaped cells is present. A hypodermis is absent. The cortex consists of three to four cell layers and is composed of parenchyma cells which contain starch granules. An endodermoid sheath of two to three cell layers surrounds the central region. The central area contains the vascular tissue which is scattered throughout and is composed of parenchyma cells packed with starch granule. The vascular bundles also anastomose in this region and are mixed either being amphivasal, or with xylem arranged in a u-shape or bi-collateral.

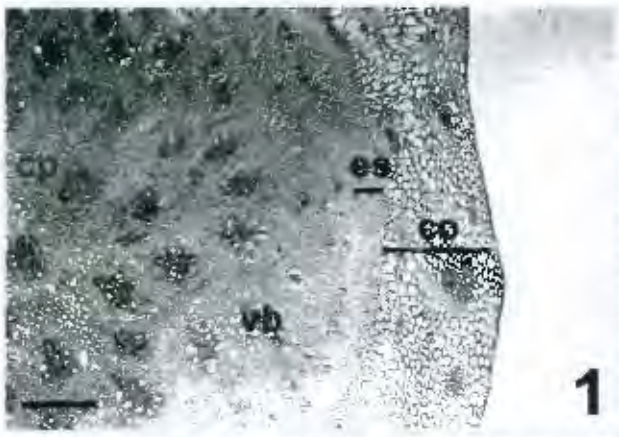
T/S basal inflorescence axis

The basal inflorescence axis is bounded by a single layered epidermis composed of brick shaped cells. A parenchyma band of two to three cell layers in thickness is present and surrounds the central region. The central area contains the vascular tissue which is scattered within the region. The central area consists of unspecialised parenchyma cells and the central area tends to break down to form a hollow pith. The vascular bundles are mixed either with the xylem arranged in a u-shape or bi-collateral and are surrounded by a single layered bundle sheath.

Plate 26. Anatomy of *Pentameris thuarii* (Figs. 1-4) and morphology and anatomy of *Merxmuellera rufa* (Figs. 5-8).

Figure 1. T/S base of vertical stem layers showing cortex (co); endodermoid sheath (es) and amphivasal vascular bundles (vb) in the central area (cp).
Figure 2. T/S base of vertical stem central area showing amphivasal vascular bundles (vb) in the central parenchyma (cp).
Figure 3. T/S aerial internode showing bi-collateral vascular bundles (vb) and hollow pith (pi).
Figure 4. T/S node of vertical stem showing sheathing leaf (slf) and sclerified central parenchyma (cp) which contains bi-collateral vascular bundles.
Figure 5. Morphology of base of *Merxmuellera rufa* showing position of rhizome (rhiz); runner (run); base of inflorescence axis (bia) and the transition (tr) area between the rhizome and the inflorescence axis (ia).
Figure 6. Drawing showing the detail of the rhizome plus runner portions of *Merxmuellera rufa*. Leaf bases of rhizome removed to show the swollen internodes (swi). Runner with axillary bud (ab). (n) = node; (ar) = adventitious root; (tr) = transition; (in) = inflorescence axis; (bia) = basal inflorescence axis.
Figure 7. T/S rhizome of *Merxmuellera rufa* showing reduced hypodermis (hyp) and expanded cortex (co). (sc) = sclerified region of central vascular area.
Figure 8. T/S runner of *Merxmuellera rufa* showing expanded cortex (co) and endodermoid sheath (es) which surrounds the central vascular area.

[Bars = 29 μm].



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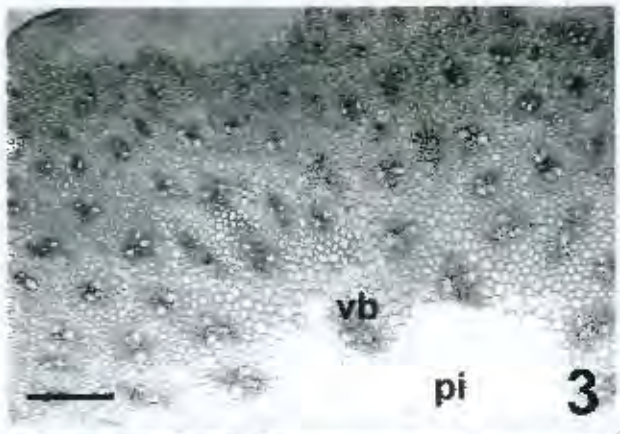

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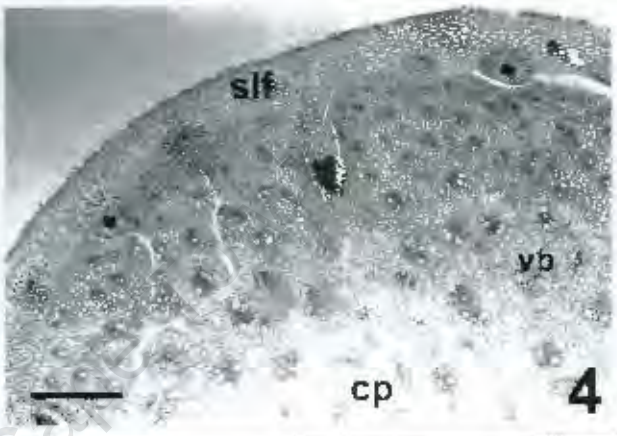

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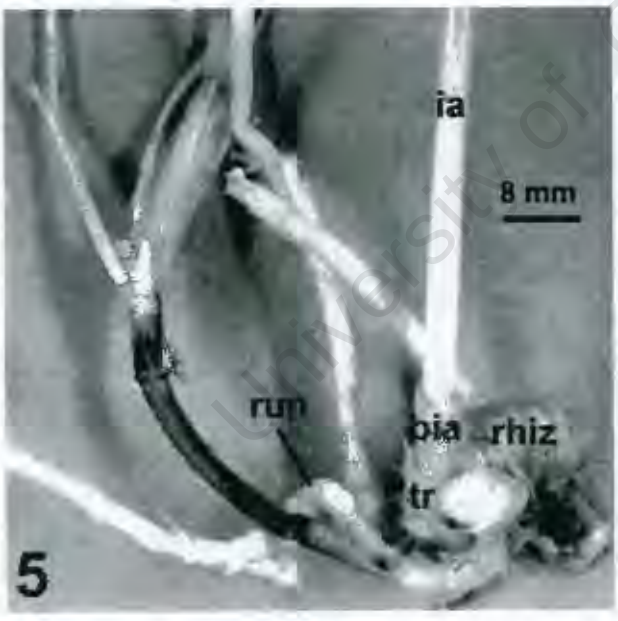

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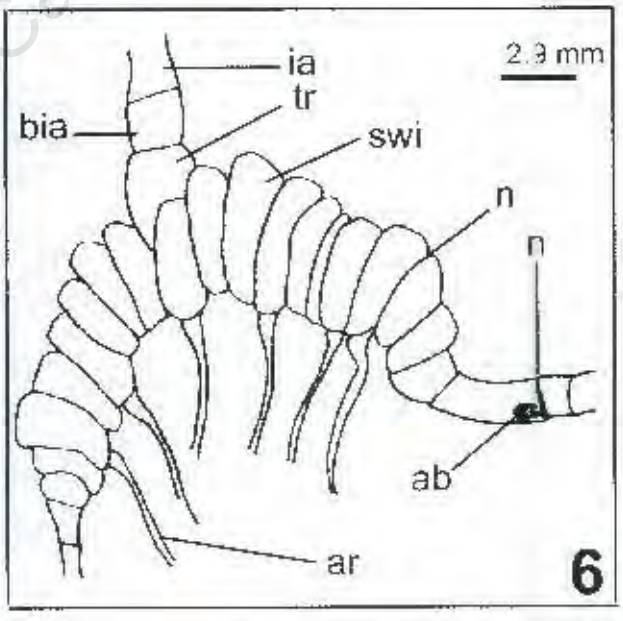

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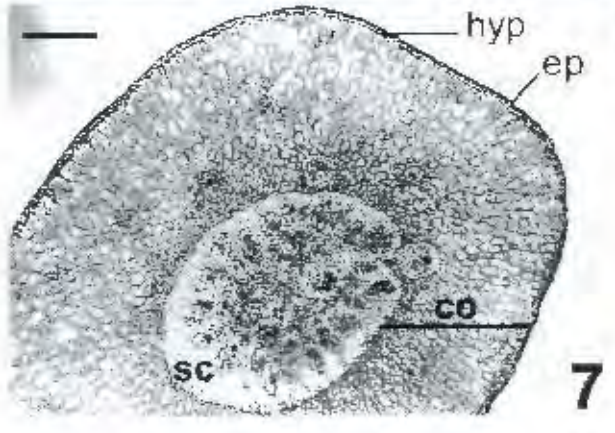

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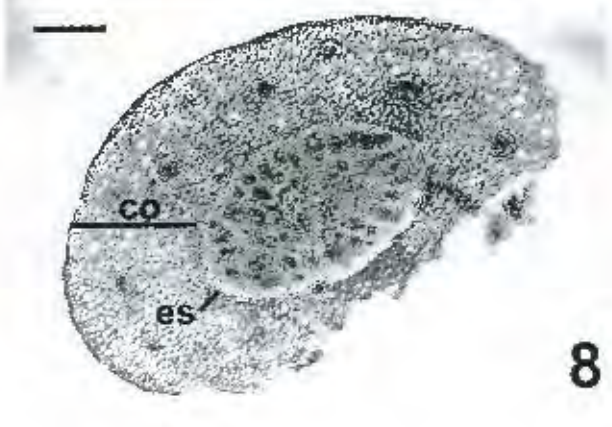

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T/S inflorescence stalk

The inflorescence axis is bounded by a single layered epidermis consisting of brick shaped cells. Directly below the epidermis is a sclerenchyma band which consists of two to three cell layers in thickness. The central area breaks down to form a hollow pith, the vascular tissue scattered around the pith in the unspecialised parenchyma cells of the central region. The vascular bundles are mixed either with the xylem arranged in a u-shape or are bi-collateral and are enclosed by a single layered bundle sheath.

Growth form affinities and differences

The expanded internodes of the rhizome in addition to the presence of a large amount of starch granules in the cells in both the cortex and central region indicates that the rhizome is an important storage organ. The arrangement and concentration of vascular bundles would also point to this. The basal innovation buds suggest the possibility for renewal growth if aerial portions are damaged/removed, but generally the new growth is by sympodially renewed branching. Linder and Ellis (1990) classify *P.aristidoides* in the geophyte group of Cape grasses on the basis of the swollen base of the plant.

The growth form of *P.aristidoides* is similar to *M.rufa* in that the rhizome internodes are swollen. No runners were observed in *P.aristidoides* however. The anatomy of the various portions of the plant of *P.aristidoides* show marked differences, with the transition between the rhizome and upright aerial portions being quite distinct.

(iv) Pseudopentameris macrantha

Morphology

Plants with a stout, creeping rhizome, the plant often up to 1.5 metres in height. The rhizome is not fleshy and is without hairy sheathing leaf bases. The leaf bases of the rhizome are scale-like, short and are formed at the nodes. There are aerial innovation buds which allow intravaginal branches (tillers) to be formed above the soil surface. The apical portion of the rhizome turns upright to form aerial axes, with an upright portion of two to three internodes before the axis becomes green. The renewal sympodial unit of the rhizome is formed from an axillary bud just below the portion which turns upright, and is situated in the axil of the scale leaf. There are also axillary buds along the length of the rhizome in the axil of every scale leaf which have the potential to develop into new rhizome internodes, effectively resulting in branching of the rhizome axis. Roots arise along the length of the subterranean portion at nodes and also continue to do so in the

area that turns upright. The plant is generally unbranched in the basal regions, but tends to expand laterally by branching from aerial axillary buds.

Anatomy

T/S rhizome base

The rhizome is bounded by an epidermis composed of brick shaped cells. A hypodermis consisting of two to three cell layers of brown staining cells is present. The cortex is expanded and consists of approximately six cell layers of parenchyma cells with slightly thickened cell walls. A sclerified layer (endodermoid sheath) binds the central area which contains the vascular tissue and is composed of parenchyma cells which contain sparsely distributed starch granules. The vascular bundles are closely arranged within the central area and are amphivasal and enclosed by a single layered bundle sheath.

T/S rhizome (creeping portion)

In this region the hypodermis is expanded to approximately ten cell layers and the cell walls are slightly thickened. The cortex is reduced to a single band comprising two to three layers of blue staining parenchyma cells. A sclerified layer (endodermoid sheath) surrounds the central area which contains parenchyma cells filled with a few starch granules and also the vascular tissue. The vascular bundles are closely arranged and are amphivasal with a single layered bundle sheath.

T/S upright turning portion of rhizome

In this region the tissue plan differs to the creeping portion by the absence of a sclerified layer and the central vascular cylinder increases in volume.

T/S rhizome-upright axis transition area

This region is bounded by an epidermis composed of brick-shaped cells. Directly below the epidermis is a parenchyma band which is comprised of approximately three cell layers. The following band is a sclerified region which contains developing vascular bundles and this surrounds the central area. The central area consists of unspecialised parenchyma cells and contains the vascular tissue which is scattered within the region. The vascular bundles are amphivasal and bi-collateral, the collateral bundles tending to be arranged in the outer ring of the cylinder.

T/S inflorescence axis internode

The inflorescence axis is bounded by an epidermis comprised of brick shaped cells with the outer walls thickened. A parenchyma band consisting of one to two cell layers is present directly below the epidermis. The sclerenchyma band contains developing vascular bundles and is approximately four cell layers in thickness. The central area is composed of parenchyma cells which break down in the centre to form a hollow pith and contains the vascular tissue. The vascular bundles are few, are sparsely distributed throughout the area and are bi-collateral, enclosed by a single layered bundle sheath.

Growth form affinities and differences

The creeping rhizome form of *P.macrantha* appears to be truly sympodial with the possibility that the presence of starch in the central vascular area is mobilised for the development of the many axillary buds that are present on the subterranean portion of the rhizome. The precise separation between upright axis and rhizome portion is difficult to locate. The anatomy of the areas along the length of the rhizome which possess roots at the nodes tends to differ from each other as well as from the aerial portions. Barker (1995) reported that the upright "stem" of *P.macrantha* had the anatomy of a rhizome. The anatomical study presented here has indicated that firstly, it is difficult to define exactly what rhizome anatomy is and secondly, that in *P.macrantha* it depends on which portion of the upright stem is examined (as suggested previously). A similar difficulty in defining the "stem" anatomically and morphologically in *P.caespitosa* was encountered (see below).

Pseudopentameris macrantha was previously quite widely circumscribed. Barker (1995) however, split *P.macrantha* into two species, *P.macrantha* and *P.caespitosa,* on the basis of floret size and growth form. Specimens with smaller florets generally have branching stems (*P.macrantha*), while those with larger florets are strictly caespitose, and the caespitose form he named *P.caespitosa*. The anatomy of the "stem" portions (sensu Barker 1995) of these two species differ in that in *P.caespitosa* the cortex contains vascular bundles and the sclerified endodermoid sheath is generally absent. However, as alluded to earlier, it is very difficult to precisely define characteristics of the "stem" regions

(v) Pseudopentameris caespitosa

Morphology

Plants up to half a metre in height with a caespitose form, branching from basal portions of the plant. There is a main basal portion to the plant, which then branches to give rise to

several aerial axes. These in turn have axillary buds in the lowermost internodes which frequently branch to produce further aerial axes. Roots are confined to developing from the nodes of the basal part of the plant. The inflorescence axes bear terminal inflorescences. Further aerial branching does not take place in *P.caespitosa*.

Anatomy

T/S base of plant

The epidermis is a single layer and is composed of brick shaped cells. A hypodermis consisting of four to five cell layers is present and is composed of loosely arranged cells with thin cell walls. The cortex is composed of unspecialised parenchyma cells and is approximately ten cell layers in thickness. The cortex also contains vascular bundles. An endodermoid sheath (sclerified band) consisting of two to three cell layers is present and contains developing vascular bundles. The central area also contains vascular bundles which are very closely arranged, amphivasal and are enclosed by a sclerified bundle sheath. Starch is absent from all of the tissues.

T/S basal portion of aerial axis (single stemmed area)

An epidermis is present and is composed of brick shaped cells. Directly below the epidermis is a parenchyma layer consisting of three to four cell layers. This surrounds the central region which consists of unspecialised parenchyma cells and also contains the vascular tissue. The vascular bundles are scattered within the central area and are mixed, being either bi-collateral or with the xylem arranged in a u-shape, and are enclosed by a sclerified bundle sheath.

T/S lower inflorescence axis

The epidermis consists of a single layer of cells which are brick shaped and have the outer wall thickened. A cuticle is present and stomata are absent. Directly beneath the epidermis is a sclerenchyma band composed of approximately five cell layers and also containing developing vascular bundles. The central area is composed of unspecialised parenchyma cells which break down in the centre to form a hollow pith. The vascular bundles are scattered within this region and are bi-collateral with a single-layered bundle sheath.

Growth form affinities and differences

The upright, caespitose growth form of *P.caespitosa* differs from the creeping rhizomatous form of *P.macrantha* and the various portions of the plant also differ in their tissue arrangement. The caespitose form, while stout, is regularly found within Poaceae as well as Restionaceae. The basal branching that is observed is usually through development of the axillary buds located on the lower nodes of the basal portion of the plant. This is described as tillering by Clark & Fisher (1986); Bell (1991). The branching is usually intravaginal in these forms which leads to tiller clumps i.e. tufts. If the branching is extravaginal (i.e. breaking through the leaf sheath) then this leads to the development of rhizomes/stolons which in turn form intavaginally branched tufts at their nodes (Clark & Fisher 1986; Bell 1991). Branching can also occur from upper nodes, intavaginally, which results in the formation of aerial tillers (Clark & Fisher 1986; Bell 1991). In *P.caespitosa*, the tillering is confined to the basal nodes of the plant. The precise recognition of the "rhizome" and aerial axes in these caespitose forms can be difficult as much of the plant is orientated in a vertically upright growth position. If the most terminal axis is followed from tip to base, the merging between the aerial axis and the upright rhizome portion can be observed, but the merging region differs anatomically to both the "rhizome" portion and the aerial axis.

(vi) Pentaschistis pallescens

Morphology

Plants with closely spaced internodes contributing to a short, vertical rhizome which is several centimetres above the soil surface. The leaf sheaths are deciduous and roots arise from the nodes and are thus aerial for some portion before entering the soil. Above this single stemmed region the plant branches to form aerial axes which in turn branch at basal nodes. There are no aerial cauline innovation buds and the basal branches give rise to terminal inflorescences. The plants are confined to moist areas, often growing in streamside verges.

Anatomy

T/S upright base

The epidermis is comprised of a single cell layer of flattened cells. The cortex is expanded to approximately eight cell layers in thickness and is composed of parenchyma cells containing starch granules. Tannin deposits also occur in this region. A sclerified region (endodermoid sheath) is present and consists of one to two cell layers. Associated with

this band is a ring of amphivasal vascular bundles, which merge into the central area. The central area is composed of unspecialised parenchyma cells and contains vascular bundles scattered throughout. The vascular bundles are amphivasal and are enclosed by a sclerified bundle sheath.

Growth form affinities and differences

The single stemmed portion which gives rise to roots at the nodes is similar to the basal portion of older plants of *P.thuarii*. The vertical portion of the rhizome in *P.pallescens* does not become lignified and also branches to form a series of tillers from the basal portions of the plant, which differs to the pattern in *P.thuarii*. Where the inflorescence axes are formed, no further branching is observed. The presence of basal cauline buds would suggest that the renewal growth could continue from any of the cauline buds that are located in the axils of the leaf sheaths of the basal branches. Plants which are confined to sheltered streamside verges may not frequently be burnt and this would result in a continued proliferation of basal branches. If the aerial portions were removed, renewal could occur from the basal cauline buds located at the basal portion of the plant.

(vi) Merxmuellera cincta

Morphology

Plants forming large, persistent tussocks and attaining up to two metres in height. Plants with stout subterranean rhizomes with internodes closely spaced and often swollen. Roots arise at nodes along the length of the axis. Renewal growth is from an axillary bud situated below the current aerial axis on the rhizome node in the axil of the leaf sheath. Aerial axes are formed from the upward turning of the apex of the rhizome internode. An axillary bud is positioned in the axil of the leaf sheath of the first internode of each aerial axis. The first two internodes of the aerial axes are closely spaced, but the following internode is elongated and the internodes remain elongated in the aerial portion.

Anatomy

T/S rhizome

An expanded hypodermis consisting of between three and five cell layers in thickness appears to be the outermost layer. An epidermis or periderm could not be identified. The cortex consists of parenchyma cells, is approximately five to six cell layers in thickness and contains a few vascular bundles. The parenchyma cells are packed with starch granules. The endodermoid sheath, composed of two to three cell layers, encloses the

central region which is composed of parenchyma cells. Starch granules are also densely concentrated in the parenchyma cells of this area. The vascular tissue is scattered throughout the area, but tends to anastomose from the centre outwards towards the roots. Roots appear to arise from the region just outside the endodermoid sheath (possibly a PTM?). The vascular bundles are amphivasal and are surrounded by a sclerified bundle sheath.

T/S basal inflorescence axis

The basal inflorescence axis is bounded by a single layered epidermis. The cortex is expanded to approximately six cell layers in thickness and is composed of parenchyma cells and contains some vascular bundles. The endodermoid sheath is composed of two to three cell layers and has a few, elongate vascular bundles associated with it. The central region contains most of the vascular tissue and is composed of parenchyma cells which contain a few sparsely concentrated starch granules. The vascular bundles are amphivasal and are enclosed by a sclerified bundle sheath.

T/S lower inflorescence axis

The lower inflorescence axis corresponds to the first elongated internode of the aerial axis and is surrounded by an epidermis composed of cells with thickened walls. The cortex is approximately three cell layers in thickness and contains a few vascular bundles. The endodermoid sheath comprises two to three cell layers and lacks any vascular bundles. The central area is composed of unspecialised parenchyma cells and contains the vascular tissue. The vascular bundles are arranged in a distinct pattern, with amphivasal bundles scattered towards the exterior of the central area and bi-collateral vascular bundles arranged in a ring within the centre of the area.

T/S inflorescence axis internode

The epidermis is composed of brick shaped cells and is followed directly by a thin band of parenchyma cells. A sclerenchyma sheath is present, but is dominated by a ring of elongate vascular bundles. The central area is composed of unspecialised parenchyma cells and contains the vascular tissue which is arranged into three regions. The outermost vascular bundles are amphivasal. This is followed by a ring of more elongate vascular bundles which are bi-collateral and centrally, both amphivasal and bi-collateral bundles are present and are generally scattered within the area.

T/S inflorescence axis node

The inflorescence axis node is bounded by a single layered epidermis composed of brick shaped cells. Directly below the epidermis is a thin band of sclerenchyma cells. An enlarged parenchyma region containing, large elongate cells takes up a large proportion of the cross section. The central area also contains vascular tissue which consists of both amphivasal and bi-collateral vascular bundles which are scattered within the central area.

Growth form affinities and differences

The robust tussock form that is formed from the stout subterranean rhizome of *M.cincta* has basal innovation buds on the first internode of each of the aerial axes. However, Linder & Ellis (1990) had difficulty classifying the ecological strategy of *M.cincta* because the tussocks do not display evidence of resprouting after fire. The authors placed *M.cincta* into the coppice category largely because of the basal innovation bud position. The accumulation of dense starch granules in all of the parenchyma cells of the rhizome suggest that the rhizome performs some storage function. Whether this is for renewal growth, flowering each season or coppicing after fire is a question that needs further investigation.

(vii) Pseudopentameris obtusifolia

Morphology

Plants with a knotty base which is vertically orientated and gives rise to basal shoots (branches or tillers) (Pl. 27, Fig. 1). The buds are located in the axils of the leaf sheath and are often present on most of the lower internodes of the basal part of the plant (Pl. 27, Fig. 2A). The aerial axes also have axillary buds present on the nodes in the axil of the persistent leaf sheath (Pl. 27, Fig. 2B). The buds seem to be initiated in a spiral arrangement which is consistent with the leaf arrangement. Thus the plant is able to branch both aerially and basally. The leaves are tough and spiny and seem to be formed at the more apical portions of the new branches and thus are associated with seasonal growth (Pl. 27, Fig. 1). The plants can be up to a metre in height and are generally found in mature Fynbos stands, but are often restricted to rocky outcrops where there is less competition among plants in the dense stands of mature Fynbos. The plants thus form a "graminoid-shrublet" with a terminal inflorescence axis. In herbarium specimens collected in the first year after fire the growth form is strictly caespitose, with no aerial branching at all.

Anatomy

T/S base

The epidermis is composed of a single layer of brick shaped cells. The cortex is comprised of approximately five cell layers and lacks vascular bundles. The endodermoid sheath is sclerified and comprises three to four cell layers and contains developing vascular bundles. The central area is composed of unspecialised parenchyma cells and contains the bulk of the vascular tissue (Pl. 27, Fig. 3). The vascular bundles anastomose outwards towards the roots which tend to form on the exterior region of the endodermoid sheath and break through the cortex. The vascular bundles are amphivasal and are enclosed by a single layered bundle sheath (Pl. 27, Fig. 3).

T/S main axis

The epidermis is composed of a single layer of brick-shaped cells. The cortex comprises six to eight cell layers and is composed of rounded parenchyma cells. The endodermoid sheath has a PTM to the exterior, which gives rise to a cauline bud. The endodermoid sheath consists of approximately five cell layers and vascular bundles are not associated with it. The central area is composed of unspecialised cells and contains the vascular bundles, which are amphivasal.

T/S node of main axis

The epidermis consists of brick-shaped cells which are lignified. Directly below the epidermis is another lignified area (approximately three cell layers) staining deep brown and composed of thick walled cells, probably a hypodermis. The cortex is composed of two to three cell layers of translucent parenchyma cells. The PTM is approximately four to six cell layers in thickness and the cauline bud originates from this band. The cauline bud has numerous traces which move from the central area in a longitudinal fashion, through the sclerenchyma band and PTM to feed directly into the bud. The central area is composed of unspecialised parenchyma and contains the vascular bundles which are amphivasal and are enclosed by a single layered bundle sheath.

T/S aerial axis

The epidermis is composed of brick-shaped cells, but is not well differentiated. A cuticle is absent. Stomata are absent. A sclerenchyma band composed of two to three cell layers of thick-walled cells is present and contains vascular bundles. The central area is composed of unspecialised parenchyma cells, which break down centrally to form a

Plate 27. Morphology and anatomy of *Pseudopentameris obtusifolia* (Figs. 1-3) and anatomy of *Arundo donax* (Figs. 4 & 5).

Figure 1. Morphology of *Pseudopentameris obtusifolia* showing vertical orientation of stems (max) and persistent leaf bases (olf) with current leaf growth confined to the upper nodes (lf). Branching of the stems occurs at the base of the plant (ba) and may also occur aerially.
Figure 2. Plan drawing of stem morphology of *Pseudopentameris obtusifolia*. **[A]** Detail of bud location at base of plant showing where branch initiation (br) takes place and spiral arrangement of axillary buds (ab). Stippled lines indicate position of leaf base (slf). **[B]** aerial portion of stem showing location of axillary buds and sheathing leaves (slf).
Figure 3. T/S base of *Pseudopentameris obtusifolia* showing cortex (co); endodermoid sheath (es) and amphivasal vascular bundles (vb). (vt) = vascular trace to leaf base; (cp) = central parenchyma.
Figure 4. T/S aerial axis of *Arundo donax* showing the cortex (co) and location of sclerified cells (sc) associated with the bi-collateral vascular bundles (vb) and the hollow pith (pi) in the centre.
Figure 5. T/S inflorescence axis of *Arundo donax* showing sclerenchyma pole (scp) associated with outermost vascular bundles. The central parenchyma (cp) is solid. The vascular bundles (vb) are bi-collateral.

[Bars = 27 μm**]**.


olf
lf
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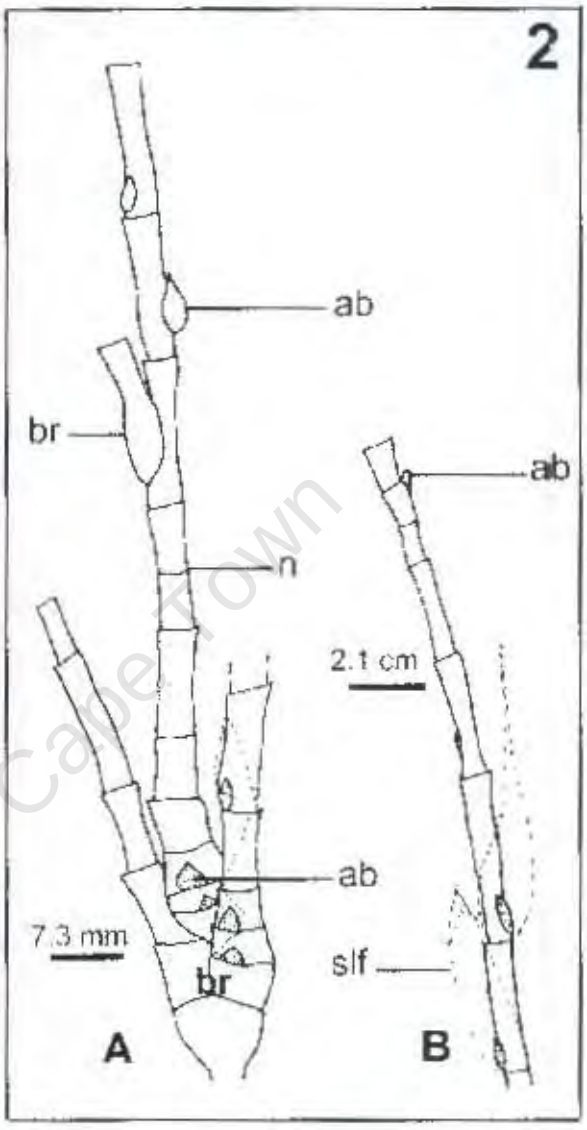
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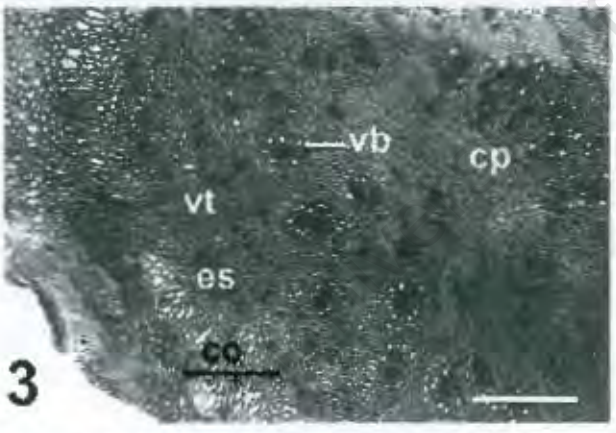
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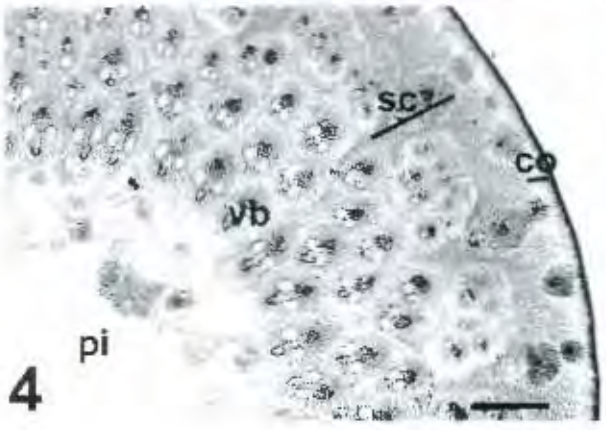
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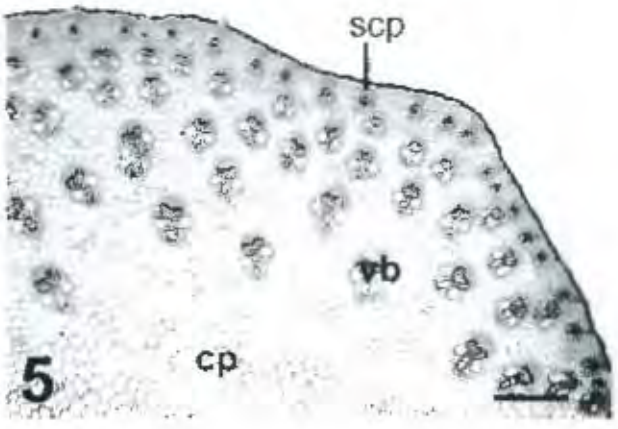
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hollow pith. The central area contains bi-collateral vascular bundles arranged in a ring and enclosed by a one-layered bundle sheath.

T/S aerial axis below inflorescence

The epidermis is composed of a single layer of brick-shaped cells with the outer walls slightly thickened. A cuticle is present and stomata are located in a level position at intervals along the epidermis. Directly below the epidermis is a sclerenchyma band composed of five to eight cell layers and containing cells with concentrically thickened cell walls and a few vascular bundles. The central area is composed of unspecialised parenchyma, it does not break down to form a pith and contains the vascular tissue which is arranged in a ring. The vascular bundles are bi-collateral and are enclosed by a single layered bundle sheath.

Growth form affinities and differences

The growth form of *P.obtusifolia* conforms closely to the "graminoid shrub form" that is described by Dahlgren et al. (1985). The similarity of these graminoid shrub forms throughout the monocots (e.g. *Borya*, *Calectesia* and *Xerophyta*) is probably only superficial, with possible homology between the vertical stems and clearly, cases of convergence in each case. The possession of both basal and aerial cauline buds allows a high degree of flexibility within the life history of the plant. Basal innovation buds allow the plant (seedling) to establish in the first year after fire and ensure a successful flowering event. The aerial cauline buds allow aerial branching which ensures persistence in a competitive vegetation type. In addition, basal innovation buds, suggest the possibility of basal rejuvenation following damage of aerial portions. However, the retreat of the mature forms into rocky outcrops indicates that this possibility is not often employed, the longer term persistence in the vegetation is probably better achieved by location rather than resprouting.

The morphology and anatomy of the "stem" portions along the length of the plant seem to show some similarity and appears to be consistent from the base upwards where the stems are ensheathed by the persistent, dead leaf bases. The precise area of where the stem becomes the flowering axis is not clear as it emerges apically from the new leaf growth area. The floral axis is quite different to the stems because of the difference in leaf morphologies, the floral axis having reduced leaf sheaths and fewer laminate leaves at the nodes, particularly in close proximity to the inflorescence.

There appears to be a noticeable trend in the growth form of the Arundinoid Cape grasses that have been examined in this study, namely that the seedling growth form (i.e. in the first year after fire) differs from the mature growth forms (>three years). This was particularly noticeable in *Pentameris thuarii* and in *Pseudopentameris obtusifolia*, where the mature forms have elaborate cauline bud systems and the stems become "single stemmed" basally with age. Unfortunately, the comparison between seedling anatomy and adult anatomy in *P.thuarii* could not be determined in this study, due to seedling mortality. It is possible that such a trend may be present between *P.macrantha* and *P.caespitosa*. The larger flowers and caespitose form may be related to the after fire "flush" that is seen in the fist year in many Fynbos plants, while the more "rhizomatous" form and branching stems with smaller flowers may be the mature phase persisting in the Fynbos vegetation. Further morphological characteristics were not examined by Barker (1995), but, in defence of recognising two species, they often co-occur. The precise nature of co-occurrence was not elucidated by Barker (1995), but at Silvermine, where the two species were collected for this study, they co-occur in mosaic patches which have been subjected to different fire regimes. Further examination of the ecology, life history and population structure in such localities would be desirable for these two species.

(viii) Arundo donax

Morphology

Plants with stout, woody subterranean rhizome. Aerial axes are produced by regular sympodial branching from the apex of rhizome internodes. The renewal of rhizome internodes is from an axillary bud on the last internode of the rhizome just below the upturned aerial portion, which often terminates with an inflorescence. The aerial axes in *Arundo* are branching, each branch tending to be a vegetative shoot. Basal innovation buds seem to be suppressed. The branching is by extravaginal tillering so that the branches break through the thick, sheathing leaf bases, which usually ensheath the entire internode of the aerial axis.

Anatomy

T/S aerial axis

The epidermis is composed of brick-shaped cells with the outer walls slightly thickened. Directly below the epidermis is a parenchyma band, comprising two to three cell layers. This effectively constitutes a cortex (due to the position). The strange feature of this region is the associated developing vascular bundles on the inner surface of the band (Pl.

27, Fig. 4). Following on from the parenchyma band, the tissue arrangement is odd. There is no sclerenchyma band or endodermoid sheath which forms a continuous cylinder as is commonly found in either a rhizome sort of construction or an aerial axis construction. Instead, the vascular bundles in the region below the parenchyma band are thickened and elaborately expanded into at least three cell layers (Pl. 27, Fig. 4). The bundles are very closely arranged in this region concentrated into groups, effectively and functionally creating a "sclerified" region, but, as stressed before, not a continuous cylinder. The further peculiarity of the tissue arrangement is that finger-like portions of parenchyma traverse between the groups of vascular tissue, merging into a central tissue area which is composed of parenchyma cells which tend to break down centrally, forming a hollow pith (Pl. 27, Fig. 4). The vascular bundles are all bi-collateral. The nodal region displays the same anatomy and tissue arrangement, except that the node is solid.

T/S inflorescence axis

The epidermis is composed of brick shaped cells with slightly thickened outer walls. Directly below the epidermis is a system of peripheral vascular bundles, each situated directly beneath a sclerenchyma pole (Pl. 27, Fig. 5). The sclerenchyma poles do not occur unless in association with the vascular bundles. These structures (i.e. pole plus bundle) are arranged in a regular ring within a parenchyma band which surrounds the central area containing the vascular tissue (Pl. 27, Fig. 5). The central area is composed of unspecialised parenchyma cells and breaks down centrally to form a hollow pith. The vascular bundles are bi-collateral and are enclosed by a single layered bundle sheath.

Growth form affinities and differences

Anatomically, the aerial axis of *A.donax* is difficult to describe. There are two possible ways of interpreting such a tissue arrangement. The first being that the "parenchyma band" is an unsclerified (positionally) sclerenchyma band. The further areas are simply a modified central region, with a hollow pith centrally. Such a tissue arrangement is similar to most grass inflorescence axes. However, such an interpretation is inadequate as the complexity of the vascular bundle groupings is not adequately explained. The second interpretation is that the parenchyma band is a cortex containing vascular bundles, the following region a sort of sclerified region with a central area and a hollow pith. Neither of the interpretations is adequate and will tend to force the stem into one or another category i.e. inflorescence axis or rhizome. In a similar vane, the kind of vascular bundle does not serve to "identify" the organ more clearly either. Other features such as a

continuous leaf sheath along the internode and extravaginal branching make the interpretation of the organ incredibly difficult, with features of both a rhizome organ and inflorescence axis organ. For the coding of parameters (Chapter 3), the descriptions given in the anatomy section above is exactly how the organs were treated i.e. for the aerial axis: a parenchyma band, no sclerenchyma band, a hollow pith etc. The lack of a sclerenchyma band directly below the epidermis may be an uncommon feature for a grass inflorescence (aerial) axis, but in other monocots, the presence or absence of a sclerified band is highly variable.

When the anatomy and tissue arrangement of the inflorescence axis is considered and compared with the aerial axis there are a large number of similarities. The main differences are in the arrangement and structure of the peripheral bundle system and the location of sclerenchyma, which, in both organ portions is peculiar, not being arranged in the more usual continuous cylinder.

Bell (1991) points out that the aerial branching in *Arundo* is odd, being extravaginal, whereas most grasses will display intravaginal aerial tillering. Extravaginal branching usually leads to the formation of rhizomes or stolons (Clark and Fisher 1986; Bell 1991) and the vegetative branches of *A.donax* are morphologically and anatomically similar to the main axis. The exact interpretation of the organ portions on the basis of anatomy and morphology remains enigmatic.

There is a superficial similarity of *Arundo* with cane-like bamboos with aerial branching, but the basal sympodial branching and the (almost) solid axes (compared to very hollow axes and hollow nodes) is quite different to the complex branching and morphology of bamboos. Bamboo vegetative branches are complex, the aerial axillary buds often having a complex series of axillary buds of their own which are able to produce either vegetative or floral branches (McClure 1993; Wong 1986; Bell 1991).

(viiii) Tribolium obtusifolium

Morphology

Plants are usually caespitose with intravaginal tillering basally, forming short tussocks and producing terminal inflorescence axes. However, another form of *T.obtusifolium* occurs. It is a caespitose plant which develops runners and co-occurs in the same locality as the previous form (Pl. 28, Fig. 1). The runner form is only found in seasonally, moist hollows and the runners are able to produce aerial portions and ultimately new caespitose tussocks with their own runners. Linder & Davidse (1997) suggest that the formation of this structure is due to disturbance. The runners are generally formed by extravaginal

branching which occurs from the third or fourth node of the upright, basal axis of the plants. The portion of runner resulting from extravaginal tillering is often referred to as a rhizome or a stolon (sensu Clark & Fisher 1986; Bell 1991). The distinction between these two extravaginal tillers appears to be whether they are subterranean or superficial on the substrate, and, additionally whether it is monopodial or not. The runner of *T.obtusifolium* never enters into the soil, it always remains on the surface, attaching to the soil at intervals by several roots at the nodes, which are in contact with the substrate. The moist hollows seems to be a condition which stimulates this vegetative cloning of the plants. However, each of the clones is able to produce its own flowers. In clone material that is in flower, the runners are always dried out and appear non-functional. This coincides with the drying out of the hollows. The runners can extend for up to 100 centimetres before turning upright to form a new plant. In all of the material examined, there was no evidence of axillary buds which would give rise to new plants. Hence, the runners appear to be sympodial. Monopodial runners seem to be restricted to creeping, mat-forming grasses (Holttum 1955, Clark & Fisher 1986; Bell 1991). The internodes of the runners are very elongated and the leaf sheaths are restricted to the nodes.

Anatomy

T/S rhizome

The epidermis is composed of a single layer of brick shaped cells. A thin cortex comprising two to three cell layers is present. The endodermoid sheath is distinct and is composed of approximately five layers of small sclerified cells. The central area is composed of unspecialised parenchyma cells and contains the vascular tissue. The vascular bundles are sparsely distributed in this area and are amphivasal and enclosed by a single layered bundle sheath.

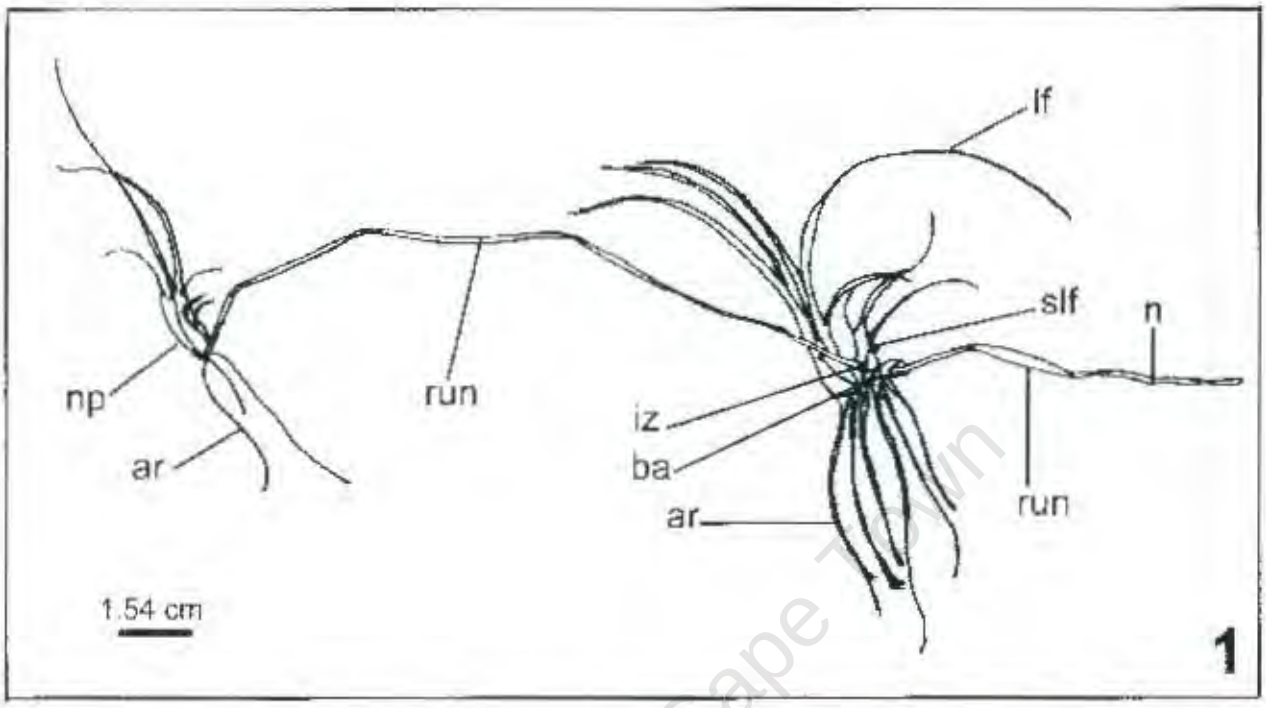
T/S runner internode

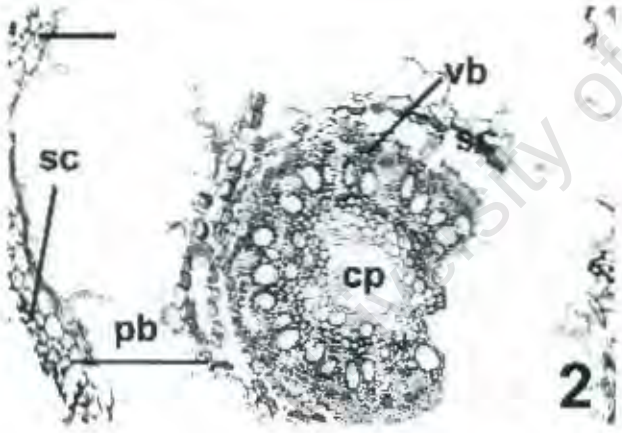
The epidermis is composed of brick shaped cells with the outer wall thickened. The tissue band directly below the epidermis is composed of three cell layers and consists of highly sclerified small, rounded cells. A parenchyma band consisting of up to ten cell layers is present, the parenchyma cells being large and isodiametric (Pl. 28, Fig. 2). The central area is bounded by another sclerenchyma band comprised of two cell layers (Pl. 28, Fig. 2). The vascular tissue is only found in the central area and is arranged in a ring, with the central area comprising parenchyma cells. The bundles are very closely arranged together in this ring, so that the bundle sheaths merge into each other and it is difficult to

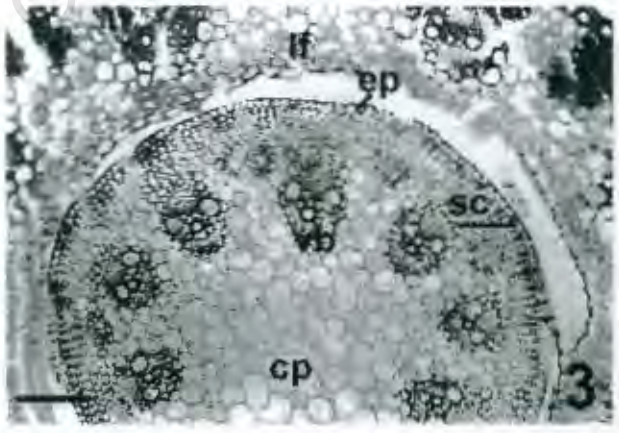
Plate 28. Morphology and anatomy of *Tribolium obtusifolium*.

Figure 1. Morphology of runner form of *Tribolium obtusifolium* showing initiation of runner (iz) breaking through axil of sheathing leaf base (slf). (ba) = base of plant; (ru) = runner; (n) = node; (ar) = adventitious root; (lf) = leaf; (np) = new plant.
Figure 2. T/S runner showing the two sclerenchyma bands (sc); the parenchyma band (pb) and the central region with bi - collateral vascular bundles (vb) arranged into a ring and the hollow, central pith (cp).
Figure 3. T/S inflorescence axis enclosed by leaf (lf), showing sclerenchyma band (sc) directly below the epidermis (ep) and bi-collateral vascular bundles within the central area (cp).

[Bars = 9 μm (Figs. 2 & 3)**]**.







distinguish individual bundles (Pl. 28, Fig. 2). The vascular bundles are bi-collateral and the bundle sheath cells have their lower walls thickened.

T/S inflorescence axis

The epidermis consists of brick shaped cells, with all the cell walls equally thickened. A cuticle is present. Directly below the epidermis is a sclerenchyma band which comprises two to three cell layers (Pl. 28, Fig. 3). The central region consists of unspecialised parenchyma cells and contains the vascular bundles, which are arranged in a ring. The vascular bundles are bi-collateral and are enclosed by a single layered bundle sheath (Pl. 28, Fig. 3).

Growth form affinities and differences

The extravaginal tillers (runners) that are produced by *T.obtusifolium* are commonly found within the grasses (Holttum 1955; Clark & Fisher 1986; Bell 1991). A similar kind of vegetative proliferation is seen in *Chlorophytum comosum.* However, the nature of the branch is entirely different. The runners of *C.comosum* are simply lax inflorescence axes i.e. terminal axial structures, whereas in *T.obtusifloium* the branches actually break through the leaf sheath and are thus, extravaginal. The function of the two structures is the same. The process of the formation of new plants also differs, with the runner of *T.obtusifolium* turning upright to form aerial portions, while in *C.comosum* the new plants are formed by false viviparity. This comparison between two similar structures which are often termed "stolons" serves to illustrate that they can be very different developmentally. In addition to this, these two structures differ anatomically with the "stolon" of *C.comosum* having the same anatomy as its inflorescence axis, while that of *T.obtusifolium* differs to the anatomy of its inflorescence axis, having an expanded parenchymatous band and an additional sclerenchyma band.

CONCLUSIONS

A number of important points have emerged from the comparison of the morphology and anatomy of the growth forms of monocots sampled in this study.

1. In unrelated taxa there are often similarities in the overall habit of plants. The examination of morphology and an in-depth view of the anatomy of the various parts of the plants often showed that the similarity is superficial and could be considered as cases of convergence. Such examples include the "graminoid shrub" growth form in monocots

as seen in *Dasypogon bromeliifolius*, *Borya nitida*, *Calectesia cyanea* and *Pseudopentameris obtusifloia*; the similarity in corm morphology and development in Hypoxidaceae and Iridaceae and the similarity in vascular pattern between *Borya nitida* and Dioscoreales to mention a few. On the other hand, similarities in basic anatomical histology, both positionally and functionally could often be seen among unrelated taxa. This revealed that there is a general pattern of plant parts among the monocots examined and is considered further in point 4.

2. The differences that were discovered among the taxa were often linked more closely to the kinds of habitats that the plants occurred in as well as the kind of form of the plant, rather than to the fact that the taxa were unrelated (or related). This suggests that extrinsic factors have influenced the ultimate growth pattern that is achieved by the plant, but that there is a phylogenetic constraint which is seen in the initial development of the plant (and refers to point 3). The often repetitive patterns that are described in the various plant parts are testimony to the possibility of a general pattern (a phylogenetic constraint) suggesting a complex of historical events which have led to the evolution of the certain variations in growth form of monocots.

3. The developmental phase (juvenile phase) is important in determining monocot form. Most of the seedlings examined initiated modifications to the basic structures within the first year of growth, so in *Zantedeschia*, *Eriospermum*, and *Wachendorfia* small swollen structures equivalent in position and function to adult tubers had formed. Similarly, in *Lachenalia splendida* the swollen leaf base of the first leaf was developed and the seedling also mirrored the life history of the adult, losing aerial portions at the end of the growth season. In *Chlorophytum comosum*, the formation of root tubers also occurs early in the developmental phase. The only seedling that did not mirror the adult form, was that of *Thamnochortus spicigerus*, the rhizome was not well developed until at least two years of growth and the aerial portions displayed juvenile foliage in the first two growth seasons. The importance of the juvenile phase was alluded to by Tomlinson and co-workers in their studies of arborescent monocots. Tomlinson further suggested that arborescent monocots with their extended establishment phase are the basic monocot habit and that the herbaceous forms (and variations thereof) are merely extended juvenile phases in the life history of monocots with *Tillandsia usnoides* being an extreme example displaying precocial flowering (see Tomlinson 1970a). In this study, the modification of the hypocotyl in the seedling seemed to be an important clue as to the kind of growth form that is reflected in the adult e.g. short hypocotyls in horizontal rhizomatous forms in *Myrsiphyllum scandens* and *Canna indica*; compact, very reduced hypocotyls in short,

vertical rhizome forms in *Chlorophytum comosum*, *Lachenalia splendida*; swollen hypocotyls in "tuberous" forms in *Zantedeschia aethiopica*, *Eriospermum*, and *Wachendorfia*. In this study, most of the seedlings examined required an establishment phase, albeit that they were herbaceous forms, except for *Canna* which takes six months from germination to elaborate vegetative growth and flowering and some Fynbos grasses where flowering is effected in the first year after fire. This may be related to both the growth form e.g. in storage forms such as *Zantedeschia, Wachendorfia* and *Lachenalia* (and in *Canna*) and the habitat e.g. Restionaceae in which the low nutrient status shapes the growth rates and subsequent carbon allocation of the plants (and in Fynbos grasses where fire and competition in the landscape are important factors).

4. A general pattern of form in morphology and anatomical features can be highlighted and is probably due to some initial functional feature which has become historically a taxic similarity or phylogenetic constraint. For example, rhizomes which are subterranean generally have scale leaves, which are reduced and don't function in photosynthesis, but still retain a full vascular connection with the main vascular cylinder (see Bell 1980b); or vertical, aerial axes which terminate in flowers often have a sclerenchyma band which surrounds the central vascular region. There is however, a lack of constancy and regular repetition of specific structures/tissues which is likely to reflect variation at one level or another and this depends at which level the examination is taking place, or modification of functional requirements e.g. sclerenchyma bands are not always present (*Canna*) or parenchyma bands can be positionally equivalent, but differ on a functional level where in many internodes, the parenchyma cells will be filled with starch granules.

5. The variation in the pattern of xylem and phloem arrangement in the vascular bundles from one plant portion to the next is possibly related to the vascular construction pattern of monocots described in detail by Tomlinson and co-workers. The sympodial habit by necessity must have a complex network of vascular connections from the "central cylinder" to the roots, leaf sheaths (both in aerial and non-aerial axes) and to the renewal bud which must develop into the new sympodium. As has been shown, the vasculature consists of an inner and an outer system. The outer system is often not developed in herbaceous forms, but the evidence of it in the system is seen in central bundles, which end blindly after changing direction and moving towards the exterior. Due to the continuous nature of the vascular system (with direct connections in the vascular bundles between a node and the preceding internode) the vascular system has to be examined from the start of the branch to the tip as has been the case in many vascular construction studies. However, a question that is not often considered is how the xylem and phloem

ontogeny is affected from the start of the branching process to the end, from a three dimensional view point and how this affects the positional pattern of these tissues in the vascular bundle at various points along the branch (i.e. from one plant portion to the next) and why the pattern should differ, giving rise to the variation in vascular bundle types that are described in this study.

To summarise, there is a certain amount of similarity as well as variation which can be considered for further interpretation. It is possible that the variation in certain features of the internodes and growth forms examined can be tested in a rigorous framework. The testing of hypotheses concerning monocot growth forms is the subject of Chapter 3, but the main questions worth considering now are:

1) Is the variation measurable so that certain features can be deemed important in distinguishing between certain internodes or growth forms

2) Are the plant portions discrete or is the whole sympodium (branch or module) a continuation of a series of processes and

3) Can certain growth forms be recognised and are these a result of history, function or extrinsic factors?

CHAPTER 3

Analysis of growth form parameters and organ identification

INTRODUCTION

Theoretical perspectives on analytical techniques

The main objectives of this chapter are to determine whether structures that comprise the axial system in monocots are discrete or continuous and which of these structures (if any) are homologues. Thus, the recognition of similarity of structures occurs at two levels: within plants and between plants. The initial assumption of form in this study of monocot growth forms is that there are no discrete structures (or categories). This leads to the interpretation that there is no such thing as an organ and thus, no distinct organ categories can be recognised. (A continuum, although not recognising categories, signifies some sort of structure in the data where one organ merges into another without a distinct boundary apparent). Once this assumption has been tested and falsified i.e. some sort of structure has been found within the data, then, a second set of hypotheses should be formulated. These can also be divided into two phases. The first of these uses the same data set, and will be undertaken in this thesis, that is to identify the types of structure in the data. The second of these is an opening for new research where hypotheses about the "types" of structure (or groups) can be formulated and tested where new experiments and data collection are designed.

According to Gordon (1981) a data set comprises *n* objects each being described by several variables. The aim of any classification is to investigate the structure within the set of objects and in particular to ask whether the objects fall naturally into a number of small groups of objects such that the objects within a group are more similar to one another than any outside of the group. If objects cluster then a classification exists. In contrast, if objects don't cluster, then no classification exists. One may also wish to examine the structure within the variables.

Gordon (1981) clearly identifies the differences between *classification*, *assignment* and *identification*. It is apparent that classification is often thought of as being all three of these things. Gordon refers to the fact that *classification* assumes that the number and composition of groups are not known at the start of the classification. Methods of

classification should, therefore, be (philosophically) exploratory in nature. After the classification has been erected, then processes of *assignment* to specified groups and *identification* of objects by descriptive variables should be possible. One of the goals of this chapter is to facilitate the placement of objects (organs) into specified groups which are identifiable by a limited number of variables (descriptors). In this chapter, the aims are to (1) set up a *classification* of organs; (2) try to create a way to easily *assign* organs to the specified groups and (3) to create a number of "identifiers" or "descriptors" (variables) which allow the *identification* of a set of organs.

The exploratory nature of a classification should be followed by some sort of confirmatory analysis (Gordon 1981, Krzanowski 1988). However, this is often difficult as data which are analysed by classification procedures are rarely of the kind which permit straightforward statistical testing. Gordon (1981) suggests this to be due to the fact that such data can rarely be regarded as samples from one or more multivariate normal distributions, and that the data which have been analysed are all that are available to the investigator. Further data subject to the same conditions may be difficult to collect. Thus, to my mind, the classification should act as a framework for formulating and testing specific hypotheses - much like a phylogeny forms the basis for testing hypotheses about biogeography or adaptational scenarios. For this, a new set of data should be collected. So for the growth form data, the functional significance of such groups needs to be considered using a new set of information, and similarly, how the actual organs respond to manipulation or changes in conditions etc. should also be assessed using a new set of data. This thesis focuses on the exploratory phase and predictions about the results can only be made if new data sets are collected to test the many possible hypotheses that may arise from the classification.

It is important to describe which type of classification method is most pertinent to the growth form data. The Trollian concept (Troll 1937) of plants proposes that the organs root, stem, leaf and trichome are all independent and distinct categories of plant division, they are not interrelated and thus show no nested hierarchical nature to these organs. So, from this perspective, cluster analysis would not be an appropriate method of classification. Instead, something like a k-means clustering would be more suitable so that the degree of isolation between specified categories can be quantified. In the k-means method, the procedure is to initially categorise objects into groups and then test the difference in the means between each category. Therefore, using this method, the groups must be defined *a priori*. As this is not the intention of this thesis, it is only feasible to identify the structure in growth form data from an exploratory perspective, using a method that can detect the underlying pattern of the relations between multiple variables.

Holttum (1955) interpreted the variation in growth form in the monocots as variations on a theme. This approach would suggest that there is a single basic pattern and deviation from this occurs to give several "offshoot" groups. Data collected from this perspective would best be represented in some form of geometric method where points are represented in n-dimensional space and the proximity of points to each other is a measure of the similarity of two objects. However, there is the possibility that nested relationships could occur in any of the "similar" groups. As such, some form of clustering method should be able to clarify the hierarchical relationships within the "offshoot groups". Clustering methods do however impose structure on the data - usually a partition or a set of partitions (Kruskal 1977; Gordon 1981). In the ideal situation, no preconceived categories or within group structure should be invoked initially in the analytical procedure. A method that reflects natural groupings to the extent to which they are present is desired in the first instance. For this reason, to avoid a preconceived notion of structure, a geometric analytical approach was followed initially in the analysis of the monocot growth form data. Throughout the analytical approach Gordon's (1981) suggestion that the data should not be obliged to form groups i.e. the data do not form isolated dissimilar clusters, should always be borne in mind.

In addition, Holttum's (1955) proposal of monocot growth forms also hints at the possibility that "categories" such as those proposed by Troll (1937) may not necessarily apply to monocots. The organ categories in Troll's (1937) system are based on a dicot plant model and as such may be inappropriately extrapolated to monocots. The organ categories are in most cases difficult to homologise with monocot organs and similarly, non-seed plants and lower vascular plants. A model for monocot growth form and "organs" is desirable as Trollian concepts and ideologies surely cannot be applicable to the monocots. Other major contributors to the understanding of how monocots grow, their vascular construction and function such as Zimmermann & Tomlinson (1972) and Tomlinson (1970a; 1980; 1995) have complemented the Holttum (1955) idea of monocot growth form.

Complications in classifying monocot organs are that the growth is modular and repeating units can either be the same throughout, or show modification into different structures both structurally and functionally. This leads to the possibility that the whole monocot system is malleable according to functional needs or extrinsic pressures. As such, organs need to be assessed in terms of a phylogenetic constraint as well as the extrinsic factors that may be responsible for forced changes. Secondly, modular growth implies that each unit is independent and this poses a problem because the types of classification measures that are available, cannot take this into consideration. It should be recognised that each organ which is comprised of repeating units (internodes) may be an individual organ (both structurally and functionally) or, may consist of several organs strung together,

structurally and functionally distinct from one another. This means that the concept of an individual is difficult to comprehend and recognising individual structures in a clonal organism is a fuzzy area as distinct boundaries are difficult to define. In fact, how to delineate an individual could be a study of its own. It is not the intention of this chapter to consider the clonality of monocots because we need a way to recognise the organs themselves.

Choice of variable type

The type of variables that are best used in this kind of analysis is an important consideration, as the statistical distribution curve of the data determines what kind of classification analysis is most appropriate. In addition to this, the question of how one wishes to recognise the groups is also important. For the growth form data and ultimately the identification of organ types (post classification) it is necessary to have a qualitative description of variables from a practical perspective. Furthermore, for the procedure to be broadly applicable to a range of monocot taxa, a qualitative system would also be preferable. A classification incorporating the detail of taxonomic sampling that is required for such a study, measurement data would take years to collect. This is not to say that quantitative data should not be incorporated, it may be useful to include measures in addition to the qualitative data e.g. the diameter of xylem vessels within different organs could be related to the size of the plant or to the water transport capacity of the vessel.

For the aforementioned reasons, the type of variables that were collected and coded are qualitative - they are nominal variables as well as conditionally present variables where applicable. Such variables (features or patterns) can ultimately behave as descriptors for various organs in the identification process, which is one of the ultimate aims of the classification system. It would be more difficult to describe an organ based on measurements than on binary states. In the mathematical calculations for proximity, an object is better described by a series of binary variables than a single multistate variable (Sokal & Sneath 1963; Gordon 1981, Krzanowski 1988). In the modern approach to classification using cladistic methods, the idea of creating a series of binary variables for a single multistate variable is generally not considered to be appropriate (Stevens 1984; Pimental & Riggins 1987; Maddison 1993; Hawkins et al. 1997). However, calculations of proximity are different to parsimony algorithms for branch addition in cladistics and as such the two methods are not comparable on this point. For this reason, there should be no problem using binary variable coding in similarity calculations as proposed by Sokal & Sneath (1963). In a similarity study such as this, one is only interested in a calculation for proximity in terms of defining the dissimilarity between groups, whereas in the cladistic

approach, the branch addition is affected by the character states themselves - so if each feature is given three characters effectively (by creating several binary characters for a multistate character) this feature is weighted, being scored more often. However, in the phenetic analysis Sokal & Sneath (1963) suggest that, proximity between pairs of objects is probably better assessed if the variables are in a binary form - this may result in a small amount of deweighting of a particular feature, but in terms of the calculation of similarity, *Pij* can be viewed in terms of presence and absence of the variable. In this situation the use of the Jaccard coefficient would be an appropriate measure of similarity.

Sampling

Initially, a single plant was examined from the top to the base for morphological and anatomical characteristics. A regular, rhizomatous growth form was selected for this purpose and the Restionaceous plant, *Thamnochortus spicigerus* was examined. The details of the data selection and recording are outlined in Chapter 2. Variation in features between certain "typical" organs could be seen after close examination and in the anatomy. The exact point of change over from one organ to another was difficult to determine i.e. the exact end of the rhizome and the start of the inflorescence axes. Thus, all possible portions between this area were included in the analysis and each data point used in this chapter is a single internode [Chapter 2, Figure 2.1 (A-C)]. Using internodes as representative portions, the list of taxa in Appendix 2.1 were sampled, incorporating all possible ambiguous zones into the data collection procedure. In this way, a representative sample for monocot growth forms is assumed.

Approach to data analysis

The main goal of this chapter is to find a "natural" structure in the data, in an exploratory manner. Further, it was desirable to use a method which allowed for an easy visual representation of the relatedness between any of the groups that may be found in the data analysis. Following recognition of "groups" it is important to test their integrity and then determine whether there is any structure within the groups. Lastly it important to assess whether there is an underlying structure in the variables that were used in the study to obtain an understanding of the driving forces behind group formation. Thus, the approach to the data analysis in this chapter was as follows:

1) To convert and score all observations as binary variables
2) To calculate a dissimilarity matrix (using the Jaccard coefficient) for the observations

3) To use multidimensional scaling analysis (MDS) to find "natural" group structure
4) Then to assign the data points (internodes) in *n* dimensional space to groups which reflect the natural structure shown in the MDS
5) Then to analyse the grouped data
   5.1) and test the significance of between group variation with MANOVA
   5.2) and to use randomisation of group membership to assess whether the pattern is not due to chance
6) Use cluster analysis to determine within group structure
7) and lastly, measure the association between variables to determine latent factors

METHODS AND MATERIALS

Coding the data

The morphological and anatomical characteristics of the sampled monocots were examined and compared for different groups as well as forms in order to assess the similarities and differences. Morphological and anatomical features of plant portions[1] were compiled into a basic list according to how the groups and forms differed from each other. These features were then converted into a list of binary variables comprising an either or situation for each of the internodes that were being considered (Table 3.1). Each plant piece was then coded according to the binary character list and given an either/or code (1 = presence of a feature; 0 = absence of a feature; and 999 = inapplicability for conditionally present variables) and a data matrix was constructed for 157 internodes and 90 variables (Appendix 3.1)

Table 3.1. List of variables used to code plant portions in growth form analysis.

	Variables
1	internode subterranean (1) not subterranean (0)
2	internode on surface of substrate (1) not on surface of substrate (0)
3	internode aerial (1) not aerial (0)
4	internode orientation horizontal (1) not horizontal (0)
5	internode orientation vertical (1) not vertical (0)
6	internode orientation intermediate between horizontal/vertical (1) not intermediate (0)
7	internode branching (1) internode not branching (0)

[1] The term internode is used to describe plant portions that were selected according to Figure 2.1 A-C, Chapter 2. Internodes are obviously only present in plant portions which are divided into nodes and internodes and therefore apply to axial portions of the plant. For roots, the sections were taken from the mid-region, except in cases where swellings were present, and then sections were taken from those regions.

Table 3.1 Continued.

	Variables
8	branching intravaginal (1) not intravaginal (0)
9	branching extravaginal (1) not extravaginal (0)
10	innovation buds aerial (1) not aerial (0)
11	innovation buds subterranean (1) not subterranean (0)
12	innovation buds on surface of substrate (1) not on surface (0)
13	nodes present (1) nodes absent (0)
14	leaf bases ensheathing length of internode (1) not ensheathing length internode (0)
15	leaf bases photosynthetic (1) leaf bases non-photosynthetic (0)
16	internodes closely spaced (1) not closely spaced (0)
17	internodes with intermediate spacing (1) not with intermediate spacing (0)
18	internodes widely spaced (1) not widely spaced
19	internode giving rise to another internode (1) not (0)
20	internode arising from another internode (1) not (0)
21	internode arising from and giving rise to another (1) not (0)
22	internode life history, perennating (1) not (0)
23	internode life history, short lived (1) not short lived (0)
24	internode life history intermediate (1) not (0)
25	internode photosynthetic (1) not photosynthetic (0)
26	internode forming swellings at some point (1) not forming swellings (0)
27	swellings terminal (1) not (0)
28	leaf bases swollen (1) not swollen (0)
29	leaf bases hairy (1) not hairy (0)
30	roots present (1) roots absent (0)
31	root contractile (1) not contractile (0)
32	vascular tissue arranged in a discrete vascular bundle (1) not in a bundle (0)
33	vascular bundle proliferating to extranumery xylem & phloem elements (1) not proliferating (0)
34	xylem exarch (outside phloem) (1) not exarch (0)
35	xylem endarch (inside phloem) (1) not endarch (0)
36	xylem mesarch (in-between phloem) (1) not mesarch (0)
37	internode polystelic (1) not polystelic (0)
38	vascular bundle distribution medullary only (1) not medullary (0)

Table 3.1. Continued.

	Variables
39	vascular bundle distribution medullary and peripheral (1) not medullary and peripheral (0)
40	medullary vascular bundle type amphivasal (1) not amphivasal (0)
41	medullary vascular bundle type bi-collateral (1) not bi-collateral (1)
42	medullary vascular bundle type uni-collateral (1) not uni-collateral (0)
43	medullary vascular bundle type u-shaped (1) not u-shaped (0)
44	medullary vascular bundle type v-shaped (1) not v-shaped (0)
45	medullary vascular bundle type t-shaped (1) not t-shaped (0)
46	medullary vascular bundle type mixed amphivasal and u-shaped (1) not mixed (0)
47	medullary vascular bundle type mixed u-shaped and collateral (1) not mixed (0)
48	medullary vascular bundle type mixed amphivasal and bi-collateral (1) not mixed (0)
49	medullary bundle sheath developed (1) not developed (0)
50	medullary bundle sheath cells with thickened walls (1) not with thickened walls (0)
51	medullary bundle sheath chlorenchymatous (1) not (0)
52	medullary vascular bundles anastomosing (1) not anastomosing (0)
53	area occupied by central ground parenchyma enlarged (1) not enlarged (0)
54	central ground region forming hollow pith (1) not forming pith (0)
55	central ground region containing canals (air/mucilage) (1) not containing canals (0)
56	central ground parenchyma cells with thickened walls (1) not with thickened walls (0)
57	starch present (1) absent (0)
58	starch distribution present in cortex (1) absent in cortex (0)
59	starch distribution present in hypodermis (1) absent (0)
60	starch distribution present in central ground parenchyma (1) absent (0)
61	starch distribution present in cortex plus central ground parenchyma (1) absent (0)
62	starch distribution present in cortex plus central ground parenchyma plus hypodermis (1) absent in these areas (0)
63	endodermoid sheath present (1) absent (0)
64	sclerenchyma band present (1) absent (0)
65	sclerenchyma band cells with concentrically thickened cell walls (1) cell walls not so (0)
66	cuticle present (1) absent (0)
67	epidermal cell shape brick shaped with outer wall thickened (1) not like this (0)

Table 3.1. Continued.

	Variables
68	epidermal cell shape brick shaped all walls equally thickened (1) not like this (0)
69	epidermal cell shape upright rectangular with outer wall thickened (1) not like this (0)
70	chlorenchyma present (1) absent (0)
71	chlorenchyma breaking down (1) not breaking down (0)
72	chlorenchyma with thickened cell walls (1) not thickened (0)
73	chlorenchyma band containing vascular tissue (1) not containing vascular tissue (0)
74	stomata present (1) absent (0)
75	stomatal position level (1) not level (0)
76	stomatal position sunken (1) not sunken (0)
77	parenchyma band present (1) absent (0)
78	parenchyma band thickened (1) not thickened (0)
79	parenchyma band containing vascular tissue (1) vascular tissue absent (0)
80	roots endogenously formed (1) roots not endogenously formed (0)
81	hypodermis present (1) hypodermis absent (0)
82	suberised cells present (1) absent (0)
83	cortex present (1) absent (0)
84	cortex containing vascular bundles (1) vascular bundles absent (0)
85	cortex cells with thickened walls (1) walls not thickened (0)
86	cortex with chloroplasts (1) not (0)
87	exodermis present (1) absent (0)
88	velamen present (1) absent (0)
89	endodermis present (1) absent (0)
90	pericycle present (1) absent (0)

Multivariate methods

Non-metric multidimensional scaling analysis (MDS)

Multidimensional scaling analysis (MDS) involves a number of steps. To begin with, MDS requires that the starting matrix must be a similarity (or dissimilarity) matrix. The similarity (distance) between points in a geometric space can be calculated in several ways (see Sokal & Sneath 1963) and depends on the nature of the variables. Thus, different measures are

used for continuous variables as compared to qualitative variables. Once the similarity matrix has been calculated, the points are projected into k dimensional space.

A single distance measure was used in this study, the Jaccard coefficient (Sneath & Sokal) as is found in the program Ntsys-pc (Vers. 1.70, Rohlf 1992). This distance measure is best suited to binary variables, where the positive state was given the code 1 and the negative state the code 0. The Jaccard coefficient (J) was chosen in preference to the simple matching coefficient (SM) [which is the default in Ntsys-pc (Vers. 1.70, Rohlf 1992)] as the measure for similarity because it is not desirable for the absence of a state (in truly binary coded data) to make a large contribution to the measure of similarity. The Jaccard omits considerations of negative matches (Sokal & Sneath 1963). This coincides with the goals of this study - it would be very difficult to justify describing organs by features which they lack and similarly it is undesirable to infer similarity between two objects in this case if they lack a certain feature which is globally absent to the particular set in which they are found. This is not to say that absence cannot be a true alternative - it may be in some situations. It may be much more accurate to assess similarity on the presence of features. Binary data by its nature would however require that the pairs (both unmatched and matched) are equally treated (weighted). The Jaccard coefficient allows for this and is probably the best suited coefficient to binary data when negative matches are not included as is recommended by Sokal & Sneath (1963) and Krzanowski (1988).

The J-coefficient is calculated according to the following equation (Jaccard 1908, as outlined in Ntsys-pc (Vers. 1.70, Rohlf 1992) manual and following the simple treatment of variable states shown in Table 3.2):

Equation 1:

$$\text{Jaccard coefficient of similarity } (J) = \frac{a}{(n - d)}$$

where: m (no. matches) = a + d
u (no. unmatches) = b + c
n (total sample size) = u + m

Thus: $$S_{ij} = \frac{a}{a + b + c}$$

Table 3.2 . Two way table illustrating the frequencies of all pairs of two objects *i* and *j*. Modified from Gordon 1981 and Ntsys-pc (Vers. 1.70, Rohlf 1992) manual.

		Object *j*	
		Variable (state 1)	Variable (state 0)
Object *i*	Variable (state 1)	a	b
	Variable (state 0)	c	d

The similarity matrix was calculated by comparing distances between internodes. The MDS analysis performed in Ntsys-pc (Vers. 1.70, Rohlf 1992) follows that proposed by Kruskal (1964a), (1964b). The MDS ordination technique is generally considered to be better suited to categorical data than a principal components analysis (PCA), for example, which requires normal distribution in continuous variables. MDS also differs from PCA in that the distances in k dimensional space have a monotone relationship to the original distances (whereas in PCA the projection of points in k-dimensional space explain a maximum percentage of the variation found). Thus, similar objects in an MDS projection should be closely spaced, while dissimilar objects would be further apart. In this study, the MDS was started with a random initial configuration for the points, not with the co-ordinates from a principal co-ordinates analysis (PCO) analysis. The co-ordinates from a PCO may be used for the starting configuration of the MDS (see Ntsys manual, 11-6) as the number of iterations required to explain monotonicity may be reduced. However, because the starting matrix of binary variables is not normally distributed the use of geometric ordination procedures would be used hesitantly in this study. Although, in the PCO analysis, the means of data points in the resulting similarity matrix are used, it is still uncertain how binary variables may ultimately affect the structure of the similarity matrix. This effect would be carried through to the eigenvalue calculations and would affect the distribution of the point in space.

The measure of stress used to assess how bad the fit of the distances in the configuration space to the monotone function of the original distances, was calculated using the following equation:

Equation 2:

$$\text{Stress 1} = \sqrt{\frac{\sum (\hat{d}_{ij} - \hat{d}_{ij})^2}{\sum \hat{d}_{ij}^{\,2}}}$$

The stress value determines how close the projected matrix is to the original matrix. values close to zero give 100% agreement, while those close to one give a 100% disagreement. The points are usually projected into a specified number of dimensions and the levels of stress examined to see how dimensionality reduces stress. A greater number of dimensions may result in lower stress values. From a practical viewpoint, two dimensions are used in this study for ease of interpretation of the data points. Zero stress is apparently always achievable, but may require hundreds of iterations to achieve this level. The maximum number of iterations to achieve a minimum value of stress was set to 40 in this study (the maximum in the Ntsys programme options). Guidelines for the range of stress values have been determined by several researchers and are followed as outlined in the Ntsys-pc (Vers. 1.70, Rohlf 1992) manual (0.40 = Poor; 0.20 = Fair; 0.10 = Good; 0.05 = Excellent; 0.00 = Perfect).

The MDS analysis was initially undertaken for all the internodes (as presented in Appendix 3.1). Subsequently, several manipulations of this basic data set were undertaken, after the resulting patterns of this analysis had been interpreted and tested using multiple analysis of variance (MANOVA). Manipulations included the removal of "identified" groups and the calculation of a new distance matrix with projection of a new MDS. Each time, groups were identified and tested using MANOVA. The within group structure was examined using cluster analysis to determine relationships between internoces within the identified groups.

Multiple analysis of variance (MANOVA)

The MDS analysis revealed a pattern of relationship in two dimensions between the different internodes examined, suggesting some definition and classification system for organs. Thus, points in certain areas of the two dimensional space were assigned to specific groups which could be visually determined. These predetermined, user defined groups were then tested: firstly, to determine whether the groups (i.e. organs) were distinct and significantly different from each other and secondly, to determine if the group detection was correct. The design of the MANOVA was a one-way ANOVA with fixed effects, using two dependent variables and only calculating the between groups variance. The user defined groups were assigned a grouping variable code (1 and 2.1, 2.2, 2.3 etc.) and this formed the independent variable. The two dimensional co-ordinates for each point in the MDS were used as the two dependent variables (i.e. Dimension 1 and Dimension 2 in configurational space). MANOVA was used for several data sets (i.e. complete and axial system) and the difference between groups was assessed. MANOVA assesses significance at the $p < 0.05$ level through the Rao R statistic. Least squares difference (LSD) tests were used to illustrate exactly which of the

groups differed from each other. The means between the two dependent variables were considered and p values compared for the assigned groups.

In order to test whether the user defined groups were present due to chance, subjective choice or whether they reflected real groupings, grouping variable codes were assigned randomly to the internodes. The MANOVA Rao R test statistic was recalculated for the resulting random groups following the procedure described above.

The MANOVA approach used in this chapter, is similar to a canonical variates approach, in that the point co-ordinates of the final configuration of the MDS are used. However, canonical variate analysis generally utilises co-ordinates of the initial matrix in the two dimensional space, and thus, the method would work best on quantitative data. Canonical variates can be applied to binary data, but is cautioned against due to the presence/absence effect on the vectors. As such, the method may not offer "meaningful" (in a statistical sense) interpretation of group allocation and has rarely been used as a method to "test" group differences. Rather, this approach is more appropriately used in a descriptive fashion (Krzanowski 1988). Multivariate normal distribution of the data are a prerequisite for any testing with the canonical variates approach. The two dependent variables (i.e. MDS dimension co-ordinates) that are used for each of the MANOVA tests in this study are normal distributed, and thus, a "meaningful" interpretation of the group differences could be obtained.

Cluster Analysis

The patterns obtained from MDS and the tested groups (MANOVA) were further examined using a clustering approach. Internodes corresponding to rhizomes in Figure 3.2 and listed in Table 3.7 were extracted from the main data set and a similarity matrix calculated for the internodes. The Jaccard coefficient was used for this again, as previously outlined. The clustering method of UPGMA was selected because the method calculates the average distance between all pairs of objects in two different clusters and is said to be efficient for both naturally "clumped" data and also naturally "chained" data. Accordingly, this method would be the most applicable for the current situation where the difference between groups is not really "clumped", but within group differences may be. Selecting groups for clustering following this procedure i.e. first exploring the structure in the data with MDS and then testing the patterns with MANOVA should ensure that distinct and natural groups are identified by the clustering process, eliminating the possibility of finding hierarchical structure where there is none (clustering techniques have the problem of finding structure in random data sets).

Internodes corresponding to inflorescence axes and inflorescence axis-like organs plus the transition groups shown in Figure 3.2 and listed in Table 3.7 were also extracted from the main data set. A similarity matrix using the Jaccard coefficient was calculated for the internodes and UPGMA was followed for the clustering procedure. A phenogram of the resulting groups is presented for the inflorescence axis and inflorescence axis-like transition internodes. The phenogram representation shows levels of similarity (proximity) as well as groups (i.e. internodes most similar to each other) represented by the clusters.

Discriminating variables

With binary data, the assessment of how the variables are contributing to the discrimination between specified groups is limited. Without normally distributed, continuous variables, discriminant function analysis is not possible. This would obviously be the ideal way of determining which of the variables were responsible for group structure. An alternative approach would be to use the biplot method, where the arrangement of variables in k-dimensional space is plotted simultaneously with the OTU's, and the length of the vectors used as a measure of the contribution of each variable to a particular group. However, binary data does not give an accurate reflection of vectors in this approach, due to the presence/absence effect of the data. The biplot method also assumes that there is an association between the parameters, which may not necessarily be true. Thus, the biplot method was not considered appropriate for this study.

The frequencies of the presence of variable state 1 was calculated for all 90 variables for the five user defined groups. For Group1, the roots of *Xerophyta*, *Borya* and *Epidendrum* were excluded on the basis that they are most likely outliers. Subsequently, the frequency of presence for that variable was calculated by dividing by the total number of OTU's (internodes) in that group, values close to zero indicate rarity of the particular feature, values close to one indicate commonality of a particular feature. Line plots were used to display the frequencies for each variable. Variables with a 50% and greater presence were considered to be important discriminators for the various groups. The method of using the frequency of state 1 in the various groups is similar to the discrimination method described by Sneath (1962). Sneath's method is for two state characters and utilises the algebraic difference between the frequencies of a given state in two taxa. The most discriminating characters have the highest value (either positive or negative) in Sneath's example.

Association between variables

It is possible that the variables when combined together in a particular way can contribute to a factor which causes similarity among the variables. Such variables are termed latent

variables, as on their own they do not contribute to factor structure and are not easily identifiable.

It is desirable in an analysis such as this to determine whether there are any latent variables which may be contributing to the formation of the organ groups found. Such latent variables may be structural components or physiological features. In fact, measuring the association between variables is a way to test whether the driving force in organ group formation in this study is a result of structure (phylogenetic pattern) or functional characteristics (ecological responses).

There are two problem areas that can be encountered when measuring affinity between variables. Firstly, if the variables are not truly independent and are logically correlated, then naturally they will have a high association. It is hoped that this first problem is accounted for in the choice of variable type, the procedure of variable coding and the use of conditionally present variables. The second problem is the sample bias that can be present in a data set such as this. Most examined and scored features are structural variations, with few being directly linked to a functional nature.

Association between binary variables is thought to be best measured by first calculating a tetrachoric correlation matrix (Sokal & Sneath 1963, Krzanowski 1988) and then exposing the matrix to factor analysis. Highly associated variables will have high similar values (i.e. values close to 1). The vectors obtained for the k-dimensional projection of variables in space will represent the latent variables responsible for certain group detection. This is an incredibly complex set of points in space, and often the results of such analyses are not only difficult to interpret, but may also have little statistical relevance (see Krzanowski 1988) in terms of testability.

A normal correlation matrix was calculated using Pearson's correlation coefficient in Statistica, as the tetrachoric correlation equation cannot cope with conditionally present variables (i.e. missing data). The missing data were deleted on a pairwise basis in the Pearson's calculations and a correlation matrix for variables 1-90 (excluding 32, 75, 76, 84, 88, 89 which had perfect correlation values [and may not be completely logically independent]) calculated. Factor analysis was carried out using the principal components option and a projection of the variables in k-dimensional space represented in a scatterplot.

RESULTS

Multi Dimensional Scaling Analysis (MDS)

All internodes (incl. roots)

The projection of points in two dimensions is shown for the MDS analysis on the total data set of monocot internodes collected in this study in Figure 3.1. Internodes corresponding to roots separate out from a main group (axial structures) in both the first and second dimensions (Group 1, diamonds, Figure 3.1). The group integrity (or proximity of points) of the roots does not appear close, some group broadly (*Holothrix* root, *W.glomerata* root, *T.spicigerus* root, *Myrsiphyllum tuber*, *Holothrix* tuber, *Albuca* contractile root, *Polystachya* root, *Phalaenopsis* root), while others appear to be outliers (*Xerophyta* root, *Epidendrum* root, *Borya* root, symbolised by plus signs in Figure 3.1). The main group (Group 2, triangles, Figure 3.1) includes all of the organs which comprise the "axial" system of the monocots sampled in this study.

Internodes corresponding to the axial system (roots excluded)

In order to gain clarity within this main group (Group 2), all roots were excluded from the analysis. The MDS analysis was rerun, calculating a new similarity matrix and a new scaling projection of the points in dimensional space. Four groups (Groups 2.1 - 2.4) were visually discernible as symbolised in Figure 3.2. In the first dimension, along the x-axis, a group corresponding to internodes which are rhizomatous in origin is distinct and is represented by open circles (Group 2.1, Figure 3.2). The other group which can be visually recognised along the x-axis is composed of inflorescence axes and related internodes shown by filled triangles (Group 2.4, Figure 3.2). Towards the base of this inflorescence axis group there are several separate internodes which could possibly be considered as extremes of the group. These are the stolon of *Chlorophytum comosum* (triangle tagged 11), the basal inflorescence axis of *Johnsonia pubescens* (triangle tagged 20), the basal inflorescence axis of *Pentaschistis aristidoides* (triangle tagged 26), the basal inflorescence axis of *Merxmuellera cincta* (triangle tagged 23), and the mid pseudobulb of *Maxillaria variabilis* (triangle tagged 22). Another isolated point (triangle tagged 37) in this group is the aerial axis of *Smilax anceps*. Two smaller groups (Groups 2.2 and 2.3) can be distinguished which are positioned in-between the rhizome (Group 2.1) and inflorescence axis (Group 2.4) groups. Groups 2.2 and 2.3 are separated in the second dimension from the Groups 2.1 and 2.4, along the y-axis. Group 2.2, represented by filled squares is composed of internodes from runners plus transition region internodes. Group 2.3 represented by stars, is composed of another set of internodes from runners and transition areas. An internode which could be placed in either transition

group (i.e. Group 2.2 or Group 2.3) or the inflorescence axis group (Group 2.4) is the mid neck region of *Wurmbea spicata* (triangle tagged 44). However, in proximity, it is closer to the bulk inflorescence axis group (Group 2.4) and thus is considered as part of that group.

Multiple analysis of variance (MANOVA)

All internodes (incl. roots)

In order to test the distinctness of the visually apparent groups in Figure 3.1 the approach of testing the significance of between groups variance was undertaken. The first detectable group was considered to be the main "root group" and these OTU's were assigned the grouping variable of one. Thus, the main root group (diamonds, Figure 3.1) was assigned to Group 1. The points symbolised by stars (Figure 3.1), *Xerophyta* root, *Borya* root and *Epidendrum* root were excluded from the MANOVA tests as they were considered to be outliers. The second visually identifiable group was composed of the remaining organs comprising the axial system of the sampled taxa. These organs were allocated to Group 2. These grouping variables are the dependent variable in the MANOVA and the co-ordinates of Dimension 1 formed the one set of independent variables, and those for Dimension 2 the other set of independent variables. The results of the MANOVA for the total organ data set are summarised in Table 3.3. A significant Rao's R statistic was obtained for the MANOVA at the $p < 0.05$ level. The Wilks' Lambda value was also significant at this level.

Table 3.3. Results of the MANOVA for the complete data set of monocot organs sampled for the groups assigned 1-2. Stars represent significance at the p<0.05 level.

Summary of all effects					
Effect	Wilks' Lambda	Rao's R	df1	df2	p-level
1	0.651173*	37.76620*	2	141	0.000000*

With a significant Rao R statistic, the groups can be considered to be distinct and significantly different from each other. The results of the LSD tests are shown in Table 3.4 as a confirmation of the significant difference, highlighting that the difference occurs in both the first and the second dimensions.

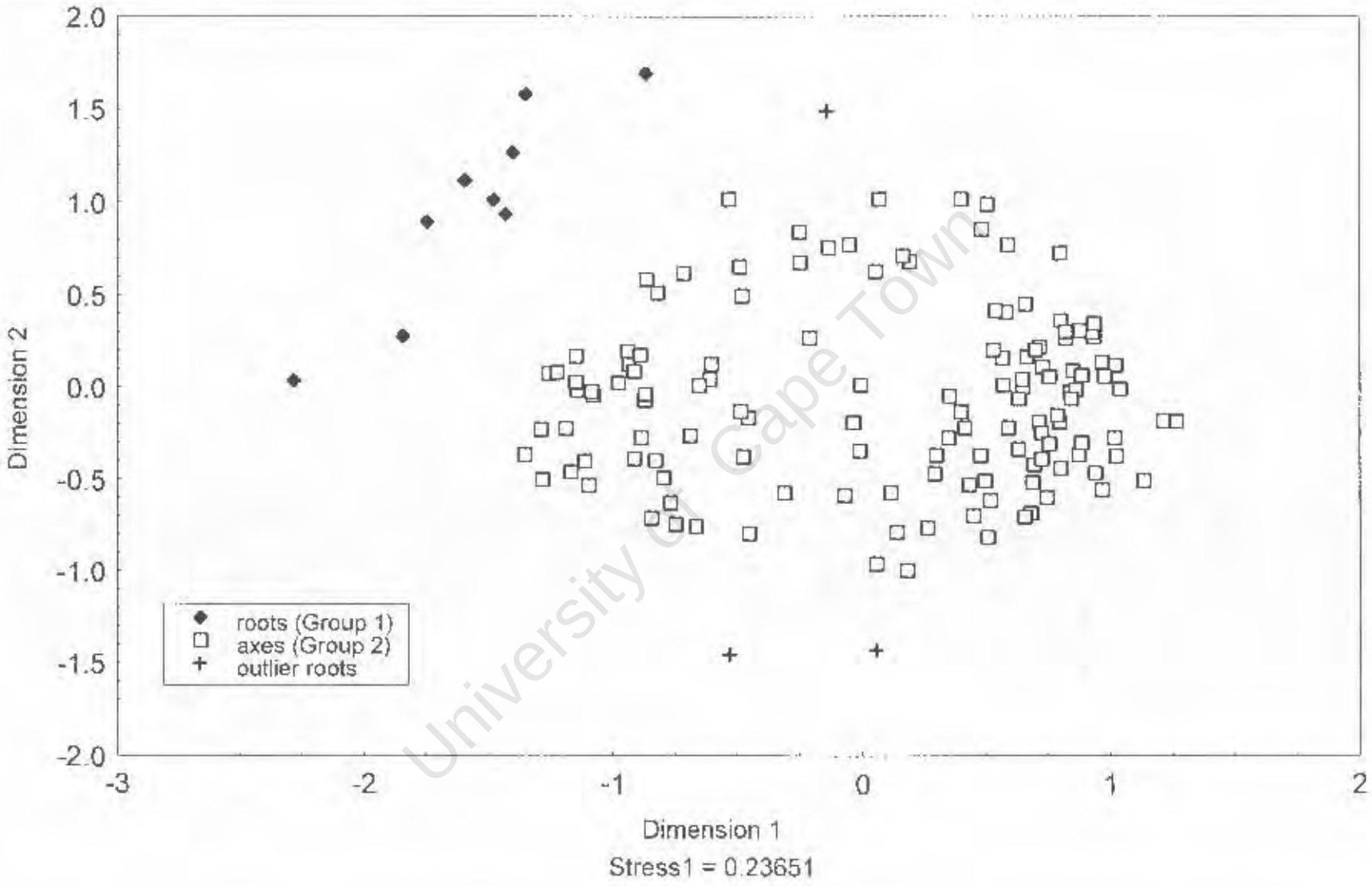


Figure 3.1. Scatterplot of points (representing root portions and axial system internodes) in two-dimensional space from the MDS analysis with all internodes included. Diamonds represent root portions and squares the axial system. Outlier roots are indicated with plus signs.

Table 3.4. Results of the LSD tests for the complete data set of internodes for the groups assigned 1-2. Stars represent significant difference in means between the groups.

To test whether the assigned groups were in fact distinct and recognisable on the basis of real features and not simply a statistical artefact, a randomisation procedure was applied to the MANOVA test. Each of the organ points of the complete data set was randomly allocated one of the grouping variables (either 1 or 2) and the MANOVA recalculated for the independent variables. The results of the randomised MANOVA are presented in Table 3.5. A non-significant Rao's R statistic and Wilks' Lambda value was obtained, confirming that the user-defined group allocation is better than random. The results of the LSD test on the randomised dependent variable showed that none of the groups differed significantly from each other (Table 3.6).

Table 3.5. Results of the MANOVA test for the complete set of sampled organs for the randomised procedure of group assignment.

Summary of all effects					
Effect	Wilks' Lambda	Rao's R	df1	df2	p-level
1	0.999955	0.003143	2	141	0.996862

Axial system

With roots excluded from the data set, the projection of points by MDS in the scatterplot shown in Figure 3.2 the grouping pattern suggests four groups. Thus, for the grouping variable, the codes 1-4 were assigned to all points corresponding to each of the groups respectively, outlined in Figure 3.2. The taxa and their corresponding internodes allocated to the four groups are presented in Table 3.7.

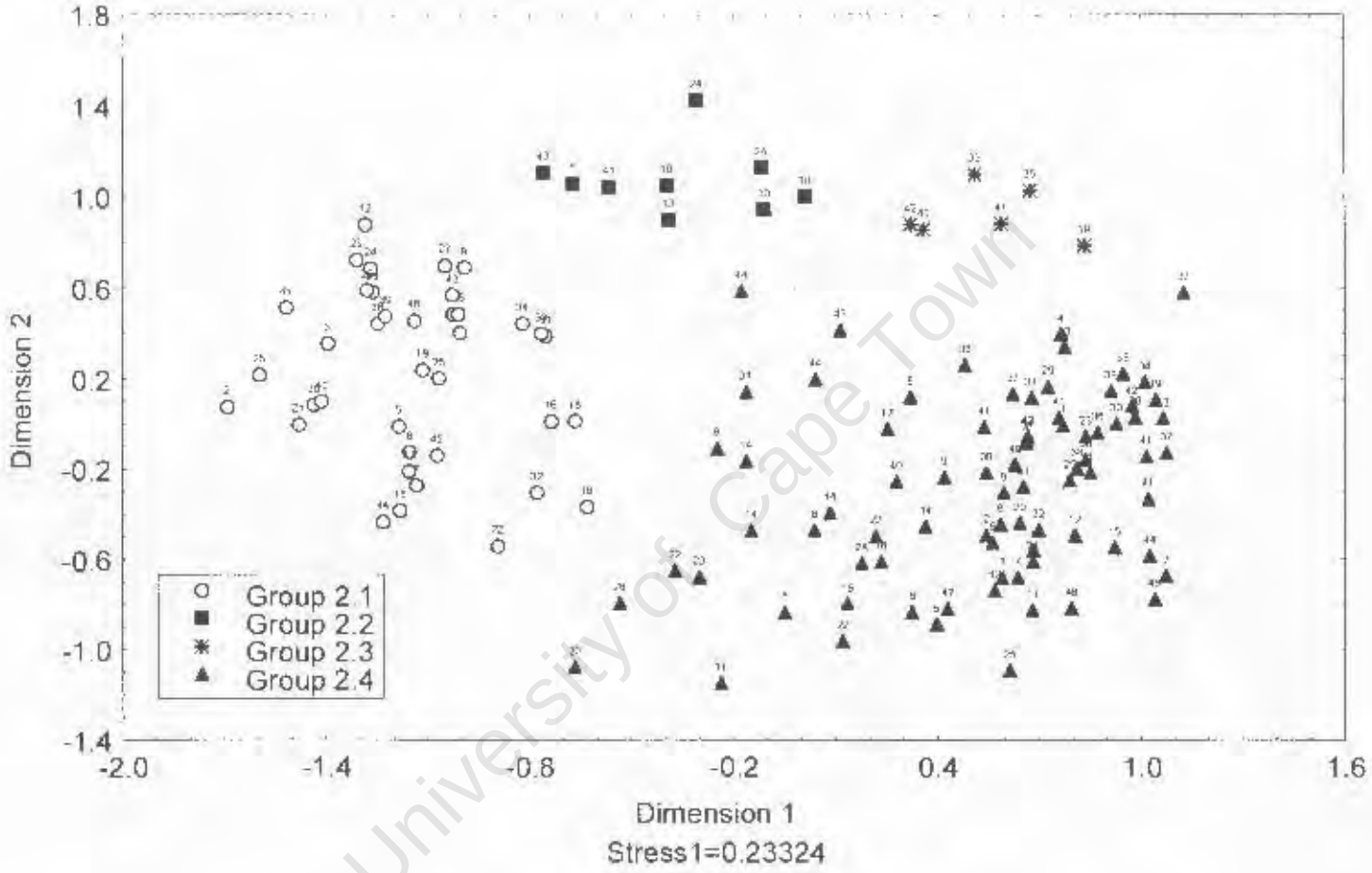


Figure 3.2. Scatterplot of points (representing axial system internodes) in two-dimensional space from MDS analysis with roots excluded and only axial system internodes included. Circles represent Group 2.1 (rhizome internodes), squares represent Group 2.2 (transition region and runner internodes); stars represent Group 2.3 (transition and runner internodes) and triangles represent Group 2.4 (inflorescence axis internodes). The numeric labels are listed according to taxon and internode portion in Appendix 3.2.

Table 3.6. Results of the LSD tests for the complete data set with the grouping variables randomly allocated to internodes.

The MANOVA was designed as described for the complete data set. The dependent variable was the grouping variable with the codes 1-4 assigned to the four groups (2.1, 2.2, 2.3, 2.4) as outlined above. The two independent variables were the co-ordinates for each of the points in Dimension 1 and Dimension 2 respectively. The results of the MANOVA for the axial system data set are presented in Table 3.8. A significant Rao's R statistic was obtained for the MANOVA at the $p < 0.05$ level. The Wilks' Lambda value was also significant at this level.

Table 3.7. Internodes assigned to groups 2.1, 2.2, 2.3 and 2.4 for the axial system MANOVA tests.

Group 2.1	*Anigozanthos manglesii* rhizome; *Aponogeton distachyos* rhizome; *Baometra uniflora* corm; *Billbergia nutans* rhizome; *Borya nitida* stem; *Canna indica* rhizome; *Chlorophytum comosum* rhizome; *Conostylis prolifera* runner; *Dasypogon bromeliifolius* stem base; *Epidendrum cinnabarinum* upper axis, lower axis; *Eriospermum pumilum* tuber; *Holothrix villosus* rhizome; *Ischyrolepis cincinnata* rhizome base; *Johnsonia pubescens* stem base; *Lachenalia klinghardtiana* rhizome; *Maxillaria variabilis* pseudobulb stalk; *Merxmuellera cincta* rhizome; *Merxmuellera rufa* rhizome; *Myrsiphyllum scandens* rhizome; *Paurida minuta* corm; *Pseudopentameris obtusifolia* rhizome base; *Pentameris thuarii* vertical rhizome; *Pentaschistis airistidoides* rhizome, rhizome-inflorescence axis; *Pentaschistis pallescens* rhizome base; *Polystachya ottoniana* pseudobulb; *Pseudopentameris caespitosa* vertical base; *Pseudopentameris macrantha* rhizome base; *Restio harveyi* rhizome base; *Thamnochortus lucens* basal rhizome; *Thamnochortus spicigerus* rhizome; *Tribolium obtusifolium* rhizome; *Tulbaghia alliacea* rhizome; *Wachendorfia thyrsiflora* rhizome; *Wurmbea spicata* corm; *Xerophyta humilis* stem; *Zantedeschia aethiopica* tuber
Group 2.2	*Billbergia nutans* runner; *Chondropetalum deustum* rhizome, basal inflorescence axis; *Chondropetalum rectum* rhizome, basal inflorescence axis; *Merxmuellera rufa* runner, basal inflorescence axis; *Wachendorfia thyrsiflora* underground runner
Group 2.3	*Ischyrolepis cincinnata* runner; *Restio harveyi* runner; *Tribolium obtusifolium* stolon; *Thamnochortus lucens* rhizome-inflorescence axis; *Thamnochortus spicigerus* basal inflorescence axis; *Willdenowia glomerata* runner

Table 3.7. Continued.

Group 2.4	*Albuca fragrans* aerial inflorescence axis; *Albuca fragrans* inflorescence axis; *Anigozanthos manglesii* inflorescence axis; *Aponogeton distachyos* inflorescence axis; *Arundo donax* aerial stem; *A.donax* inflorescence axis; *Baometra uniflora* basal neck; *B.uniflora* inflorescence axis; *B.uniflora* lower flowering stalk; *B.uniflora* upper neck; *Billbergia nutans* basal inflorescence axis; *B. nutans* inflorescence axis; *B. nutans* inflorescence axis; *Borya nitida* basal inflorescence axis; *B.nitida* mid inflorescence axis; *Chondropetalum rectum* aerial inflorescence axis; *Calectasia cyanea* aerial stem; *C.cyanea* flowering stalk; *Canna indica* aerial inflorescence axis; *C.indica* inflorescence stalk; *Chlorophytum comosum* inflorescence axis; *Conostylis prolifera* aerial inflorescence axis; *C.prolifera* inflorescence axis; *Chondropetalum rectum* lower inflorescence axis internode; *Cyanella hyacinthoides* basal inflorescence axis; *C.hyacinthoides* basal neck; *C.hyacinthoides* flowering stalk; *C.hyacinthoides* mid neck; *Dasypogon bromeliifolius* flowering inflorescence axis; *Epidendrum cinnabarinum inflorescence axis; Eriospermum pumilum* flowering stalk; *E.pumilum* lower inflorescence axis; *Holothrix villosus* inflorescence axis; *Ischyrolepis oncinnata* aerial inflorescence axis; *Johnsonia pubescens* inflorescence axis; *Lachenalia klinghardtiana* inflorescence axis; *Merxmuellera cincta* inflorescence axis; *Maxillaria variabilis* basal inflorescence axis; *M variabilis* upper inflorescence axis; *Myrsiphyllum scandens* aerial shoot; *M.scandens* flowering stalk; *Pentaschistis aristidoides* flowering stalk; *Pseudopentameris caespitosa* inflorescence axis; *Pseudopentameris macrantha* inflorescence axis; *Pseudopentameris obtusifolia* inflorescence axis; *P.obtusifolia* lower inflorescence axis; *P.obtusifolia* vertical main axis; *Pentaschistis pallescens* basal branching zone, flowering stalk; *Pentameris thuarii* inflorescence axis; *Phalaenopsis frosty hunter hybrid* flowering stalk; *Polystachya ottoniana* mid inflorescence axis; *Restio harveyi* aerial inflorescence axis; *Spiloxene alba* flowering stalk; *Spiloxene minuta* inflorescence axis; *Smilax anceps* stem; *Tulbaghia alliaceae* basal inflorescence axis; *T.alliaceae* inflorescence axis; *T.alliaceae* flowering stalk; *T.alliaceae* inflorescence stalk; *Thamnochortus lucens* inflorescence axis; *Thamnochortus spicigerus* basal inflorescence axis; *T.spicigerus* inflorescence axis; *T.spicigerus* inflorescence stalk; *T.spicigerus* inflorescence stalk; *T.spicigerus* seedling inflorescence axis; *Tribolium obtusifolium* inflorescence axis; *Wildenowia glomerata* inflorescence axis; *Wachendorfia thyrsiflora* inflorescence axis; *W.thyrsiflora* inflorescence stalk; *Wurmbea spicata* flowering stalk; *W.spicata* mid neck; *W.spicata* neck; *Zantedeschia aethiopica* inflorescence stalk; *Z.aethiopica* spathe stalk; *Zingiber officinale* reproductive axis; *Z.officinale* vegetative axis Distinct internodes: *Johnsonia pubescens* basal inflorescence axis; *Maxillaria variabilis* mid pseudobulb; *Merxmuellera cincta* basal inflorescence axis; *Pentaschistis aristidoides* basal inflorescence axis Isolated internodes: *Chlorophytum comosum* stolon; *Smilax anceps* inflorescence axis

Table 3.8. Results of the MANOVA for the axial system in monocots for internodes assigned to groups 2.1 - 2.4. Stars indicate significance

Summary of all effects					
Effect	Wilks' Lambda	Rao's R	df1	df2	p-level
1	0.106030*	89.74513	6	260	0.000000*

The post-hoc assessment of the grouped data, using the LSD tests for the axial system show that in Dimension 1, Groups 2.1 and 2.2 differ from each other and from Groups 2.3 and 2.4, but that Groups 2.3 (inflorescence axis-like runners) and 2.4 (inflorescence axes) do not differ significantly from each other. In Dimension 2 all groups differed significantly from each other excepting Groups 2.2 and 2.3 (Table 3.9). The LSD test confirms the general visual pattern that was suggested in the MDS, a cluster of points which correspond to rhizomes (Group 2.1), plus a cluster of points which correspond to inflorescence axes (Group 2.4) and additionally two intermediate clusters corresponding to

runners and transition areas (Groups 2.2 and 2.3) respectively. These transition groups are not distinctly different from each other with the result that some internodes can be members of either the first transition group (Group 2.2), the second transition group (Group 2.3) or of the inflorescence axis internode group (Group 2.4).

Table 3.9. Results of the LSD tests for the axial system data set with grouping variables 1-4 corresponding to the four user-defined groups, Groups 2.1 - 2.4. Stars indicate significant difference in means between the groups.

[illegible]	(2.1) -1.13225	[illegible] -0.342756	(2.3) 0.5484217	[illegible]
[illegible]	------------	0.000000*	0.000000*	0.000000*
Group 2.2	0.000000*	------------	0.000025*	0.000000*
Group 2.3	0.000000*	0.000025*	------------	0.818700
Group 2.4	0.000000*	[illegible]000000*	0.818700	------------
[illegible]ension 2				
	(2.1) 0.2208329	(2.2) 1.074[illegible]	(2.3) 0.9213684	[illegible]
Group 2[illegible]	------------	0.000000*	0.000106*	[illegible]00000*
Group 2.2	0.000000*	------------	0.479032	0.000000*
[illegible]p 2.3	0.000106*	0.479032	------------	0.000000*
Group 2.4	0.000000*	[illegible]	0.000000*	------------

The randomisation procedure was followed as for the complete data set, where the grouping codes 1-4 for the four groups (2.1 -2.4) was randomly allocated to internodes and the MANOVA analysis carried out. A non-significant Rao's R was obtained for the randomised variable allocation (Table 3.10), again confirming that the group allocation based on Figure 3.2 is better than random.

Table 3.10. Results of the MANOVA for the randomised allocation of internodes to the four groups, Groups 2.1 -2.4.

Summary of all effects					
Effect	Wilks' Lambda	Rao's R	df1	df2	p-level
1	.956971	0.963509	6	260	0.450429

The results of the LSD tests on the randomised dependent variable for the co-ordinates of points in Dimension 1 and Dimension 2 (Table 3.11) showed that no distinct, significantly different groups were revealed using this procedure in either of the dimensions. Randomising the grouping variable in the procedure outlined above, tests the allocation of

internodes to the four user specified groups (Groups 2.1 - 2.4), again confirming that a grouping pattern is recognisable in the axial data set.

Table 3.11. Results of the LSD tests for the randomised allocation of grouping variables 1-4 to the internodes assigned to Groups 2.1 - 2.4.

	(2.1) -0.050023	(2.2) 0.1739677	(2.3) 0.725939	
	----------		0.532114	0.535488
	0.267075		0.628058	
	0.532114		----------	
	0.535488		0.232776	
		Dimension 2		
	(2.1) 0.0756777	(2.2) 0.1	(2.3) -0.0553034	(2.4) 0
	----------		0.328630	
	0.101418		0.504879	0.777180
	0.328630		----------	0.
	0.839732	0.777180	0.257716	

Cluster Analysis

Rhizome group internodes

The internodes which correspond to the MDS rhizome group of Figure 3.2 (open circles) show a certain amount of within group structure which is evident in the phenogram (Figure 3.3). The general pattern shown in the phenogram and that of the MDS (Figure 3.2) is broadly similar, only a few internodes here and there change proximity locations.

In Figure (3.3), there are two internodes which are most dissimilar to any of the other internodes in the clustering analysis. These are the rhizome-inflorescence axis area of *Pentaschistis aristidoides* and the runner of *Conostylis prolifera* (labelled O1 and O2 respectively). There are clearly two main clusters of rhizome internodes outlined in the phenogram at level 0.40 (labelled 1 and 2). These are the orchid pseudobulbs and axes of *Polystachya ottoniana*, *Maxillaria variabilis* and *Epidendrum cinnabarinum* (Cluster 1) and then a bulk group of internodes from rhizomes (Cluster 2). Cluster 2 is further divided into two main clusters at the 0.50 level (2.1 and 2.2, Figure 3.3) which can broadly be defined as vertical, non-swollen rhizomes (2.1A, B & C); rhizomes which tend to be swollen (2.2A) to unswollen (2.2B & C); tending from vertical (2.2A) to horizontal (2.2B & C Figure 3.3). These clusters reflect a functional grouping on the basis of growth orientation as well as thickness of rhizome internode portions.

Inflorescence axis and transition internodes

The phenogram presented in Figure 3.4 shows very poor clustering, where the branch lengths are all more or less equal up to the full length of the phenogram. This pattern suggests that there is an absence of sudden transitions between the clusters. The clusters correspond to the intermediate group internodes (squares and stars, Fig. 3.2) and the inflorescence axis group internodes (triangles, Fig. 3.2) shown in the MDS projection in Figure 3.2. Two main clusters can be distinguished at the lowest level of similarity (0.29). These two main clusters (labelled 1 and 2) are the intermediate group internodes (1) and the inflorescence axis group internodes (2). Cluster 1 is divided into two further clusters (1.1 and 1.2, Figure 3.4) which roughly correspond to groups 2.2 and 2.3 of Figure 3.2, consisting of runner and transition area internodes. Cluster 2 consists of most of the internodes of the inflorescence axis group and is divided into many clusters at various levels of similarity, each of which is poorly separated from the other.

Discriminating variables

The line plots for the portions corresponding to roots (Group 1, Fig. 3.1) and for the axial system internodes (Groups 2.1 -2.4, Fig. 3.2) of the MDS analysis, are shown for variables 1-45 in Figure 3.5 and for variables 46-90 in Figure 3.6. Variables with a greater than 50% frequency are labelled for each of the five groups and the 50% frequency line is indicated in each line plot. Examining the points which occur above the 50% frequency line in each of the line plots is a way of visually determining which variables define the five groups. Table 3.12 shows which of the variables are most frequently present in each of the five groups, with a greater than 50% frequency highlighted in bold font. In Table 3.13, the most important, shared variables between two groups for the five groups (Groups 1-2.4) are shown.

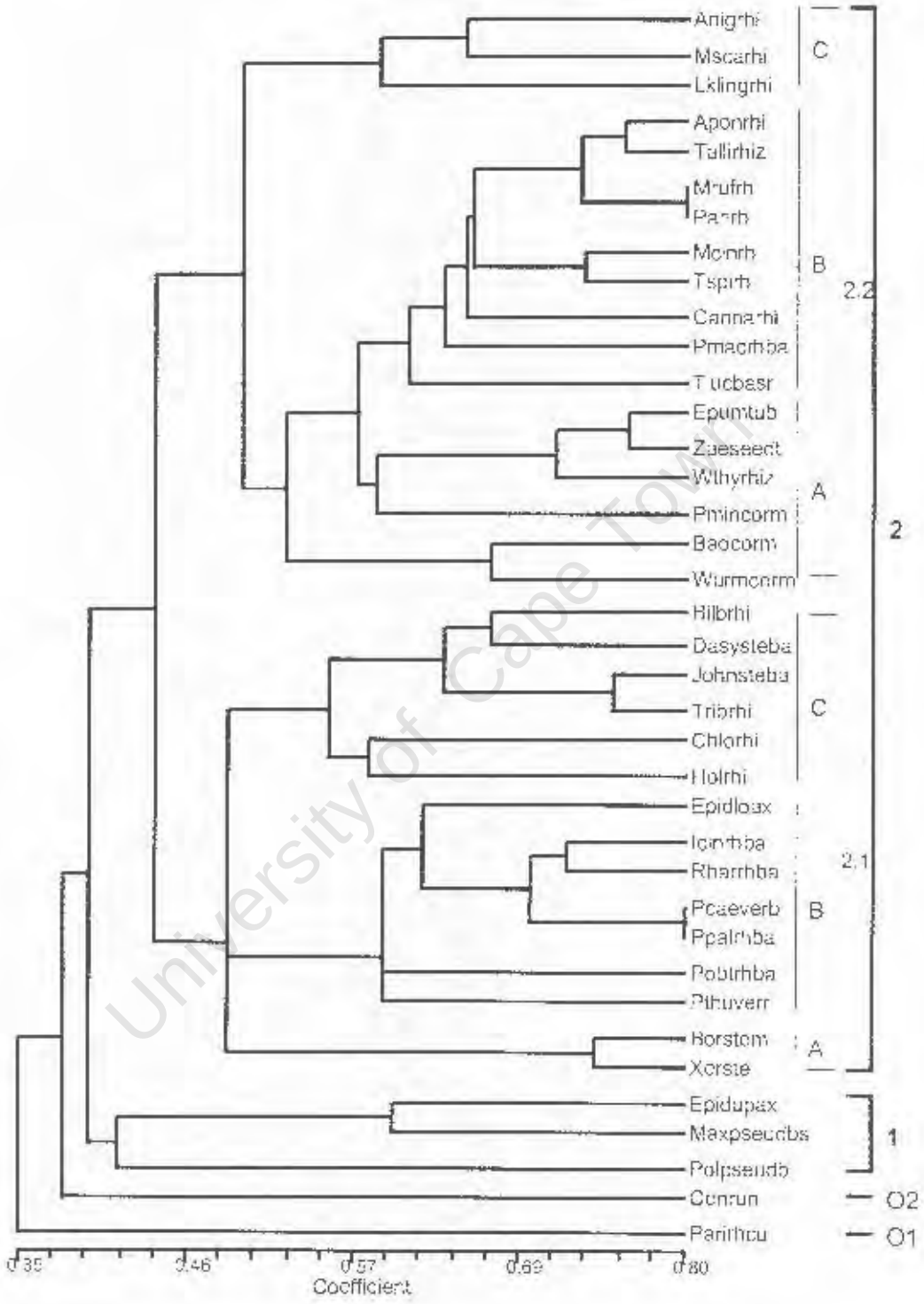


Figure 3.3. Phenogram with UPGMA clustering algorithm based on a Jaccard coefficient similarity matrix representing cluster hierarchy of rhizome internodes which form part of Group 2.1 (Fig. 3.2). Captions for OTU's (internodes) appear in Appendix 3.3.

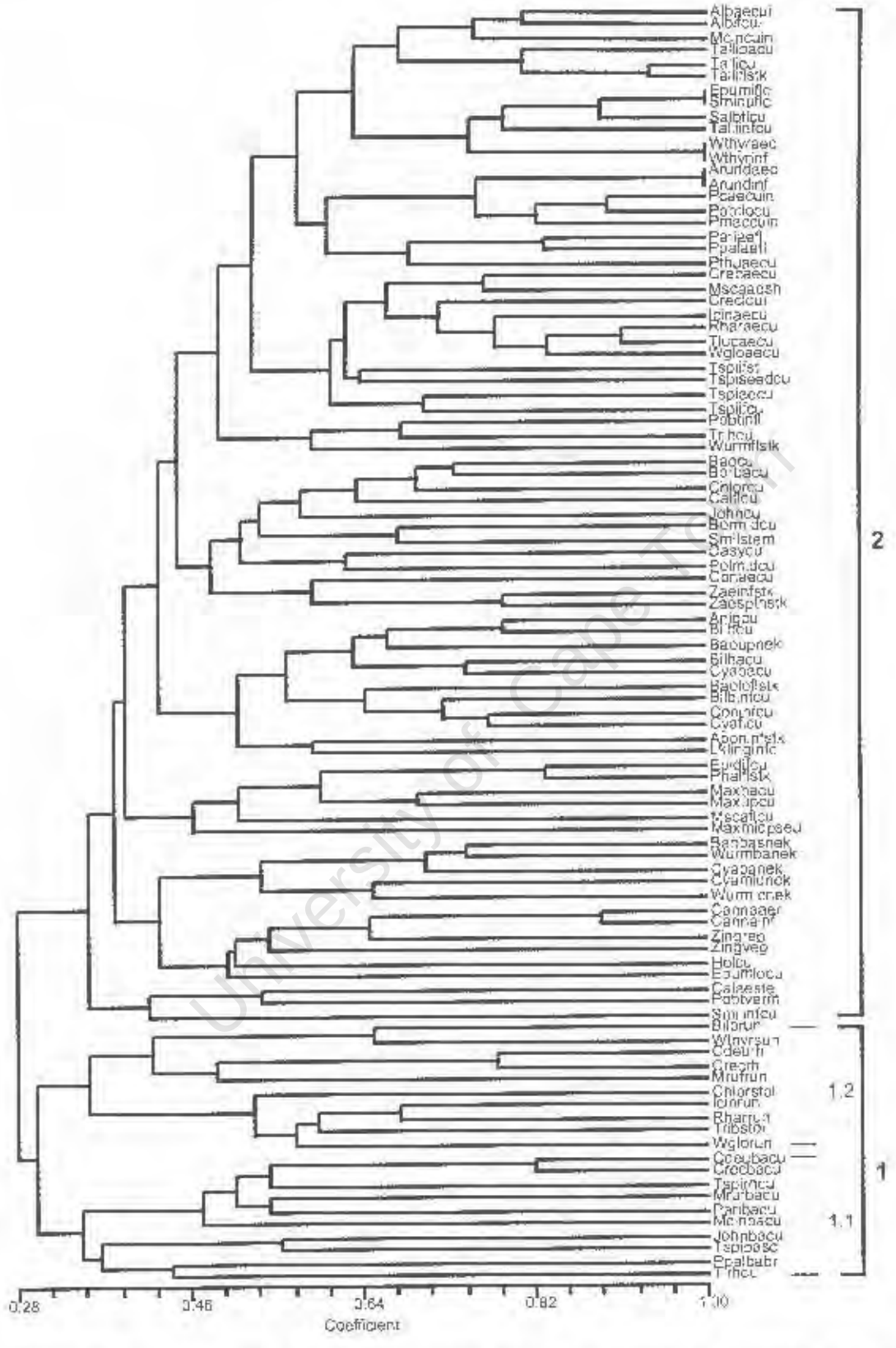


Figure 3.4. Phenogram with UPGMA clustering algorithm based on a Jaccard coefficient similarity matrix representing cluster hierarchy of internodes comprising intermediate groups (Groups 2.2 and 2.3, Fig. 3.2) and the inflorescence axis group (Group 2.4, Fig. 3.2). Captions for OTU's (internodes) appear in Appendix 3.4.

Table 3.12. Discriminating variables which are most frequently present in each of the Groups (1-5). Bold font indicates which of the variables have a greater than 50% frequency of presence.

	Variables for internodes
GROUP 1 (roots)	**20 (arising from another)**, 27 (terminal swellings), 31 (contractile roots), **35 (endarch xylem)**, 36 (mesarch xylem), 37 (polystely), **83 (cortex)**, 86 (chloroplasts in cortex), **87 (exodermis)**, 88 (velamen), **89 (endodermis)**, 90 (**pericycle**)
GROUP 2.1 (rhizomes)	9 (extravaginal branching), **16 (closely spaced internodes)**, **19 (giving rise to another)**, **22 (perennial)**, **40 (amphivasal vb.'s)**, 61 (starch in cortex & central area) 62 (starch in cortex, central area, hypodermis), **81 (hypodermis)**, 85 (thickened cortex)
GROUP 2.2 (transition and runners)	**4 (plagiotropic)**, 12 (superficial buds), 71 (chlorenchyma breaking down), 72 (chlorenchyma thickened)
GROUP 2.3 (transition and runners)	2 (**superficial**), **17 (internodes intermediately spaced)**, 56 (thickened central area), 59 (starch in hypodermis)
GROUP 2.4 (inflorescence axes)	3 (aerial), **5 (orthotropic)**, **15 (leaf bases photosynthetic)**, **23 (short lived)**, **25 (photosynthetic)**, 33 (extranumery xylem and phloem elements), 42 (uni-collateral vb.'s, 44 (v-shaped xylem), 55 (central area with canals), 69 (upright rectangular epidermal cells), 73 (chlorenchyma band with vascular tissue), 74 (stomata), 75 (level stomata), 76 (sunken stomata), 78 (thickened parenchyma band), 79 (parenchyma band with vascular tissue)

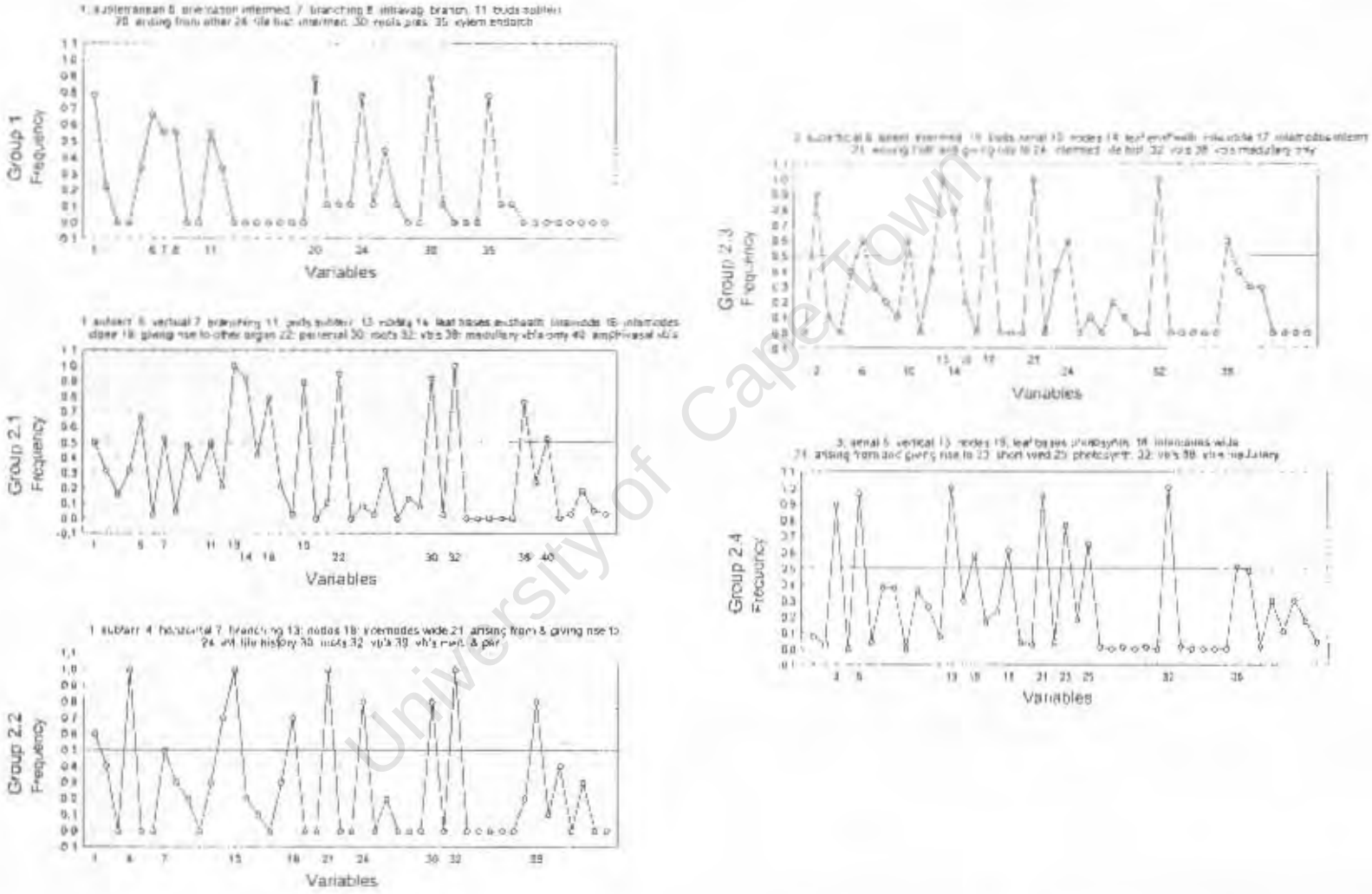


Figure 3.5. Line plots of frequencies for variables 1-45 for Groups 1 - 2.4. Variables with a greater than 50% frequency are labelled on each line plot and the 50% frequency is indicated by a solid line. Group 1 = roots; Group 2.1 = rhizomes, Group 2.2 = transition and runners; Group 2.3 = transition and runners, and Group 2.4 = inflorescence axes.

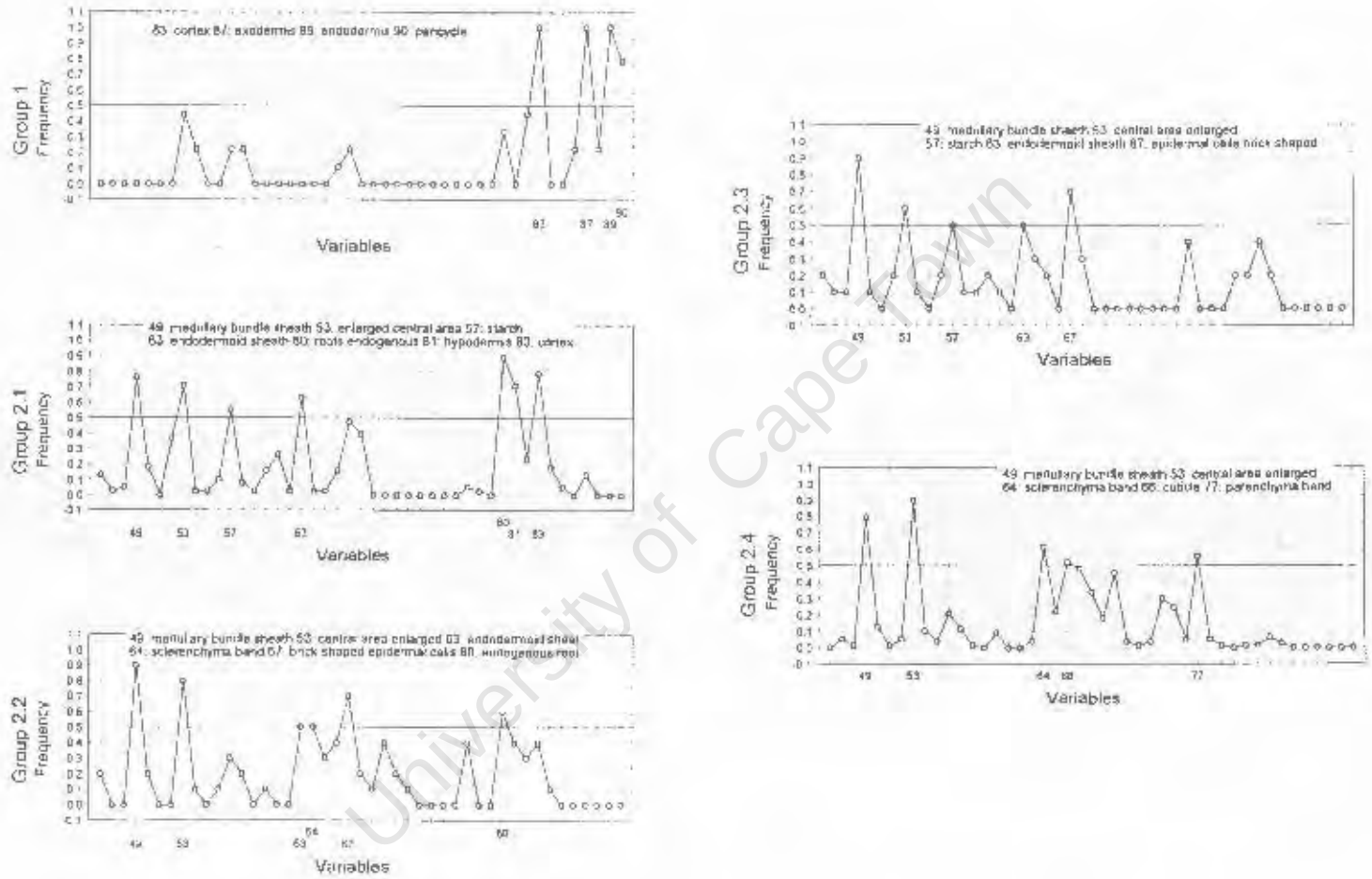


Figure 3.6. Line plots of frequencies for variables 46-90 for Groups 1 - 2.4. Variables with a greater than 50% frequency are labelled on each line plot and the 50% frequency is indicated by a solid line. Group 1 = roots; Group 2.1 = rhizomes; Group 2.2 = transition and runners; Group 2.3 = transition and runners; and Group 2.4 = inflorescence axes.

Table 3.13. Table showing shared variables between two groups each time for the Groups (1-2.4).

	Group 1	Group 2.1	Group 2.2	Group 2.3
Group 1	----------	----------	----------	----------
Group 2.1	11 (subterranean innovation buds), 83 (cortex)	----------	----------	----------
Group 2.2	1 (subterranean), 24 (intermediate life history, 58 (starch in cortex)	53 (enlarged central area), 80 (endogenous root formation)	----------	----------
Group 2.3	6 (orientation intermediate)	14 (leaf base ensheathing internode), 28 (leaf bases swollen), 29 (leaf bases hairy), 57 (starch), 60 (starch in central area), 84 (cortex containing vb.'s)	67(brick shaped epidermal cells)	----------
Group 2.4	8 (intravaginal branching), 54 (central area hollow)	45 (t-shaped vb.'s) 52 (anastomoses), 68 (epidermal cell walls equally thickened)	18 (widely spaced internodes), 39 (vb.'s medullary and peripheral), 64 sclerenchyma band), 70 (chlorenchyma)	10 (aerial buds)

Association between variables

The scatterplot of variable association in k-dimensional space is shown in Figure 3.7. The vectors that were determined on a purely visual recognition basis are indicated on the figure. The vectors correspond directly to groups of variables which define rhizome internodes, root portions, inflorescence axis internodes and intermediate internodes. These groups of variables were also detected and highlighted using frequency calculations in the line plot graphs (Figures 3.5 and 3.6; Table 3.12).

The factors are difficult to tease out and interpret. But, the vectors correspond perfectly to the internode groups of the MDS analysis and either there is complete circularity in this method or, the factors are structural in nature and contribute strongly to the vector projection. Separation along Factor 1 results in the detection of the rhizome and inflorescence axis vectors with the intermediate vector in-between. Separation along Factor 2 separates the root vector from the remaining vectors. These vector projections, suggest that the root system is quite separate from the axial system in monocots.

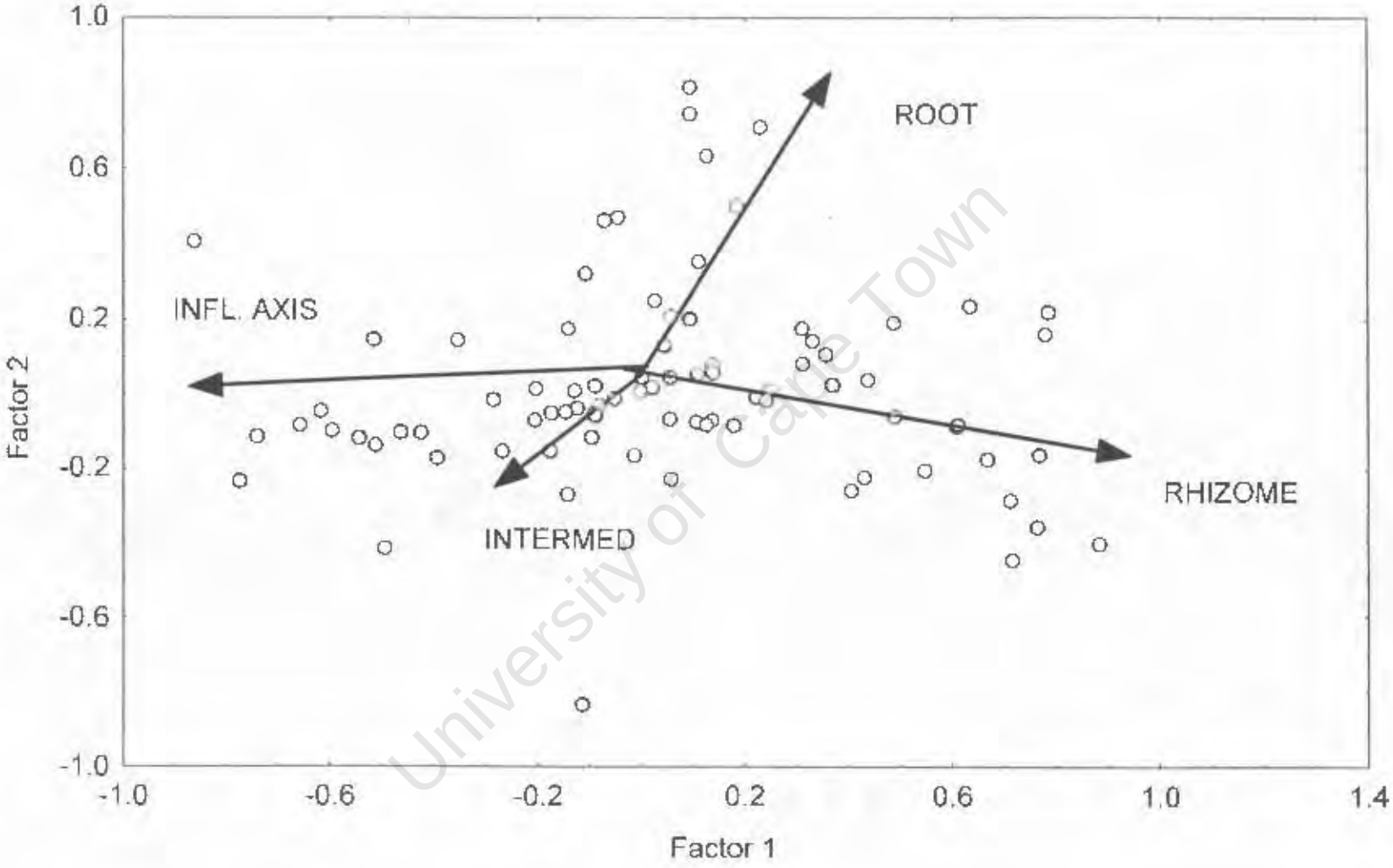


Figure 3.7. Scatterplot showing variable association in two dimensional space. Vectors correspond to groups defined in MDS analysis (Figs. 3.1 and 3.2).

DISCUSSION

Binary data: merits and problems with its use in this study

Growth form is a complex integration of many characteristics which make up a plant. In order to interpret growth form logically, it is necessary to consider growth form not as the whole, but to break it down into elementary components which when combined contribute to the overall growth form and structure of a plant. Such components can be extrinsically determined factors like localised environmental conditions, while others may be intrinsic, like the basic design of a certain portion of the plant.

Every attempt is made in this chapter, to take account of growth form as a whole, examining individual plants from tip to base and coding variation for each "zone" of the plant. This approach is adopted in order to avoid recognising preconceived organ categories. In any classification process, the whole is composed of component subunits comprising that classification. The subunits referred to in this case are internodes. The internodes are further examined for variation in features by using a binary approach i.e. presence or absence of features. This approach closely follows that which is used in numerical taxonomic analyses. Thus, growth form features (parameters) are treated as independent entities. However, as Sokal & Sneath (1963) have indicated, it is difficult to assess empirical correlations between features, as the association between characters can be a result of deterministic factors, like a specific environmental condition or genetic coding (arrays of characters responsible for one function). There is not necessarily any notion of hierarchical arrangement between features, since binary data does not suggest any degree of nestedness.

As with any attempt to measure variation, transforming observations into measurements is problematic. This is less often the case when the variation is easily measurable as an absolute measure or a count. However, when the variation is expressed as a series of identifiable patterns and the observations are coded as binary variables, the analysis is likely to be more problematic. One problem encountered in this study, for example, was that of inapplicable characters. Many authors suggest ways of dealing with inapplicable characters such as treating them as missing data, giving them the zero code (or negative code) when applicable or best of all recognising them as non-comparable characters (Gordon 1981, Sokal & Sneath 1963, Hawkins in press). Unfortunately, not all characters can be treated with the zero code if the feature is not present in the particular OTU, nor can they be given the missing code unless the structure in question is lacking. Ideally, the inapplicable score (N/A in Paup (or no comparison (NC suggested by Sokal & Sneath 1963)) is most appropriate for many of the characters that

one encounters in one OTU, which are lacking in another due to the whole structure being absent, not just the associated feature.

In Ntsys-pc (Vers. 1.70, Rohlf 1992), inapplicable characters can be treated as missing data, giving them the 9999 code (missing data code). This was not desirable in this study for many reasons, the most important being that the OTU's are structural entities themselves, as opposed to entire organisms or taxa. Thus, missing data codes don't adequately deal with the notion of conditionally present features. However, missing data are treated in a computationally appropriate way in Ntsys-pc (Vers. 1.70, Rohlf 1992), in that no comparison is made between data points in any of the calculations if the missing data code is encountered.

Another approach that could have been adopted is to code the inapplicable variables with state 0. However, in proximity calculations this is not desirable as in a pairwise comparison these variables will have a "value" and hence some measure of similarity will be calculated, albeit it small. This is not desirable in the situation where variables are conditionally present and require a definite and distinct separation from other OTU's in which the variables are present. Inapplicable coding would be the most appropriate approach here (or missing as treated in this study) rather than zero state coding. Zero state coding is not uncommon and has been used in several instances (e. g. Pleijel 1995), but is not the recommended method of character coding in cladistic studies (Stevens 1984; Maddison 1993; Hawkins et al. 1997; Hawkins in press).

To solve the problems encountered with inapplicable characters, it could be argued that it would be better to combine the characters into a single multistate character. This is theoretically correct, but is problematic in practice where a structure is missing, as much information is lost when it is treated as an alternative state rather than a possible character. Furthermore, problems may arise when proximity calculations between the OTU's need to be made, as in this study. It is recommended that the calculations used for assessing similarity (see Introduction) are best achieved on homogenous data sets. For this reason alone, having a data set which comprises binary data in addition to numerous multistate characters could lead to inconsistencies in calculations of proximity and therefore, inaccurate projection of relationships between points (OTU's) in n dimensional space.

During a preliminary, exploratory analysis, multistate coding of the variables and a similarity matrix based on percent disagreement was projected in MDS on an earlier, incomplete data set. The same basic structural pattern was obtained as for that with the Jaccard coefficient in this study, with many of the points falling into the same groups that are recognised in the current study. As such, on a purely superficial level, it seems that

the coefficient of similarity does not adversely affect the exploratory data analysis. However, following a puritanical and computationally correct approach, using binary coding and the Jaccard coefficient as the measure of similarity for this kind of data, should be the best suited option for the OTU's in this study.

Similarity measures - the Jaccard coefficient and the effects on proximity assessment

One problem with using the Jaccard coefficient, is that inapplicable data cannot be *specially* accounted for - it has to be coded as *missing data*, where the Jaccard calculations make no comparison when missing data are encountered in the pairwise assessment. This means that lack of data and conditional presence are treated in the same way. It would be better to treat missing data as equivocal (allowing it to have either a 0 or 1 state in this case) and only conditional presence as no comparison. Fortunately, all the "missing" coded data in this analysis is of the conditional presence type, there are no "unknowns". However, if one had to include fossil organ internodes, this would become a real problem.

Another alternative would be to use a simple matching coefficient which differs from the Jaccard, by including negative matches, offering the alternative that "absence" or the negative state can be a real, defining character. In this study, a matrix of similarities based on a simple matching coefficient was calculated and projected in MDS. The result was little different to that obtained from the Jaccard calculation, in fact, the Jaccard calculation tended to produce an MDS with greater separation between major "groups" and lower stress values. Tyteca & Dufrêne (1993), in an analysis of the taxonomy of Western European orchids, also found that certain distance measures produced more satisfactory results overall in both PCA and clustering. In their study, they used a continuous data set and found that of the range of distance methods, the Mahalanobis distance was most suited to the data. This suggests that the distance measure must be carefully selected to avoid erroneous results in later portions of analyses such as MDS, PCA or clustering.

Stress calculations - which is the best approach to "badness of fit" in MDS?

In the method of non-metric multidimensional scaling described by Shepard (1962a; b), the computational approach is to maximise a monotonic relationship between the inter-point distances and the dissimilarities. Thus, the larger the dissimilarity, the larger the corresponding distance. Therefore, the method uses the rank ordering of the

dissimilarities rather than metric information. Gordon (1981) suggests that it is more like a method of ordinal scaling. Kruskal (1964a, b) developed the method to describe the function of monotonicity by proposing the calculation of least squares monotonic regression. In the method, a set of dissimilarities is determined to obtain a geometrical configuration whose inter-point distances minimise the values of Stress in the given equation. The starting co-ordinates used in this study were random and thus, the geometrical configuration had to be found by an extensive iterative procedure. Accordingly, at the start, there are a number of distances corresponding to the configuration in the specified dimensions which will have an initial stress value when they are compared with the dissimilarities. Minimising the stress value iteratively is a measure of the "badness" of fit of the initial configuration to the set of dissimilarities. The main problem with this kind of iterative calculation, is that iterations may become trapped in poor local minimum solutions which may be far removed from the global minimum (Gordon 1981, Everitt & Dunn 1991). A way around this would be to change the starting configurations of points and search for improved stress values. This was undertaken for the total organ data set using configurations obtained from analyses in more than two dimensions as starting configurations. This procedure had little effect on lowering the stress value. The stress equation used did however affect the values of stress. The Stress1 equation used in this analysis gives lower stress values as the denominator is simply the sum of squared initial configuration distances rather than the difference between configuration distances and a set distance d* (as in equation Stress2). This may lead to small denominator values which ultimately increase the value of stress regardless of the difference between the configuration distances and the original distances (i.e. the monotonic relationship). It is likely that the Stress2 equation may be better utilised for the situation when the starting configuration of points comes from a principal co-ordinates analysis (PCO), and the configuration distances are already ordinally placed.

The random starting configuration option was chosen for two reasons. The first being that the variables for the internodes do not show a multivariate normal distribution due to their binary nature, which may affect calculations of variance in geometric methods. The second reason is that starting with an initial configuration imposes a certain amount of structure in the data set and hence on the points in configurational space. Ultimately, the inter-point distances may be artificially imposed. The intention was to use the MDS analysis as an exploratory form of data analysis and therefore if any structure is present in the data set it should be simply and monotonically presented in the configuration of the points in two dimensional space. By using an MDS analysis, the proximity between the points can be taken at face value - the closer the points are to each

other, the more similar they are, while the further apart the less similar. There is no complication with rotation, variance and confidence intervals around each specific point in the projection as is the situation in a principal components method.

The MDS patterns and the recognition of groups

The root system

The MDS projection in Figure 3.1, which shows the spatial arrangement between all the internodes revealed two main groups. The major distinction is between a group composed of root portions and a group comprising the axial system. There are also the three root outliers which were subsequently excluded from further analyses. These are the roots of *Xerophyta, Epidendrum,* and *Borya*. These root portions are all aerial roots, arising some way towards the apex of the axis in each case, which may account for their position in Figure 3.1. The root of *Epidendrum* is also odd in that the cortex contains chloroplasts and also has mesarch xylem. The roots of *Xerophyta* and *Borya* being part of the whole resurrection lifestyle, are only produced when hydrating conditions are available and tend to be protected by sheathing leaf bases as they grow downwards, closely adpressed to the axis. These characteristics are not encountered in any of the other roots that were examined in this study, possibly accounting for their unusual placement in Figure 3.1.

The root group includes three subterranean "tubers". These are the tubers of *Myrsiphyllum scandens, Chlorophytum comosum* and *Holothrix villosus*. The anatomy of the tubers of *Myrsiphyllum* and *Chlorophytum* were, in each case identical, to the root organ anatomy except that there was a large degree of cortical expansion in the tubers. It is likely that these tubers serve as nutrient stores, and in particular, starch was present in the cortex of *Myrsiphyllum*. The root system of monocots was included in the study so that the nature of orchid tubers of orchids could be assessed. The tuber of *Holothrix* (tribe Diseae of which the general condition is to have tubers) is located within the root group in Figure 3.1. This is an interesting position as it has long been considered that the tubers of orchids are special organs - intermediate root-stems. The tuber certainly behaves like a stem because it overseasons producing the shoot material from its apex at the start of the growth season. Such characteristics have led to much confusion in terminology, with some authors proposing that the tubers are root tubers (Arber 1925; Pate and Dixon 1982), while others stem tubers (Dressler 1981, 1993) or that the tuber is intermediate between roots and stems (see Pridgeon & Chase 1995, Chapter 2).

Several decades ago, the developmental anatomy of the root plus tuber (orchidoid droppers and sinkers) was carefully examined by Ogura (1953) and Kumazawa (1956) who proposed that the "stem tissue" was merely ensheathed in the root and tuber tissue

and in cases where tuber dropping occurs the root functions to carry the new "stem tissue - bud" with the tuber to a new location. The anatomy of the root plus developing tuber of *Holothrix* found in this study, is congruous with this conclusion. In addition, if the anatomy of the apex of the fully developed tuber is examined, the meristematic position of the "aerial" portions of the plant are located within a groove in the tuber tissue. Thus, the tuber tissue is separate from the shoot/stem tissue in *Holothrix* (Chapter 2). Therefore, the tuber of *Holothrix* should be considered as consisting of two organ systems, that of the root system and that of the axial system. For this reason the tuber falls directly into the root group as anatomically, it has no peculiar features that distinguish it from a root, other than being polystelic. There is the possibility that such an elaborate "root" has evolved because of its particular function - that of taking the new seasons sympodial growth to a new location in the soil. The most plausible reasoning, albeit totally hypothetical, would be that from a basic node plus the new seasons shoot bud, the roots would have to grow around that portion of the sympodium, then separate it from the central sympodium and thereby "carry" the shoot tissue within it as it grew away from the parent plant. This would link with the fusion hypothesis i.e. that polystely would have arisen by fusion of several roots - making a polystelic tuber with stem tissue contained within. However, this hypothesis is rejected in more modern approaches in which the idea of stele splitting is favoured. The tuber functions like a stem, having a divided vascular system (albeit discrete steles, not vascular bundles), due to the increased area that must be covered by the tuber and the function of supplying the shoot with resources. The phenomenon of roots taking on a stem-like function, as the tuber of *Holothrix* does, is uncommon in monocots. However, roots of some *Phalaenopsis* species can be induced to form adventitious plantlets, known as a *keiki* (see Hodgson 1991). It is more usual for the rhizome to take on a root function as in *Cordyline australis* and *C.banksii* in which the main axis produces a lateral, downwardly growing branch (vertical rhizome) which acts as a surface on which new roots arise, behaving like a tap root (Tomlinson & Esler 1973).

Another root portion that is included in the root group is the contractile root found in *Albuca*. Although these are anatomically similar to ordinary roots, they differ morphologically and functionally. Contractile roots have many folds and convolutions towards their bases where they depart from the axis, although this cannot be detected in a T/S of the area as there is no special tissue in this area. Similar observations were made by Arber (1925). In *Arisarum vulgare* (Araceae), on the other hand, Pütz & Froebe (1995) have found anatomical differences in contractile roots which correlate to the functioning of the roots. There is a radial expansion in the cortical cells which is coupled with longitudinal shortening and the radial expansion develops a force which causes the

root to push sideways against the soil. This is postulated to allow for movement in the soil channel. Following this, the cells collapse, which passively facilitates shortening. Functionally, in the above processes, contractile roots serve to pull the bulb down into the soil at the end of each growth. Thus, contractile roots are only produced on a seasonal basis and develop at different times to the roots which are formed at the start of the growth season (described in Chapter 2). The lack of difference in structure is accounted for by their position in the root group, but it may be interesting to further develop ideas about the features of their functioning and in some way include this into the model so that function becomes more distinct.

The axial system

As shown in the MDS scatterplot in Figure 3.2, the axial system is comprised of two main groups with two intermediate groups. This pattern shows that it is difficult to make an absolute distinction between rhizomes and inflorescence axes, with many situations where features of both organs are shared, resulting in a continuum between two structures with intermediates recognisable.

It has been suggested (Kruskal 1977) that the position of points within groups i.e. the small differences in proximities are volatile in MDS and that the precise locations of the points can change considerably according to iterative procedures and changes in configurational points. For this reason the arrangement of the points within groups in Figure 3.2 was further analysed in a clustering approach. Small differences in proximity are well explained by hierarchical clustering, while the large differences in proximities are more often ambiguous offering little insight into position and relationships. As such, the combination of the two approaches as used here should offer solutions for both situations - MDS for initial group detection (large differences in proximities) followed by hierarchical clustering to detect within group relationships (small differences in proximities).

<u>The rhizome group - Group 2.1</u>

Multidimensional Scaling

This group comprises a wide variety of internodes from structural and functional rhizomes. The pseudobulb of *Polystachya ottoniana* and the pseudobulb stalk of *Maxillaria variabilis* are included in this group. Both of these structures appear superficially very similar, but in *M.variabilis* the pseudobulb stalk subtends the pseudobulb which is formed from the node above, positionally where one finds the basal inflorescence axis. The pseudobulb of *P.ottoniana* on the other hand, has no such structure subtending it. The corms of *Wurmbea spicata*, *Baometra uniflora* and *Pauridia minuta* are also found

in this group, along with the vertical axes of *Epidendrum cinnabarinum*, *Pentameris thuarii* and *Dasypogon bromeliifolius*. Swollen rhizomes of *Canna indica*, *Wachendorfia thyrsiflora*, *Merxmuellera rufa* and *Tulbaghia alliaceae* are also found in this group along with the tuber of *Eriospermum pumilum*. Short vertical rhizomes of bulbs are also found like that of *Lachenalia klinghardtiana*, and short rhizomes of *Tribolium obtusifolium*, *Ischyrolepis cincinnata* and *Holothrix villosus*. Other rhizomatous forms are also in this group like *Thamnochortus spicigerus*, *Anigozanthos manglesii*, *Pseudopentameris macrantha* and *Aponogeton distachyos*.

Clustering

In Figure 3.3 three main clusters (labelled 1; 2.1 & 2.2) were evident. The possibility exists that there is some underlying factor that causes the upper axis of *Epidendrum cinnabarinum*, the pseudobulb of *Polystachya ottoniana* and the pseudobulb stalk of *Maxillaria variabilis* to cluster together (Cluster 1). It is unlikely to be due to a phylogenetic similarity as then the rhizome of *Holothrix villosus* and the lower axis of *E.cinnabarinum* would be expected to group with them. The only explanation lies in the epiphytic growth habit, which must be an underlying feature since no coding of parameters specifying this were used in the analysis. Accordingly some combination of parameters must be determining this.

The main cluster (cluster 2) is split evenly into two clusters (2.1 and 2.2, Figure 3.3) broadly on the basis of orientation as well as thickness. The changes from cluster to cluster are not definite, as some gradation between these two characteristics occurs. Cluster 2.1A, B & C is composed of rhizome internodes which are vertical and non-swollen; cluster 2.2A is composed of swollen, vertical rhizome internodes; and cluster 2.2B is predominantly composed of swollen and non-swollen, horizontal rhizome internodes.

In cluster 2.2A, many of the internodes of the rhizomes are swollen, which on an anatomical level is expressed as an expansion of the cortex and the central ground parenchyma and occasionally the hypodermis too. In addition, these rhizomes can be classified as storage rhizomes as most often starch is abundant in the expanded tissue areas. The clusters additionally signify rhizomes which are found to be instrumental in determining certain growth forms. In the vertical rhizomes group (cluster 2.1B) the internodes are expanded in a vertical manner and as a result give rise to an upright stature of the plants. The stilt grass, *Pentameris thuarii* is present in this cluster group as an extreme example of the vertical rhizome habit and other "stem" grasses are also present in this group e.g. *Pseudopentameris obtusifolia*. Other members such as *Restio*

harveyii have shorter internodes and thus the pattern weakens from one side to the next of the cluster. The second group of vertical rhizomes (cluster 2.1C) generally have short internodes such that the rhizome is crowded by leaf bases and not visible e.g. *Tribolium obtusifolium*, *Johnsonia pubescens* and *Billbergia nutans*, while in *Dasypogon bromeliifolius* the "stem" is visible in mature stands, but the internodes are nevertheless closely spaced.

The other cluster which reflects growth form is that of 2.2B. Cluster 2.2B is indicative of regular rhizomatous growth forms, the organs being horizontal and positioned underground. Interestingly, both storage and water transporting forms occur in this cluster with no specific division into either type. Examples of the storage forms are *Merxmuellera cincta*, *Tulbaghia alliaceae* and *Canna indica*, while those that are water transporting are like *Thamnochortus spicigerus* and *Pseudopentameris macrantha*.

Cluster 2.2C is a small cluster which defies classification and contains a mix of short vertical (*Lachenalia klinghardtiana*) and regular (*Myrsiphyllum scandens*, *Anigozanthos manglesii*) rhizomes.

The intermediates - Groups 2.2 and 2.3

Multidimensional Scaling

In Figure 3.2 the MDS projection, two intermediate groups were identified. These were composed of internodes ranging from rhizome-inflorescence axis transition areas, through basal inflorescence axes to runners of various description. Table 3.7 shows the taxa and internodes for Groups 2.2 and 2.3. Due to the precise location of closely spaced points in an MDS projection being volatile, the precise location of the points in space will not be taken to reflect a related context of within group structure of the intermediate groups. The MDS gives a good idea of the composition of these two groups and does not need to suggest any further relationship between the internodes.

Clustering

In the cluster analysis of the intermediates plus inflorescence axes shown in the phenogram in Figure 3.4 the two intermediate groups found in the MDS are retrieved (labelled cluster 1.1 and 1.2) and additionally show a certain amount of internal structure. A few internodes are misplaced in the cluster analysis, relative to the MDS. The stolon of *Chlorophytum comosum* is located within the intermediate cluster 1.2, while in the MDS was an outlier of Group 2.4. Other internodes swap between the two groups such as those of *Chondropetalum deustum*. This is not really a problem, as the MANOVA tests indicated that the distinctness of the intermediate groups was not significant in both

dimensions, indicating that group membership may be labile in either direction. It is possibly better to recognise the intermediate organs as a single cluster (labelled 1 in Figure 3.4). The division in internodes occurs on the one side into rhizome-inflorescence axis transition portions and basal inflorescence axes, to runners, stolons and rhizomes on the other side. Such a clear cut division seems rather artificial and idealistic. The interpretation drawn from the MDS analysis is less artificial, where group proximity to either rhizomes or inflorescence axes is a better descriptive factor than whether the organs are runners or not. For example, the basic anatomy of the runners of *Wachendorfia thyrsiflora, Billbergia nutans, Chondropetalum deustum* and *Chondropetalum rectum* is similar to that of the rhizome group, with a few inflorescence axis-like anatomical features and peculiar long internodes etc. and would be better described as "rhizo-inflorescence axes", signifying their true intermediate nature. Similarly, the runners of *Willdenowia glomerata, Tribolium obtusifolium, Restio harveyii* and *Ischyrolepis cincinnata* are more reminiscent of inflorescence axes in basic anatomy, with structural and functional modifications to the chlorenchymatous tissue, and the proximity of this group is much closer to inflorescence axes in the MDS. Such relationships are lost in the cluster analysis and for the within group structure of a small sample of internodes like this, where the dissimilarities are not reflected in clustering, the overall picture that the MDS projects is a more feasible interpretation.

The inflorescence axis group - Group 2.4

Multidimensional Scaling

The MDS scatter shown in Figure 3.2 suggests that a single, large inflorescence axis group is discernible. The distinctness of this group is not always clear as some intermediate organs of Group 2.3 could also be members of this group as previously indicated. The basic elements of this group consist of basal inflorescence axes, ordinary inflorescence axis internodes, inflorescence axes and flowering stalks. Also included in the group are the rather indistinct organs produced at the apex of corms which are buried underground and only aerially become photosynthetic and then produce either inflorescences or flowers terminally.

Clustering

The clustering pattern is highly complex with many small clusters forming with no plausible features by which to distinguish them. There is no division into position of organ such as basal inflorescence axis, inflorescence axis, inflorescence stalk, upper inflorescence axis (flowering stalk) etc. Often the inflorescence axis clusters are related in

the taxic sense i.e. some grasses, some restios, orchids etc., but the pattern is not consistent. In other clusters it is a functional grouping such as inflorescence axes arising from swollen/storage rhizomes, or photosynthetic inflorescence axes or simply similarity in basic structure between corm necks and inflorescence axes. It is not certain whether the patterns shown in clustering reflect any true underlying grouping criterion. In support of this contention, no obvious variation or distinctness was apparent when the internodes were being examined and coded for the various parameters. It is possible that one of the major faults with clustering procedures is encountered here i.e. the retrieval of hierarchical structure where there is none.

Discriminating variables

In the root group (Group 1, Fig. 3.1), many of the variables are not found in any of the other groups as it is clearly a different organ system. The frequency calculations and line plots are only a way of elucidating which variables are important. However, the sorts of variables that appear important could be reflected by sample bias e.g. if only vertical rhizomes were sampled. In this study, the range of growth forms that were sampled is likely to overcome this problem. The following variables are found most frequently (50% or more) in the root group (See Figures 3.5 and 3.6), although this does not imply that all members of the group necessarily have the feature nor that the feature is exclusive to the group. Some of these features are however, exclusive root characters, such endodermis and pericycle:

- (35) endarch xylem
- (87) exodermis
- (89) endodermis
- (90) pericycle.

In the rhizome group (Group 2.1, Figure 3.2) the following variables are important (see Figures 3.5 and 3.6). However, not *all* rhizomes have these features and nor are they exclusive to the rhizome group, for example, amphivasal vascular bundles are commonly found in rhizomes, but bundles with u-shaped xylem also occur and often the bundles are of a mixed nature, with both types present. This group shares most variables with Group 2.2:

- (16) closely spaced internodes
- (19) internode giving rise to other internodes
- (22) perennial
- (40) amphivasal vascular bundles

- (81) hypodermis.

The first of the intermediate groups (Group 2.2, Figure 3.2) has few exclusive features which may define it. Many of the variables are shared with the other groups (Figures 3.5 and 3.6). The only important variable is:

- (39) vascular bundles medullary and peripheral.

The second of the intermediate groups (Group 2.3, Figure 3.2) similarly has few features which are obviously important, many of the variables are shared with the other groups (Figures 3.5 and 3.6). Some of the important variables found in this group are:

- (2) internode located on surface of substrate
- (10) aerial innovation buds
- (17) internodes with intermediate spacing.

In the inflorescence axis group (Group 2.4, Figure 3.2) there are many variables which are important in the group in addition to a few variables which are shared with some of the other groups (Figures 3.5 and 3.6). Some of the important variables are:

- (15) leaf bases photosynthetic
- (23) internode short lived
- (25) internode often green and photosynthetic
- (66) cuticle
- (77) parenchyma band.

The method of using frequencies and line plots to gauge the variables contributing to group structure is adequate in revealing the important discriminatory variables for each of the groups. Thus, if one wished to identify a particular portion of a monocot plant e.g. part of the axial system, an internode could be examined and its features compared with those presented in Figures 3.5 and 3.6. If the internode has the following features e.g. aerial position; vertical orientation; a cuticle and a parenchyma band, it is likely that the portion from which the internode is taken from could be described as being similar to those found in the inflorescence axis group (Group 2.4). As such, it is possible use the important variables outlined above to postulate group membership for a particular internode.

The main problem is that there is no way of obtaining an exclusive variable and *denovo* sharing of variables by all the members of a specified group, because the variables tend to be shared. However, in the present study, such a goal is probably not desirable as there are clearly not discrete groups. Many internodes can be placed in more than one group and this method shows nicely which shared variables are important in this instance. The assessment of variables in this way is quite useful where there is not a categorical grouping of organs.

Association between variables

The association between the variables shown in the scatterplot in Figure 3.7 illustrates clearly that two factors are important, separating the variables into distinct clumps. Accordingly, vectors are plotted over the concentrated clumps and the direction of vectors is related to groups of variables which are likely to be important in defining the organ groups delimited in the previous analyses of MDS and clustering. It seems that Factor 1 defines the axial organ system, with a continuum apparent and intermediate organs recognisable, while Factor 2 defines the root system.

The precise nature of these factors is difficult to determine. Many of the variables which have clustered together in dimensional space are related structural features and tissue patterns which are present within the particular groups. It is therefore likely, that organ systems are defined on a structural basis, by the presence of certain features and patterns and ultimately by some underlying phylogenetic determinant. The vectors (organ groups) are also defined by a similar determinant force. This result suggests that organs will in some way be distinct and definable by certain characteristics (groups of associated variables). The variation from the basic structural features and the modification in pattern leads to the variety of forms such as were evident from the clustering analysis of the rhizome group (Figure 3.3). These modifications are most likely in response to some sort of functional force e.g. the need to have an organ which can store starch for the following season's growth results in the internodes expanding and becoming fleshy with a concomitant expansion in the cortex to accommodate the starch storage requirements. A similar set of functional groups is probably present in the root system too as many roots show modifications in their basic structural pattern towards a particular function e.g. the photosynthetic cortex of *Phalaenopsis* roots or the peculiar roots of the resurrection plant *Borya nitida*. However, a wider sample of roots would be required to test this in a comprehensive manner and this falls beyond the scope of this thesis.

CONCLUSIONS

Rhizomes tend to vary more widely, showing more functional division into groups and also seem to have a pivotal role in determining what the overall growth form of the plant is likely to be than inflorescence axes do. There was far less observed variation in form in the inflorescence axis organs, excepting where specialisation to specific conditions has occurred, such as water dwelling plants (*Aponogeton distachyos*) and drought exposed plants (some Restionaceae, see Chapter 2 for detailed consideration of the variation and specialisations).

In a paper examining the vegetative morphology and inter-fire survival strategies in Fynbos grasses, Linder & Ellis (1990) showed that the kind of stem base that these grasses have determines two crucial aspects of their life history - that of growth form and that of fire survival strategy. The results presented here support this contention and suggest that such relationships may exist on a broader level in monocots as a whole. Modifications in rhizome form has lead to a whole suite of survival strategies in monocots (overseasoning, fire survival, water colonisation, drought tolerance etc.). The idea that all modifications of monocot growth form are variations on a basic theme (Holttum 1955) is supported by the results of this study.

From this set of analyses it is clear that MDS is a useful tool in elucidating the underlying group structure in growth form. The results illustrate that monocot organs cannot be categorically defined as there are organs of intermediate nature to consider in the classification. The notion of discrete organs and sets of discrete features defining them cannot be considered when it is apparent that a continuum in growth form exists with many shared features and group membership being labile. The cluster analysis was most useful in defining the closer proximities and therefore the relationships between the internodes within the defined groups. In the rhizome group in particular, the functional variation was clearly demonstrated by the hierarchical agglomerative procedure. The correlation and ultimate association between sets of variables indicated that the basic structure of particular organs is important in defining the different organ systems and additionally the defined groups of the axial system. It is evident that the growth forms of particular monocots are defined by a very fine balance between history and function, the phylogenetic constraint being most important in maintaining the basic structure of the organs and the functional requirements of the particular organ being extrinsically shaped and modified as conditions and needs change, eventually resulting in a growth form that is suited to a particular niche and thus survival strategy.

The analyses involve a certain notion about monocot growth forms. The model based on the patterns shown in the MDS analysis indicates a distinct root system with a continuum occurring within the axial system. Such a notion is one of a functional shoot system in monocots. The shoot can be viewed as a series of processes which are inter-linked. Thus, intermediates must be given consideration in any attempt to recognise organs in monocots. The disparities between a functional view of plant form and a pattern approach in identifying homologous structures are many and will be further addressed in Chapter 4 where the homology and terminology of monocot organs is considered.

The results from this study serve as a firm grounding towards further work on the remaining organ systems of monocots and if a continuum approach is considered, the

problems encountered with the interpretation of monocot leaf morphology have the potential to be overcome. Clearly, monocot organs do not group together on the basis of taxic similarity but rather, in the first instance on structural similarity and in the second instance on the functional nature of the organ.

CHAPTER 4

An examination of organ homology in selected monocots: proposals for a simple terminology

'Definitions are tricky things. Some think that definitions are, or ought to be, independent of time and space, just as natural laws are or ought to be.' .....'the sum of the angles in a triangle is always and only 180°, regardless of time and space. True indeed, as long as parallels do not cross, but somebody will eventually point out that parallels do not meet in the infinite!'

Rieppel (1994).

INTRODUCTION

Concepts and types of homology

Concepts of homology refer to different explanations (e.g. idealistic, historical and biological) while types of homology refer to comparisons within (iterative or serial) and between (taxic) organisms (Sattler 1994). Explanations of homology are usually based on structural features which are present among several different groups. This is referred to as taxic homology because taxic homology implies a hierarchy of groups (de Pinna 1991). Within group explanations of homology are referred to as transformational homology, iterative homology or serial homology (de Pinna 1991). Similarly, transformational homologues can be compared between different organisms and thus may also be taxic homology implying some relation and hierarchy among the organisms (de Pinna 1991). There has been much debate over the explanations of homology and as a result, many definitions have been developed. There is no right or wrong definition, it is entirely dependent on the approach that is utilised for identifying homologues (Hall 1994; Wagner 1994). Whichever definition is accepted, there will always be advantages and disadvantages to the choice (Wagner 1994). In addition, there is often overlap between the types of homology i.e. taxic and transformational. As a result, the term homology is often confused and is fraught with a plethora of definitions.

Taxic homology

The idealistic explanation

Owen is often credited with first defining the differences between homology and analogy (Panchen 1994). But, the concept of homology is ancient, being traceable to Aristotle (Hall 1994). Panchen (1994) reviews Richard Owen's concept of homology and in this says that Owen's definition of a homologue is: the same organ in different animals under every variety of form and function. Owen's definition is based on the explanation that homologous structures were derivable from the same structure in the archetype (Panchen 1994). Owen offered an idealistic explanation of homology, in believing that an archetypal vertebrate skeleton existed. The morphological concept of homology could also be included within this explanation because the definition refers to structural identity (Wagner 1994) which must relate back to a basic or general structural pattern.

The phylogenetic, evolutionary or historical explanation

An evolutionary (historical and/or phylogenetic) explanation of homology is based on the theory of evolution i.e. descent with modification which provides the causal explanation for homology (Rieppel 1994). Under this explanation, the definition of historical homology is not circular (Rieppel 1994). Darwin wrote that unity of type is explained by unity of descent and thus, arose the explanations of homology as similarity due to common descent (Rieppel 1994). In cladistics, homology has been equated with synapomorphy (Patterson 1982). A cladistic explanation of homology (or synapomorphy) is that homology is an hypothesis of similarity due to common ancestry to be tested by congruence (Patterson 1982; de Pinna 1991; Nelson 1994; Rieppel 1994; Stevens 1984). The more characters (similarities) congruently supporting a hierarchy of relationships, the stronger the evidence for regularity of character distribution among taxa and hence evolution (Rieppel 1994). Cladistic homology approaches typology because the taxa are abstract constructs, albeit that cladistic homology works at the level of the monophyletic taxon. The taxa represent ideal categories, types or essences, but are not based on the notion of a real archetype. Taxa are relations between organisms and are as a result composed of material organisms (Nelson 1994). Cladistic homology (or synapomorphy) cannot be applied to the level of the individual or structures and thus is similar in concept to typology of structures where a comparative approach is necessary.

The biological explanation

The biological definition of homology is based on the idea that homology is shared similarity of developmental units due to shared developmental constraints (limitations to

phenotypic variability) or pathways, rather than common ancestry (Rieppel 1994; Wagner 1994). Commonality of development at some level is important for structures to be recognised as homologues (Hall 1995). The similarity is caused by locally acting regulatory mechanisms of organ differentiation (Wagner 1994). The biological explanation is based on developmental processes during ontogeny that shape the generation of a structured material entity. The processes are self assembly, fixation of a temporal pattern of activity into a spatial pattern and spontaneous pattern formation (Wagner 1994). Thus, although many structures appear passive in organisms e.g. the mollusc shell, the pattern of shell deposition is actively maintained by a particular developmental pathway (Wagner 1994).

Iterative (serial) homology

The explanations for this kind of homology involve the comparison of entities within organisms, usually within the same individual. It is the correspondence between different features/organs/segments (or repeated features/organs/segments) in the same individual at the same time (Hall 1995; Roth 1994). Owen distinguished serial homology from special homology (Hall 1995). The repeated features are recognisable as homologues because they are variations on a common structural theme (Hall 1995). As a result, the recognition of serial homology is based on some concept of an archetype (basic structural plan). Serial homologues are also clearly based on common developmental processes (Hall 1995). Serial homology can be complicated by transformation within the series, so that the final structure in the series may differ to the initial structure e.g. leaves and petals (Hall 1995). It has been suggested that homeotic genes control the establishment of serial homologues (Hall 1995, Albert et al. 1997). If a requirement of shared common descent is part of an explanation of homology, then serial repeated structures can only be homologues when the same structures are compared between different organisms (Hall 1995). Thus, in this view serial homology cannot be accepted as homology at all. However, serial homology may offer insight into the relation between pattern and process. Repeated expression of the same structures is controlled by homeotic genes, and teratologies and homeosis are examples of where the genetic basis for expression is removed. Homeosis shows a clear link between pattern and process in the expression of structures (see Sattler 1994).

Pattern versus process in explanations of homology

There main reason for the wide range in proposals for a definition of homology is that homology is operationally defined from two diametrically opposed approaches: one based on pattern and the other based on process (causal explanation). In pattern based approaches the structural identity of features is important (e.g. historical explanations), while in a process based approach the processes that are responsible (e.g. biological explanations) for shaping the feature being examined are important (Sachs 1982; Shubin 1994). Sachs (1982) suggests that while process is an important determinant in the development of plant organs, the determination of an apex (or meristem) as shoot, root or leaf occurs early in the developmental phase. Tomlinson (1984b) has suggested that a good basis for establishing homologies would be the equivalence of primary meristems because similar structures originate from the same kind of meristem. Thus the inclusion into morphological categories can be based on process. However, the notion of homology is still the equivalence of parts, whether there is a historical connotation, biological mechanistic basis or idealistic groundplan. Underlying the differences in opinion about the definition is the need for similarity: either positional or special similarity or both (see Inglis 1966). Homology has been described by de Pinna (1991) as primary and secondary homology. In primary homology, the equivalent structures are operationally defined on the basis of similarity. This is the case for synapomorphy (shared sameness of characters), for topographical equivalence (similarity in position); special similarity (similarity in histology or ontogenetic life phase) or whether by a shared function (similarity in developmental process). It is only in the concept of cladistic homology that secondary homology is considered. Secondary homology is a statement about the congruence between shared characters (synapomorphy or homology). Patterson (1982), in addition to the congruence test, proposed the tests of similarity and conjunction. However, de Pinna (1991) argued that the only way to test statements of homology is through the method of parsimony and an assessment of character congruence, thereby negating the validity of the conjunction test. If characters are incongruent then there is non-homology and the statement of synapomorphy (homology) is refuted.

Modular construction and the importance of process in homology

Tomlinson (1984a; 1984b) points out that homology has been examined from the viewpoint of unitary construction with zoocentric principles and should be independently considered in plants due to their modular construction. Tomlinson (1984a) suggests that this is difficult because it is problematic to measure transformation in a part for part

comparison. Without determining equivalence of structures, an evolutionary examination of form is not possible (this is a basic premise in the cladistic paradigm). Yet establishing equivalent structures should be the basis of any sort of comparative morphology of form. It is difficult to determine what structures are equivalent without thinking of the plant as a whole, the units considered being part of a much larger process in the constructional design of the modular organism. This is an unfortunate contradiction, as homology recognition requires the reduction of the whole into smaller units which are independent and reflect a pattern (measurable as characters) rather than a process. Mabberley & Hay (1994) have also proposed that this is problematic when viewing form from the process point of view.

A further consideration is that the whole plant life cycle should be included in any assessment of homology. Tomlinson (1984a) proposed that the mature stage of the plant is only one portion in the space-time continuum that plants occupy. In order to correctly establish potential relation between parts, it is important that the homology criteria are applied to all stages of plant development (Sattler 1994). This can be done by examining the development of selected seedlings and following the developmental fate of the various parts of the seedling. This ensures that the correct correlations between the seedling and the adult are made and so strengthens the possibility of identifying homologous organs. The hypocotyl of the seedling plays an important part in establishing structurally and functionally different rhizomes (Chapter 2), and thus appears to be the basic structure which is modified in the sympodial growth habit.

Problems with a taxic (pattern) approach to homology

Sattler (1984) proposes that a concept of homology based on common ancestry can only apply to entities that show a direct genealogical/phylogenetic relationship e.g. genes, chromosomes and whole organisms, not parts such as organs, organ systems or modules because they do not directly become transformed into one another. He further argues that homology of organs cannot be inferred from a knowledge of the genealogy of the plants which bear the organs. Thus, organ homology cannot be reduced to gene homology (Sattler 1984). However, recent developmental research shows that genes can control organ formation (Albert et al. 1997; Bell 1992, Coen & Meyerowitz 1991; Smith & Hake 1994), therefore, organs *per se* can be reduced to sets of genes which control their expression. Perhaps organ homology can be reduced to gene homology if the genes controlling individual organ expressions can be isolated. If the expression of mutant structures is considered e.g. in floral whorls, then the expression is by genealogy. Sattler

(1984) has questioned how the organs of the mutant are homologised with the natural form and has used this argument to illustrate that organ homology is independent of historical notions. The notion of partial homology according to Sattler (1994) allows the possibility of comparing structures both in terms of a 1:1 correspondence (sameness of features) when dealing with features and in partial correspondence when whole structures are compared.

Problems with a categorical approach to homology recognition

Sattler (1994) suggests that the first step in proposing homologies should be based on correspondence between structures. He suggests that the common thread running through homology recognition is relation (or correspondences) between parts. Homology must be a 1:1 correspondence of parts. Stevens (1984) proposes that 1:1 correspondences are unique elements in structures and should be evaluated using the criteria of homology proposed by Kaplan (1984). Other similarities are either forced into the 1:1 correspondence or discounted (Sattler 1994). This reduces diversity of variability into categories and variation (which is often important phylogenetically, biologically etc.) is not considered in homology identification. Sattler (1994) proposes that to understand the biological variation and to represent living structures, the concept of partial homology (partial correspondence) has to be included in any operational approach to identifying homologues. The concept of partial homology applies to all organisational levels, even molecules (Sattler 1994). The concept of partial homology is problematic if notions of homology are based on an idealistic archetype consisting of discrete categories or on the idea of homology as synapomorphy (cladistic homology). Idealistic notions of discrete categories do not allow the recognition of intermediates. If homology is viewed as synapomorphy, then a notion of partial homology is inadmissible because monophyletic groups cannot be defined by anything other than shared derived characters (synapomorphy). A shared "intermediate" feature may be interpreted as a morphological "hybrid", much like a transitionary organ would be. Thus, many concepts of homology are based on a 1:1 correspondence of features. Sattler's (1994; 1996) concept of correspondence incorporates both ahistorical and historical concepts of homology where correspondences refer to structures or to function or to behaviour.

Sattler (1994) has proposed that many examples of partial homology and transgressions are evident in both the vegetative and reproductive regions of the plant. Weber (1980) illustrated the transgression between phyllome categories and bract in the tepals of Zingiberaceae, and proposed that the phylogenetic origin of these structures in

monocots would be difficult to determine. Another example of transgression may be false vivipary, where a reproductive series reverts to vegetative series. Instead of a flower being initiated in an axillary position (or subtended by bract), a new shoot axillary bud is developed, yielding a new vegetative series. Similarly, branching inflorescence axes could be an example of homeosis - which may develop according to extrinsic pressures. Sattler (1994) proposes that homeosis is essential to homology and plant morphology, but of course, that it contradicts the importance of the topographic criterion and 1:1 correspondence. However, with mounting evidence that homeosis exists naturally and that organ position and developmental fate can be regulated by homeotic genes, the phenomenon cannot be ignored and the resulting structures must be considered in whichever framework one is working in. Concepts of homology based on a categorical approach can be nicely illustrated by some examples (e.g. stamens, petals and sepals are modified leaves, and in mammals, where transformational homology is based on a categorical approach, where the mammalian ear ossicles are homologous with the quadrate and articular jaw bones (Panchen 1994). But, when structures are displaced, then a categorically based concept of homology has problems e.g. forelimb of the newt and arm of man are homologous structures, but occupy different positions on the body (Panchen 1994). In the case of homeotic organs, similarity between structures is based on special quality (Sattler 1994). Special quality i.e. a functional or histological one will show the relation of the part. However, both position and special quality could change.

Homology as pattern and process

However, Sattler (1996) views structure as function in terms of processes. This is where Sattler's (1984; 1994) concept of homology differs from the approaches discussed above because the opposition between pattern and process is eliminated. Thus, morphological relations (correspondences) become dynamic and the disparity between structure (pattern) and function (process) becomes obsolete. He highlights that operationally, homologues are recognised in more or less the same way regardless of what the underlying concept of homology is. Homologues are operationally defined by similarity (special quality) and position. In ahistorical concepts homologues recognised in this way establish homology, while in historical concepts they provide potential homology only, and need to be tested further by congruence. In partial correspondence (partial homology) a structure does not share all characteristics with another one. Thus partial homologues cannot be categorically placed. In Sattler's multivariate approach (Jeune & Sattler 1992; Sattler & Jeune 1992) to recognising homologues, homology can be measured

quantitatively by linear distance. In Jeune & Sattler's (1992) system for example, a typical leaf would have zero distance from the leaf category and would indicate 1:1 correspondence, while an intermediate would fall some way out of the typical leaf zone. The greater the distance, the less the correspondence and hence, homology. If a simple leaf is compared with a shoot the distance in p-dimensional space is great and the two structures are different. In Sattler & Jeune's (1992) analysis, stamens are intermediate between both phyllomes and caulomes. Structural categories are not mutually exclusive and as such, they do not exist as entities nor as essences. Thus, atypical structures or teratologies are only aberrant because they do not fit into the specified categories of the classical model of de Candolle. With the recognition of a continuum and intermediates the notion of a typical structure becomes fuzzy (Sattler 1996). A category refers to a practical name for a said structure which is more common than an atypical structure.

Typology, homology and terminology

Typology (based on an idealistic notion of an archetype) must have arisen as a comparative method for assessing homologues. The philosophical position of a "type" is one of theoretical constructs (Tomlinson 1984a). Typology has been criticised (see Rieppel 1994), but in many respects it has formed the basis for much of the understanding in many biological studies. A typological approach to recognising plant structures is practical and easy to work within a comparative framework. This approach may work well in an initial approach to identifying homologues and also in any sort of evolutionary framework. However, at an operational level, when the actual demarcation of organ boundaries is attempted, typology fails. Typology also fails when the term "stem" is too rigidly defined, not allowing for the incorporation of "less typical" stems. Troll (1937) alluded to these points with respect to monocot rhizome modifications. Typology cannot incorporate intermediate structures because they have characteristics of more than one category. Typology thus requires strictly defined and demarcated categories. This rigidity can be relaxed to a certain extent, by creating theoretical notions that are simplistic and which express the very basic structure of the plant form under consideration. A theoretical construct of plant form should only apply at the specific level of the plants being considered. For example, difficulties will be experienced in recognising homologous structures if a basic form depicting monocot form is proposed and then is applied broadly e.g. to Bryophytes. The transformation of features between these two distantly related and structurally divergent groups is so great as to be of meaningless interpretation at the level of Bryophytes. Along the evolutionary grade, taxa as well as features have been

lost, gained or transformed and it is difficult to consider form without a perfect fossil collection. There are undoubtedly broad based features of growth patterns which relate to distantly related taxa and indeed to biological organisms as a whole, but the direct link of these patterns to particular structures and growth forms is tenuous, unless compared within a delimited group. Similarly, monocot form is sufficiently different in many respects to dicot form to warrant separate interpretation of structures. It is therefore, important to separate concepts from processes.

Operational approaches to homology and aims of this chapter

Shubin (1994) suggests that an analysis of homology should consist of three steps: 1) formulating hypotheses of homology, 2) testing the hypotheses with phylogenetic analysis, and 3) determining their mechanistic explanation. Of these three steps, the first step forms the basis of this chapter and this thesis, and no testing of the hypothesis by phylogenetic analysis is attempted in this thesis. There are also two extreme views which arise out of the pattern versus process approaches namely, holism i.e. there is no individuality (developmentally) to propose homologies and reductionism i.e. organisms decomposed to traits without consideration of their biological functioning (Shubin 1994). These two views are important in plant morphology. With the many explanations that are present for the term homology, it is difficult to decide which approach is the best to adopt. This in part depends on your philosophical viewpoint, but generally should be determined by the goals of your study. If a comparative assessment of sets of characters is the end goal, then a character based cladistic approach to recognising homology should be utilised. On the other hand, in an exploratory examination of structural features such as this study, the notion of positional similarity should be strongly adhered to. Testing hypotheses of homology should and can be carried out at a later stage. In this thesis (Chapters 2 and 3), a pattern based approach to homology has been adhered to such as that described by Kaplan (1984), where similarity and position of structures are the most important criteria for recognising similar features. Dissimilar features and differences in topography of structures are considered as non-homology. This approach has been adopted in this study because the main objective is to assess the equivalence between a number of structures. The intention of this chapter is to examine structures in light of the characteristic features which define them. A multivariate approach to recognising homology in this chapter shows that pattern reflects process.

In monocots, numerous terms have been proposed for various vegetative structures over the years. Some of the terms can be broadly applied to all monocots,

however others have been proposed for very specialised forms of the structure in narrow studies within particular groups e.g. Orchidaceae. As a result, there is no clarity about which of the terms refer to the same structures and similarly, which of the structures are actually equivalent (i.e. homologues). Similarly, there is no consensus over what a basic growth form is for monocots so that the structures can be examined within a comparative framework. The need for clarity on these points forms the basis of this chapter. The intent is to determine which portions of the monocot plant constitute equivalent structures using the results obtained in the multivariate analysis in Chapter 3 as a framework. Thus, the concept of homology in this chapter is based on similarity in structural features as reflected by multivariate analysis. There is also a need to interpret the observed variation in growth form and to obtain patterns. This way, it is hoped that some idea of a basic growth form of monocots will be achieved (based on both adult and seedling plants - Chapter 2). The basis of this approach is formed from the results of the MDS analysis (Chapter 3) in which equivalent structures are determined and on which the basic growth form is based. With an idea of the equivalent structures and a simplistic model of growth form in mind, it is much easier to assess the current terminology.

The aims in this chapter are to:

1) propose general, broadly defined terms which relate to equivalent structures, even in their modified state. Narrow definitions lead to rigid terms with defined boundaries which don't allow the flexibility which is required to account for variation in such a diverse group of plants and

2) propose simplistic models which reflect a *concept* of growth form so that a general pattern can be obtained which allows for a practical, operational system which is not specific in nature.

If monocot growth forms can be viewed in terms of simplistic models with general definitions for the structures making up the forms, then both equivalence and variation can be easily interpreted, making the system easily operational in any sort of comparative approach.

METHODS AND RESULTS

A multivariate approach to recognising similarity in structures

The multidimensional scaling plot (Figure 3.2) of plant portions shown in Chapter 3 represents a direct measure of similarity between plant portions: the closer the portions are to each other, the more similar they are. A multivariate approach to recognising similarity (Figure 3.2) between the plant portions suggests that in the sample of

monocotyledons examined, categories are difficult to distinguish. One of the main reasons for this is that the *rhizome*[1] and *inflorescence axis* categories, consistent with current terminology and organ recognition, are not discrete. In addition to this, the internodes which are topographically between the *rhizome* and *inflorescence axis* appear to form an intermediate region, sharing characteristics of both categories. This is important as it has bearing on the fundamentals of recognising structures. What is apparent is that while there is a continuum in the data, the *inflorescence axis* internodes and *rhizome* internodes are separated in the space continuum, suggesting a certain amount of distinctness and thus dissimilarity. It is therefore possible, that a *rhizome* internode and an *inflorescence axis* internode forms part of a series in which one structure is transformed into another, slightly modified structure, presenting the possibility of serial homology. The transition region between the *rhizome* and the *inflorescence axis* presents the existence of a partially homologous structure as many characteristics are shared commonly between the two structures. The pattern reflected by the MDS plot of Figure 3.2 should be considered to represent a general pattern of monocot axial structures. Thus, a growth form model of an individual plant can be constructed on the basis of the similarity between the internodes. This growth form model would then be a construct of the general monocot growth habit and would form the basic model for any monoctyledonous plant.

If the plant portions alone are considered, there appears to be no difference between *rhizomes* displaying plagiotropic and orthotropic growth, or those that have been modified into storage organs such as corms or pseudobulbs. With this pattern, it is possible that all the rhizome portions examined in this study and shown in Figure 3.2 in Group 2.1 are similar structures, forming a single cohesive group. The two homology criteria of topography and special quality are fulfilled by this group and therefore, it is plausible to call the plant portions represented in Group 2.1, homologues. Similarly, there is no apparent spatial difference between the plant portions found in Group 2.4. Thus, inflorescence axes both in the mid portion and upper portions where they form flowering stalks are equivalent. Therefore it is plausible to compare, for example, the aerial axis of *Myrsiphyllum* with the flowering stalk of *Myrsiphyllum* and at a broader level, with the inflorescence axis of a *Lachenalia*. The plant portions of Group 2.2 were shown in Chapter 3 to have features which are shared between both *rhizome* and *inflorescence axis* and are therefore not similar to either by any quantitative degree. However, the

[1] The names used to represent the groups recognised in the MDS are italicised because they are consistent with current terminology. These terms may be different to those proposed later in this chapter.

position and distance of many of the portions in the MDS plot, indicates to some extent the groups to which the portions are more similar, runners being more similar to *rhizomes*, while basal inflorescence axes are more similar to *inflorescence axes*. The problem, however, is that the group is not distinct (i.e. was not significantly different from *rhizome* or *inflorescence axis*) and this leads to a difficulty in suggesting the homologues of such structures. The MDS results suggest that the spatial pattern reveals partial homologues between, for example, the runners of Group 2.2 and *rhizomes* (Chapter 3, Figure 3.2). The same conclusions can be reached for the plant portions of Group 2.3 which may be considered partially homologous to *inflorescence axes* (Chapter 3, Figure 3.2).

Growth form models in selected monocots

The concept of growth form must be holistic. Therefore, a growth form concept must incorporate the plant body which is made up several units. The units must be comparable between plants of the same species and at a broader level, in distantly related taxa. The units in this study, are considered to be composed of the plant portions (or internodes) which were used in the MDS analysis and which are shown to be either equivalent structures or members of a different unit. Thus, a concept of a growth form is a hypothetical construct, but it is based on the realistic similarity or equivalence of structures. The basic monocotyledonous growth form pattern illustrated spatially by the MDS plot seems to be consistent and recurrent across the wide variety of taxa sampled. The basic pattern can be delimited into two general growth form models. Two basic models are considered here as the cluster analysis in Chapter 3, Figure 3.3, indicates two main clusters. These being delineated more or less on the basis of growth orientation, either orthotropic or plagiotropic. The differences in growth orientation often result in different overall plant habits: a tufted growth habit or a rhizomatous habit. Both habits reflect the same MDS pattern in terms of the units which comprise each growth form. With this simplistic approach the wide diversity in structural features can actually be interpreted under either the tufted or rhizomatous model. Thus, the monocot habits examined can be interpreted as either tufted or rhizomatous.

This differs slightly from Holttum's (1955) proposal of monocot growth habits in which only the tufted form was considered the general growth form and all other modifications were variations of the basic tufted theme. The tufted habit, Holttum (1955) proposed, was a necessary consequence of the lack of cambium. The direct result being the formation of axillary buds at nodes only, the development of an adventitious root system at nodes towards the basal part of the stem, a reduced upper stem strength and

the finite vascular supply. The main limiting factor of a plant with this habit is the demand and supply of water. If the plant were to branch in the upper portions, the water demand may be met, but without upper stem strength, branching must be restricted to the base of the plant. The way for this to be maintained is for each branch to have a definite lifespan and thus terminate in a flower. After flowering, branch growth ceases. Renewal growth must then occur from the axillary buds at the base of the stem. This is repeated so that several basal branches are produced and the resulting form is the tufted habit which has an unlimited lifespan. Holttum (1955) then proposed how he though this basic tufted habit could have been modified through time into the variations in growth habits of monocots as a whole. He proposed that in the early stages of branch development of the tufted form that each new branch would extend horizontally underground for some portion. This would result in the aerial part of the stem arising some distance away from the parent stem. This would also allow for new roots to grow into new soil regions. This growth habit is what he termed regular rhizomatous growth. Holttum (1955) suggested that the regular rhizomatous growth habit was adaptable to seasonal resting phases. He proposed that all underground storage organs have developed from this growth habit. The necessary modifications to the regular rhizomatous habit would be that the renewal growth would arise from a subterranean axillary bud which would develop internodes with adequate storage tissues. In the unfavourable season, the aerial portions of the stem would die back and the storage structure would remain viable until the following season when renewal growth could occur again from subterranean axillary buds. The modified storage structures which Holttum (1955) considered to have arisen from the regular rhizomatous growth habit are corms, bulbs, pseudobulbs and fleshy sympodial rhizomes. It is difficult from Holttum's proposals of modification of the regular rhizomatous growth habit to imagine how the corm is derived. He described the structure as "a segment of rhizome which grows erect bearing a single terminal leafy (and flowering) stem.....". Further, he discussed the difference in renewal bud position in the pseudobulb of *Spathoglottis* and *Gladiolus*, noting that the renewal growth of each occurs in different orientations. With the distinction between orthotropic and plagiotropic orientation of various monocot stems (whether subterranean, aerial etc.) it becomes important to draw a distinction between a tufted growth form model and a rhizomatous growth form model. This is because it is difficult to derive an orthotropic storage organ like a corm from a plagiotropic, regular rhizomatous form. The meristem potential of the renewal bud is generally predetermined and will follow the growth orientation which is genetically controlled, thereby making it difficult to derive orthotropic growth from an initial plagiotropic form. For this reason, two

basic growth form models are proposed (Figures 4.1 and 4.2) in this study which are based on the growth orientation of the first formed (rhizomatous) portion of the stem.

The tufted model

The tufted model for monocot growth habits was first introduced by Holttum (1955) as the basic monocot habit, which could be modified to form the wide variation of monocot habits. Figure 4.1 shows a hypothetical construct of the tufted growth form. The basal portion of the plant branches closely and successively forming aerial axes which terminate in an inflorescence. In this study several plants can easily be assigned to the tufted growth form model. The tufted growth form model, in the basic form lacks any form of aerial branching. However, modifications of the tufted model can be illustrated and this is based on the plants that have been examined in this study. The tufted model and the modifications that are proposed are presented in the following key:

Key to the tufted model

A. Caespitose
   a. Aerial branching absent
   b. Aerial branching present

B. Caespitose, basal intravaginal plagiotropic tillering
   a. Aerial branching absent
   b. Aerial branching present

C. Caespitose, suppressed basal branching
   a. Aerial branching absent
      1. Basal extravaginal tillering
      2. Basal internodes with storage tissue
   b. Aerial branching present

A. Caespitose habit

In this proposed growth form, the habit is much like Holttum's (1955) tufted habit in which the branching is restricted to the basal portion of the stem and each stem terminates in a flower (or inflorescence) which terminates the life of the stem. This form has been described in this model as a caespitose habit with aerial branching absent. In the monocots examined in this study, several can be shown to fit this model. However, the basic tufted model described by Holttum (1955) can be modified and these modifications are described here in this model as caespitose with aerial branching.

Aa. Aerial branching absent

Plants without aerial branching are *Canna indica*, *Johnsonia pubescens*, and *Thamnochortus lucens*.

Ab. Aerial branching present

Those with the caespitose form and which display aerial branching are *Pentaschistis pallescens* and *Pseudopentameris caespitosa*.

B. Caespitose habit with basal intravaginal plagiotropic tillering

The basal branching is reduced relative to the basic tufted model and the growth focus is in plagiotropic tillers. Plants with this habit tend to form runners on the surface of the soil which have most usually been termed stolons. In this habit, the basic tufted form is modified so that the successively branched basal stems become lax and thus no longer display orthotropic growth. The renewal buds are also usually located in the basal parts of the plants on the surface of the substrate.

Ba. Aerial branching absent

A plant which can be interpreted as having this growth form is *Tribolium obtusifolium*, which lacks aerial branches.

Bb. Aerial branching present

Ischyrolepis cincinnata and *Restio harveyii* are plants with this growth form which have aerial branches. In these two taxa, the lower internodes of the aerial axes tend to show branch suppression and the upper internodes branch profusely, forming a single stemmed appearance at the lower portions of the plant. In *Willdenowia glomerata* the aerial branches are sparse, often only one to two per node. The lax branch forming the runner is slightly unusual in that it continues to grow underground. The renewal bud is also located just below the surface of the substratum.

C. Caespitose habit with suppressed basal branching

The basal branches are suppressed so that a single, upright rhizome portion is formed and renewal growth is entirely in an orthotropic direction. Basal portions of the plants tend to have very short, compact rhizome internodes which show little tissue differentiation and additionally, lack any form of swelling. Plants with this growth form as a result of the unspecialised rhizome, seem to develop other organs as the storage modified regions.

Ca. Aerial branching absent

Examples of the plants in this study which display this growth form are *Chlorophytum comosum* which has swollen root tubers; bulbous taxa such as *Lachenalia klinghardtiana*, *L.splendida* and *Albuca fragrans* in which the sheathing leaf bases are modified into storage structures and *Holothrix villosus* which develops the specialised root-stem tuberoid structures.

Ca1. With basal extravaginal tillering

The basal branches are suppressed, so that the upright portion of the rhizome becomes the central growth region and often is composed of many internodes which are closely arranged. Growth accretion is in an orthotropic direction, except for the formation of "new" growth which develops as axillary extravaginal branches. These structures have usually been referred to as offsets, runners or suckers. A plant examined in this study with this growth habit is *Billbergia nutans*.

Ca2. With modification of the basal internodes to form storage organs.

The basal branches of the general tufted model are suppressed, but often the buds are retained as axillary buds that ultimately grow into new plants. The rhizome internodes are laterally as well as vertically expanded and display seasonality in the growth of various portions of the basal part of the plant. Growth is always in an orthotropic direction so that the basal portions of the plant tend to die at the end of each growth season, only to be replaced by a series of renewed rhizome internodes. The basal internodes and the sheathing leaf bases often form a closely linked relationship, with the leaf bases being modified subterraneanly to protect the structure in various ways. More apically produced leaves have a different role, and serve to provide the basal portions with photoassimilates for the following growth season. The aerial axes are usually in a terminal position and are also produced on a seasonal basis. Plants with this growth form may also have an extended seedling phase in which the hypocotyl seems to be responsible for developing the swollen internode portion of the base of the plant. Plants with this growth form were found to display a large amount of variation within this growth model. Examples that were examined in this study are *Zantedeschia aethiopica*, *Wurmbea spicata*, *Baeometra uniflora*, *Cyanella hyacinthoides*, *Eriospermum pumilum*, *Pauridia minuta*, *Spiloxene alba* and *Spiloxene minuta*. The modifications of the basic growth habit in *Z.aethiopica* are the lack of sheathing leaf bases for the protection of the storage structure and the continuous production of leafy shoots. In *B.uniflora*, *W.spicata*, and *C.hyacinthoides* there is an extended region above the storage structure which is produced seasonally at the onset of

leafing and is ultimately an extension of the flowering axes. This feature ensures that the storage structure can be buried to some depth in the substrate to prevent water loss and exposure. The development of the storage structure is phasic and follows the growth and flowering season closely as described in Chapter 2. In *P.minuta* and the *Spiloxene* species examined the storage structure is in a shallow position in the substrate and as a result an extended neck region is not developed, a similar region is located ensheathed by the aerial leaf sheaths. In *Eriospermum* the special feature of hysteranthy is developed displaying an extreme example of phasic growth.

Cb. Aerial branching present

Basal branching is suppressed and there is often profuse aerial branching which increases the amount of area occupied in the aerial portions of the plants and this may be related to living in competitive, densely vegetated habitats. However, this is only true for the adult plants examined. Seedlings of *Pentameris thuarii* and *Pseudopentameris obtusifolium* on the other hand, will show both basal and aerial branching and this may be related to less competitive habitats in the seedling establishment phase, such as occurs in post-fire Fynbos landscapes. Plants examined which have this growth form are *Borya nitida*; *Dasypogon bromeliifolius*; *Xerophyta humilis*; *Calectasia cyanea*; *Pentameris obtusifolium* and *Pentameris thuarii*.

A modification of this proposed model is the monopodial growth habit of many epiphytic orchids, but which is most easily explained by the growth form of *Phalaenopsis*. Several modifications have taken place from the basic, tufted sympodial model. Basal suppression of the sympodially renewed branches has taken place. This forms a single axial vertically growing plant with aerial branches. The internodes extend vertically via vigorous growth of an internodal meristem. Aerial branches are initially vegetative (as is seen in *Phalaenopsis*) with terminal inflorescences, but then some of the vegetative branches are exclusively utilised for reproduction. The reduction of the vegetative branch follows, so that a seemingly axillary inflorescence axis is formed. Both vegetative and reproductive axillary axes are found in *Phalaenopsis*. In the more specialised epiphytic orchids, the growth direction along a branch via vigorous internodal meristem activity, no longer requires the dependence on prior sympodia in the sequence, each new exploratory sympodium can receive nutrients and water independently. This would encourage the senescence of older sympodial units and the apical meristem would be modified to continue vegetative growth instead of developing into a reproductive axis. The independent units would then be able to branch either vegetatively or reproductively in an axillary position. This growth form therefore displays a slight difference to the basic tufted

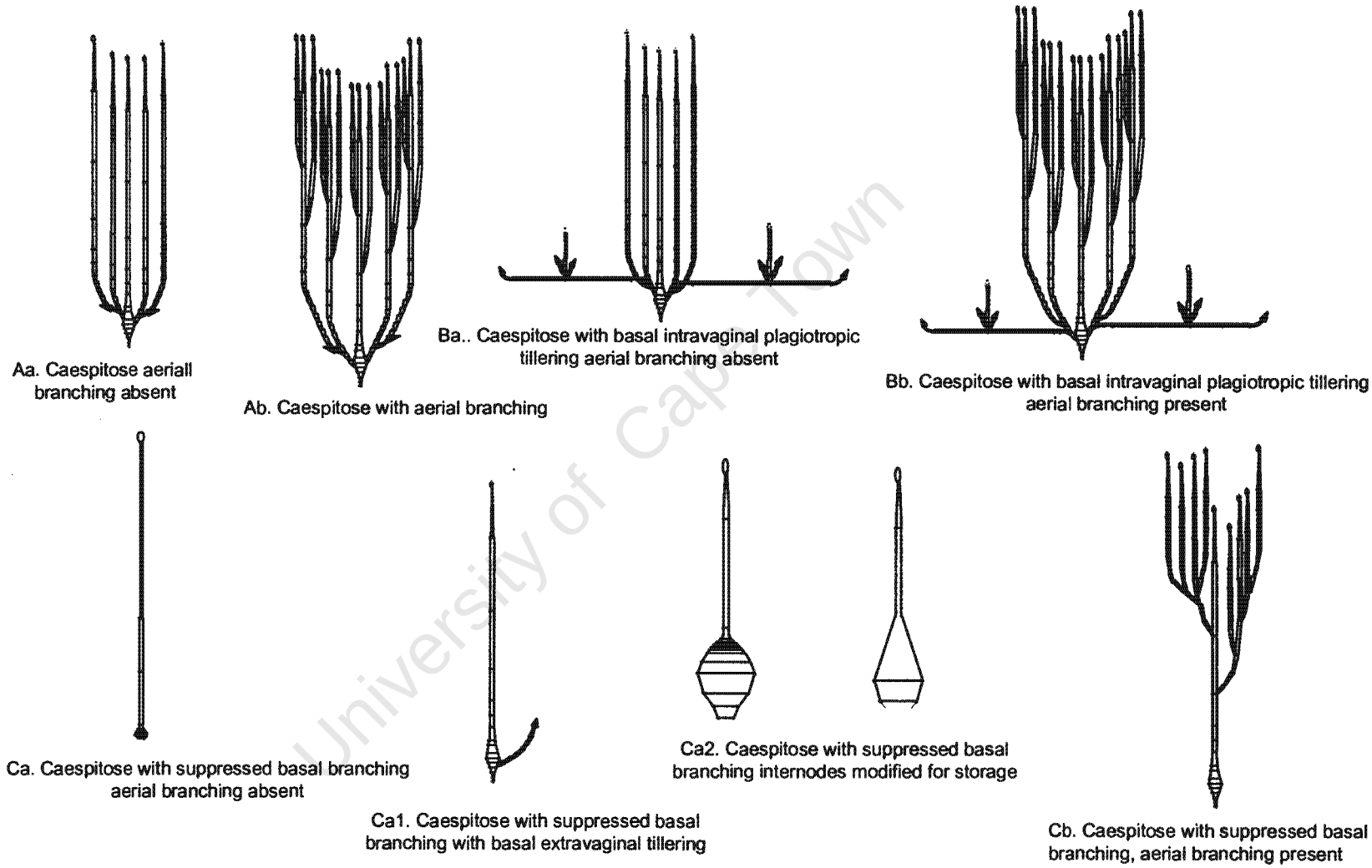


Figure 4.1. Caespitose growth form and variations. Circles indicate determinate axes. Arrows indicate renewal growth direction.

model in that the rhizome internodes have become elongated and thus the whole axis of a monopodial orchid is equivalent to the compact region of a general tufted form. In the general tufted form the apically derived structure elongates forming the inflorescence axis. This is the opposite in the monopodial form because the apical meristem is utilised for a different function and as a result, there is a greater expression of axillary branches with specialised reproductive function.

The rhizomatous model

In the rhizomatous growth model, the renewal growth is sympodial and is generally non-orthotropic (Figure 4.2). Growth is most often plagiotropically orientated, but, may also be negatively geotropic or somewhere between plagiotropic and slightly vertical. The plagiotropic portion of the plants may or may not be buried into a substratum and in the case of epiphytic orchids in particular, the units will be located on the growth surface. Each portion will develop plagiotropically for some distance before turning upright and growing orthotropically, ultimately terminating in an inflorescence. In the case of negatively orthotropic forms, the growth direction is orthotropic relative to the substrate, whether negatively geotropic or not. The main difference between this growth model and the tufted model is in the general unidirectional and plagiotropic orientation of the renewal portions of the plant. In this growth form, the rhizome may or may not branch and similarly, the aerial inflorescence axes may be simple or branching. In addition, the *rhizome* portion of the plant may be modified, with expanded internodes that serve a storage function of either nutrients or water or both. The growth orientation and branching of rhizomes may be linked to deterministic factors such as distichy. Bell & Tomlinson (1980) and Tomlinson (1984b) have shown that patterns of rhizome geometry in monocots such as Zingiberaceae are linked to the plane of distichy. The plane of orientation of leaf distichy results in different orientations of rhizome systems: vertical distichy results in linear systems, while horizontal distichy results in branched systems (Tomlinson 1984b).

Key to the rhizomatous model

A. Unidirectional sympodial renewal growth
    a Internodes slender
        1. Simple inflorescence axes
    b. Internodes swollen
        1. Simple inflorescence axes
        2. Branching inflorescence axes

B. Rhizome with axillary branches
   a. Short, non-swollen internodes
      1. Simple inflorescence axes
      2. Branching inflorescence axes
   b. Short swollen internodes
      1. Simple aerial axes
   c. Long rhizome internodes
      1. Simple inflorescence axes
      2. Branching inflorescence axes

A. Rhizomatous habit with unidirectional sympodial renewal

The renewal growth is from an axillary bud between the base the current inflorescence axis and the rhizome internode. As a result, the renewal growth continues in the same direction with each branching event.

Aa. Slender internodes

The internodes which compose the growth units of this particular growth form do not display any form of expansion either macromorphologically or in the form of tissues. The renewal growth tends to be unidirectional with many sympodia growing intermeshed into a closely allied clump. An example of a plant with this growth form is *Maxillaria variabilis.* The basal portions (pseudobulb stalk) of the plant comprise a unidirectional rhizome. The pseudobulb itself, is equivalent to an aerial vegetative axis (Chapter 3).

Aa1. Simple inflorescence axes

The aerial axes in *Maxillaria variabilis* are of two kinds. The first is a vegetative axis which terminates in a fleshy storage internode termed a pseudobulb. The second is an inflorescence axis which appears in a lateral position, but is probably a reduced axillary branch (see Chapter 2). This reproductive axis does not have any swollen internodes associated with it. Moreover, the multivariate analysis (Chapter 3) shows that the pseudobulb and the reproductive axis are equivalent structures. Similar conclusions were reached by Rasmussen (1986) who proposed that pseudobulbs were not individual organs, but constituted part of the whole axis.

Ab. Swollen internodes

In *Tulbaghia alliaceae* the internodes of the rhizome portion are quite fleshy and seem to contain moisture in addition to starch granules. In *Aponogeton distachyos* the rhizome internodes are also swollen, but not very fleshy. *Merxmuellera cincta* forms stout, slightly fleshy *rhizome* internodes with the cortex tissue area expanded to store starch granules. In *Polystachya ottoniana* the swollen internodes towards the base of the plant form the sympodial *rhizome* system. The growth direction is usually unidirectional, but branching may also occur slightly laterally in renewal portions. The older units die back after two seasons of growth.

Ab1. Simple inflorescence axes

In *Aponogeton distachyos*, the simple, orthotropically growing axes cannot really be considered as aerial as they are submerged under water, which can be considered a "substratum" and thus the inflorescences themselves are produced terminally on the surface of the substratum. In *Tulbaghia alliaceae*, the simple aerial inflorescence axes tend to be quite fleshy. The inflorescence axes of *Polystachya ottoniana* are terminal and always simple.

Ab2. Branching inflorescence axes

Merxmuellera cincta is able to form axillary aerial branches, each of which terminate in an inflorescence axis. An extreme example of aerial branching is observed in *Elegia capensis* along the length of the inflorescence axes (Figure 4.3.1 & 2), where, superficially multiple axillary branches appear to be present. These branches are presented in a whorl-like arrangement at the nodes in the axil of a scale leaf. The serial transverse reconstruction of branching at the node, reveals that the axillary bud is initially a single bud. The bud is flattened and initially develops so that it encircles the inflorescence axis (within the axil of the leaf). Following this phase, the flattened bud begins to divide, branching from the edges of the semi - circle towards the centre. The branches may be vegetative or reproductive in nature, but the uppermost nodes tend to produce reproductive branches only. In *Restio quadratus* on the other hand, there are several axillary buds present at each node (Figure 4.3.3) which develop separately into axillary branches.

B. Rhizomatous habit with axillary rhizome branching

Ba. Short non-swollen internodes

Plants have very sparsely branched rhizomes. The internodes are not expanded and the anatomy shows a high degree of tissue sclerification. This kind of rhizome offers the aerial axes support and provides the physical properties to transport water to the aerial extremities. Such rhizomes are found in *Arundo donax*, *Myrsiphyllum scandens*, *Smilax anceps* and *Thamnochortus spicigerus.*

Ba1. Simple inflorescence axes

Thamnochortus spicigerus is a plant with this growth form. However, the seedling growth form displays branching aerial axes in a very diagnostic form of "seedling" growth. This seedling growth may be reverted to following flowering and additionally after fire when resprouting occurs.

Ba2. Branching inflorescence axes

Arundo donax is a special example of this growth form model as the aerial branching is extravaginal as opposed to the usually intravaginal aerial branching axes of many of the monocots examined. In *Myrsiphyllum scandens* the aerial axes are modified in that the internodes are elongated and prickles are formed at the nodes. In addition, the aerial branches are indeterminate and special flowering axes are formed in an axillary position. A similar situation is observed in the aerial axes of *Smilax anceps*. In addition to axillary floral axes, axillary, paired tendrils are formed and prickles are also located along the internodes.

Bb. Short, swollen internodes

In this growth form the internodes are closely linked to one another in the *rhizome* portion of the plant. The internodes tend to be buried below the soil surface and renewal growth is from the most recent internodes via an axillary bud which is buried below the soil surface. However, axillary buds located at intervals along the length of the internodes do allow branching along the length of the *rhizome*. Anatomically, the swollen internodes show an expanded cortex or a mixture of expanded cortex and central area. Often starch granules or proteinaceous storage materials are located in these tissues. In cases where rapid exploration of newly defoliated areas occurs, the *rhizome* internodes remain unswollen and the focus is on elongation into new soil areas. Thus at intervals, there may be portions which are non-swollen, followed by a series of swollen internodes. A *rhizome*

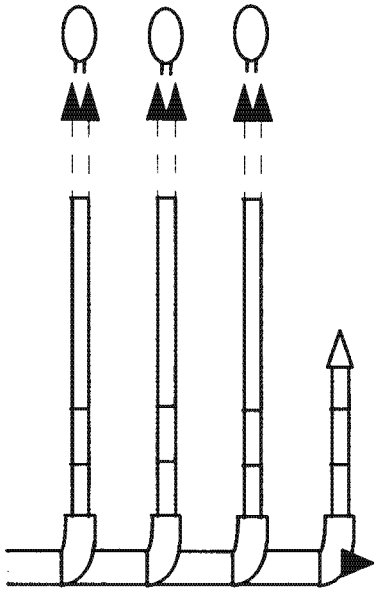
growth pattern like this was observed in *Merxmuellera rufa*. The internodes of the plagiotropic portions of *Wachendorfia thyrsiflora* are modified in that they show a certain amount of phasic growth, with up to four units expanding in a single growth season. The rhizome internodes also branch from axillary buds and these branches can have elongated internodes which behave as runners and often show no swelling. Thus, the plagiotropic portion may have several branched portions, ranging from the fleshy internodes to the elongated internodes of the runner. Anatomically and in the multivariate analysis, the fleshy internodes and elongated internodes of the runner are equivalent structures. In addition, the fleshy internodes of the previous season shrivel and die back, so that only the current season's growth is viable.

Bb1. Simple aerial axes

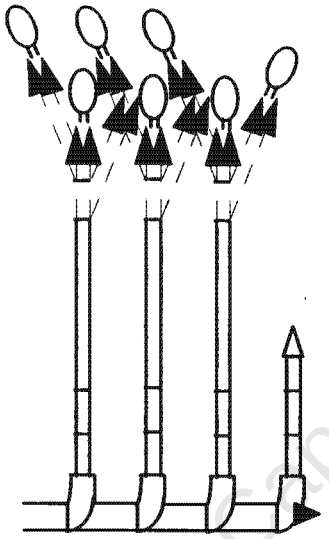
At intervals, the plagiotropic portions turn upright to form aerial axes which terminate in inflorescences. Plants examined with simple inflorescence axes are *Merxmuellera rufa*, *Pentaschistis aristidoides* and *Wachendorfia thyrsiflora*.

Bc. Extended rhizome internodes

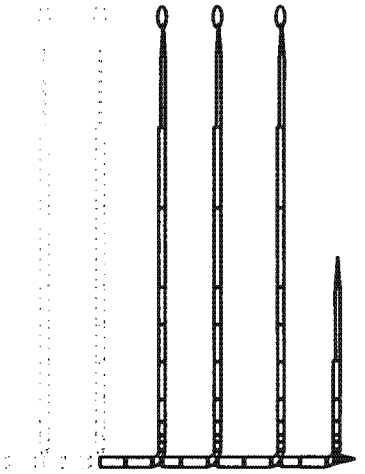
The plants with this growth form have long, rambling *rhizomes* which are composed of elongated internodes. The growth direction is most often plagiotropic, although the depth of penetration varies and some may turn geotropically for some way before resuming orthotropic growth and developing aerial inflorescence axes. These rhizomes move the growing part of the plant into new soil areas, but do not function physiologically like roots. Long rhizome forms appear to be absent in epiphytic plants. A special example of this extended rhizome growth form are the organs that formed part of Group 2 in the multivariate analysis (Figure 3.2, Chapter 3). The plants examined which form part of the group are *Chondropetalum deustum* and *Chondropetalum rectum*. They differ to the other plants examined which can be described by this model generally, in the position of development of the rhizome. The renewal buds are situated on the basal region of the inflorescence axis, which is shallowly located in the substratum. As a result, the long rhizomes formed are shallowly positioned in the soil surface. This position and growth point origin of the rhizomes may be related to the habitat in which these plants grow (see Chapter 2).



Ab1. Unidirectional rhizomatous growth, swollen internodes with simple inflorescence axes

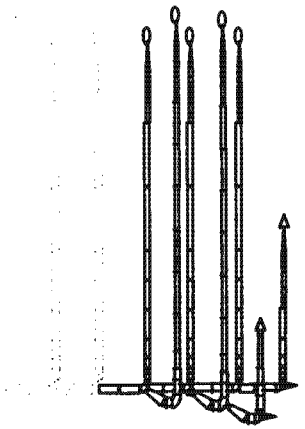


Ab2. Unidirectional rhizomatous growth, swollen internodes with branching inflorescence axes

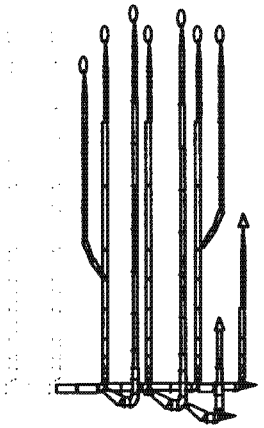


Aa1. Unidirectional rhizomatous growth, slender internodes, simple inflorescence axes

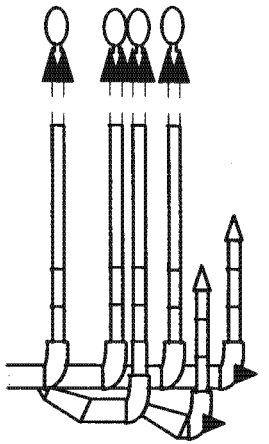
Figure 4.2. Unidirectional rhizomatous growth form and variations. Circles indicate determinate, arrows indicate growth direction.



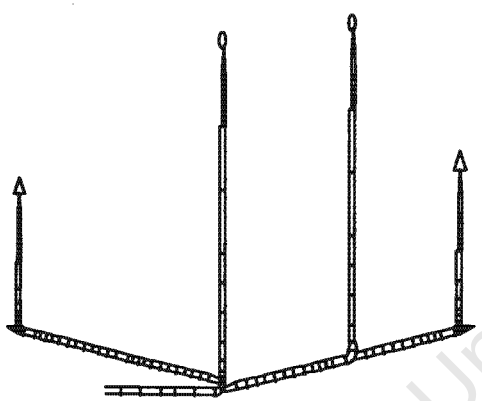
Ba1. Branching rhizomatous growth,non-swollen internodes, simple inflorescence axes



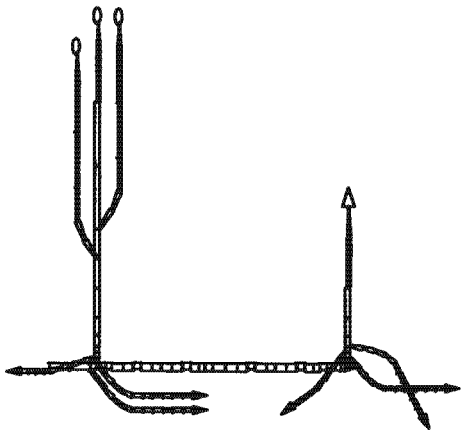
Ba2. Branching rhizomatous growth, non-swollen internodes, branching inflorescence axes



Bb1. Branching rhizomatous growth, swollen internodes, simple inflorescence axes



Bc1. Extended rhizomatous growth, simple inflorescence axes



Bc2. Extended rhizomatous internodes branching inflorescence axes

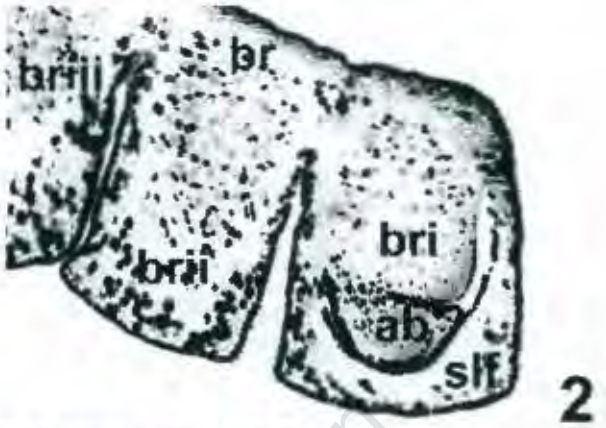
Figure 4.2 Cont. Branching rhizomatous growth form and modifications. Circles indicate determinate growth. Arrows indicate growth direction

Figure 4.3. Multiple branching at nodes in *Elegia capensis* (1 & 2) and *Restio quadratus* (3).

Figure 4.3.1. T/S of *Elegia capensis* inflorescence axis at the nodal area to show the branching region (br). The branch structure consists of a flattened, sheathing structure (sbr).

Figure 4.3.2. T/S of *Elegia capensis* inflorescence axis to show the edge of the branch area (br) (i.e. opposite where branch arises at node) and the series of multiple division resulting in multiple baranching axes (bri - briii). The multiple branches in turn have axillary buds (ab) which also develop into branches. Each one of the multiple branches is surrounded by a shathing leaf (slf).

Figure 4.3.3. L/S of a growing tip of a vegetative axis of *Restio quadratus* showing the shoot apex (ap) and the location of the many buds (mb) in the axils of sheathing leaves which develop into branches.



3

Bc1. Simple inflorescence axes

In *Conostylis prolifera*, the rhizome internodes are extended and the rhizome tends to follow different depth levels, before turning upright and forming the simple aerial inflorescence axes of the plant. The renewal bud for each rhizome unit is usually located well below the surface of the soil. In some plants, however, the rhizome growth direction is almost orthotropic and the renewal buds are shallowly located below the soil surface.

Bc2. Branching inflorescence axes

In *Pseudopentameris macrantha* the aerial axes are able to branch. Along the basal portions of these axes there are numerous axillary buds, not all of which develop. It appears as though *P.macrantha* rambles through the soil substrate as well as the aerial habit gaining as much coverage as possible. The aerial axes of *Chondropetalum deustum* and *C.rectum* are sparsely branched, with up to two branches per node, but often with only one.

Discussion

The concept of growth form is holistic, incorporating the whole plant and therefore comprising several structures, modules or units. It is important to make this distinction because terms have been based on the (individual) structures that make up the whole growth form and not the form itself. When examining growth forms in monocots there is a simple basic pattern which is retrievable. Many monocots display sympodial growth as a result of the constraints which a lack of cambium has placed on the growth system (Holttum 1955). This determinate growth pattern may be one of the main reasons why such variety in shoot form and function has arisen in monocots. Watson et al. (1997) propose that plants *are* plastic because of their modular growth, and the changes that can occur in size, shape and number of modules in plants contributes to their adaptability. The diversity of form in leaves (another determinate system) was noted by Kaplan (1984) and Hagemann (1992) in tracheophytes in general.

Of the growth form models proposed over the years for monocots, there is no consensus about which represents the basic form. The basic form may be interpreted as either a type (archetype) or a general form in the evolutionary sense. Some authors proposed a tufted herbaceous basic form (e.g. Holttum 1955), while others propose that the arborescent (or pachycaul) form is the basic form (Corner 1954; Hay & Mabberley 1991; Moore & Uhl 1973; Tomlinson 1970a). Others suggest that the stem structure may just be a constraint related to the constructional plan of the arborescent form (see Mosbrugger 1990). Whatever the origin of the variation, and the contradiction in viewpoints, the starting

"pattern" is the same i.e. tufted with modifications. This starting pattern (general form) of the tufted form, followed by modifications is also observed in related taxa such as Chloranthaceae and Piperaceae (Blanc 1986) and is also observable in some seedling ontogenies (Chapter 2). Although arborescent forms have not been examined in detail in this study, their growth form can also be viewed as a modification of the tufted form. Blanc (1986) also proposes a similar derivation for the arborescent forms in Chloranthaceae. If the phylogeny of flowering plants is considered, one of the sister groups to the monocots is proposed to be the Piperales (Chase et al. 1993, The Angiosperm Phylogeny Group 1998). Here the growth forms of these taxa are very similar to the basic monocot form (Burger 1977) e.g. tufted *Piper nigrum*; laxly tufted *Peperomia*, rhizomatous *Piper amapaense* with terminal inflorescence (see Cremers & Edelin 1995). The resemblance may be superficial as other features such as the anatomy of the stem and the shoot construction may differ. On the whole, however, it seems plausible that the ancestral monocot may well have resembled certain members of Piperales in growth form or Nymphaeales (see Doyle 1973). The seedling structure and ontogeny in geophytic Piperales has been examined by Hill (1906) and the growth form and morphological changes that occur with the geophytic habit are very similar to many monocots with geophilous organs.

Homology and equivalence

Pattern versus process in homology explanations

In examining the morphology of plant form, a structure can be divided into units which can be described by a set of features (observable as a particular pattern). A structure may also be recognisable on the basis of its positional location on/in the organism. The expression of the structure (i.e. features and position) has a genetic basis. Thus, developmental sequences responsible for initiating the structure are linked to the expression of the structure. In this way process and pattern are intimately linked. The conflict between the pattern and process approaches in homology concepts occurs because causal explanations for the observable pattern (tautology) cannot be directly invoked. Thus, in the explanation of homology, circularity is avoided if only a pattern approach is utilised in the operational stage of homologue recognition. However, as discussed, pattern is not independent of process and the process has an indirect effect on the observable pattern. Similarly, homology explanations based on shared developmental processes also exclude the pattern as an informative stage of the homologue recognition.

Some workers have opted for an almost pluralistic approach. Roth (1994) favours homology as correspondence caused by continuity of information. Here correspondence

between two features is similarity in position, shape, structure, chemical composition etc. and continuity is through some genealogical process such as gene duplication or as serial repetition of structures. Other workers, such as Cusset (1994); Jeune & Sattler (1992); Sattler (1994, 1996) and Sattler & Jeune (1992), have opted to view pattern as process so that structural pattern is seen as a dynamic rather than a static phenomenon. In most morphological studies the emphasis is on the static phenomenon of a structure (the pattern), separating the processes which govern the pattern (i.e the dynamic aspect).

Ritterbusch (1980) has examined plant morphology using both aspects. This is an important approach because it allows the examination of homology as a series of transformations, modifications of a basic form into more elaborate forms. This approach i.e. pattern and process has been useful in this study because features of growth orientation are shown to be important in the determination of unit structures and the resulting form which they comprise. In particular, the shoot unit that is under consideration here, could not be interpreted in any other manner. The sequence of development from axillary bud initiation through to expression of the terminal inflorescence axis must be viewed as a specified process, that of a flowering branch (see Tomlinson 1987). The various portions of plant involved in this sympodial branching process reflect certain characteristics, which are interpretable as a collection of features (pattern) which constitute a certain structure e.g. the plagiotropic underground internodes (rhizome). Changes in the relation between pattern and process in ontogenesis result in slightly different expressions of the units concerned, leading to modifications of the basic form (Ritterbusch 1980).

Additional factors that can affect the expression of units in the sequence are genetic and are controlled by groups of genes which result in the transference of function (*sensu* Corner 1958) from one unit to another (Hall 1995). The fact that expression of units is not a constant feature suggests that rigid definitions of homology cannot effectively relate to equivalence of parts in plant morphology. Furthermore, the metameric structure of plants predisposes them to transformational changes in structures (White 1984) and adds another difficult dimension to recognising equivalent structures. All of these features and relations are especially applicable to monocots and cannot be discounted when examining growth forms and comparing equivalent structures.

Similarity based on a multivariate approach

Multivariate analysis has been used previously to test the placement of intermediate categorical forms within a typological framework (Cusset 1994; Sattler & Jeune 1992; Jeune & Sattler 1992). In these multivariate analyses, intermediates occur spatially

between typical categories such as root, stem and leaf indicating that structural categories are not discrete. In Sattler's and co-workers approach, the typical categories of classical plant morphology model (de Candolle's) are utilised *apriori* as markers in the n-dimensional space. The intermediate structures are then coded and their position in the same n-dimensional space as the markers is examined. Thus, natural groupings of structures and therefore, similarity between structures, cannot be found using a categorical framework to test the position of structures.

The pattern and position of structures is often such a fundamental part of determining plant form that it seems feasible that a methodological approach based on similarity in n-dimensional space should reveal the relatedness of the structures. Multivariate similarity measures between points (plant portions) in a spatial scatterplot offer a way of easily examining the similarity in structures and thus should be an effective way of determining equivalence between parts. The approach to recognising equivalent structures is simple: the closer the structures, the more similar they are. However, in the multidimensional scaling analysis of Chapter 3, several intermediate groups could be identified (Figure 3.2), and so the categories of rhizome and inflorescence axis are not discrete. Therefore, the multivariate approach complicates the recognition of homologues, because intermediates and partially similar internodes (structures) are identifiable (see Chapter 3). The multivariate method seems to break down the (hypothetical) boundaries between plant structures, particularly where transformation occurs e.g. rhizome to aerial inflorescence axis (see also Cusset 1994; Jeune & Sattler 1992; Sattler & Jeune 1992 approaches and results therein). The coding of variables into two states in this study (and others e.g. Sattler & Jeune 1992) leads to discontinuous results, so the choice of variable and the way it is coded does not appear to influence the continuity of the pattern obtained in the multivariate analysis (Chapter 3).

Multivariate analysis shows equivalence in a quantitative manner between structures so that a measure of difference between structures is obtained. Non-metric MDS is entirely suited to this because the distance between the points (structures) is a 1:1 measure of difference in n-dimensional space. Thus, in the results of MDS (Chapter 3), partial correspondence between rhizomes and aerial inflorescence axes is illustrated, whereas the root system was quite different from the shoot system (save for some roots with special qualities and shown as outliers). However, the morphological similarity (distance between points, is as discussed in Chapter 3, dependent on the methodological calculations and coding of features) and therefore correspondences are relative to the similarity measures used in this thesis.

Recognition of a continuum

Similarity, or 1:1 correspondence (equivalence or sameness of structures), is a way of determining homology. In this view, the MDS pattern (Chapter 3) would have to be interpreted as: portions in the rhizome group (Group 2.1) share a high correspondence of features, but rhizome runner portions (Group 2.2) have a partial correspondence of features with rhizomes. The notion of partial correspondence suggests that the units which represent the main cluster of points in the MDS scatterplot (i.e. Groups 2.1 and 2.4) are not discretely defined. In morphological studies where continuous categories can be determined the morphology is described as fuzzy or open morphology (see Cusset 1994, Rutishauser 1995; Rutishauser 1999; Sattler 1996). Thus, if the whole structure is considered, it is feasible to say that rhizomes and rhizome runners are partially homologous and/or that rhizomes and aerial inflorescence axes are partially homologous as there is an intermediate between the two structures (the basal portion of the inflorescence axis and the transition area) which shows features of both of the other structures and the one structure is transformed into the other along a space-time dimension. This pattern would be consistent with the notion of a continuum, which may reflect a process e.g. the whole shoot system of a sympodial monocot. The process is: initiation of an axillary bud on one sympodial unit, the development of the axillary bud into rhizome, and then ultimately inflorescence axis by the apical bud. The structures therefore, all form part of a single system, there is no further branch/axillary bud in the sympodium. Aerial buds interrupt the system as the process is truncated at each level by the addition of new growth units. This truncation represents a breakdown in the continuum of the process, but, Zimmermann & Tomlinson (1972) have shown that vascular connections between the units are maintained, illustrating the continuous nature of the vascular system. The question, is an aerial tiller homologous to the initial aerial inflorescence axis, may be asked. In terms of the process and continuum concept, this is difficult to establish, but using a pattern based, 1:1 correspondence approach there will generally be a 1:1 correspondence of features, save for the difference in origin of the two structures. Thus, the rhizome and the aerial inflorescence axis could be interpreted as serial homologues at the level of shoot, showing vegetative to reproductive transformation. The basal portion of the inflorescence axis and the transition area cannot be accounted for as this area seems to be the central region of transformation and can't be considered as one or the other structure. The caulome of classical morphology, i.e. stem, allows for the inclusion of both vegetative and reproductive axes and in this sense incorporates both rhizome and inflorescence axis, but not the transition region.

Serial homology as an explanation for monocot growth form

If the rhizome and the inflorescence axis are considered as serial (or partial) homologues, then inflorescence axes which branch retain the feature of the previous series i.e. axillary buds such as is found in vegetative axes. Inflorescence axes are displaying partial replacement, they still have the positional feature of the first series (rhizomes), but will have the new features of the aerial inflorescence axis e.g. tissue patterns and leaves instead of cataphylls. A transformation from rhizome to leafy shoot has been experimentally induced in *Cordyline* by physical removal of the apical dominance and the addition of various hormones (Fisher 1972; 1973a). A similar phenomenon is illustrated in monopodial growth, where in some forms axillary buds yield inflorescence axes directly. This transformation was illustrated by Andersen et al. (1988) and Rasmussen (1985; 1986) in orchids in which there is a transition from a first series branch (i.e. axillary vegetative) with terminal inflorescence axis, to a reduced branch with terminal inflorescence axis, and finally, an inflorescence axis. The problem of where inflorescence axes fit into the scheme of homologues is problematic and has been under discussion for several years. The proposal of the term 'Ramicaul' is an example of this. Stern & Pridgeon (1984) suggested that there should be recognition for the second order branch of an orchid i.e. the aerial vegetative (becoming reproductive) axis. Rasmussen (1985) observed that the structure is not a branch at all and therefore the term was meaningless, merely adding confusion to an already complex system. Tomlinson (1987) agreed in principal with Rasmussen (1985) as he defined the branch as a process. But Tomlinson (1987) also pointed out that in terms of recognition by features, it is different to the rhizome portion and could not criticise Stern & Pridgeon (1984) for suggesting a workable terminology. The conflict occurs really in the philosophical perspective of the two workers (Tomlinson 1987) - the conflict between process and pattern. Indeed, the problem can be expanded to monocots as a whole as Rasmussen (1985) suggests. However, if the rhizome and inflorescence axis are interpreted as serial (or partial) homologues, then the aerial portion in terms of process is no different to the basal part, but shows transformation which is reflected by a the addition of few new features and therefore should be worthy of a term which distinguishes it from the first series.

Taxic versus serial homologues

An historical explanation of homology and the comparative approach must utilise taxic homologues. This is solely a pattern based approach, the underlying causal phenomenon for the similarity or equivalence is similarity through common descent. The underlying causal processes must be separated from the homology explanation. However, such

explanations cannot be applied to repeated features within organisms i.e. serial homology. When serial homologues are to be recognised a pattern or process approach or both can be adopted. The processes are more easily identifiable in either gene composition or in meristem location and function in serially repeating units and thus, can be utilised in recognising homologues. Thus, the two types of homology require very different explanations. The conflict between pattern and process is clearly a conflict between taxic homology and serial homology. Comparison of structures within an organism versus comparison of structures between organisms is clearly at two different levels. The problem arises when the first goal is to homologise serially repeating structures within a single organism and then to determine which are equivalent serially repeating structures in other organisms. This is where the real conflict between pattern and process occurs. But, if serial homologues can be correctly identified within a single organism using an approach such as that adopted in this thesis (multivariate analysis), then there should not be confusion at the level of taxic homology. If a set of identifiable features or shared processes (e.g. homeotic genes) can be used to identify serial homologues within a single organism, then the shared features should serve to identify other repeating structures within other organisms and comparisons between taxa can be made confidently.

In this study the continuum appears at two levels: the level of taxic homology and the level of serial homology. When making comparisons of monocot structures between taxa (taxic homology) there are intermediate structures such as rhizome runners, which share features of both rhizomes and of inflorescence axes. When the whole branching process of the axillary rhizome bud is examined and the features of the internodes examined, there is a continuum present from rhizome through to the inflorescence axis. Within a single plant (serial homology) intermediate regions of this continuum can be identified as the rhizome-inflorescence axis transition area and the basal inflorescence axis.

Recognising serial and taxic homologues with a continuum concept

Thus, with the phenomenon of serial construction in plants and the presence of intermediate areas, the strict recognition of 1:1 correspondence in parts may often fail. This illustrates that there is disparity between the *concept* of homology and the practicality of actually measuring and/or homologising units. Panchen (1994) has discussed this in relation to taxa. The concept of a homologue is based on an idea of the basic/general form (bauplan or archetype) of the structure (i.e. typological) and the practicality is based on the examination of *real* features (i.e. essentialistic). For this reason, the end point i.e.

recognition of homologues will depend entirely on the rigidity of the concept. This is why intermediates cannot be dealt with in current concepts of homology because the concept of shared similarity breaks down. In the multivariate method used in this study, the pattern reflected suggests that the continuum in plant structures is heterogeneous, that some areas have a dense concentration of points. This suggests, as discussed in Chapter 3, that a basic pattern can be recognised. This same heterogeneous pattern has been found by Cusset (1994), Jeune & Sattler (1994) and Sattler & Jeune (1994). Such a pattern suggests that the concept of a *bauplan* is feasible, but the boundaries and structural variations need to be considered from a fuzzy logic view point, so that the recognition of intermediates can be possible. The central region of the dense point scatter should be where the structure can be recognised by a set of features, hence corresponding to the notion of the *bauplan*, and also to the concept of homologue. This set of features should be able to be utilised as a set of discriminants by which similar structures are recognised (i.e. points falling into the same dense scatter in this study). The features found important in this regard (see Chapter 3) were able, to a certain extent act as group identifiers. However, few exclusive features to a particular group were found and this is a further indication of the complexity of variation that is found within the continuum. Thus, it is certainly possible to recognise homologues among monocot organs, these corresponding to the dense areas of points on the scatterplot in Figure 3.2 using a multivariate approach. However, the problem of variation and a lack of 1:1 correspondence remains a problem, which conceptually cannot be dealt with in a rigid, categorical definition of homology.

Growth form models in selected monocots

Sympodial growth form

It is hoped that the taxa sampled in this study represent both the phylogenetic and growth form diversity of the monocots. When the variety of form in monocots is examined, two basic growth form patterns are converged upon repeatedly and the variety is simply variations of either of the basic forms. These forms are the tufted habit and the rhizomatous habit (see Figures 4.1 and 4.2). If the Holttum (1955) model is considered, then only one basic form exists, that of the tufted sympodial form and all variation seen is from that form. Holttum (1955) also considered that the annual habit present in several grasses, is a modification of the tufted form in response to seasonally dry habitats. In this study, the tufted and rhizomatous forms are recognised separately. This is because the process of branching results in different orientation of the forms either orthotropic (tufted) or plagiotropic (rhizomatous).

In the two basic models described here for monocot growth forms, the wide variety of modifications that are addressed in this study are simply slight variations in growth and to a certain extent, structural and/or functional characteristics. In many of the models that are proposed for monocots and grasses in particular, there is much emphasis on the aerially branching portions. If viewed simply, i.e. that aerial axes can either branch or they cannot, the diversity in models is reduced substantially. This would lead to a reduction in the prolific and practically difficult terminology that has arisen over the years describing these units. The focus of model construction should be placed on the rhizome (homology) in monocots and accordingly, the variation can be dramatically simplified and easily understood. In this way, a comparative approach can be undertaken and aerial branches of grasses can be compared to the other monocot taxa. A similar simplification of models is proposed by Cremers & Edelin (1995) who have suggested that too much subdivision is constructed on the basis of modified aerial portions and that when the basal portions are considered, many of the proposed models fit the already existing models.

Andersen et al. (1988) proposed habits and modular forms in the genus *Eria* for the purpose of determining evolutionary changes, ranging from simple to complex. They also propose that the terminal position of an inflorescence is a basal condition in the genus and that the change from homoblasticity to heteroblasticity occurs from basal to terminal lineages. However, the simple to complex series proposed in *Eria* can't be generalised for monocots as a whole, as reduction may have occurred.

In this study, the intention is not to redress tree architecture and plant growth form models, since this has been described in detail by Hallé et al. (1978). Rather, the purpose of defining growth form models in this study was to construct a simple form to which certain portions of a monocot plant can be compared, so that ultimately congruence in portionas can be obtained. This results in a set of terms refering to similar structures which apply to monocots as a whole. The congruence is based on the initial assessment of positional similarity and followed up by the quantitative similarity confirmed by the MDS method. What these models provide is a simple outline of the variation that has been observed and how to recognise different variations from the basic form. They are not designed to fit into any big architectural scheme of plants as a whole. Instead they help to identify homologous organs among monocots. Thus, if Figure 4.1 is examined, the concept of a tufted form is presented, showing the variations of this form and illustrating which portions of the plants are equivalent structures in each case.

Monopodial growth form

If the shoot of a monocot incorporates both the vegetative and reproductive axes and if these structures are serially homologous, then there is no need to separate monopodial systems as has usually been the case (see Holttum 1955). The monopodial form can easily be considered as a modified tufted habit. It is not necessary to consider the axillary branch in a reproductive axis as peculiar or a deviation under this notion. There are many monocots where both aerial and reproductive axes have the potential to branch (see Figures 4.1 and 4.2). Where the monopodial form differs from the sympodial form is that the apex has the ability of continued growth. Whichever hypothesis is considered, it is conceivable that the monopodial habit can be derived by three different modes of modification and independent occurrence of the feature. In the first of these, Holttum (1955) also considered that the monopodial axis was a specialisation, proposing that change from terrestrial to epiphytic forms was the driving force behind this feature. Epiphytes could grow in a single direction along tree branches, exploring their habitat without the need for basal innovation. The terminal flowering position is simply transferred to the axillary branches and the growth apex is reserved for renewed vegetative growth. The lower internodes at a certain distance away from the control of the apical meristem get cut off and die away. In a continuously growing environment there is also no further need for basal innovation. In the second mode, Rua and Gróttola (1997) consider the monopodial runners of grasses to be modified synflorescences (aerial reproductive tiller) which become plagiotropic and proliferate in axillary positions. Thirdly, it is also possible to consider that a basal tiller unit of a grass can become plagiotropically orientated and the same process leading to apical vegetative dominance as previously described takes place. Again, growth orientation plays a major role in the option of which portion of the tuft is modified.

Constructional constraints

The degree of variation in form is also going to depend largely on the constructional constraints of the basic monocot habit. Constructional constraints have been described by Mosbrugger (1990) as being external when functional or constructional and phylogenetic when internal. The external constraints ultimately affect the physical attributes (architecture) of the plant, while the phylogenetic constraint only allows a certain moulding of a set of fixed features. In monocots the foremost constructional constraint to growth form is the lack of cambium. However the mechanical design of monocot stems may also be a constructional constraint (Mosbrugger 1992). In addition to this, the size that certain forms can attain is dependent on the diameter of the stem and the maximum number of

roots that can support the aerial system. Niklas (1995) has examined the tissue patterning in herbaceous stems correlated with stem height and has classified them into types according to the kind of stresses to bending that they are likely to experience. The interesting finding is that herbaceous stems which are slender seem to have the same tissue pattern i.e. a rigid rind surrounding an incompressible core of tissue. Thus, the similarity among aerial inflorescence axes that were examined in this study may be a result of their constructional design, which serves functionally to prevent buckling as described by Niklas (1995).

Proposals for a simple terminology

The terms that appear in the literature for monocot morphologies are extremely varied and many are synonymous (see Table 4.1). What is unclear is which of the terms are equivalent parts and thus which of the terms actually describe homologues. This is important for comparative studies as it is desirable to compare the same portions (structures/organs) among differently related taxa, whether for phylogenetic or functional studies. In monocot seedlings there is a similar problem with terminology and confusion over what portions are homologous (see Tillich 1995). Many of the published works on monocot morphology are taxon specific report on a specialisation or strange feature. This has lead to new terms being introduced for the special structures within the study group. The problem is that there is no reference point from which to work. There does not seem to be a specific set of terms which describe the different homologous regions of a monocot plant. At one level there is a terminology which is general to a genus or a family, while at the other level there is a terminology general to angiosperms. But, monocots due to the absence of cambium share a set of constraints to form and thus a morphology, but no terminology. In general, the categories which have been constructed for land plants and dicots specifically by Troll and others are applied to the monocotyledonous habit. If a strict application of this approach is taken, then a rhizome and an inflorescence axis should be called the same thing, a caulome (reproductive and vegetative stem). However, such a broad term is not the solution either as the difference between the two structures is profound, both in morphology and function. This difference is however, based on a set of features relating to the growth and the anatomy of the structures (pattern). It could be argued on the other hand, from a functional viewpoint, that there is no need to worry about what to call the structures. A caulome adequately describes the pipe-like structure which is responsible for transporting water and solutes in the plant. What needs to be elucidated is that there must be a distinction between the term and the definition which

goes along with the specific term. The term must refer to a structure which can be shown to be equivalent among all monocots, while the definition must be broad enough to encompass a certain amount of variation. Narrow definitions will lead to a categorical definition which cannot account for the variation observed. If necessary, where specialisations are unaccounted for by a broad definition, then an additional term describing this must be considered.

Table 4.1. Some examples[2] of the terms that have been published for structures which make up a sympodial unit in the monocot growth form.

Subterranean structures	Aerial structures	Surface structures
corm; *rhizome*; *tuber* (stem, root) (Lawton & Lawton 1969; Burkill 1960); *root-stem tuberoid* (Pridgeon & Chase 1995); *parent tuber, daughter tuber, replacement tuber* (Dixon 1991); *bulb*; *offset*; *sucker* (Skutch 1932; Fisher 1976; 1978); *subterranean stem*; *narrow stem with long internodes* (Tomlinson 1961a); *creeping rhizome*; *stolonoid* (Dixon 1991) *stolonoid root* (Pridgeon & Chase 1995); *dropper* (Robertson 1906; Ogura 1952; Kurzweil et al. 1995); *turion* (Blackmore & Tootill 1984; Heywood 1993)	*pseudobulb*; *peduncle*; *stem* (Barker 1993, 1995; Burkill 1960; Tomlinson 1961a; Kurzweil et al. 1995); *inflorescence axis*; *culm*; *inflorescence stalk* (Dixon 1991); *monochasium - monopodium* (Ritterbusch 1971); *bulbil* (Burkill 1960; Bell 1991); *vegetative shoot - reproductive shoot* (Rasmussen 1982; Andersen et al. 1988); *secondary stem* (see Dressler 1981 for refs therein); *ramicaul* (Stern & Pridgeon 1984)	*runner*, *stolon*, *offset*; *dropper* (Robertson 1906; Ogura 1952); *keiki* (Hodgson et al. 1991)

Sympodial units

The terms describing the structures that comprise each sympodial unit are variable and often misleading. The first problem encountered is what to call each sympodial unit of the monocot plant. This involves recognising that the construction of the monocot habit is modular. Variation in the terms describing these units is vast, from grass terminology the tiller (e.g. Clark & Fisher 1986), through to the phytomer (e.g. Madison 1970), paracladium (e.g. Troll 1949, 1951; Rua & Grottola 1997; Vegetti & Weberling 1996), or synflorescence (Vegetti & Anton 1996), module (after White 1984), metamer, phyton, I'

[2] Note that this table is only an illustrative example of some of the terms that have been encountered in the literature, and is not meant by any means to be an exhaustive account. Where terms are general and appear frequently in the literature, reference sources are not cited. Terms which appear less frequently and/or apply to a specialised structure have been referenced.

article etc. (see Bell 1991). In *Calla palustris* (Araceae), Scribailo & Tomlinson (1992) describe the plant as consisting of "sympodial, ephemeral, seasonal shoot units" which includes "creeping horizontal axes and an "inflorescence axis (spadix)" as well as a "renewal shoot" with "overwintering terminal buds" and "neoformed leaves". The basic structure of a monocot sympodium in this example, is not referred to by the more usual terms that refer to the sympodium such as peduncle (inflorescence axis) and creeping rhizome (horizontal axes). LaFrankie (1986) describes the shoot in *Melanthemum* as consisting of three discrete portions: a rhizome, a leafy stem and a terminal inflorescence. Further he notes "Although these sections are entirely distinct, they are not separate organs but represent different developmental stages of a single shoot". Thus, if they are not separate organs as LaFrankie considers, should they be afforded special rank by being given a name or does *shoot* encompass all of the discrete portions? Often the term *shoot* is used to refer to the most recent portion of the sympodium and is associated with the apical meristem (e.g. Martin & Tucker 1985). In functional approaches, such as that of Sharman (1942), the shoot has been described in terms of nodes and internodes for *Zea mays*. This interpretation of the shoot highlights the different needs of the process versus pattern approach, as examining the course of vasculature and the movement of solutes does not require a distinction between basal and aerial internodes of the plant. The problem encountered in these examples is a philosophical one, but, it really does affect the terminology of monocot plant portions. In a pattern based approach, the differences between the portions comprising the shoots is demonstrable using a multivariate approach (Chapter 3). For practical purposes, such as descriptive biology and flora accounts (even physiological experimentation), it is important to be able to take a monocot and recognise a portion of the plant as a specific structure e.g. rhizome, and similarly, to be able to identify homologous structures in other taxa.

Rhizomes

The first descriptions for the term rhizome actually refer to roots (see Bell 1991), but in more recent years the term refers to a horizontal, underground stem. The term rhizome is problematic because the definitions are many and often very rigid (see Table 4.2). Burkill (1960) states that a rhizome should have three qualities which relate back to Ker-Gawler's description: it should be cauline in nature; it should be horizontal and there is some degree of thickness to the structure. If thickness is not a feature, then the structure is termed a stolon. However, in grasses a stolon can only be formed by intravaginal tillering (Clark & Fisher 1986). The term stolon is interchangeable with runner (Bell 1991) and refers to an organ which grows on the surface of the substrate with long, thin

internodes and usually bearing foliage leaves and axillary buds. In Bell's definition there is no criterion of intravaginal branching. In grasses, a rhizome is formed by extravaginal tillering (Clark & Fisher 1986). The more usual definition of this term (see Table 4.2) is not adequate because, as shown in this study, many of the "aerial axes" that were examined actually grouped within the rhizome group (Chapter 3) and some axes are actually descending e.g. *Cordyline* (Bell & Tomlinson 1980; Tomlinson & Fisher 1971). Similarly, the subterranean criterion has been criticised by Bell & Tomlinson (1980), Dressler (1981) and Rasmussen (1985) because epiphytic orchid rhizomes are not subterranean. Similar problems exist for the many descriptions of the storage forms of rhizomes (e.g. tubers, corms, bulbs) such that tubers have been described as vertically orientated, swollen rhizomes (e.g. Holttum 1955) or corm described as a squat upright axis (Bell & Tomlinson 1980). These definitions directly contradict the more usual usage of the term rhizome and at the same time add modifications to currently existing terms (see Table 4.2). Bell & Tomlinson (1980) encountered many of these problems and incorporated a variety of organs such as stolons, suckers, offsets and tubers in their definition of rhizome for the purpose of examining architecture in clonal growth. Troll (1937) also includes a large variation of rhizomes e.g. swollen rhizomes, branching rhizomes, elongated internode rhizomes (runners, stolons) etc. in his term "rhizome", but separates bulbs, stem tubers ("hypokotylknollen") and rhizome tubers ("Ausläuferknollen"), and pseudobulbs ("Sprosknollen") from "rhizomes". Mention should be made that the terminology that is considered here, only relates to morphological (rhizomes) stems and modifications i.e those structures which reflect a specific stem structural pattern. Functionally, roots may also act as rhizomes e.g. root suckers and droppers, which carry the new shoot some distance away from the parent axis. Many rhizomes may also act as roots e.g. descending axes in *Cordyline*. A clear distinction must be made between terms referring to structures which are morphologically stem - like in quality as opposed to functionally stem - like. This is where pattern i.e. a set of distinct attributes, is so important in the recognition of plant structures.

With the use of many definitions for various rhizome kinds, whether thin, short, thick, vertical or storage forms, two main problems emerge. The first is that when rhizomes are modified e.g. into a bulb or a corm, the definitions suggest that these structures are different organs. Thus, morphologists interpret a bulb, corm or tuber as a different organ to a rhizome. The results obtained in Chapter 3 and the models that are proposed in this chapter exclude such a possibility. Bulbs, tubers or corms are not distinct organs, separate, or different from rhizomes, they group together within the rhizome group. Further, the distinction between these modified underground "organs" is not very precise e.g. "thickened underground stem" (Table 4.2)

seems to define both corms and tubers. This reiterates the point that although bulbs, corms and tubers are modified "stems", there is very little morphological difference warranting their separation as distinct organs from rhizomes. The second problem is that many of the terms refer to the same structures, but have very different names. For example, offset, sucker (stem) or turion seem to refer to very much the same kind of branch, but different terms seem to be applied to specific families/genera for the same structures.

When examining the various names for structures which represent rhizome or rhizome-like structures in Table 4.2, the definitions rest predominantly on the idea that rhizomes are *stems* or *shoots*. However, a clear definition of what theoretical notion of shoot or stem is being followed is often lacking. The concept of *shoot* has received much attention. Sattler (1974) has pointed out that according to the classical model of de Candolle, shoot refers to the categories of caulome (vegetative and reproductive stem) and phyllome (leaf). Two main problems arise from the definitions referring to shoots: (1) from a morphological and categorical viewpoint rhizomes cannot be referred to as shoots (albeit that functionally, they may behave as *shoot*), unless the reproductive (and/or leafy) portion of the axis is included in the definition, because rhizomes (on their own) do not (usually) bear phyllomes, particularly subterranean, horizontal forms, to which most of the definitions refer; (2) the term stem, following the classical definition as defined by Heywood (1993) (see Table 4.2), implies two things (i) that stem refers to homologous organs in any group of flowering plants and (ii) that rhizome and inflorescence axis (and synonyms) are the same structure (both forming a main axis and bearing leaves with axillary buds (but rhizomes and inflorescence axes clearly have distinct features - see Chapter 3, and on this basis represent modifications (in both) of *stem* and may represent serial homologues).

Table 4.2. List of authors and definitions for the term "rhizome" or "stem" referring to rhizome.

Author	Definitions
	Bulb
Bell (1992)	an underground perennating and storage organ consisting of a reduced *stem* surrounded by fleshy leaves
Blackmore & Tootill (1984)	A fleshy undergroung perennating organ. A highly modified shoot, the bulk of which is made up of colourless swollen scale leaves or leaf bases. The central apical bud contains the immature foliage leaves, the future flower and rudimentary adventitious roots at its base

Table 4.2 Continued.

Author	Definitions
	Bulb
Figuier (1892)	an underground stem covered with scales
Gray (1879)	an exceedingly abbreviated stem, reduced to a flat plate, from the lower surface of which roots are produced, from the upper surface, leaves in the form of scales, these scales being either reduced and thickened leaves or the thickened bases of ordinary leaves
Hartmann et al. (1990)	a specialised underground organ consisting of a short, fleshy, usually vertical stem axis bearing at its apex a growing point or a flower primordium enclosed by thick fleshy scales
Heywood (1993)	an underground organ comprising a short disk-like stem, bearing fleshy scale leaves, buds and surrounded by protective scale leaves; it acts as a perennating organ and is a means of vegetative reproduction
Holttum (1955)	a short stem with swollen leaf bases as the storage organs
Strasburger (1903)	a shortened shoot with a flattened, discoid stem and fleshy, thickened scale leaves with storage material
Vines (1896)	a shoot consisting of a short, discoid stem, bearing a number of scaly leaves closely arranged on its upper surface and roots on its lower surface
Wordsell (1915)	structure consisting of an excessively shortened axis bearing fleshy, food storing scale leaves and a central rudiment of foliage shoot and inflorescence, a modified vegetative shoot
	Bulbil
Bell (1991)	a small bulb that is a short stem axis bearing fleshy scale leaves or leaf bases and producing adventitious roots occurring on aerial stems in axillary positions, replacing flowers or in axils of scale leaves of bulbs
Blackmore & Tootill (1984)	a small bulb that develops from an aerial bulb
Figuier (1892)	separate buds in the axils of leaves
Gray (1879)	small aerial bulbs, or buds with fleshy scales, which arise in the axils of leaves
Heywood (1993)	a small bulb or bulb-like organ often produced on above ground organs
Strasburger (1903)	a special form of modified buds
Vines (1896)	an aerial bulb
Wordsell (1915)	a small axillary shoot having the general structure of a bulb but which is probably a modified flower

Table 4.2. Continued.

Author	Definitions
	Corm
Bell (1992)	a subterranean storage and perennating organ consisting of a short, swollen *stem* base
Blackmore & Tootill (1984)	a short, swollen underground stem that serves as an organ of perennation
Figuier (1892)	a thickened underground stem
Gray (1879)	comparable to a short rootstock or tuber and also a bulb, a subterranean fleshy stem of rounded or depressed figure and solid texture
Hartmann et al. (1990)	the swollen base of a stem axis enclosed by dry scale-like leaves ... a solid stem structure with distinct nodes and internodes
Heywood (1993)	a bulbous, swollen, underground stem base, bearing scale leaves and adventitious roots; a perennating organ
Holttum (1955)	a short segment of rhizome which grows erect, bearing a single terminal leafy (and flowering) stem and stores food for the next seasons' growth
Vines (1896)	a rounded or flattened stem which occupies a relatively larger proportion of space than that of the bulb
	Offset
Gray (1879)	a short *stolon* or *sucker*
Blackmore & Tootill (1984)	a short shoot that arises from an axillary bud near the base of the stem and gives rise to a daughter plant at its apex
Hartmann et al. (1990)	a characteristic type of lateral shoot or branch that develops from the base of the main stem in e.g. date palm, pineapple or banana
	Rhizome
Bell (1992)	a plagiotropic underground *stem*
Blackmore & Tootill (1984)	An underground stem that grows horizontally and, through branching, acts as an agent of vegetative propagation
Figuier (1892)	a stem, creeping horizontally, more or less covered by soil, giving off buds above and roots below
Gray (1879)	(Rhizoma -rhizome or rootstock) a horizontal or oblique perennial *stem* which lies on the ground or is buried beneath its surface.
Hartmann et al. (1990)	specialised stem structure in which the main axis of the plant grows horizontally at or just below the ground surface
Heywood (1993)	a horizontally creeping underground stem which perennates and bears roots and leafy shoots

Table 4.2. Continued.

Author	Definitions
	Rhizome
Strasburger (1903)	(rootstock) underground shoots bearing scale leaves and axillary buds, and roots, usually perennial, often thickened
Vines (1896)	a horizontal, perennial and subterranean shoot
	Rootstock
Blackmore & Tootill (1984)	a short, erect underground stem. It is the equivalent of a vertical rhizome or any underground part of a plant
	Runner
Bell (1991)	a thin horizontal stem above ground consisting of one or more long internodes at the distal end of which is a rosette of foliage leaves or a heteroblastic sequence of leaves and from which additional runners diverge. Runners do not root at any point along their length
Blackmore & Tootill (1984)	a creeping stem that arises from an axillary bud and runs along the ground, giving rise to plantlets at the nodes ... or apex ... often formed by rosette plants ... and usually possess greatly lengthened internodes
Figuier (1892)	procumbent shoots
Gray (1879)	a fusiform *stolon* naked and tendril like except at tip where it roots, develops a bud and so a new plant
Hartmann et al. (1990)	a specialised stem that develops from the axil of a leaf at the crown of a plant and grows horizontally along the ground and forms a new plant at one of the nodes
Holttum (1955)	usually monopodial, bearing erect leafy and flowering stems which grow from lateral buds
Strasburger (1903)	a shoot on the soil surface bearing scale leaves with axillary buds and roots at nodes, forming new plantlets from axillary buds
Vines (1896)	(or stolon) an elongated, lateral, creeping shoot on or below the soil surface which takes root at some distance from the parent plant and which by the dying away of the intermediate portions, becomes a new individual
	Sobole
Bell (1991)	a single underground horizontal stem turning erect at its distal end, growing out from the otherwise erect stem (Palmae and Araceae)
	Stem
Heywood (1993)	the main supporting axis of a plant. It bears leaves with buds in their axils. Usually aerial, but can be subterranean

Table 4.2. Continued.

Author	Definitions
	Stolon
Bell (1991)	a stem growing along the substrate surface or through surface debris with long thin internodes and bearing either foliage or scale leaves, monopodial or sympodial.
Bell (1992)	a short plagiotropic shoot which develops a new plant at the tip eventually serving connection with the parent
Blackmore & Tootill (1984)	a long branch that is unable to support its own weight and consequently bends down to the ground, where nodes touch the soil a new plant may develop from the axillary bud
Figuier (1892)	a sucker, at first aerial, and then rooting
Gray (1879)	prostrate branch which strikes root at the tip and then develops ascending growth which becomes an individual plant
Hartmann et al. (1990)	a modified stem that grows horizontal to the ground
Wordsell (1915)	a subterranean, horizontally growing elongated shoot
	Sucker
Blackmore & Tootill (1984)	an adventitious shoot that develops from the root
Gray (1879)	ascending *stem* arising from a subterranean creeping base
Hartmann et al. (1990)	a shoot that arises on a plant from below ground, usually from an adventitious bud on a root, but also to shoots arising from adventitious buds at crown of stem
Wordsell (1915)	a vigorous shoot springing from the *stem* base or the root
	Tuber
Bell (1991)	stem tuber is a swollen shoot usually underground and bearing scale leaves with axillary buds. Root tubers lack leaf scars
Blackmore & Tootill (1984)	a swollen part of a stem or root, usually modified for storage, and lasting for one year only, those of the succeeding year not arising from the old ones, nor bearing a position relative to them ... stem tubers may be distinguished from root tubers by the presence of buds
Figuier (1892)	a thickened underground stem
Gray (1879)	a thickened and short subterranean branch, beset with buds
Hartmann et al. (1990)	a swollen, modified stem structure that functions as an underground storage organ
Heywood (1993)	an underground stem or root that perennates and which is swollen with food reserves
Strasburger (1903)	a fleshy and swollen axis, serving as a reservoir of reserve materials
Vines (1896)	a shortened shoot with swollen stem and small scaly leaves

Table 4.2. Continued.

Author	Definitions
Wordsell (1915)	swollen root or shoot consisting almost entirely of parenchyma stored with food material
	Tubercle
Gray (1879)	a small tuber or an excrescence: or something between a tuber and root ... imitating a corm and charged with a bud at the upper end, near their origin
	Turion
Blackmore & Tootill (1984)	a type of perennating bud formed by certain aquatic plants shed from the plant to lie dormant on the river bed or any vegetative shoot or sucker
Heywood (1993)	a short scaly branch that is produced from a rhizome

Inflorescence axes

Rasmussen (1985) has elaborated on the variation of terms that have been proposed for the floral bearing axes in orchids, and has suggested that this problem is not restricted to orchids, but is a problem in all monocots. Like the term rhizome, the term "aerial axis" or aerial inflorescence axis has been suggested for the upright portion terminating in the inflorescence. Again, Dressler (1981) proposed that this was inadequate for orchid axes, as many epiphytes display negative geotropism, so that they are certainly not "upright" axes. In grasses and Restionaceae, the term culm has been widely used following Cutler (1969) and earlier authors (see Table 4.3). There appears to be no standardisation for the terms that are utilised to describe the variation in monocot flower-bearing structures. Many of the terms in use e.g. scape, pedicel, peduncle etc. (Table 4.3) refer to the same portion of stem (the reproductive stem) and the recognition of portions i.e. flower stalk (pedicel) implies that these are distinct from the main inflorescence axis. The results obtained in Chapter 3 suggest the contrary and thus, the need for elaborate terms representing the inflorescence axis must be questioned. Rasmussen (1985) suggested that the Systematics Association Committee for descriptive terminology (e.g. 1962) should be incorporated to help solve the problems with naming that are inherent in monocot morphology. Gray (1879) proposed a number of (nomenclatural) rules which should be followed where terminology is considered. Gray (1879) suggests that de Candolle's (1813) treatment of botanical terminology served as a basis and little modification of the terms he proposes have taken place. Of these rules, the most important are (Pg. 359):

- "... that each organ or part shall have a substantive name, and that modifications of organs shall be designated by adjective terms",
- "each object ought to be known by only one name"
- and "no term ought to be used with two different meanings"

However simple this approach may be, Gray (1879) offers examples of the complexity that is encountered when terms are being proposed e.g. the carpel is highly modified from one family to the next and each bears a different name, albeit that they may be homologous structures. Gray (1879) highlights that no matter how precise a system is, there will always be ambiguity of meanings. Therefore, using homology as a basis for naming can lead to difficulties where a great deal of modification has taken place (variation etc. would be lost by referring to all fruit modifications as *carpel* and one could argue this too for the term *rhizome* and all its modifications) and as discussed, where intermediate structures can be identified.

Table 4.3. List of authors and definitions for terms referring to inflorescence axes or aerial stems.

Authors	Definitions
	Culm
Blackmore & Tootill (1984)	the jointed stem of members of the Gramineae and Cyperaceae
Figuier (1892)	stem or stalk of grasses
Gray (1879)	a name applied to the peculiar closed-jointed stem of Grasses and Sedges, whether herbaceous, as in most Grasses, or woody or arborescent, as in the Bamboo
	Pedicel
Blackmore & Tootill (1984)	the stalk attaching individual flowers to the main axis of the inflorescence
Figuier (1892)	a stalk supporting a single flower
	Peduncle
Blackmore & Tootill (1984)	main axis of the inflorescence
Figuier (1892)	the general flower-stalk or floral axis
Wordsell (1915)	the stalk bearing an inflorescence
	Pseudobulb
Hartmann et al. (1990)	a specialised storage structure consisting of an enlarged, fleshy section of the stem made up of one to several nodes
Wordsell (1915)	an aerial tuberous shoot borne by epiphytic orchids

Table 4.3. Continued.

Authors	Definitions
	Rachis
Blackmore & Tootill (1984)	the main axis of a compound leaf or of an inflorescence
Wordsell (1915)	central axis of an inflorescence or leaf
	Scape
Blackmore & Tootill (1984)	the leafless stem of a solitary flower or inflorescence
Figuier (1892)	a naked flower stalk
Gray (1879)	a stem or branch which rises from beneath or near the surface of the ground and bears flowers but no proper foliage. It belongs to the inflorescence and springs from one of the subterranean forms of stem
Wordsell (1915)	a leafless peduncle springing from the centre of a rosette of foliage leaves and bearing a single terminal flower or capitulum

Terms based on multivariate pattern and growth form models

On the basis of the results obtained in the MDS analysis in this study and the proposals for viewing monocots in terms of two simple growth form models, the distinction between rhizome and inflorescence axis becomes necessary. There is no doubt that the monocot habit reflects a continuum of serial homologues and that the boundaries between the structures are not discrete (e.g. Figure 3.2). In practice it is difficult to place names onto this pattern. The MDS pattern (Chapter 3) shows that many of the portions examined which are representative of a wide variety of structures are equivalent and thus, one could easily simplify terms down to the very basic structure which is shown in the simplest model of the growth form (see Figure 4.3). Thus, a corm or a tuber or a pseudobulb may be a plagiotropic rhizome with swollen internodes (Figure 4.3), while an aerial rhizome such as that of *Pseudopentameris obtusifolium* would be an orthotropic rhizome (Figure 4.4). Something like a *Wachendorfia* organ could be termed a plagiotropic rhizome with swollen internodes (Figure 4.4).

When the inflorescence axes are considered, there is a functional variation that is reflected in the anatomy which allows the detection of a difference between the rhizome and the inflorescence axis. This is related to the constructional design of the stem (see Niklas 1994) and also what the inflorescence axis is co-opted to do e.g. photosynthesis in Restionaceae culms. Therefore, it is feasible to suggest that a term is used to distinguish this part of the sympodium from the rhizome, rather than calling the whole branch a shoot,

caulome, module or phytomer. It seems that the term inflorescence axis would suffice as many of the axes terminate in an inflorescence in monocots. The term is unfortunately not broad enough, as it does not encompass a "monopodially" growing axis or the separate vegetative and reproductive shoot units that are present in some orchids. The other area which poses a problem is the transition area at the base of the inflorescence axis. The intermediate nature of the portions are such that they are not sufficiently or consistently diagnosable by a particular set of features. Thus, they do not really warrant recognition and naming, albeit that they may be serial homologues.

Conclusions

What is proposed here is that the terms that apply to a general monocot form be considered when modifications are examined. Each part of a sympodial unit should be thoroughly examined for positional and identifiable features that point to which portion of the sympodium it fits into. Such a simplification in terminology would allow for ease of comparison among taxa for many disciplines. Thus, comparatively, the terms would refer to homologous structures. A simplification of the variations in growth forms into the two basic forms as proposed here, would also allow for relatively simple operational recognition of equivalent structures. Realistically, this is an oversimplification as many terms already exist and adding new terms could lead to more confusion. However, if the terms relate to basic structures, there should be little problem in recognising certain structures and then deciding what modification has occurred. Thus, a basic set of working terms could be along the lines of the following (depicted in Figure 4.4):

(1) rhizome, either plagiotropic or orthotropic

(2) inflorescence axis

(3) basal inflorescence axis or rhizome-inflorescence axis transition area

(4) extravaginal runner (rhizome-like runner)

(5) intravaginal runner (inflorescence axis-like runner).

Where terms are not broad enough, or such modification of the structure is present, then additional descriptive features can be added to the terms. This will (and has) invariably be the case when specialised structures in specific taxa are examined.

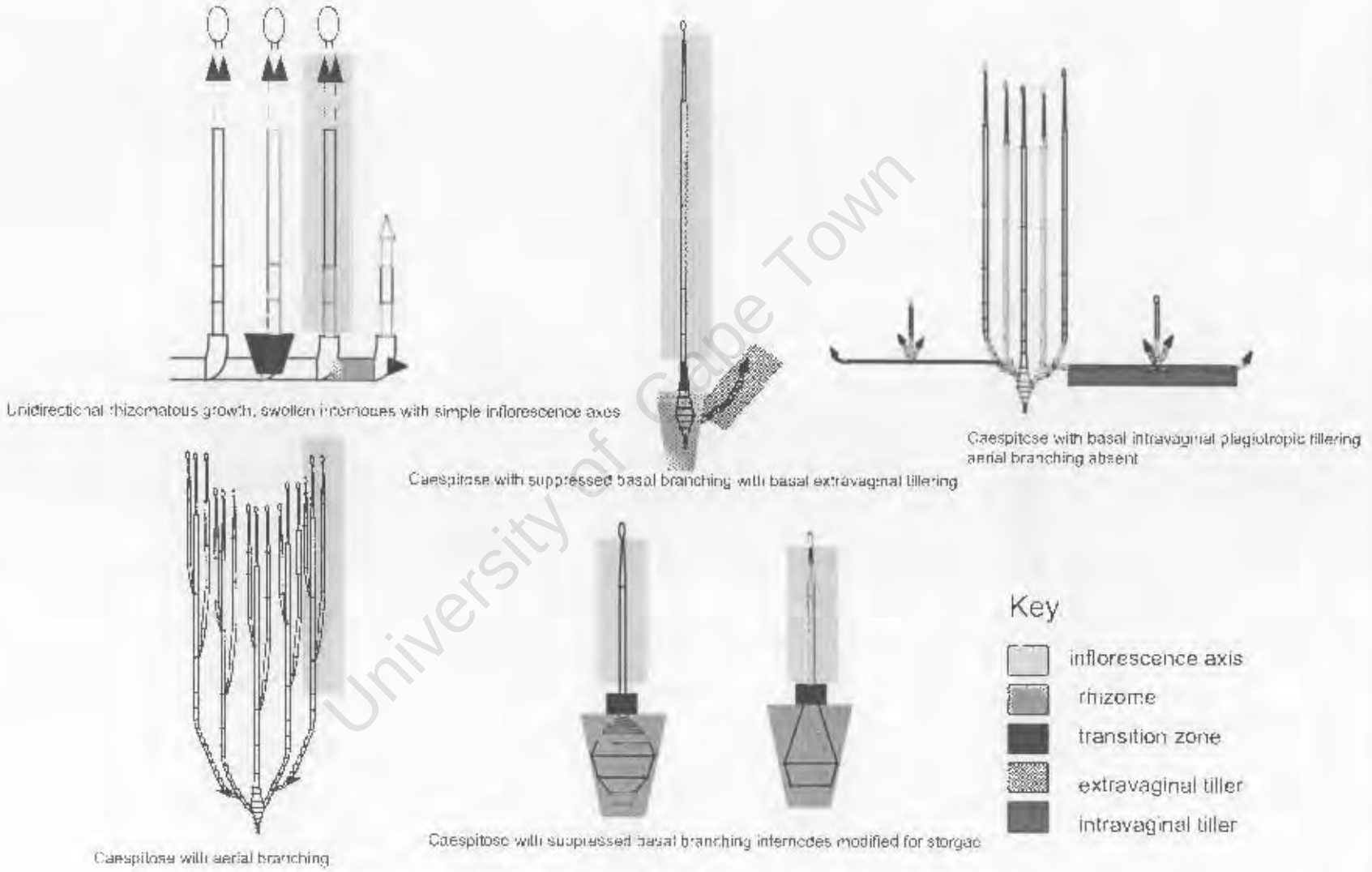


Figure 4.3. Simplistic models of the tufted and rhizomatous growth forms showing equivalent structures and proposed terms

CHAPTER 5

Synthesis and Conclusions

INTRODUCTION

This study presents a classification of the variation of monocot growth habits and establishes a protocol to recognise the structures which are component parts of particular forms. Classification approaches to recognising plant organs in the past have been based on idealistic notions of types (e.g. Troll 1937) and categorical entities (e.g. classical plant morphology model of de Candolle) into which structures are placed (cf. Arber 1950; Cusset 1994; Hagemann 1992; Jeune & Sattler 1992; Sattler 1974; 1996; Sattler & Jeune 1992). Thus, the framework for recognising plant organs has been based largely on rigidly defined models of plant structure. This thesis attempts to break down the boundaries that exist between categories of structures by adopting a non-categorical approach to recognising structures. Plants are divided up into internode components and information about the morphology, anatomy, growth, life history and function for each internode is recorded. The variation in features of the internodes are analysed using a multivariate approach and the similarity between each internode portion assessed. The pattern of multivariate similarity reflects a continuity between internode portions, which can be interpreted as both whole structures and whole growth forms. Thus, the recognition of structures is based on similarity of features, rather than whether the structure fits into a discretely defined category or not.

The monocot growth habit has several unique features, related to a lack of cambium and the sympodial habit, which set the group apart from other flowering plants (Holttum 1955, Corner 1954, Tomlinson 1970a; 1995). The deterministic method of sympodial renewal growth is modular in design and axes have the ability to become modified so that a large amount of variation in the axial systems of monocots exists. The axial system of monocots usually comprises two (functional) components, a vegetative stem and a reproductive stem, each made up of several repeating units. When an attempt is made to classify the axial system of monocots according to the classical plant morphology model of de Candolle, difficulties are encountered because both stem components have very distinct features, but both may comply with the necessary features of a stem (see Sattler 1974) i.e. main axis with lateral appendages and axillary buds.

Thus, it is difficult to decide which portion should be regarded as "stem", equivalent to "stem" in other flowering plants.

While the sympodial habit has no doubt resulted in the modifications of the axial system in monocots, there is no consensus as to which form is basic in the grade of variation. Holttum (1955) has proposed that the tufted form is general and all variations are modifications on this basic form. Tomlinson (1970a) has proposed that the herbaceous sympodial form of monocots is an example of paedomorphic development and that large, arborescent monocots are the general growth habit. Thus, an attempt is made in this thesis to determine which is the basic habit in monocots, taking into account the forms of sister taxa. Various aspects (e.g. seedlings, vasculature, branching, meristem distribution and function etc.) relating to monocot growth form have been examined, and in particular, the focus has been on specific plants or particular groups. However, a consolidated approach, where an overview of monocot growth habits is obtained is desirable. The approach in this thesis has been to examine whole plants, a range of taxa and a diversity of growth habits. All plants examined are sampled in the same way and thus, comparison between like parts is easily made.

MORPHOLOGY AND ANATOMY OF GROWTH FORM

The morphology and anatomy of internodes of subterranean and aerial axes and roots from a range of monocot growth habits is examined in order to describe the variation and to determine whether a general pattern (or a set of features) is recognisable in particular plant portions. Although, the approach is to examine growth form without recognition of *a priori* categories, a comparison between equivalent structures is desirable. Thus, the end goal was to find similar structures and to be able to compare them between a range of taxa. The idea is that a pattern will reflect a natural grouping which will determine which of the structures are similar. These can be labelled *a posteriori*, and can be representative of a category, if desirable.

An examination of the morphology and anatomy of the internodes revealed several interesting trends which could readily be identified both qualitatively in observations and quantitatively in the multivariate approach:

(1) There has been a tendency to recognise particular or specialised structures as distinct organs (see Tables 4.2 and 4.3). The rigorous MDS analysis of such particular "organs" e.g. pseudobulbs, corms tubers etc. has shown that this is not the case (Figure 3.2). This is particularly noticeable if the morphology and anatomy of such structures is carefully examined e.g. pseudobulbs of Orchidaceae can be recognised as swollen internodes of

either inflorescence axes or rhizomes and there is no special set of features which distinguish them from axes as separate organs. Rather, they must be recognised as either part of the rhizome or inflorescence axis, depending on their nature. In some of the plants examined, runners are produced which may either be subterranean or superficial. In many, the features of the internodes were similar to both rhizome portions of the axis and sometimes, to the inflorescence axis portions. The recognition of these structures as either rhizome or inflorescence axis was impossible (as shown in the MDS analysis), and it was also not possible to recognised these "structures" as distinct categories separate from rhizome or inflorescence axis either (Figure 3.2 and MANOVA Chapter 3). The distinction between so called corms and tubers, both from a morphological and anatomical standpoint is not clear. Storage forms such as corms and tubers lack structural tissues due to the expansion of parenchymatous tissues for storage of food reserves. In these forms, the vascular supply to the storage regions is much reduced and only the currently growing portion contains distinct vascularisation. Examining the morphology and anatomy of whole plants from the base to the tip highlights the difficulty involved in demarcating areas which represent discrete boundaries between one part of the axial system e.g. rhizome to the next part e.g. inflorescence axis. In many of the plants examined there was not a distinct nor absolute change over in features to coincide with one "organ" to the next (cf. La Frankie 1986).

(2) Functional aspects which are related to growth seem to have a central role in some of the features of particular growth forms. Within monocots, there seems to be a transference of function, or more specifically functional convergence, from one structure to another. Thus, roots may function like rhizomes. This is observed in the tuber and "extended root" (dropper) of *Holothrix villosus*, whereby, the stem meristem is positioned at the apex of the tuber and/or dropper carrying the bud to a new location in the substrate away from the parent plant. Although stem-like in function, the anatomy and morphology of the structure indicates that it is a root. Similarly, the aerial axes of Restionaceae are the sole photosynthetic structures, although they are cauline in anatomy. Although the flower bearing portions of the axial system (i.e. inflorescence axis) tended to group together in the MDS analysis (Figure 3.2), there is anatomical variability in the tissues comprising the internodes. Some show specialisation towards photosynthetic function (e.g. culms of Restionaceae) or to buoyancy (e.g. *Aponogeton distachyos*), while others serve to present the flower or inflorescence (e.g. *Baeometra uniflora*). Tissue patterning within axial portions of monocots appears to show basic trends (Figure 3.2), which are either attributable to a basic pattern (history) or constructional constraints (e.g. Mosbrugger

1990; Niklas 1995), although this modification in structural tissues offers insight into the growth habit of some forms. Fast growing axes, both subterranean and aerial e.g. *Canna indica*, seem to lack strengthening tissues, except in climbing forms e.g. *Smilax* and *Myrsiphyllum* where sclerification is elaborate. Structural support in the form of sclerenchyma bands or as poles associated with vascular bundles are a predominant feature of water transporting axes e.g. Restionaceae.

(3) Some of the plants examined had very similar, shared features. These could be related to the convergence in habitat of the plants, rather than common ancestry. This was particularly noticeable in the sub-shrub growth form (tufted model Cb, Figure 4.1) which characterises *Borya nitida*; *Dasypogon bromeliifolius*; *Xerophyta humilis*; *Calectasia cyanea*, *Pentameris obtusifolium* and *Pentameris thuarii*. Similar shared morphological features are found in the "long rhizomes" of *Chondropetalum rectum* and Australian genera such as *Alexgeorgea*.

(4) Seedlings of monocots tend to offer much information about the biology of the plant, the growth form and the phylogeny of particular groups. The seedlings of *Wachendorfia thyrsiflora* develop the growth habit which the adults display very early in their development. Similar trends were observed in seedlings of *Lachenalia splendida* and *Zantedeschia aethiopica*. In *Thamnochortus spicigerus*, by comparison, the seedlings take up to three years to develop the adult growth habit. In all of the seedlings examined, excepting for those of *Canna indica*, the focus of growth is on vegetative development and production of specialised regions of the axial system, rather than flowering. The seedlings of *Canna indica* display an opposite growth trend, where flowering is achieved after six months of growth. In the seedlings of the storage rhizome growth forms examined (e.g. *Z.aethiopica*) the hypocotyl region of the seedling appears to be the region which undergoes modification into a storage internode, which later develops into the "tuber".

PHILOSOPHY OF FORM

With the variation in growth habits that is observable in monocots and the obvious modification of structures which comprise the axial system, several questions relating to the concept of plant form were considered. The first is to determine whether there is a basic growth habit as Holttum (1955) suggested and whether the variations in form are simply variations of a basic theme. The second, relating to the parts comprising monocot plants is whether discrete, homologous organs can be recognised. Lastly, an important

consideration is whether variation is measurable so that a set of features can be used to distinguish between different "organs" and growth forms.

With idealistic notions of types and the classical model of plants being categorical, the concept of plant form is fraught with many difficulties. The intention of this thesis was to try to recognise "natural" groups of plant internodes using multivariate analytical techniques, rather than start from preconceived categories (de Candolle model) of organ types (Goethean types). The multivariate approach proved useful in achieving many of the goals of this thesis and the following results were obtained:

- internodes tended to group together on the basis of structural and functional similarity;
- the structures comprising the axial system of monocots are not discreet;
- within plants, the axial system is comprised of serial homologues i.e. the rhizome internodes and the inflorescence axis internodes, which are separated by an intermediate region;
- this continuum represents the functional shoot system (branch) of a monocot plant and
- between plants, some structures share features of both rhizome and inflorescence axis and thus appear to represent intermediates.

If monocot growth forms can be viewed in terms of simplistic models with general definitions for the structures making up the forms, then both equivalence and variation can be easily interpreted, making the system readily operational in any sort of comparative approach. Thus, the equivalence of structures is determined by the pattern of points shown in the MDS analysis and therefore, the growth habits can be viewed as comprising these equivalent structures. The problem in recognising homologues has been a conflict between pattern based approaches and process based ones (e.g. de Pinna 1991; Hall 1995; Kaplan 1984; Sachs 1982; Sattler 1994, Tomlinson 1987). The MDS analysis, while utilising features of internodes and thus pattern based in its inception, reflects process (i.e. morphology of a branch in a monocot plant). Using the MDS pattern, homologues can be identified by recognising the areas of dense point accumulation. However, intermediates cannot be recognised as homologues because they fall in-between the dense point areas.

In the cluster analysis, the relation within groups, e.g. rhizomes, could be highlighted. From this, two growth patterns could be identified and two basic growth form models could be constructed on this basis. The first of the models is a tufted growth habit which results from a vertically orientated axial system, while the second model is a rhizomatous growth habit which results from a horizontally orientated axial system. A

series of features relating to groups of internodes can be utilised to recognise similar structures. The "structures" which comprise the axial system of the monocots are the homologues identified in the MDS analysis and thus, any terms which are given to these structures refer to equivalent things. The terms apply to the two basic growth habits and as a result are general. Modifications of portions should necessarily be called by the same name and anecdotes relating to the variation can be added to definitions on a descriptive basis. Although this solves the problem of ambiguity and synonymy, much of the variability in form may be lost if this is not included as part of the definition.

CONCLUSIONS

This study has highlighted some important aspects relating to monocot growth forms.

1) The concept of plant form and how it relates to monocots is such that a basic form (two growth habit models) in monocots is recognisable and it may be considered as a "type", but the recognition of this basic growth form does not need to be idealistic in approach if an attempt to retrieve natural group structure is taken using multivariate techniques.

2) The axial system in monocots (representing a functional process - the development of an axillary branch) constitutes a continuum from the vegetative to the reproductive function. The vegetative is the rhizome and the reproductive is the inflorescence axis which is separated by a transition region, and the whole axial system is a modified series. Thus the rhizome and inflorescence axis should be viewed as serial homologues and inflorescence axes may or may not retain some features of the previous series (rhizome) such as axillary buds and thus, the ability to branch.

3) Organs such as bulbs, tubers, corms, pseudobulbs, culms etc. are modifications of two homologous structures, rhizome or inflorescence axis. Thus, comparative approaches must utilise the basic homologous form and the recognition of some of these structures as distinct organs from either rhizome or inflorescence axis is not really appropriate.

4) The conflict between pattern and process in homology recognition is highlighted in this study using multivariate techniques. This is because, the continuum in growth form is present at two levels - within the plant (serial homology, probably process based) and between taxa (taxic homology, probably historically based). Homologues can be recognised at both levels if a pluralistic approach to homology recognition is considered.

5) The results of this study suggest that a multivariate approach to examining plant form leads to a greater understanding of plant construction and the processes relating to the

organ systems. Such an approach to examining the leaf system and how it relates to the axial system of monocots in terms of structural pattern, development and function, may be useful.

6) The basic growth models proposed for monocots in this study are most similar to growth habits in sister taxa such as those found in some Piperales (see Chapter 4). This similarity along with the seedling structure of monocots suggests that the herbaceous sympodial habit may be the general habit in monocots. An extended "juvenile phase" in monocots other than arborescent forms negates the possibility of neoteny as an explanation for the sympodial habit of monocots. Arborescent forms must be considered as modifications of the basic tufted habit which is also reflected in the establishment growth of the seedlings.

While this thesis has examined a wide variety of forms representative of a number of taxa, it is by no means exhaustive. However, the pattern obtained in the MDS analysis suggests that much of the variation that is present represents modification in either the rhizome or inflorescence axis components of the axial system and that many monocots will show this pattern. The number of intermediate forms that are present are fewer than the number of general forms, a trend which has also been observed in other plant groups (Jeune & Sattler 1992). No doubt there will be other interesting cases of intermediate structures that are present in monocots. A basic terminology relating to equivalent structures can be constructed for the purposes of comparative analyses. However, if some of the terms are too broad ranging e.g. if rhizome includes all modifications, that some of the intrigue and functional biology relating to many of the modified structures may be ignored.

This thesis has reported on morphological and anatomical aspects and how they relate to plant form. Several aspects follow or from the grounding that this thesis provides and require further research:

- examination of other organ systems in monocots using a multivariate approach may solve issues relating to homology and development e.g. in monocot leaves;
- the functional aspects in terms of habitat and evolution of many axial systems of monocots is an area in which future research must be directed. Nutrient cycling within monocots, particularly highly clonal forms such as root tuberous orchids is in need of further examination;
- similarly, the relationship between meristem position and inception to life history strategy needs further elaboration;

- the growth form models proposed here are broad ranging. Detailed growth form models within taxa may lead to an improved understanding of biological and phylogenetic aspects relating to plant form e.g. evolution of annualness in some groups (see e.g. Rua and Gróltola 1997) and
- comparative approaches, such as phylogenetic methods, can be used to test the evolution of particular growth forms in a set of taxa e.g. whether there is a relationship between the orthotropic and plagiotropic models or whether they have evolved separately.

CHAPTER 6

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APPENDIX 2.1

Voucher list

VOUCHER LIST OF THE PLANTS SAMPLED AND EXAMINED FOR GROWTH FORM MORPHOLOGY AND ANATOMY.

TAXON	NO.	LOCALITY
Albuca fragrans Jacq.	Munro 7	Jonkershoek, Western Cape, S. Africa
Anigozanthos manglesii D. Don	Munro 71	Darlington, Western Australia
Apodogeton distachyos L. f.	Munro 70	Wynberg Park ponds, Western Cape, S. Africa
Arundo donax L.	Munro 61	Univ. Cape Town grounds, Western Cape, S. Africa
Baeometra uniflora (Jacq.) Lewis	Munro 68	Newlands forest, Western Cape, S. Africa
Billbergia nutans H. Wendl. ex. Reg.	Munro 69	Propagated from cuttings (cult.)
Borya nitida Labill.	Munro 75	Darlington, Western Australia
Calectasia cyanea R. Br.	Munro 60	Reid's lookout, Grampian's Nat. Park, Victoria, Australia
Canna indica L.	Munro 53	Sown from seed (cult.)
Chloropbytum comosum (Thunb.) Jacq.	Munro 111	Sown from seed
Chondropetalum deustum Rottb.	Esterhuysen 32899	Kaaljagsberg, Cape Peninsula, Western Cape, S. Africa
Chondropetalum rectum (Masters) Pill.	Munro 34	Riverlands, Malmesbury, Western Cape, S. Africa
Conostylis prolifera Benth.	Munro 73	Jarradale forest, Western Australia
Cyanella hyacynthoides L.	Munro 99	Signal Hill (rump), Western Cape, S. Africa
Dasypogon bromeliifolius R. Br.	Munro 76	Badgingarra, Western Australia
Elegia capensis (Burm. f.) Scheipe	Munro 112	Jonkershoek, Western Cape, S.Africa
Epidendrum cinnabarinum Salzm. ex Lindl.	Munro 105	Cult. Kenilworth, Western Cape, S. Africa
Eriospermum pumilum T. M. Salter	Munro 63	Rondebosch Common, Western Cape, S. Africa seed reared from locality plants
Hoplothrix villosa Lindley	Munro 81	Helderberg Mts, above nat. reserve, Western Cape, S. Africa
Ischyrolepis cincinnata (Masters) Linder nec.	Munro 78	Echo Valley, Kalk Bay Mt., Western Cape, S. Africa
Johnsonia pubescens Lindley	Munro 77	Badgingarra, Western Australia
Lachenalia klinghardtiana Diriter	Munro 110	Steinkopf, N. Capo, S. Africa
Lachenalia splendida Diels	Munro 108	Propagated from seed from Graham Duncan, Kirstenbosch
Maxillaria variabilis	Munro 103	Cult., Duckitt Nurseries, Darling, Western Cape, S. Africa
Merxmuellera cincta (Nees) Conert	Munro 54	Sir Lowry's Pass, Western Cape, S. Africa
Merxmuellera rufa (Nees) Conert	Munro 26	Steenberg Plateau, Western Cape, S. Africa
Myrsiphyllum scandens (Thunb.) Oberm.	Munro 59	Nowlands Ravine, Table Mt., Western Cape, S. Africa
Paurala minuta (L. f.) Durand & Schinz	Munro 67	Rondebosch Common, Western Cape, S. Africa
Pentameris thuarii Beauv.	Munro 5	Jonkershoek, Western Cape, S. Africa
Pentaschistis aristidoides (Thunb.) Stapf	Munro 24	Steenberg Plateau, Western Cape, S. Africa
Pentaschistis pallescens (Schrader) Stapf	Munro 39	Platteklip Gorge, Table Mountain, Western Cape, S. Africa
Phalaenopsis fresty hunter x 'Puma canyon' amboinensis	Munro 102	Cult. hybrid, Duckitt Nurseries, Darling, Western Cape, S. Africa
Polystachya ottoniana	Munro 104	Cult., Duckitt Nurseries, Darling, Western Cape, S. Africa
Pseudopentameris caespitosa Barker	Munro 22	Steenberg Plateau, Western Cape, S. Africa
Pseudopentameris macrantha (Schrad.) Conert	Munro 23	Steenberg Plateau, Western Cape, S. Africa

Voucher List Continued.

TAXON	NO.	LOCALITY
Pseudopentameris obtusifolia (Hochst.) N. P. Barker	Munro 60	Mts. above Kleinmond, Western Cape, S. Africa
Restio harveyii Masters	Esterhuysen 3390	Camps Bay, Cape Town, S. Africa
Restio quadratus Mast.	Munro 20	Newlands forest, Western Cape, S. Africa
Smilax anceps	Munro 43	Devil's Window, Mpumalanga, S. Africa
Spiloxene alba (Thunb.) Fourc.	Munro 68	Rondebosch Common, Western Cape, S. Africa
Spiloxene minuta (L.) Fourc.	Munro 66	Rondebosch Common, Western Cape, S. Africa
Thamnochortus lucens Poir.	Zeyer 1741	Camps Bay, Cape Town, S.Africa
Thamnochortus spicigerus (Thunb. Sprengel	Munro 12	Olifantsbos, Cape Point, Western Cape, S. Africa Seed reared from locality plants
Tribolium obtusifolium (Nees) Renvioze	Munro 85	Riverlands, Malmesbury, Western Cape, S. Africa
Tulbaghia alliacea L. f.	Munro 64	Rondebosch Common, Western Cape, S. Africa
Wachendorfia thyrsiflora L.	Munro 4	Jonkershoek, Western Cape, S. Africa Also grown from seed purchased @ Silvermill Seeds, Kenilworth
Willdenowia glomerata (Thunb.) Lindor ined.	Munro 10	Steenberg Plateau, Western Cape, S. Africa
Wurmbea spicata (Burm. f.) Durand & Schinz	Munro 101	Signal Hill (granite outcrops), Western Cape, S. Africa
Xerophyta humilis (Bak.) Dur. & Schinz	Munro 50	Great Dyke, Zimbabwe
Zantedeschia aethiopica (L.) Sprengel	Munro 109	Grown from seed purchased @ Silvermill Seeds, Kenilworth
Zingiber officinale Roscoe	Munro 107	Propagated from rhizome material purchased from local grocery store

APPENDIX 3.1

Data matrix

DATA MATRIX FOR 147 PLANT PORTIONS AND 90 VARIABLES - BINARY CODING. INCLUDES ALL ORGANS FROM ROOTS TO INFLORESCENCE AXES. CONDITIONALLY PRESENT VARIABLES ARE CODED WITH A MISSING DATA CODE -999.

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APPENDIX 3.2

Plant portions used for growth form analysis

LIST OF TAXA, FAMILIES AND PLANT PORTIONS UTILISED FOR GROWTH FORM ANALYSIS.

TAG[1]	TAXON	FAMILY	PLANT PORTION
1	*Albuca fragrans* Jacq.	Hyacinthaceae	inflorescence axis internode; inflorescence stalk; contractile root
2	*Anigozanthos manglesii* D. Don	Haemodoraceae	inflorescence axis internode; rhizome
3	*Aponogeton distachyos* L. f.	Aponogetonaceae	inflorescence stalk; rhizome
4	*Arundo donax* L.	Poaceae	inflorescence axis internode; inflorescence stalk
5	*Baeometra uniflora* (Jacq.) Lewis	Colchicaceae	basal neck, upper neck; corm; inflorescence axis internode; flowering stalk
6	*Billbergia nutans* H. Wendl. ex. Reg.	Bromeliaceae	basal inflorescence axis; inflorescence axis internode; inflorescence stalk; rhizome; runner
7	*Borya nitida* Labill.	Boryaceae	basal inflorescence axis; inflorescence axis internode; root; stem
8	*Calectasia cyanea* R. Br.	Calectasiaceae	stem; flowering inflorescence axis
9	*Canna indica* L.	Cannaceae	aerial stem; inflorescence axis; rhizome
10	*Chondropetalum deustum* Rottb.	Restionaceae	basal inflorescence axis; rhizome
11	*Chlorophytum comosum* (Thunb.) Jacq.	Anthericaceae	inflorescence axis internode; rhizome; stolon; tuber
12	*Conostylis prolifera* Benth.	Haemodoraceae	inflorescence axis internode; inflorescence axis; runner
13	*Chondropetalum rectum* (Masters) Pill.	Restionaceae	inflorescence axis internode; basal inflorescence axis; lower inflorescence axis internode; rhizome
14	*Cyanella hyacynthoides* L.	Tecophilaceae	basal neck; mid neck; basal inflorescence axis; flowering stalk
15	*Dasypogon bromeliifolius* R. Br.	Dasypogonaceae	inflorescence axis internode, stem base
16	*Epidendrum cinnabarinum* Salzm. ex Lindl.	Orchidaceae	inflorescence axis; lower axis; upper axis; root
17	*Eriospermum pumilum* T. M. Salter	Eriospermaceae	flowering stalk; lower inflorescence axis; tuber
18	*Holothrix villosa* Lindley	Orchidaceae	inflorescence axis internode; rhizome; root; tuber
19	*Ischyrolepis cincinnata* (Masters) Linder ined.	Restionaceae	inflorescence axis internode; rhizome base; runner
20	*Johnsonia pubescens* Lindley	Johnsoniaceae	basal inflorescence axis; inflorescence axis internode, stem base (rhizome)
21	*Lachenalia klinghardtiana* Dinter	Hyacinthaceae	inflorescence axis; rhizome
22	*Maxillaria variabilis*	Orchidaceae	basal inflorescence axis; inflorescence axis internode; pseudobulb stalk; mid pseudobulb

[1] This number refers to the number that each taxon is given as a tag in Figure 3.2.

Plant portion list Continued.

TAG[2]	TAXON	FAMILY	PLANT PORTION
23	*Merxmuellera cincta* (Nees) Conert	Poaceae	basal inflorescence axis; inflorescence axis internode; rhizome
24	*Merxmuellera rufa* (Nees) Conert	Poaceae	basal inflorescence axis; rhizome; runner
25	*Myrsiphyllum scandens* (Thunb.) Oberm.	Asparagaceae	aerial axis; flowering stalk; rhizome; tuber
26	*Pentaschistis aristoides* (Thunb.) Stapf	Poaceae	basal inflorescence axis; flowering stalk; rhizome; rhizome-inflorescence axis
27	*Pseudopentameris caespitosa* Barker	Poaceae	inflorescence axis internode; vertical stem (rhizome)
28	*Pnalaenopsis frosty bunior x 'Zuma canyon' amboinensis*	Orchidaceae	flowering stalk; root
29	*Pseudopentameris macrantha* (Shrad.) Conert.	Poaceae	inflorescence axis internode; rhizome
30	*Pauriola minuta* (L. f.) Durand & Schinz	Hypoxidaceae	corm
31	*Pseudopentameris obtusifolia* (Hochst.) N. P. Barker	Poaceae	inflorescence stalk; inflorescence axis internode; rhizome base; main axis
32	*Polystachya ottoniana* Reichb. f.	Orchidaceae	inflorescence axis internode; pseudobulb; root
33	*Pentaschistis pallescens* (Schrader) Stapf	Poaceae	flowering stalk; stem; rhizome base
34	*Pentameris thuarii* Beauv.	Poaceae	inflorescence axis internode; vertical stem (rhizome)
35	*Restio harveyi* Masters	Restionaceae	inflorescence axis internode; rhizome base; runner
36	*Spiloxene alba* (Thunb.) Fourc.	Hypoxidaceae	flowering stalk
37	*Smilax anceps* Willd.	Smilacaceae	flowering stalk; stem
38	*Trilhagnia alliacea* L. f.	Alliaceae	basal inflorescence axis; inflorescence axis internode; inflorescence stalk; flower stalk; rhizome
39	*Thamnochortus lucens* Poir.	Restionaceae	rhizome-inflorescence axis; inflorescence axis internode; rhizome base
40	*Trifolium obtusifolium* (Nees) Renvolze	Poaceae	inflorescence axis internode; rhizome; stolon
41	*Thamnochortus spicigerus* (Thunb. Sprengel	Restionaceae	inflorescence axis internode; basal inflorescence axis; inflorescence stalk; flowering stalk; rhizome; rhizome-inflorescence axis; root; seedling inflorescence axis
42	*Willdenowia glomerata* (Thunb.) Linder ined.	Restionaceae	inflorescence axis internode; root; runner
43	*Wachendorfia thyrsiflora* L.	Haemodoraceae	inflorescence axis internode; inflorescence stalk; rhizome; runner
44	*Wurmbea spicata* (Burm. f.) Durand & Schinz	Colchicaceae	mid neck; basal neck; corm; flowering stalk
45	*Xerophyta humilis* (Bak.) Dur. & Schinz.	Velloziaceae	root; stem
46	*Zantedeschia aethiopica* (L.) Sprengel	Araceae	inflorescence stalk; spathe stalk; tuber
47	*Zingiber officinale* Roscoe	Zingiberaceae	reproductive axis; vegetative axis
48	*Spiloxene minuta* (L.) Fourc.	Hypoxidaceae	flowering stalk

[2] This number refers to the number that each taxon is given as a tag in Figure 3.2

APPENDIX 3.3

Labels

INTERNODE LABELS FOR FIGURE 3.3.

Anigrhi = *Anigozanthos manglesii* rhizome; Aponrhi = *Aponogeton distachyos* rhizome; Baocorm = *Baeometra uniflora* corm; Bilbrhi = *Billbergia nutans* rhizome; Borstem = *Borya nitida* stem; Cannarhi = *Canna indica* rhizome; Chlorhi = *Chlorophytum comosum* rhizome; Conrun = *Conostylis prolifera* runner; Dasysteba = *Dasypogon bromelifolius* stem; Epidloax = *Epidendrum cinnapalinum* lower axis; Epidupax = *Epidendrum upper axis*; Epumtub = *Eriospermum pumilum* tuber; Holrhi = *Holothrix villosus* rhizome; Icinrhba = *Ischyrolepis cincinnata* base; Johnsteba = *Johnsonia pubescens* stem; Lklingrhi = *Lachenalia klinghardtiana* rhizome; Maxpseudobs = *Maxillaria variabilis* pseudobulb stalk; Mcinrh = *Merxmuellera cincta* rhizome; Mrufrh = *Merxmuellera rufa* rhizome; Mscarhi = *Myrsiphyllum scandens* rhizome; Panrhcu = *Pentaschistis aristidoides* rhizome-inflorescence axis transition area; Parirh = *Pentaschistis aristidoides* rhizome; Pcaeverb = *Pseudopentameris caespitosa* base; Pmincorm = *Pauridia minuta* corm; Pmacrhba = *Pseudopentameris macrantha* rhizome; Polpseudb = *Polystachya ottoniana* pseudobulb; Ppalrhba = *Pentaschistis pallescens* base; Pthuverr = *Pentameris thuarii* stem; Rharrhba = *Restio harveyii* rhizome base; Tallirhiz = *Tulbaghia alliaceae* rhizome; Tlucbasr = *Thamnochortus lucens* rhizome; Tspirh = *Thamnochortus spicigerus* rhizome; Tribrhi = *Tribolium obtusifolium* rhizome; Wthyrhiz = *Wachendorfia thyrsiflora* rhizome; Wurmcorm = *Wurmbea spicata* corm; Xerste = *Xerophyta hunilis* stem; Zaeseedt = *Zantedeschia aethiopica* tuber.

APPENDIX 3.4

Labels

INTERNODE LABELS FOR FIGURE 3.4

Albaecul = *Albuca sp.* inflorescence axis; Albifcu = *Albuca sp.* inflorescence stalk; Anigcu = *Anigozanthos manglesii* inflorescence axis; Aponinfstk = *Aponogeton distachyos* inflorescence axis; Arundaec = *Arundo donax* stem; Arundinf = *Arundo donax* inflorescence axis; Baobanek = *Baeometra uniflora* basal neck ; Baocu = *Baometra uniflora* inflorescence axis; Baoloflstk = *Baometra uniflora* flower stalk; Baoupnek = *Baeometra uniflora* upper neck; Bilbacu = *Billbergia nutans* basal inflorescence axis; Bilbcu = *Billbergia nutans* inflorescence axis; Bilbinfcu = *Billbergia nutans* inflorescence stalk; Bilbrun = *Billbergia nutans* runner; Borbacu = *Borya nitida* basal inflorescence axis; Bormidcu = *Borya nitida* mid inflorescence axis; Calaeste = *Calectasia cyanea* stem; Calflcu = *Calectasia cyanea* flowering stalk; Cannaaer = *Canna indica* inflorescence axis; Cannainf = *Canna indica* inflorescence stalk; Cdeubacu = *Chondropetalum deustum* basal inflorescence axis; Chlorcu = *Chlorophytum comosusm* inflorescence axis; Chlorstol = *Chlorophytum comosum* stolon; Conaecu = *Conostylis prolifera* inflorescence axis; Coninfcu = *Conostylis prolifera* inflorescence stalk; Crecaecu = *Chondropetalum rectum* inflorescence axis; Crecbacu = *Chondropetalum rectum* basal inflorescence axis; Creclcul = *Chondropetalum rectum* lower inflorescence axis ; Crecrh = *Chondropetalum rectum* rhizome; Cyabacu = *Cyanella hyacinthoides* basal inflorescence axis; Cyabanek = *Cyanella hyacinthoides* basal neck; Cyaflcu = *Cyanella hyacinthoides* flowering stalk; Cymidnek = *Cyanella hyacinthoides* mid neck; Dasycu = *Dasypogon bromelifolius* inflorescence axis; Epidifcu = *Epidendrum cinnapalinum* inflorescence stalk; Epumific = *Eriospermum pumilum* inflorescence stalk; Epumlocu = *Eriospermum pumilum* lower inflorescence axis; Holcu = *Holothrix villosus* inflorescence axis; Icinaecu = *Ischyrolepis cincinnata* inflorescence axis; Icinrun = *Ischyrolepis cincinnata* runner; Johnbacu = *Johnsonia pubescens* basal inflorescence axis; Johncu = *Johnsonia pubescens* inflorescence axis; Lklinginfc = *Lachenalia klinghardtiana* inflorescence axis; Maxbacu = *Maxillaria variabilis* basal inflorescence axis; Maxmiseu = *Maxillaria variabilis* mid pseudobulb; Maxupcu = *Maxillaria variabilis* upper inflorescence axis; Mcinbacu = *Merxmuellera cincta* basal inflorescence axis; Mcincuin = *Merxmuellera cincta*; Mrufbacu = *Merxmuellera rufa* basal inflorescence axis; Mrufrun = *Merxmuellera rufa* runner; Mscaaesh = *Myrsiphyllum scandens* aerial axis; Mscaflcu = *Myrsiphyllum scandens* flowering stalk; Pariaefl = *Pentaschistis arisfidoides* flowering stalk; Paribacu = *Pentaschistis aristidoides* basal inflorescence axis; Pcaecuin = *Pseudopentameris caespitosa* inflorescence axis; Phalflstk = *Phalaenopsis frosty hunter hybrid* flowering stalk; Pmaccuin = *Pseudopentameris macrantha* inflorescence axis; Pobtinfl = *Pseudopentameris obtusifolia* inflorescence stalk; Pobtlocu = *Pseudopentameris obtusifolia* lower inflorescence axis; Pobtverm = *Pseudopentameris obtusifolia* stem; Polmidcu = *Polystachya ottoniana* mid inflorescence axis; Ppalaefl = *Pentaschistis pallescens* = flowering stalk; Ppalbabr = *Pentaschistis pallescens* basal inflorescence axis; Pthuaecu = *Pentameris thuarii* inflorescence axis; Rharaecu = *Restio harveyii* inflorescence axis; Rharrun = *Restio harveyii* runner; Salbflcu = *Spiloxene alba* flowering stalk; Smilinfcu = *Smilax anceps* inflorescence axis; Smilstem = *Smilax anceps* stem; Sminuflc = *Spiloxene minuta* flowering stalk; Tallibacu = *Tulbaghia alliaceae* basal inflorescence axis; Tallicu = *Tulbaghia alliaceae* inflorescence axis; Talliflstk = *Tulbaghia alliaceae* flowering stalk; Talliinfcu = *Tulbaghia alliaceae* inflorescence stalk;

Tlrhcu = *Thamnochortus lucens* rhizome-inflorescence axis transition; Tlucaecu = *Thamnochortus lucens* inflorescence axis; Tribcu = *Tribolium obtusifolium* inflorescence axis; Tribstol = *Tribolium obtusifolium* stolon; Tspiaecu = *Thamnochortus spicigerus* inflorescence axis; Tspibasc = *Thamnochortus spicigerus* basal inflorescence axis; Tspiifcu = *Thamnochortus spicigerus* upper inflorescence axis; Tspiifst = *Thamnochortus spicigerus* inflorescence stalk; Tspirhcu = *Thamnochortus spicigerus* rhizome-inflorescence axis transition area; Tspisedcu = *Thamnochortus spicigerus* seedling axis; Wgloaecu = *Willdenowia glomerata* inflorescence axis; Wglorun = *Willdenowia glomerata* runner; Wthyraec = *Wachendorfia thyrsiflora* inflorescence axis; Wthyrinf = *Wachendorfia thyrsiflora* inflorescence stalk; Wthyrsun = *Wachendorfia thyrsiflora* runner; Wurbanek = *Wurmbea spicata* basal neck; Wurmflstk = *Wurmbea spicata* flowering stalk; Wurmidnek = *Wurmbea spicata* mid neck; Zaeinfstk = *Zantedeschia aethiopica* inflorescence stalk; Zaespthstk = *Zantedeschia aethiopica* spathe stalk; Zingrep = *Zingiber officinale* reproductive axis; Zingveg = *Zingiber officinale* vegetative axis.